THE CARNIVORES
OF
WEST AFRICA

BY

D. R. ROSEVEAR

BRITISH MUSEUM (NATURAL HISTORY)

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Publication No. 723

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D. R. ROSEVEAR

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by
Rita Parsons
and 172 line drawings
by
Patricia Wolseley, Monika Shaffer,
Rita Parsons and the author

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NOTE

Definition of the area taken herein as representing West Africa and of other topographical terms will be found on page 518.

". . . I should have much stronger expectations than I dare yet entertain, to see philosophy solidly established, if men would more carefully distinguish those things that they know from those that they ignore or do but think, and then explicate clearly the things they conceive they understand, acknowledge ingenuously what it is they ignore, and profess so candidly their doubts, that the industry of intelligent persons might be set on work to make further enquiries and the easiness of less discerning men might not be imposed on".

ROBERT BOYLE
The Sceptical Chymist
1661

"Ce que nous connaissons est peu de choses, ce que nous ignorons est immense".

The last words of
PIERRE SIMON, MARQUIS DE LAPLACE
1827

PREFACE

The research for this, the third volume on the West African mammals, was made possible by the generous support for three years of the Wellcome Trust, to whose Trustees, Director and staff I am most sincerely grateful. I must also once more express my thanks to the Trustees of the British Museum (Natural History) for the facilities again accorded to me. This present work to all intents and purposes brings to a close an association with the Mammal Room extending over almost forty years, and I cannot too strongly express my deep appreciation of the ever-friendly help and encouragement I have received throughout from the members of this section and most particularly in recent times from Dr. Gordon Corbet and all his subordinate staff in their various capacities. I also gladly acknowledge my indebtedness to the Museum's Librarian, Mr. M. J. Rowlands, and his assistants who have repeatedly and readily gone out of their way to give me their help.

I have been much encouraged by various correspondents who have found the previous volumes useful, and by the help I have received from collectors and field and museum workers who have kindly furnished me with specimens or items of information. These are more fully acknowledged in the appropriate places; but I would here mention A. J. Hopson, G. S. Child, R. H. Kemp, Sonia Jeffreys and Gerald Durrell for notes concerning distribution or behaviour; Dr. P. H. J. van Bree of Amsterdam and Dr. Renate Angermann of Berlin for the loan of specimens; and J. J. C. Mallinson for photographs. I owe a very special debt to Theo S. Jones for his unflagging interest in this entire project, for his continual encouragement and for his practical help, despite an over-busy existence, in reading through the typescript and supplying numerous valuable notes from his wide experience in the field. The typescript has been read, too, by Robert Hayman who, although now in well-earned retirement, has once again as so often before kindly offered me helpful suggestions, thus adding yet more to my long-standing indebtedness to his wide knowledge of African mammalogy.

No one who studies the morphology and taxonomy of the Carnivora can fail to be deeply impressed with the encyclopaedic knowledge of the Order possessed by the late R. I. Pocock, the outcome of a lifetime's acquaintance as much with living or recently dead specimens in zoos as with mere skulls or dried skins. I should be truly wanting in gratitude if I failed to acknowledge how very much this present work owes to the innumerable clearly illustrated papers of this remarkable and indefatigably inquisitive student.

All who use this book will agree that it owes a great deal of its value to the painstaking work of the artists who have assisted in its production, Rita Parsons, Patricia Wolseley and Monika Shaffer. I have been fortunate in finding such willing helpers and I am indeed grateful for their cheerful co-operation in the exacting task of achieving accuracy and clarity. I must add my thanks also to Sylvia Oliver who has almost faultlessly typed the whole of my lengthy manuscript, skilfully and uncomplainingly taking in her stride a variety of unfamiliar languages, technical terms, columns of figures, niceties of spacing and abbreviations, often bedevilled with maddening complexities of punctuation.

Though less immediately concerned with the day-to-day production of the work, I cannot overlook how much I owe initially to Lord Grey of Naunton whose foresight and faith originally got the whole of this project off the ground; and to Sir Terence Morrison-Scott whose friendly help and persistence in the face of financial difficulties kept it airborne over a period of years. All, however, would have been useless without the never-failing support and encouragement of my wife and her forbearance through several decades of collecting, skull cleaning and, ultimately, printer's litter. Lastly I make a wholeheartedly sincere acknowledgment of my indebtedness to Mr. Stanley Raw, F.R.C.S., but for whose surgical skill this work would never have reached its conclusion.

To all of these, as well as to many other unnamed friends and helpers, I am more deeply grateful than words can properly convey. It is only to be hoped that this account of a truly fascinating group of animals goes some way to justifying their faith, and that, in a region not very rich in local literature, the work will be found to fill a gap and continue to serve a useful purpose for some years to come. The subject is a complex one, far more so than is commonly imagined even by those who justifiably claim a considerable knowledge of the animal world. Those who study the often involved taxonomic sections will gather something of this author's disquiet regarding mammalogical taxonomy in general, with its insistence on reference to anciently named types often chiefly notable for their ridiculously sketchy diagnoses, and with its placid acceptance into an already encumbered nomenclature of new names—without question, until it is too late and synonymy is, under the present system, burdened with them for eternity. Turning from the museum to the field it is interesting to note the remarkable change which the last two decades have witnessed, in that the habits and behaviour of African mammals, once the recognized speciality of the professional hunter, have now become a fashionable field of intensive scientific study supported by large funds and expensive equipment. This, as the exact niches in nature filled by each species are more clearly appreciated, must result in benefit to the animals themselves—as, indeed, it has already done for some at least of those dealt with in this volume, which not so very long ago were almost universally regarded as harmful and expendable predators.

D. R. Rosevear

Hartley Wintney
Hampshire
April, 1972

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GENERAL INTRODUCTION

The system of classification adopted throughout this work is in the main that of Simpson (1945) with relatively minor amendments in the lower taxonomic ranks. That author divides the Eutherian (placental) mammals into four cohorts, the Carnivora forming part of the cohort Ferungulata, the other three cohorts being the Unguiculata, comprising the insectivores, chiroptera and primates; the Glires, consisting chiefly of rodents; and the Mutica, the whales and dolphins.

Cohort FERUNGULATA Simpson, 1945

As far as recent, living, mammals are concerned the Cohort Ferungulata covers the following Orders: Carnivora (Flesh-eating mammals), Tubulidentata (Aardvarks), Proboscidea (Elephants), Hyracoidea (Hyraxes, known also as Dassies or Conies), Sirenia (Manatees, Dugongs), Perissodactyla (Odd-toed Ungulates) and Artiodacryla (Even-toed Ungulates).

From the point of view only of existing mammals some of these seem to make strange bed-fellows; especially in that the carnivores, that is to say the wild cats, dogs, genets, mongooses and so forth, should be regarded as having any kind of near relationship with the artiodactyls or antelopes and their close kin—in relation to which, both superficially and in general mode of life, they appear not only to have nothing in common but to stand, rather, at opposite poles. The explanation of this seeming paradox lies, of course, in the fossil record, with the complications of which this present account cannot involve itself beyond the brief statement that differentiation from a common ancestor into what are now broadly the hunter and the hunted took place in early Tertiary times. It must be further added that Simpson's views on this matter are not those of all palaeontologists.

The Ferungulata are regarded as comprising five Superorders, of which we are here concerned only with the Ferae. These latter may be broadly regarded as covering beasts of prey, the remaining Superorders consisting, by and large as far as living mammals are concerned, of herbivorous, or occasionally insectivorous, species.

Superorder FERAE Linnaeus, 1758

Order CARNIVORA Bowdich, 1821

On the other hand, the Ferae comprise a single Order, named by reason of the predominantly predacious habit of its constituent members the Carnivora, from the Latin *caro, carnis* flesh, and *voro* to devour. The animals included under this heading are divided into two Suborders, the Fissipeda or land-based carnivores, and the Pinnipedia, which spend the greater part of their active lives in the sea, upon which they are wholly dependent for their food. The land carnivores are to be found everywhere with the exception of the southern polar regions and a few islands. The pinnipedes, that is to say the seals and their kin, are of wide distribution in the oceans of the world but only one genus, *Monachus*, is partly tropical, and that is not known to occur within the limits chosen for this book, the monk seal (*M. monachus*) being recorded no further south along the western coast of Africa than Cape Blanco (Rio de Oro). This present account, therefore, is in effect concerned only with the Fissipeda. It must be added that there is an increasing tendency amongst systematists to accord to these two divisions full ordinal, rather than subordinal, rank; but though there are plausible arguments to support this such a classification does, in fact, tend to obscure the close relationship that exists between the two sections.

Suborder FISSIPEDA Blumenbach, 1791

The two Suborders of Carnivora are named from, and to some extent founded on, the general build of the feet. The Fissipeda are characterized by having the digits more or less clearly independent of each other, even though in some cases connected by interdigital webs. The name is, for this reason, derived from the Latin words *fissum* cleft and *pes, pedes* foot. In the Pinnipedia, on the other hand, the digits, notably those of the forelimbs, in conjunction with the contiguous bones function as a single unit adapted as a paddle for swimming, encased for this purpose in a common integument—though there are, of course, exceptions of greater or lesser degree to this broad plan. The name, thus, is built from the Latin word *pinna* a feather because the structure, in general shape, and in the unitary way it functions as a means of propulsion, recalls a bird's wing rather than the normal run of mammalian foot.

The fissipede carnivores consist, in West Africa, of wild dogs (i.e. jackals and foxes), the hunting-dog, striped weasel, striped polecat, honey badger, otters, civet, palm-civet, genets, mongooses, hyaenas and wild cats of various kinds including the lion, leopard, cheetah and others less well-known. These are disposed in 5 families, 27 genera and 45 species embracing about 59 different forms. Of the two families which are lacking entirely from the African fauna the more notable is the Ursidae or bears. The other, the Procyonidae, though of considerable importance in both northern and southern America and in eastern Asia, comprises less widely known animals such as the raccoons, coatis, kinkajou and pandas.

General description. The carnivores, especially the fissipede carnivores, are an extremely interesting group. They are certainly more intimately associated with man, in the capacity of close friend or bitter enemy, than any other Order of mammals. They have fairly big brains and are more often than not highly intelligent; they live by their wits; and under domestication, therefore, they are quick to grasp a situation and to learn. Without question, both the domestic cat and the domestic dog have, each in its own special way and in return for assured food and snug shelter, turned themselves into man's most intimate and seemingly understanding associates. Further, many of the normally wild species take unexpectedly kindly to captivity and become amazingly responsive to close association with human beings. Yet in the wild state there are no more unremitting foes to man's cattle, sheep and poultry, as well as to wild game, than the majority of fissipedes.

The suborder exhibits a wide range of size, varying in West Africa from a little weasel with a head & body length of only a few centimetres and weighing about 200 grammes (½ lb) to an animal of the vast bulk of a lion which may weigh 200 kg (4 cwt) or more. Between the different families there is a good deal of variety of shape; but in a general sense the bodies throughout are mostly relatively slender, long, of subcylindrical form, frequently without any very marked constriction at the neck, highly muscular and often, especially in the cats, of extreme suppleness and agility. Variety of external appearance is brought about by differences in the shapes and relative proportions of the head, the tail, the legs, and the feet, apart from any question of texture and pattern in the pelage. In much of the suborder the common form of head is long, tapering in a greater or lesser degree to a pointed muzzle; but the cats differ markedly from this general shape in having a much rounder head with a notably short muzzle.

Ears. Ears often form a very conspicuous feature. They are long and upstanding in the dogs and hyaenas, sometimes sharply pointed; but in the serval cat they are very rounded besides being tall and broad. In other cats they may be rounded but of much less size. They reach their greatest reduction in the ratel, otters and mongooses. The backs are clad with short hairs, the inside of the pinna with long hairs, often densely; and in the cats the backs mostly bear a black or black and white patch, quite characteristic of the species. An apical tuft exists in the caracal. A curious aural character occurring in large sections of the Carnivora is a doubling of the rim of the pinna near the base of the outer margin, forming a little pocket, known as the bursa, with an anterior and a posterior flap. The latter is usually semi-lunar; the former emarginate. A bursa is always present in the Canidae, Felidae, Viverrinae and Paradoxurinae; it is completely absent from the Hyaenidae, the West African Mustelidae and the Herpestinae. Near the base of the inner margin of the pinna is a small process known as the tragus; and opposite this on the outer margin is another process, the antitragus, having a notch into which, in some cases, the tragus can fit tightly and help to effect closure of the entrance to the ear passage. On the inner face of the pinna are three or four shallow folds or ridges crossing it in various directions. These also, in those species which find it necessary, aid in closing the ear when the pinna is collapsed and folded. The terminology for these is not well fixed.

Rhinarium. The rhinarium in this suborder, that is to say the region at the extreme anterior end of the muzzle surrounding the nostrils—the "nose" in common parlance—is naked over a larger or smaller area and, in the Canidae at least, has a slow secretion of mucus. The nostrils themselves may be narrow and slit-like or rather more open and comma-like; and the whole form of the rhinarium is generically, or even specifically, characteristic. This has been studied and illustrated by Pocock in a number of published papers; and there are figures also in J. A. Allen (1924).

Eyes. The eyes of the carnivores are mostly of a moderate, or sometimes relatively small, size; and they are situated well to the fore on the head, vision being thus effectively binocular, permitting that accuracy in the judgment of distance necessary to the successful striking of prey. Acuity of vision is in general good but in fact varies quite appreciably not only between species but amongst individuals too. It is a matter of common observation that some breeds of dog, or different members of a single breed, can see much better than others; and this applies as much to wild species of carnivores as it does to domestic animals. There is little doubt that cheetahs have considerable sharpness of sight over long distances, whereas otters are in a different category and, indeed, have eyes probably far better adapted to seeing under water than on dry land. Yet however acute the power of vision may be, it is in many, if not all, cases aided to a great extent by the faculties of smell and hearing, both of which are better developed than in human beings, sometimes to an incomparably greater extent. Equipped with a highly sensitive sense of smell, a carnivore can build up a mental picture of its surroundings almost beyond the comprehension of man. Sound frequently has no very great range, may be easily obstructed or blurred, and is often transitory; but scent sometimes lasts for long periods and may carry far, and it enables a suitably equipped animal to "see round a corner" where sight is of no avail. Its chief drawback lies in the degree to which it is affected by air currents; for whereas it may lie for long in sheltered undergrowth it will in open country certainly be carried considerable distances by the wind. Carnivores, therefore, if circumstances permit choice, approach their prey from downwind, securing the double advantage of having the scent of their proposed victim brought to them whilst their own is borne away. The canidae are notable possessors of a very highly developed olfactory sense which they generally rely on in preference to sight and, where possible, use to confirm what their eyes appear to have told them. Sensitivity of nasal perception and analysis amongst some of the Canidae has been shown to be of such delicacy that one second's holding in a man's hand of a billet of wood suffices for a trained dog to be able to select it from a pile of numerous similar pieces. Cats are more dependent upon hearing as an auxiliary to vision.

Many carnivores are able to see unusually well in poor crepuscular or nocturnal light conditions, a power very necessary to the securing of prey in these circumstances. Some night-active species have irises that are highly and rapidly responsive to variation in light intensity. Accommodation in this respect is achieved in the most typical cats by a pupil which in response to a lessening intensity can change from a narrow vertical slit, customary for a bright light, to a wide circular opening. By no means all felines have this power; and in some the pupil remains, within narrower limits, broadly elliptical. It is interesting to note that eyes of a similar type with a vertical slit are found amongst the owls, also nocturnal hunters; but the horizontal pupils of ungulates and kangaroos do not serve the same function.

The effect of this enlargement of the pupillary aperture in dim conditions is augmented in the carnivores by the possession of a second means of increasing the efficacy of weak light. Anyone who has observed cats or dogs at night is acquainted with the remarkable way in which the eyes assume a green or yellow phosphorescent luminosity. Since mediaeval times this somewhat ghostly glowing of the eyes has been popularly held to be something to do with "seeing in the dark" by the mysterious projection of beams as from a lamp to illuminate the object looked at. This last, of course, is not so. The effect is due to a subcircular area of tissue at the back of the eye situated immediately behind the retina around the optic nerve, having no common name but known in anatomy as the *tapetum lucidum*. This possesses the property of virtually doubling the effective intensity of such poor light as may exist by reflecting it back again through the receptive cells of the retina instead of its being at once absorbed in the posterior layers of the eye as it is in organs unprovided with this structure. It does thus enable an animal to see virtually twice as well in the near-dark as it might otherwise do, but not by the generation of light in its own eyes. It follows that it is quite inoperative in absolute darkness—a condition which rarely exists in nature—and the eyes would emit no glow in such circumstances. This dual use of feeble illumination is, of course, of considerable advantage but nevertheless has the drawback of some loss of sharpness of vision (Tansley, 1965). Eyes of this kind are found also amongst whales and ungulates. A nictitating membrane, or so-called third eyelid, is fairly well developed in some of the carnivores, especially in the cats, though it is never wholly and constantly functional as it is in reptiles and birds.

Vision varies markedly in its sensitivity to colour. Dücker (1957, 1964) found *Genetta* and *Felis* to be totally colourblind, but the mongoose *Herpestes ichneumon* to be relatively well equipped, having a positive colour sense though exhibiting difficulty in distinguishing between nearly related hues such as red and orange or green and blue.

Legs and feet. Legs are possibly responsible for a greater variety of fissipede form than heads. They are in some cases long or very long, adapted almost wholly to running, as in the dogs or that in some ways rather dog-like feline the cheetah. In these cases the feet are digitigrade and carry moderately straight, non-retractile claws. In the typical cats the feet are also digitigrade but the legs are relatively shorter and a little stouter with greater flexibility of movement. The feet are armed with strongly curved, very sharp claws which are retractile within sheaths to preserve them from abrasion in running and walking but extensible when a firm anchorage is required, either in climbing, taking off for a spring, or in clinging to prey. Such limbs are adapted rather to a bounding than to a running gait, to slinking with lowered body, to climbing trees and other rough surfaces, and to performing powerful leaps. Between these two extremes lie a number of forms, mostly with short legs suited to a trotting gait and sometimes to climbing, either with fixed or, in the genets, partly retractile claws, digitigrade, semi-plantigrade or, in the ratel, nearly fully plantigrade. Bears, which do not occur as wild species anywhere in Africa, provide the best example of carnivores that are fully plantigrade, that is adapted to walking with the whole of the foot from toe to heel in contact with the ground. There may be four digits on each foot, or five, or a combination of the two. Where the 1st digit is present it is mostly widely separated from the rest, more particularly on the hindfoot, where it is far removed from any possible contact with the ground. In the Canidae this is popularly known as the "dew claw", possibly because of its ephemeral nature since it often disappears in adolescence. Although the digits, unlike those of the pinnipedes, remain virtually independent they are nevertheless often joined by webs at least basally though in semi-aquatic species they may be extensive.

A notable feature of the fissipede foot is its sole, consisting largely of rather rubbery, mostly independent cushions, sometimes collectively referred to, for the fore and hindfeet respectively, as the palmar and plantar pads, though these terms have also a more restricted application as explained shortly. These pedal pads, in general, fall into three categories: those situated below the distal portions of the digits, which may be conveniently referred to as the digital or apical pads; those lying in the middle of the foot, basically comprising five pads surrounding a central depression but often reduced in number or indistinguishably merged, termed by J. A. Allen (1924) interdigital pads but more often called the palmar (forefoot) and plantar (hindfoot) pads. Finally, posterior to these, there is often a narrow, longer or shorter metacarpal or metatarsal pad, frequently compound. Pads follow set patterns in different species or genera and are often wholly diagnostic; but family resemblance is more uniform in the Felidae and Canidae than in the Viverridae and Mustelidae (Pocock, 1914b).

Tails. The tail in the fissipedes is a structure of considerable variety and is, with few exceptions, usually a showy as well as a characteristically formed appendage. In the cats and the genets it is for the most part long and of considerable suppleness of movement; and it is clad with hairs of subequal, moderate length resulting in a more or less cylindrical structure. In the dogs it is far less flexible, capable of little more than stiff side to side or up and down motion from the root only. It is sometimes uniformly long haired and of striking bushiness. In the mongooses the tail is tapering, in some species markedly so; in some it is relatively short-coated, in others of somewhat asymmetrical coutour owing to the drooping carriage of its long hairs. The lion's tail is unusual amongst the African fissipedes in not only being close-haired but in carrying also a prominent, blackish, long-haired terminal tuft—hidden amongst which is the famous "thorn" of hard skin with which in ancient times it was reputed to lash itself into fury before attacking its prey. On a far smaller scale, a terminal tuft, sometimes black but much less bushy than in the lion, occurs also in some of the mongooses. Apart from variety of shape, tails in this suborder may be unicoloured, bicoloured, annulated, spotted or speckled.

Scent glands. One of the most notable features of the carnivores is the possession by many members of the Order of scent glands. These are mostly situated in the region of the sexual organs or the anal area, and their functions are recognition, sexual attraction and stimulation, demarcation of territory, warning or defence. As an example of the last in West Africa the striped polecat (*Ictonyx*) can, if alarmed, by the deliberate and abrupt contraction of the circumscribing muscles emit to a surprising distance a spray of fluid with an extremely disagreeable and long-lasting stink. Despite the existence of glands, in many cases, including that of this striped polecat, little or no offensive odour is under normal circumstances apparent to human beings; but in some animals, notably some of the dogs and hyaenas, a fetid stench unremittingly pervades the whole animal by a continual uncontrolled oozing of the offensive secretion. Involuntary emission of odour also in many species accompanies the acts of defaecation and micturition, both of which functions, but especially the latter, are in consequence used to indicate the boundaries of a territory and publish a warning against trespass by prospective intruders. In other cases, establishment of ownership, or other scent-borne message, is conveyed by the rubbing of circumanal glands against trees and rocks or by dragging the anus across the ground. Scent-marking in the Canidae, especially in respect of postures adopted, has been dealt with by Kleiman (1966).

The precise siting of fissipede scent glands is, within a relatively limited bodily reginrt very varied. They may be associated with the anus, either within the rectum oronexe,-

ally around the orifice (circumanal); between the anus and the scrotum or vulva (perineal); in association with the prepuce (preputial); between the scrotum and the penis (prescrotal); on the tail, above or below, (caudal); in hyaenas, between the root of the tail and the anus (supra-anal); or, in the palm civet, anterior to the vulva and the penis (pregenital). Usually, but not invariably, the position follows a family pattern. The secretion is sometimes liquid, sometimes of a waxy consistency as in the case of the civet. It is interesting to note that this latter secretion, while nauseating to humans when in concentration, is in dilution pleasing; and "civet", extracted with a spoon from the glandular sacs of captive animals kept for the purpose, has for many centuries commonly been one of the ingredients of a number of commercially successful perfumes in Africa, Asia and Europe.

In connexion with the wide occurrence of scent glands it must be remembered that many carnivores, except at breeding time, lead a more or less solitary existence and some more reliable means than chance encounter is needed to enable the sexes to find one another at considerable distances. The emission of powerful and significant odours that may cling for long to undergrowth or be carried far on the wind, in conjunction with a highly sensitive and critically analytical sense of smell, is an ideal way of surmounting difficulties of time, distance, intervening obstructions or darkness that may render sight useless in bringing the sexes together. Sound, though sometimes similarly used as a remote inter-sexual signal, is often not so effective in overcoming difficulties of time and space as well as having a less emotive impact.

Mammae. The mammary glands are, so far as known, mostly purely abdominal and number between one and five pairs except in the cheetah, where they are far more numerous.

Pelage. The pelage, by its length, texture, colouring and pattern, accounts for very marked differences of appearance not only between families but often between genera and species. There is, unfortunately, no clearly defined and commonly accepted terminology in English for the various types of hair found in mammalian coats. At one extreme there are bristles, or vibrissae as they are more technically termed, which are of circular section and considerably stouter than the greater part of the pelage. These occur most noticeably as the "whiskers", or mystacial vibrissae, on the upper lip; but also, in the carnivores, singly, in pairs or limited groups in other set positions, of which there are five on the head besides the mystacial area. These are submental, on the anterior part of the chin; interramal, on the posterior part of the chin; genal, on the cheeks; superciliary, above the eyes; and subocular, below the eyes. Apart from the mystacial vibrissae not all these are always present; in the fissipedes the interramal vibrissae are lacking in the Felidae alone. Vibrissae occur, mostly singly, on other parts of the body, in some cases on the legs, but more commonly at wide intervals over the back and flanks. The function of these stout and sensitive hairs, wherever they are situated, is to give tactile warning or information. Those on the face and on the body, for example, furnish vital information in the dark when creeping into a narrowing hole or through a restricted rock fissure; the whiskers and possibly other facial vibrissae clearly tell the direction of the wind; and those of the otters may play a part in the detection of prey in ill-lit or muddy waters by revealing currents set up by the powerful swish of a fish's tail. The mystacial vibrissae are generally stouter and longer than the others, and sometimes very stiff—as they are in the leopard. Indeed, in some parts of West Africa in the past the whiskers of this animal were looked upon as a certain means of causing death if chopped up and mixed with anyone's food, being reputed to penetrate, or at least cause fatal inflammation of, the stomach wall.

At the other extreme of hair is the underfur, so called because in many mammals it forms the lowest, and often rather insignificant, constituent of the pelage. But this is not always so; and in some species it is the major element—as, for example, the wool of sheep. For this reason it is not a good term but it is in general use since there is nothing else with which to replace it. Underfur is always of fine diameter, sometimes extremely fine; in the carnivores it may be short or moderately long and is often slightly sinuous. Occasionally it is almost completely lacking, as in the Banded and Gambian mongooses of the genus *Mungos*; but in the majority of cases it is dense; sometimes exceedingly so, as for example in the otters where it forms, on submergence, a waterproof coat amongst which air is trapped, thus keeping the body both dry and warm. It is also remarkably dense and, amongst West African carnivores, at its longest in the striped polecat (*Ictonyx*) in which it in effect forms the entire pelage apart from a few widely dispersed lengthy bristles. In this case it probably serves to shield the body from the effects of direct tropical sunshine and hot dry winds.

Above the underfur lies the longer outer fur, which may be so abundant as to conceal the underfur completely or, as in the case just mentioned, it may be merely a widely scattered and comparatively unimportant element. The former is by far the commoner. This part of the pelage is, in a greater or lesser degree, harsher than the underfur, being composed of stouter hairs though by no means so stout and strong as the vibrissae—to which the unqualified term bristles is best confined. More often than not there are two distinct elements in this outer coat. The more important and abundant consists of stoutish hairs of round or sometimes slightly flattened section, tapering distally to a slender point but not decreasing much in diameter towards the base. When the fur is turned back they therefore usually stand out against the background of underfur by size and sometimes by colour. In the carnivores they never exhibit a concavo-convex section commonly found in the Rodentia (Rosevear, 1969). These hairs are in this present work, for want of any better recognised term, referred to as bristle-hairs. They are often broadly annulated with different colours, the tips being almost invariably black, the basal portion very often pale or even white. In many species there is a second element in the outer fur, termed herein sub-bristle-hairs, shortened to sub-bristles. These, like the bristle-hairs, are longer than the underfur and play their part, too, in overlying and concealing it; but they are of different form, consisting of a long, slender, pale stalk (the petiole) which passes into a broader, terete or slightly flattened coloured blade ending in a darker, pointed tip. This distal part, except under magnification, resembles the bristle-hair, and the fundamental difference of form has therefore often been overlooked; the slender proximal half though of somewhat greater diameter than the underfur is nevertheless not so disparate as to stand out clearly from it when the pelage is turned back as the bristle-hairs do.

This gross morphology of the pelage can be seen with the naked eye or under low magnification. No reference is made here to the surface patterns occurring on hairs since this is a matter for the microscope or electroscan and beyond the scope of this present account. It need only be said of these that, though little or no research has yet been carried out into African carnivores, it is possible that they may follow at least generic patterns and might be of use for identification, as between other mammalian groups. It is the surface scales giving rise to these patterns that underlie the property of close adherence together known as "felting" which takes place when a mass of hairs is suitably beaten.

The coat is nearly always plentifully developed to afford a more or less complete covering to the skin; but it may range between very short, as in the lion, to very long, as in some hyaenas and the striped weasel. However, coat length and quality and sometimes the relative proportions of the constituent elements are affected very considerably by season, moult and condition of health; and owing to these factors skins in museum collections are often misleading and sometimes not susceptible to valid comparison. Wrong taxonomic deductions have sometimes been based upon them. Little is at present known of these factors in connexion with the majority of West African carnivores. In some species, apart from the normal coat there may be a well-developed collar or "mane", or a nuchal or spinal crest of exceptionally lengthy hairs. These growths are affected by age, sex and possibly season.

Pelage patterns. Pelage texture follows a general family plan. In the typical dogs it is frequently long and rather harsh; in the cats mostly much shorter and somewhat softer; the otters have fairly short but extremely dense, rather silky fur. Pelage pattern in this Order varies very widely but often similarly follows some sort of family, or at least subfamily, plan, to which, however, there are sometimes notable exceptions. The larger dogs in West Africa have coats characterized by broad, irregular blotches but the foxes are more self-coloured; a speckled, "pepper and salt" appearance occurs in many mongooses, though, again, some are predominantly unicolorous. It is amongst the cats that the widest diversity is found. Spots are common—the bold markings of the leopard, cheetah and serval are familiar; and though the pelage of the adult lion is plain its spotted heritage is clearly displayed in the cubs. A more curious incidence of the loss of spots in the Felidae is shown in the golden cat, which within a single species exhibits in the adult both spotted and unspotted forms, a difference which appears to be related to distribution and is thus racial. The West African Viverridae, that is the civet, genets and their kin, also have spotted coats.

Though spots may in some individuals coalesce into lines, pure transverse striping as the sole pattern as in the tiger does not occur in West Africa; but through the regular disposition of the light and dark annulations of the hairs of its dorsal fur one of the mongooses is cross-banded. Bold, broad, longitudinal bands are exhibited by the African polecat and weasel. The ratel is unusual amongst the African carnivores in its coloration. Most mammals have the belly white or at least paler than the back; the ratel exactly reverses this; and so to a lesser extent do the striped polecat and striped weasel.

Pattern is produced in three quite different ways. The hairs may be unicolorous throughout their lengths as in the polecat and weasel, where they are in separate bands.

wholly black or wholly white. More often, bold spots or lines are produced, as in the cheetah and other cats, by groups of hairs that are indistinguishable from the rest of the fur in their pale proximal portions but differ in having black ends. Much more rarely, and in West Africa only in the single case of the banded mongoose referred to in the previous paragraph, the pattern is brought about by the regularity with which each of the different coloured annulations on the hairs fall together along the back instead of lying heterogeneously mixed as in the ordinary "pepper and salt" coat. The backs of the ears, notably in the Felidae, often contrast with the rest of the coat. In this family they may be wholly grey, wholly black, or have bold black markings with or without an additional white spot.

Melanism. Melanism is not uncommon, but albinism appears to be very rare. Red as an outstanding feature of the pelage crops up in a number of different families of the carnivores. It occurs in the dogs, where in the foxes it sometimes constitutes the main colour. It is found also in the cats; in the genets, where it is in some cases at least a component of the spots; and in the mongooses. The striking appearance of a leopard skin when it is seen as a trophy in a room makes it seem that such an animal would be very conspicuous and easily picked out in the field; but the reverse is mostly the case; for when one of these animals is at rest in the undergrowth or amongst the foliage of a tree the pattern merges completely into the dappling of light and shade produced in the vegetation by sunlight. Only when the animal stands fully exposed in the open or is on the move can it be clearly seen. The alarmed surprise of suddenly discovering oneself in unexpectedly close proximity to a leopard in the bush must possibly first be experienced before the real truth of this can be fully appreciated. At birth and soon after, the coat is mostly short and rather silky, the adult markings either absent or very faint; but lions are born with a pattern that is lost at maturity; and in the cheetah the juvenile coat is very long and greyish-white, quite unlike that of the adult. Sometimes, as in the mongooses, the entire pelage is erectile in anger or alarm; sometimes only the hair along the spine.

Skull. A great part of the fissipedes have a rather narrow skull in which the total length is markedly more than the zygomatic breadth, the braincase often not a great deal wider than the posterior end of the rostrum. This last is itself relatively narrow and often long and tapering. In the Felidae, however, the skull is clearly rounder, its breadth across the zygomata not a great deal less than its length, the braincase broad and subglobular, the rostrum very short. Throughout the suborder there are nearly always pronounced, sometimes flange-like, supraoccipital crests, and often, in mature skulls, especially males, a sharp sagittal crest, sometimes short, but often extending the whole length of the braincase. The nasals are always narrow, often relatively short, their upper front margins always situated well posterior of the forward limit of the premaxillae and incisors, thus leaving a very open, anterior nasal aperture lacking a bony roof. The slender coiled bony laminae within the nasal cavities, known as the turbinals, which play a major part in the sense of smell support a total surface area of receptive membrane incomparably greater than that available to man.

The zygomata are always strong, sometimes very strong, and this, in conjunction with the cranial crests, is to give the necessary anchorage to the extremely powerful biting muscles. The jugal bone plays an important role since it forms the greater part of the anterior half of the arch, the maxillary zygomatic process being relatively short. With few exceptions as in the otters, the infraorbital canal is of comparatively small size. The orbit is incompletely ringed with bone, there being a longer or shorter gap between the postorbital process from the frontal and, in the majority of genera, an upwardly curving process arising from the jugal. In the ratel and some otters one or both of these orbital processes may be poorly developed or virtually absent.

The bullae may occasionally be small but are more often large or very large and betoken a highly developed sense of hearing. They furnish a point of considerable taxonomic interest, providing a distinction between the two superfamilies into which the suborder is separated. In the Canoidea the bulla is simple, consisting of a single cavity. In the Feloidea, on the other hand, it is partially or almost completely divided into two chambers, of varying relative sizes, by a septum which can usually be clearly seen in a prepared skull through the auditory meatus. The division of the bulla into two parts can generally be detected externally as a shallow furrow curving around the body of the structure. It must be added, however, that this classic conception is questioned by Hough (1948) by whom the canid auditory region is regarded as more like the felid in its essential structure than has been commonly supposed. This paper furnishes details of this region in the Canoidea in comparison with those of some other present and past Carnivora and draws conclusions regarding their significance in the phylogeny of the Order.

The bony palate sometimes terminates about the level of the back of the molar row but very often extends far posterior to this. The anterior palatal foramina are of no great size, round or oval, and lie more or less between the canines; the posterior foramina, often two pairs, are situated at very different points of the palate according to genus.

A highly important feature of the skull is the form of the mandibular condyle, that is the hinge between the lower and the upper jaws. In many mammals, including human beings, this is a fairly flexible affair permitting movement of the lower member in various directions, up and down, from side to side, or back and forth, enabling the occlusal surfaces of the upper and lower teeth to alter their relative positions and to slide across each other, and thus produce a grinding effect. This is possibly best seen in the ungulates in the action known as "chewing the cud". In the carnivores, on the other hand, the hinge consists of a long subcylindrical condyle on the mandible firmly embedded in a complementary-shaped receptacle, the glenoid fossa, in the upper jaw, completely inhibiting any side to side or back and forth action, ensuring that the jaws close, like a comparable hinged door, in one firmly fixed position. Without this, the cutting action of the carnassial teeth, as described below, would be as ineffectual as a pair of scissors with play at their axis of coupling.

Dentition. The dentition is always, even in the smallest carnivores, patently of a powerful nature (fig. 1). All the roots are closed, that is to say that once any tooth has reached its appointed size there is no further growth to replace wear as, for example, in the open-rooted gnawing-teeth of the rodents. The incisors are invariably $\frac{3}{3}$. They are relatively small but the outer one, especially above, is often larger than the others,

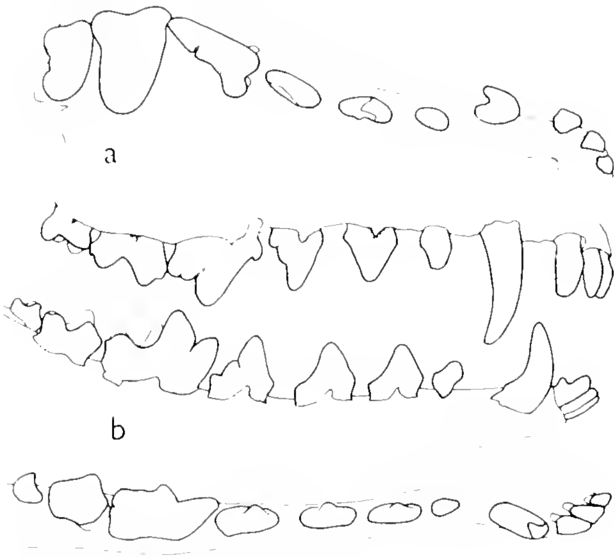


Fig. 1. Typical carnivorous teeth, showing the position of closure: a. right upper jaw, palatal view above, lateral view below; b. right lower jaw, lateral view above, dorsal view below. *Fennecus zerda*, B.M. No. 25.5.12.22, , 2

sometimes appreciably so, even to taking on a subcaniniform appearance. The jaw is nearly always strikingly dominated by the exceptionally tall, strong, curved canines—the "dog teeth" in fact—one above and one below on each side; but the cheekteeth are also of a remarkable and unique form. "Cheekteeth" is a convenient term used for all the teeth which lie posterior to the canine when it is not desired to differentiate between premolars and molars. The symbols *i*, *c*, *p* and *m* are used to denote incisors, canines, premolars and molars respectively, a figure being added above or below as index or suffix to indicate whether the tooth is in the upper or lower jaw and its position in each category reckoning from front to back. Thus, p^3 is the third premolar from the front in the upper jaw; m_2 the second molar in the lower jaw.

The total number of cheekteeth in the Carnivora is very variable according to family or genus, ranging in West Africa between 14 and 26 for the entire mouth. The premolars may be 3 or 4 above on each side of the jaw, and 2, 3 or 4 below; the molars 1 or 2 above and 1, 2 or 3 below. Complications exist in that some teeth are occasionally deciduous, being shed with advancing age, the jaw in such cases appearing not to correspond to the accepted dental formula. Moreover, in a few species certain teeth seem to be in the process of evolutionary loss, forming components of the dentition in some specimens but not in others, without being actually deciduous. The dental formula is thus variable.

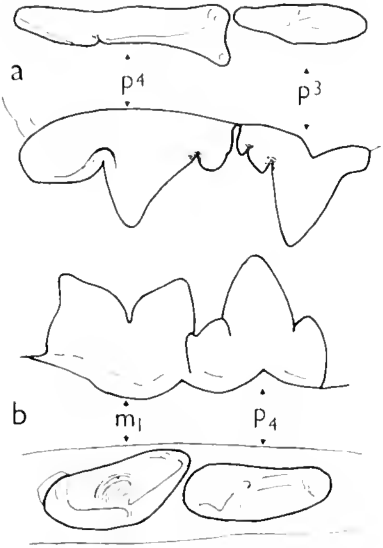


FIG. 2. Carnassial teeth, lateral and surface views: a. right upper; b. right lower. *Felis margarita airensis*, B.M. No. 67.1429, ♂, 3

The most characteristic feature of typical carnivorous cheekteeth is the modification of some of them into a highly efficient, sharp, cutting ("sectorial") form, adapted to dealing with masses of flesh and bone. This chiefly concerns the last premolar of the upper jaw (p^4) and the first molar of the lower jaw (m_1). The crowns of these are either almost wholly compressed from side to side or have at least some of their lobes thus flattened, the occlusal surfaces being in this way reduced to keen, knife-like edges which on closure slide over the face of the opposing tooth in the manner of a pair of scissors. The upper teeth always close over the outside of the lower. They are maintained in the essential firm close contact necessary to effective shearing by the rigid condyles, as explained earlier. Because of their flesh-cutting function these teeth are known as the "carnassials". In this work, as in most others, the upper carnassial is always reckoned to be the 4th premolar (p^4), it being assumed when only 3 premolars actually occur in this toothrow that it is the ancestral 1st premolar (p^1) that has disappeared and that the anterior premolar as it today exists is therefore p^2. The lower carnassial is always m_1.

The crowns of the cheekteeth lying immediately anterior to the carnassials are for the most part also laterally compressed and pointed and thus play their part too in a shearing action though in a relatively minor way. Those teeth, if any, posterior to the carnassials are of a less specialized kind suited rather to crushing than cutting, though they are often of much reduced size and then almost functionless. The detailed form of the carnassials varies somewhat from genus to genus; but, speaking in broad terms, the upper one consists of a laterally compressed outer blade divided into either two or three pointed cusps, together with a lingual, much lower, cusp which plays no role in the sectorial action (fig. 2). There are three roots; two below the blade and the third beneath the inner cusp. The lower carnassial is only two-rooted but has, in general, a broader and more complex crown than the upper one, comprising, basically, six cusps, though most are indistinct and several may be lacking. There is a good deal of variety of shape and disposition of these cusps; but most commonly it is the two anterior buccal ones which are enlarged and laterally compressed to form the sectorial blade that exercises a shearing action against the upper.

The virtual absence of grinding surfaces in the typical carnivore dentition means that chunks of flesh are cut off and swallowed whole. But not all fissipede teeth conform to this predominantly sectorial shape, which is best exemplified in the cats and dogs. In the otters, for example, there occur molars and premolars with broad crushing occlusal surfaces adequate to the disposal of the relatively soft flesh of fish and amphibians or to crushing of the shells of crustaceans (fig. 22). Teeth of a less purely sectorial form are found also in the mongooses, where they vary a good deal but in the smaller species are of a highly cusped, insectivorous type (fig. 37). The evolution away from cutting to crushing in the Viverridae has been dealt with by G. Petter (1969).

In some carnivores there is a wide interval between the canines and the anterior premolars—the post-canine gap. This permits the canines to be sunk into flesh to their full depth with a considerable band of flesh held firmly in the jaw, thus bringing about an almost unshakeable grip into a struggling prey. It is best developed in the Felidae; in other groups it is small or lacking.

Way of life. Mammals are for the most part secretive creatures. They are often nocturnal, or live concealed in dense bush or the foliage of trees, or in holes in the ground, or in crevices amongst rocks, and are therefore not easy to see let alone observe with much continuity. Most of them are, understandably, of a nervous, wary disposition reacting, by immediate retreat, to warnings conveyed by slight sounds or smell as well as by sight. Many are dangerous to approach or disturb, especially when breeding or feeding. It is not surprising, therefore, that their lives are often not so well known as those of some other, less difficult creatures. It is a fact that after many centuries of close acquaintance with and study of mammals in Europe the habits of some of them are still not understood in detail. In Africa with its much more plentiful mammalian fauna and shorter history of study this ignorance is much greater. Without question, there has been a very large number of Africans deeply conversant with the habits of mammals and other creatures. Their livelihood as professional hunters armed only with crude weapons and devoting a great part of every day or night to the pursuit of elusive quarry fostered keen and accurate observation. But though a little of this, especially as regards the more sought-after "big game" species, has from time to time been passed on to European travellers and sportsmen, the majority of it concerning the more insignificant creatures has found no place in the corpus of recorded natural historical knowledge and is now seemingly lost.

Such biographical data as we have are to a great extent the outcome of chance observations by European travellers or part-time naturalists. The study of mammalian habits calls for both patience and time. But though the former may have existed in plenty amongst keen field naturalists, the latter, owing to the daily need to pursue some more certain and lucrative occupation, has regrettably usually been lacking. Prolonged and continuous study has, to the majority, been impossible. Our knowledge of most animals is, in fact, made up of disjointed observations, often of extremely brief duration, of different individuals of a species in widely separated areas of the continent and which conceivably may not have been acting in a typical manner. Moreover, notes of behaviour have been made by observers of diverse competence and not always correctly interpreted. Habit data are thus often far sketchier and less reliable than might be supposed by those who have not examined the subject closely.

All this is now undergoing great change. Interest in wild animals has increased enormously. In consequence, part-time, intermittent amateur observation is slowly giving place to full-time continuous professional research carried out by the permanent, trained personnel of nature reserves, or specific studies by selected individuals or teams subsidized by scientific foundations. Further than this, the apparatus at the disposal of observers today is vastly more varied and sophisticated. In the past a naturalist had as his equipment at most a gun and a pair of binoculars, and could thus study an animal dead or for a brief moment alive, at some remove. It was virtually impossible to follow for any distance a large mammal in rapid progress, except occasionally with the aid of a horse—which itself introduced complications. Nowadays the observer commands the services of a Land-Rover or similar conveyance which carries not only himself and possibly a co-observer but all his complex apparatus as well at high speed across rough terrain. It is a strange thing that many animals have clearly shown that, provided reasonable caution is exercised, they are not disturbed by or, indeed, much interested in motor vehicles, which can thus follow them in the chase or approach them fairly closely at rest. Such a truck, therefore, fulfills not only the function of rapid transport but acts as a protection and a hide, enabling the observer to approach closer, to sit for long periods in relative comfort while taking notes or working his scientific apparatus without revealing his presence by movement, sound or smell. In Africa this, of course, applies mainly to the open woodlands; for while some of these advantages remain, that of free range is lost in the tangle and resistant undergrowth of the West African forest and the tall, dense grass of the Guinea woodland in the rains.

Apart from this invaluable mobility the modern field observer has at his disposal a wide range of scientific aids which either just did not exist till recent years or existed only in a relatively crude form. The improvements that have taken place in photographic material alone may seem unbelievable to those who did not know West Africa half a century, or even less, ago. Basic to much of the improved facilities is also the simple modern fact of reliable portable electricity. More esoteric methods and apparatus apart, the main aids to animal study in the field today are lightweight precision cameras with a wide selection of easily changed lenses of far greater efficiency than formerly, together with unrecognizably improved films; there are also reliable cinematography, infra-red photography, powerful flashlights and spotlights. In addition there are now sound recorders and videotapes, together with immobilizing drugs which enable even the most dangerous animals to be carefully examined while yet alive and to be distinctively marked for future recognition.

All this has brought about a change in the observation of animal behaviour and way of life that would be almost incredible to former generations of naturalists. But the new research has up to now been directed towards relatively few species—as far as this present work is concerned, towards not much more than half-a-dozen of the larger African carnivores. Such studies as have been carried out have revealed a good deal that is new besides showing that some of the old beliefs are inaccurate. For the many species which have not been investigated reliance must still be placed on old field observations, though the picture of probable habits in nature has been in some cases augmented by behaviour studies made under laboratory conditions and breeding data derived from zoos. Nevertheless, it must be remembered that animals in their natural environment may not necessarily behave exactly as they do in captivity. Nor must it be overlooked that they are individuals, each with a recognizable character of its own which may differ in some degree from a common specific pattern. Such idiosyncrasies, however, cannot of course diverge so far from the evolved norm as to jeopardize survival.

Finally in this general survey of the state of our present knowledge it must be pointed out that since what we know of the habits of most of the carnivores dealt with in this present work is still extremely sketchy and open to some doubt—as will become very apparent in the accounts given later of the various species—it is desirable that even seemingly insignificant items relating to the life of animals they may come across should be recorded by collectors or field observers. It may often appear to the naturalist that the scrap of information at his disposal must surely have been recorded before; but every note he contributes, if not original, either adds valuable confirmation to what has been asserted by others or leads to its being brought into question. Examination of thousands of collectors' labels on museum specimens reveals how astonishingly little has been recorded in the field about such commonplace matters as vegetation, time of day, season, food, stomach contents, lairs, litter size, and other similar biographical data. There is still a vast, new and interesting field open to the keen mammalogist in West Africa.

The carnivores, as their name implies, are as a group predominantly flesh-eating mammals. Yet though flesh may constitute the staple diet of the vast majority, a certain degree of vegetarianism takes place. Indeed, extralimitally some, the pandas, live almost exclusively on this type of food. Those whose experience, in the north temperate zone, is limited to the poultry-stealing red fox and a virtual absence of vineyards very possibly regard the reference in the Song of Solomon to "the little foxes that spoil the vines" as nothing other than rather puzzling figurative poetic prose. But it is almost certainly a perfectly accurate field observation; for while little is known in detail of the diet of the small foxes of West Africa it will be seen later in this work that golden jackals and other normally flesh-eating carnivores do sometimes deliberately make a meal of berries. Species inhabiting arid country may find these at certain seasons a convenient and valuable source of essential fluid.

Possibly all fissipedes on occasion take a certain amount of vegetable food. The well-known habit of domestic dogs of from time to time eating grass is shared by wild species also. This may possibly be to meet some vitamin deficiency; by reason of its intermittent nature and the small quantities involved this habit is generally regarded as being not so much a matter of diet as concerned with some regulatory action on the bowels. Yet the larger wild fissipedes do take in much more green food than appears at first sight because many of them start on their prey by ripping open the belly and consuming the entrails, the stomachs being well filled with grass. Fungi are also sometimes eaten; and later in this work a genet is recorded with its stomach full of rotten wood. In West Africa a regular alternative to an otherwise prevailingly carnivorous regime is adopted by the ratel, which frequently makes a meal of honey and insect grubs, and is known to consume also eggs, bulbs and fruits as well as small mammals. It is often erroneously assumed that the flesh taken by carnivores is always that of other mammals; yet, besides a vast number of rodents, the smaller species depend also for their food in large measure upon birds, snakes, lizards, frogs, fish, crustaceans, insects and their larvae. And though the larger species rely mainly upon antelopes for their sustenance they are not above taking some of these humbler foods too when necessity dictates. Some carnivores habitually eat carrion; others take it only rarely or when hard-pressed for fresh meat—a situation sometimes brought about by their own inability, through injury or sickness, to hunt for themselves. Smaller species in captivity have been found readily to accept prepared starchy foods, and domestic dogs are often made to depend very largely upon them; but there seems to be no evidence that farinaceous foods are ever taken by any carnivores in the wild.

Since the greater part of the diet is, in general, living and capable of swift escape, both speed and cunning are commonly called for in its procurement, as well as, in the case of larger prey, considerable strength, determination and, often, endurance. The exercise of these attributes in the chase is one of the most characteristic features of the carnivores. However, there are widely different methods of hunting. A broad distinction between those of the dog tribe and those of the cats is that the former track, chase and pull down, whereas the latter stalk, patiently await opportunity, and pounce. There are of course exceptions. At times the excursion after food has the appearance of being nothing more than a rather haphazard affair, as when a ratel or a civet proceeds solitarily at a leisurely jog-trot along a route seemingly trusting that chance will present some suitable prey. In the sociable mongooses equally random foraging becomes, however, a rather fussily noisy proceeding, individual members of the party each gathering what morsel may fall his way, unless some larger and more difficult prey, such as a snake, calls for more concerted attack. In other cases the hunt is without question a coldly planned assault on a selected victim, either on the part of a single animal or as a co-operative measure by a family or pack during which there is every semblance of messages being in some way conveyed from one member to another, serving to concert the strategy and bring the attack to a successful outcome. Such methods as these last are employed by lions and hunting-dogs. In contrast, little beyond patience is called for in the case of jackals or other scavengers which commonly live on the left-overs of large predators, and need only exercise their acute sense of hearing to pick up news of a kill to become assured of the eventual effortless acquisition of a satisfying meal.

The search for and killing of prey may take place either by day or by night, though in the latter case the victim may have been picked out earlier while there was still some fair degree of light. Hunting in relative darkness is aided, as mentioned above, by the peculiar structure of the eye by which the reflecting layer known as the *tapetum lucidum* doubles the effective strength of weak light though, probably, scent and hearing at the same time play at least an equal part. Yet despite the usual dominance of these two latter, sight is sometimes obviously the key sense, as with cheetahs initially distantly observing their intended prey and subsequently pursuing it at high speed; or with hunting-dogs in full chase leaping at intervals over intervening grass cover in order to keep on the line of their quarry.

Though food is of first importance in any animal's life the search for a convenient meal is not the sole purpose of a carnivore's daily or nightly excursion from the resting place. Protection of hunting territory or nursery grounds from intruders and, at least at seasons, the discovery of breeding partners are both of considerable moment in the activities of the majority of adults. In these vital matters sight, sound and smell all play their parts, probably in the reverse of this order in importance. As far as repulsion of trespassers is concerned sight may be employed in two ways. It may furnish the first alert to danger at a distance; but, further, at closer quarters warning postures often become a major factor in defence. These involve not only an overall threatening attitude but in some species the presentation as well of intimidating, generally black, marks on the body conspicuously brought to the opponent's view by erection of the tail or twist of the ears (Hingston, 1933). The role of sight in wooing is less; for though courtship displays are known to take place in a few species their importance in carnivores in no way approaches their standing amongst birds.

Sound enters into both personal and territorial defence in the form of the cautionary growl or hiss, the more purposeful snarl and bark, or in social species communal yapping. Its part in breeding is limited to the initial attraction at a distance of the attention of the opposite sex by a recognised mating call. But little is known of this together with the parts that touch and taste also sometimes play in the mating ritual. It is smell, however, that in a great number of carnivores overshadows all else in importance. Scent can, and does, convey clear messages of species, numbers, sex, warning or of ripeness for coupling that are far more enduring and frequently more distantly carried than those of sight or hearing. Its importance in this Order is deducible from the widespread existence and variety of odoriferous glands; and is evinced in practice by the ceaseless inquisitive sniffing of most species on the move, except possibly the cats, together with the repeated deposition of their own odour.

To judge from the development of the bullae, acuteness of hearing is common throughout the suborder in West Africa. At least in the Canidae, the upper limits of pitch received are well beyond that which is effective to human ears. Voice is extremely varied, embracing the roar of the lion, the snarl of the leopard, the purring of the cat, the ululation of the hyaena, the mournful hoo-hoo of the jackal, the musical call of the hunting-dog and the chirruping of social mongooses. These, and other characteristic notes, obviously express contentment, satisfaction, warning, fear, defiance or excitement, though it is by no means always easy to be sure which of these emotions is, in fact, the source of a particular utterance. Most carnivores can produce a variety of sounds according to mood; and there is not uncommonly a difference between the calls of the two sexes. In the case of social animals, the voice, or a change in its tone, may convey to young animals, or in the chase to other adults as well, an actual meaning, sometimes tantamount to an instruction.

The degree of sociability amongst the carnivores is widely diverse. The marine pinnipedes, not dealt with in this book, exhibit gregariousness to an extent not in any way approached by the land-based fissipedes of West Africa or, for that matter, anywhere else. A high proportion of the carnivores are to all intents and purposes solitary except at mating time or in the early stages of parenthood. Lions and cheetahs may occur as a small family group or as a combination of groups up to a dozen or so individuals, though this rarely occurs in the territory now under consideration. Hunting-dogs collect in packs, sometimes, elsewhere in the continent, of large size. The kusimanse and banded mongooses also forage in companies. These latter animals are consistently social; but gregariousness may in other species be of a transitory—though possibly recurrent—nature, the outcome of passing circumstances rather than of inbuilt sociability, as when jackals, for the most part rather solitary in habit, gather round the common attraction of a lion's kill to feed. Of other West African carnivores, foxes, most of the cat tribe, many mongooses, the genets, weasel, polecat and others are basically solitary though at post-breeding times loosely and temporarily knit into small family units.

Few carnivora actually burrow, as some other mammals do; but several of them take advantage, for breeding or shelter, of holes made by other animals such as aardvarks and porcupines. These and other holes they may enlarge and adapt to their own purposes; but probably the only real burrowers amongst the West African carnivores are to be found amongst the dogs, that is to say the fennec, the foxes and possibly, to some slight degree, the jackals. There is also the ratel, which is the most persistent and expert digger of all since it regularly unearths terrestrial bees' nests in search of food and has been known to make tunnels to effect entrance beneath stone walls protecting fowl houses. It breeds subterraneously in a hole that is almost always self-excavated. Otters make breeding chambers in river banks, usually with an under-water entrance. No nest, as such, is ever actually constructed by the carnivores but these subterranean shelters, either self-dug or adapted, are smooth-walled, warm and comfortable. Whether they are lined in any way is not recorded as far as most African species are concerned, but it is known that the fennec's is, and that grass, ferns, moss and leaves are used by other species extralimitally as bedding. Certain arboreal species shelter and breed in holes in trees; and it is possible that in West Africa, as elsewhere, squirrel "dreys" may be taken over and adapted, and perhaps some of the larger birds' nests, as for example those of the Hammer-headed Stork (*Scopus umbretta*).

Skill in climbing is developed in widely different degrees in different sections of the Suborder. This is to some extent a question not only of inborn inclination but of leg and claw shape as well. In the Canidae and Hyaenidae, apart from the ability to scramble over relatively low obstacles, there is practically no capacity for climbing in the true sense, that is to say the ascent of almost vertical surfaces to any considerable height. Leg and claw shape, together with the relative inflexibility of their articulations, are against it. The adult cheetah is not a great deal better off; but the rest of the Felidae, with their needle-sharp, abruptly curved claws and the supple movement of their limbs, are amongst the finest exponents of climbing in the mammalian world. In this they are closely followed by the genets, palm civet, polecat and, to a lesser degree, the ratel. The larger mongooses are poor and unwilling climbers; some of the smaller ones, with light bodies, quite expert.

Although most of the West African carnivores have at one time or another been kept in zoos the amount of published information regarding their breeding habits under these conditions is relatively limited. Extremely little is known of what actually takes place in the natural state though our knowledge has in recent years been welcomely augmented in this respect as regards a few of the larger and commoner species by the patient observations of specialized researchers, as recorded later in the appropriate places. The pattern of courtship, mating, gestation, number of young, and their care and upbringing varies considerably, as is to be expected in a Suborder which ranges so widely in size from the lion to the striped weasel and lesser mongooses, and in mode of life from tree-dwelling genets to aquatic otters. However, large or small, the young always come into the world in an incompletely developed state, born secluded in a den, with their eyes closed, their pelage rudimentary, their limbs too weak to enable them to walk for several days. This is in sharp contrast to the antelopes, which must face the harshness of nature from birth and can walk or even run after their mothers within an hour or two of parturition.

The long, carefully supervised childhood is accompanied by interesting developmental ploys in connexion with the upbringing of a new generation. These are play and more deliberate training, both of which are exhibited by carnivores to a greater degree than in any other group with the possible exception of the primates. This does not hold true of the whole Order; it possibly reaches its maximum development in the Felidae. Play that appears to be sheer exuberance of young spirits has none the less a more important design underlying it in that it brings into practice attitudes and movements which later in life become essential factors in seeking and killing prey. The playful pounce, the sideways strike of the kitten's paw are examples exactly parallelled in earnest by the adult in action after food.

Play is most evident and constant among the young, but in some of it the parents take part, demonstrating movements that their offspring may copy. Play is, indeed, sometimes though much less frequently, indulged in by adults without the instigation of the young; and some of it would seem to have no other purpose than pure fun. Otters, even as adults, are renowned for their apparently purposeless acrobatics and gambolling both in and out of water. Some of the later training for adult life has nothing of juvenile high spirits about it at all, being given directly and purposefully by the parents, more especially the female. Young cheetahs are made to sit and observe the mother in action after game before they themselves are allowed to hunt. In the Canidae the smaller packs of hunting dogs are essentially family groups under the direct tutelage of the mother, though eventually two or more of such groups may become associated under the leadership of a dominant male. Co-operative hunting, though it may to some extent be instinctive, nevertheless calls for the acquirement, by observation, of clan methods and the understanding of the implications of different calls. Hunting in packs does not necessarily always imply planned co-operation, or certainly not at the high level of intelligence found amongst, say, the larger Canidae and Felidae; for, as already pointed out, some of the smaller mongooses forage in company while seemingly acting each for itself alone.

Economics etc. The carnivores fill a key role in maintaining the balance of nature since without them many other kinds of animals, especially other mammals, would multiply to harmful proportions. One practical aspect of this as far as man's activities are concerned has been demonstrated in recent years, when the ruthless destruction of leopards led in many places to a vast increase in the number of baboons and, as a consequence, a grave destruction of farm crops by these marauders. The carnivores do in fact, alive or dead, play a fairly constant part in man's economy, sometimes, as in other Orders, through domestication. Dead, the pelts of several kinds, especially those with dense or strikingly patterned pelage, are valuable in the fur trade. Of these, the leopard is in Africa the chief; and it is the widely increased demand to meet this market together with the general fear and hatred in which this animal is held, combined with more effective methods of killing it that have led to its excessive destruction—with incidental repercussions such as that mentioned earlier in this paragraph. Outside the limits of this book, or indeed of the African continent, other carnivores furnish pelts of the highest value, some of the foxes and the mink ranking high in this respect; but there are other African skins which find a market as ornamental furs, such as the cheetah and to a lesser extent the serval and the otters. At a lower level, in local trade, genet and mongoose pelts fill a constant demand for bags and matchet-scabbards; and throughout a good deal of Africa the skin of the caracal finds a ready sale as an anti-rheumatic garment.

The most important economic function of the carnivores in the living state has already been glanced at—that of keeping in reasonable check all manner of animals, from rodents to antelopes, that would otherwise certainly assume, for man, pest proportions. But there are, too, certain minor economic roles. The undoubted commercial value of living carnivores as highly attractive zoo exhibits cannot be ignored in a review of the Order's economic position, though the spectacle of a lion impatiently pacing the narrow confines of a cage may not in itself be to everyone ethically justifiable—an objection which does not apply to the possibly even greater economic success of making such animals part of the attraction of a national park. The importance of the dog in many spheres, not only as the friend and sometimes protector of man but most notably as a vital aid in the discovery, seizure or retrieval of food must not be overlooked, especially in countries and communities where such use is an urgent matter of business not a "sport". Yet, as a whole, wild carnivores as living entities play little beneficial part in man's economy. The civet furnishes the perfume to which it gives its name; but apart from that it is difficult to think of any other direct service of value rendered by undomesticated species.

The adverse side of the picture is different. Wild carnivores from the largest to the smallest impinge detrimentally upon human activities, stealing and killing cattle, sheep and poultry, and sometimes even man himself, so that his hand is raised in relentless battle against all such predators. There is another, more covertly harmful role of the carnivores, their function as reservoirs and vectors of disease. Everyone is aware of the key part played by domestic dogs in the transmission of rabies. Wild species are equally guilty though their impact is, of course, less direct. There is little doubt that the carnivores as a whole are capable of spreading, directly or indirectly, a number of other diseases and intestinal parasites; and they are well-known hosts of ticks and fleas which themselves are recognized as having high medical and veterinary significance. But so far in West Africa very little investigation has been carried out into these matters.

Taxonomy. Simpson (1945) treats this at considerable length, and those to whom this aspect of the carnivores is important should consult his account. There is little purpose in a book of the present nature in entering into a wealth of not very relevant historical detail. Fundamentally there has for long been broad agreement with the general classification, if not the naming, adopted herein—which is that of Simpson (1945), itself basically that of Winge (1895). There is much about the animals included in the Carnivora, their structural morphology, dentition, external form and habits which make their apparent relationship both as a group and within that group pretty clear-cut, and for this reason their taxonomic arrangement has in essence remained much as it was in the 10th edition of Linnaeus' *Systema Naturae*, 1758. What has been more in question than the constitution of the Order as a whole or of its main subdivisions is the precise degree of relationship to one another of these subdivisional groups within the Order.

The separation of the Order Carnivora into two main categories, Pinnipedia and Fissipeda, is of very long standing, the name for the latter dating from Blumenbach in 1791, and for the former from Illiger twenty years later. The fissipedes, alone of concern to this book, are likewise divided into two main sections, herein given Simpson's Superfamily titles Canoidea and Feloidea. Precise morphological definition of the major subdivisions of the fissipedes in the modern sense dates from just a century ago when Flower came to the conclusion that three primary groups could be recognised from features of the skulls: the Aeluroidea (broadly the cats and their relatives), the Cynoidea (the dogs), and the Arctoidea (the bears). The two last, previously separated partly as being on the one hand digitigrade and on the other plantigrade, were later regarded by Winge (1895) as sufficiently close to be included in a common superfamily; and this grouping, using a variety of names, has to all intents and purposes been recognized ever since. The name Aeluroidea for the cat group is still often come across and was employed in a major work as recently as Pocock, 1951; but Simpson holds that it is invalid and otherwise objectionable and has therefore substituted the term Feloidea, used herein. The degree of relationship of the families within these superfamilies has also been subject to differences of opinion; but these matters will be dealt with in the appropriate places later.

With the exception of the Hyaenidae, which in some measure occupy an intermediate position, on skull characters the differences between the two superfamilies are clear and in most cases easily observed. The question of drawing up a brief key from external features is altogether another matter. For while all the families are individually recognizable easily enough by those who already have some experience of the animals with which we are here concerned, the characters upon which distinctions might be based are either partly shared by the two superfamilies or differ in ways that are incapable of such definition as is succinct and at the same time not productive of doubt in the minds of those who are dependent upon an artificial key. The two keys to the major scientific groups which immediately follow, and which attempt to preserve cohesion within each subfamily, illustrate these points. A third key, which entirely ignores the classic major grouping, leads to the families irrespective of their larger relationship, therefore, in a more direct fashion.

KEYS TO THE SUPERFAMILIES OF FISSIPEDA

A. Cranial characters

1. The bulla (except in the Hyaenidae) almost completely divided internally by a more or less erect septum which can generally be clearly seen (except in the otters and some mongooses) through the auditory meatus, which is in nearly every case extremely short, being devoid of any marked external lip or lips; the position of the septum is often (but not always) indicated externally by a shallow furrow dividing the bulla into two sections. In the Hyaenidae the auditory meatus is long with a well-developed external anterior lip, and the floor of this meatus is continued inwards to form a partial horizontal septum, which thus cannot be detected through the orifice. The paroccipital process spreads over the posterior part of the bulla, being sometimes very closely applied . **_Feloidea_** (*page* 160)
2. The bulla with no, or only a very small, internal septum; the auditory meatus long with a well-developed external lip or lips; no trace of any furrow across the bulla wall, except sometimes round the lips of the meatus. The paroccipital process rarely spreading much over the hinder part of the bulla . . . . **_Canoidea_** (*page* 29)

B. External characters

1. The pelage displaying one of the following characters:
   (a) a regular pattern of spots, at least on the underparts, sometimes on the spine coalesced into a stripe or stripes;
   (b) transverse stripes;
   (c) speckled or ticked ("pepper and salt"), mostly plentifully but sometimes obscurely and only on the head, neck and shoulders;
   (d) more or less self-coloured sandy-brown, and either the ears black and pencilled or the tail with a blackish terminal tuft;
   (e) the longish fur indefinitely patterned except for a black transverse stripe on the inside of the foreleg, sometimes two or more on the outside of the hindleg; the flexible tail always with a black tip and often one or more rings . . . . **_Feloidea_** (*page* 160)

2. The pelage with one of the following characters or patterns:
   (a) sleek and sheeny, the throat white with or without very irregular spots, or the tips of the hairs "frosted" white; in all cases the similarly-haired tail markedly tapers from a broad base to a slender tip;
   (b) blotched in large, irregular, varicoloured patches;
   (c) with longitudinal stripes on the flanks or dorsum;
   (d) the back wholly, or more restrictedly, grey, the underside dark;
   (e) the longish fur of indefinite pattern, the tail symmetrically bushy, the muzzle long and dog-like. . . . . . ***Canoidea*** (*page* 29)

KEYS TO THE FAMILIES OF FISSIPEDA

A. Cranial characters

1. Cheekteeth 14 or less . . . . ***Felidae*** (*page* 373)
   Cheekteeth more than 14 2
2. Cheekteeth 26 . . . . ***Canidae*** (*page* 30)
   Cheekteeth less than 26 3
3. Cheekteeth 22 or 24 . . . . ***Viverridae*** (*page* 161)
   Cheekteeth 20 or less 4
4. Cheekteeth $\frac{4\ 1}{3\ 1}$ = 18 (sometimes in *Crocuta* apparently 16 through the loss of the minute upper molar) . . . . . . ***Hyaenidae*** (*page* 341)
   Cheekteeth 16, 20 or if 18 then $\frac{3\ 1}{3\ 2}$ . . . . . ***Mustelidae*** (*page* 92)

B. External characters

1. Head rounded, muzzle short, backs of ears (except *F. lybica*) wholly or partly black; coat often spotted at least on the underside; claws (except *Acinonyx*) very curved, very sharp and wholy retractile. Cats. ***Felidae*** (*page* 373)
   Not like this 2
2. Of fairly large or large size, standing higher at the shoulders (30 inches, more or less) than at the hindquarters; coat spotted or transversely striped; jaw very powerfully built; both front and hindfeet with only 4 digits ***Hyaenidae*** (*page* 341)
   Not like this 3
3. Of small or fairly small size; the coat spotted and the tail ringed; or the coat speckled (in dark forms often obscurely) and the tail generally long-haired but not symmetrically bushy, and the legs short . ***Viverridae*** (*page* 161)
   Not like this 4
4. Coat with pronounced longitudinal dorsal stripes; or wholly (occasionally restrictedly) light grey and the underside dark; or close-lying, glistening, dark, often with a more or less white throat . . ***Mustelidae*** (*page* 92)
   Coat with varicoloured blotches, or a single side-stripe, or of an indefinite mixture with no set pattern; tail symmetrically very bushy. Dogs ***Canidae*** (*page* 30)

Superfamily **CANOIDEA** Simpson, 1931

The first major division of the fissipedes to be considered comprises four extant families, the Canidae (dogs), the Ursidae (bears, entirely absent from Africa), the Procyonidae (raccoons, coatis and other similar New World and East Asian animals), and the Mustelidae (a large and heterogeneous group of stoats, weasels, polecats, skunks, badgers, ratels, otters and several others, all characterized by powerful and sometimes highly offensive scent glands). From this it can be gathered that the whole superfamily is a pretty mixed assemblage. Even as far as the only two families occurring in West Africa are concerned, the Canidae and the Mustelidae, it covers such diverse creatures as the dog-like, carrion-eating jackals, the bulky, short-legged, honey-hunting ratel, the small and slender, warningly-coloured weasel, and the aquatic fish- and crab-eating otters. The group was once known as the Arctoidea. This was, in fact, a combination of two major groups proposed by Flower in 1869, the bears and the dogs, Arctoidea and Cynoidea; but since there were objections to the use of these terms Simpson (1945) coined the name now most commonly employed.

It is almost impossible to find characters that firmly and clearly separate the Canoidea and Feloidea. Those given in textbooks are mostly found in practice to be at least partially untrue; and, indeed, Dücker (1957) on other than morphological grounds has questioned some of the existing classification (see page 163). What follows, though for the most part of general application, takes into consideration only those species which are of concern to West Africa. There are certain obvious external differences between individual families or subfamilies; but these are often hard to define succinctly and impossible of application to the superfamily as a whole. The characters chiefly used lie in the skull and especially in and around the auditory region. In the Canoidea the tympanic bulla is to all intents and purposes unobstructed internally and the meatus is of some length, having often a lengthened lower lip. In the Feloidea, on the other hand, the bulla is almost completely divided into inner and outer chambers by a septum, and the meatus is little more than a ring—although the septum is differently placed and of possibly different origin in the Hyaenidae (Pocock, 1916c); and both in this family and in the Herpestinae the meatus is long. The paroccipital process, where present, is in the Feloidea closely applied to the posterior face of the tympanic bulla, over which it tends to spread and fuse; but in the Canoidea the process is often manifestly independent, though in some cases, as in *Ictonyx*, *Poecilictis* and *Mellivora* it simulates the feloid form. It is also said that the carotid canal is long in the Canoidea and short in the Feloidea; but this, again, is not invariably so. The dentition is widely variable throughout the two superfamilies.

Family **CANIDAE** Gray, 1821

DOGS, FOXES, ETC.

Distribution and general. The Canidae, or dogs and their close kin, are to be found in a wild state over most of the world with the exception of New Zealand, Antarctica, and a number of islands in various parts of the globe from the West Indies to Oceania. As far as Australia is concerned it is believed that the now native wild dog, the dingo, must have been introduced into this essentially marsupial island-continent by early settlers or visitors many centuries ago.

The animals included in this family form a very important section of the carnivora and, one way and another, have a great impact upon both the natural fauna and domestic stocks. This, however, has considerably lessened in recent times, due in part, by reason of human population expansion, to appreciably lesser numbers of wild canids than formerly; and in part to more effective methods of control or extermination, brought into use to combat predation upon valuable farm stock.

Canidae are to be found in very diverse ecological settings, from the arctic snows to hot and dry deserts. In West Africa wild species, with which this account is alone concerned, do not occur in the closed forest or, indeed, nearer the coast than the middle of the Guinea woodlands. On the other hand some of the foxes range well into the Sahara. Wild dogs may be to all intents and purposes solitary, except at mating and breeding times; or they may habitually occur in packs, sometimes of large size, as in the case of the wolves (extralimital) and the hunting-dogs of Africa. These packs often have a family-group foundation.

Description. Though the members of this family vary very considerably in size they are all built on a fairly well-defined plan that makes them readily recognizable as canines. In West Africa there is at one extreme the little fennec weighing about 1·5 to 2 kg and at the other the jackals which attain 5 to 8 kg. Despite such disparities of size, general overall family resemblance is seen in various parts of the body: a head, furnished with conspicuous erect ears and narrowing to a long tapering muzzle that ends in a naked black rhinarium; a deep-chested body; a long and abundantly bushy tail; and rather slender but muscular legs terminating in well-padded, digitigrade feet armed with straightish claws, well-designed for running. On the outer margin of the ear a bursa is always present, the upper part of its posterior flap not being continuous with the main rim of the pinna but arising behind it.

The pelage is generally pretty long and is always dense. Though, according to genus or species, it exhibits widely diverse colouring from blackish-brown to bright red, it is rarely entirely self-coloured but most often ticked or speckled with lighter or darker tips to the individual hairs, which may also in other ways vary amongst themselves in colour or at least tone. Areas of black or white may form a well-marked feature in certain species; but there is scarcely ever anything that could be regarded as a formal, fixed and regular pattern of stripes or spots. Even in the so-called side-striped jackal of West Africa, the black band on the flank, which gives rise to the name, is somewhat inconstant and often obscure. The extreme bushiness of the tail

(Plate 1) gives it a striking appearance and and a characteristic shape that furnishes an immediate point of recognition.

Skull. The canid skull (fig. 4) is long and narrow, the elongated rostrum reflecting the well-known sharp face of all but certain highly specialized domestic forms of the family. The braincase is rounded; but, considering the reputed intelligence of the Canidae, seems disproportionately small and to constitute a relatively minor part of the total skull volume. As far as West African species are concerned there is always at least some development of sagittal and supraoccipital crests except in *Fennecus* (fig. 8) in which the former is almost completely lacking, and the latter relatively insignificant. In *Lycaon* (fig. 10) the sagittal crest is tall and knife-like; in *Canis* (fig. 4) it is low; and in *Vulpes* (fig. 8) it is restricted to the extreme posterior part of the cranium. The frontal region is marked by fairly well-developed, subtriangular postorbital processes, often forming a slight flange over the orbit itself but lacking any finger-like extension; and since the jugal process is also short there is thus a wide gap in the circumorbital ring. The nasals are long and narrow and always reach back at least as far as the front of the orbit.

The up-curved zygomatic arch is of moderate strength, the jugal bone playing a major role in its constitution. The palate broadens posteriorly, the cheekteeth, from front to back, curving gradually out and then, more sharply, in again, the dental row from the canine to the posterior molar thus forming a flattened S. The mesopterygoid fossa is mostly broad and deep. The bullae in the West African forms are large or, in *Fennecus*, extremely large. In view of the manifest importance of the teeth in this family and the relatively strong construction of the upper jaw, the mandible appears unduly slender and weak, the slightly up-curving rami being, except in *Lycaon*, shallow; but it must be remembered that there is very little chewing carried out in this family, the teeth being mostly used for severing chunks of flesh which are swallowed whole. The coronoid process rises steeply, high above the typical carnivore subcylindrical condyle. The angular process is small and sharply divided from the main body of the ramus.

Dentition. The dental formula in the Canidae is basically $\frac{3.1.4.2.}{3.1.4.3}$ 42 throughout the family with a few (extralimital) exceptions, of which *Otocyon*, the bat-eared fox, occurring from Ethiopia to Cape Province, is the only African example. In this genus the cheekteeth may be $\frac{7}{8}$ or $\frac{8}{8}$.

In the West African genera, with which this work is concerned, the incisors, though well-developed, are relatively small, their sharp cutting edges sometimes trilobed. The canines—a name, of general use throughout mammalian dental nomenclature, deriving from their prominence in this family—are always very tall, recurved, strong and tapering to a sharp point, ideally suited to sinking deep into flesh and maintaining a secure anchorage upon a struggling prey. Their build prevents their playing any further role in mastication. The post-canine gap is at most of very moderate size, and in *Lycaon* non-existent.

All the cheekteeth (fig. 6) have cingula, most prominently developed in the posterior part of the toothrow. The four premolars of the upper jaw increase progressively in size from the first to the last, p^4, the upper carnassial, being always the tallest cheek-tooth. All, when unworn, are sharp and of triangular profile, though there may be a secondary, far lower, cusp anterior or posterior, or both, to the main one. p^1 has a single root, p^2 and p^3 two each longitudinally sited; p^4, which is of somewhat more complex construction, has a third root situated transversely to the first, surmounted by a small cusp; and there is a larger secondary narrow cusp in line with and posterior to the main one, forming an important component of the sectorial blade. The lower premolars are of the same form as the upper ones except that p_1 is simple precisely similar to p_2 and p_3.

The molars are far more complex besides being of markedly different forms in the upper and lower series. They also differ somewhat in the two subfamilies. m^1, by reason of its great breadth, is by far the bulkiest tooth in either jaw. Its cingulum is well-developed and anteriorly forms a small subsidiary cusp. Apart from this, in the Caninae the crown comprises two outer cusps, two much lower inner ones, and an internal heel. m^2 is of similar construction but lesser size. The mandibular molars are not broad. m_1, the lower carnassial, consists of a large anterior narrow blade, divided into 2 cusps; posterior to and in line with this is a third much lower external cusp; and there are two similarly small internal cusps, one opposite this last, and one opposite the rear section of the blade. m_2 is a much smaller tooth, with four cusps; and m_3, the smallest tooth in the mouth, little more than a peg, has two cusps. In the second subfamily, the Simocyoninae (*Lycaon*), the molars, both above and below, though of the same general form are rather simpler in their cuspidation.

Habits. Some of the wild dogs, the foxes, have always been recognized as habitual predators, seeking out and killing their own meals; others, the jackals, have for long been commonly regarded as, next to the hyaenas, the great scavengers, living almost entirely on the remains of the lion's or the cheetah's kill. Recent intensive observation has shown this latter notion to be less true than was thought and that the jackals do, in fact, hunt more on their own account than was supposed. This is dealt with more fully later. However, though all the Canidae are preponderantly flesh eaters they do, nevertheless, consume an unexpectedly high proportion of insects and fallen fruits. Most of them are to a very large extent nocturnal, or at least crepuscular, avoiding, except in necessity, direct exposure to the sun. Daylight shelter for the purpose of rest, or more especially for breeding and the early protection of the young, is most commonly found in holes in the ground, "earths" as they are popularly termed. But sometimes, more particularly in the case of young as yet unmated, and hence solitary, adults, temporary concealment is sought in naturally occurring crannies amongst rocks, or even in dense grass opened sufficiently for the purpose by a rotatory movement of the animal before lying down. Earths may be self-excavated but are probably most often basically holes made by other animals, hares, aardvarks, pangolins or termites, improved and adapted. There are often two or more exits.

The Canidae all appear to be monogamous, the pairs remaining together for some time. They share in feeding and bringing up the family, though in the early stages the male is often kept at some distance by his mate. Litter size amongst wild dogs seems to range between 2 and as many as 10; and there may be one or two litters a year, the age of the mother possibly being a determining factor in both. No set breeding seasons have been established for Africa. The average period of gestation is in the nature of 9 weeks but, though not well-investigated, probably varies a good deal amongst different species and may lie anywhere between 7 and 11 weeks. The young, variously known as "cubs" (foxes) or "pups" (jackals and hunting-dog) are breast fed for 6 to 10 weeks, being gradually weaned to solid food, mostly regurgitated by the parents. An interesting ceremony in this connexion is described later under the jackals.

The gait in the Canidae varies a good deal according to circumstances but follows a common pattern throughout the family. A slow walk is rarely adopted except within a limited range of a few yards extent. Over longer distances the normal means of progression is either, at slow speeds, a four-legged run, sometimes varied by bouncing the hindquarters as a unit; or, at higher speeds, a canter; or, in full pursuit, a gallop. In this last, the two hindfeet touch the ground in rapid succession, impelling the animal onwards and slightly upwards while the forelegs are stretched forwards until the two pairs of limbs are fully extended and the whole body is in flight out of any contact with the ground. The two forefeet then consecutively touch the ground, and give the animal a second onward thrust while the hindlegs are brought forward until they cross the now backwardly directed forelimbs, which leave the ground, the whole body becoming a second time suspended in flight, but this time with the legs tucked under it, not outstretched as previously.

The Canidae have no great powers of climbing; but they can overcome low obstructions in their paths both by leaping and by scrambling over those that offer adequate footholds. The hunting-dog when in full cry intermittently performs leaps to obtain a view of the prey which may be hidden by the tall grass.

Voices in the African Canidae, so far as they have been recorded, are pretty varied, not only between species but according to circumstances as well. There is, without doubt, an extensive vocabulary of signal notes, for the attraction of a mate, the control of the young or the co-ordination of the pack, that has not as yet been investigated or recorded. Nothing truly resembling the familiar bark of the domestic dog seems to be uttered by West African wild species, most of the sounds being characterised as harsh yaps, reiterated melancholy whoops or long-drawn-out notes.

Several factors serve to hold the number of Canidae in check. When young and relatively defenceless they are, unless actively protected by the parents, subject to the same attacks as other small mammals from pythons, eagles, other carnivores or driver ants. In the adult stage they may be killed by hyaenas, angry lions and the like; but the risks of destruction they run from these or similar enemies seem to be slight. Their numbers are kept in control more by diseases, and by loss of efficiency from undermined health or accident which prevent them from maintaining their place in the pack or against stronger, more active and thrusting members of their own kind. The availability of food has a considerable influence on the numerical size of the litter or the proportion of it that can be successfully reared. The relatively low density of antelope population in West Africa, for example, is directly responsible for the general rarity of the hunting-dog there and the small size of the packs in comparison with East Africa.

Taxonomy. Although the Canidae might appear to be a clear-cut, easily recognizable group, their taxonomy has, in fact, more complexity than at first seems likely. This is a matter for more specialized works and it is pointless to do more than glance at the position here. Simpson (1945) gives a long summary of the considerations and opinions involved and furnishes references to the very extensive literature on the subject.

The fossil record is unusually rich and the information which it offers leads to a diversity of possibilities in the matter of phylogeny and of consequent views. One of the chief questions at issue is the limits which should be placed upon the family and the closeness of its association with, or degree of separation from, other groups, and in particular the Ursidae, the bears. The latter, though with their heavy build and lumbering plantigrade gait apparently so dissimilar from the dogs, are, at least in Simpson's opinion, very closely related and, in point of fact, a fairly late offshoot from them. But this is of no great concern to this present work.

On a narrower issue, the extent of, or even the propriety of any, subdivision within the very uniform family Canidae is a further point in some dispute. In practical terms, three subfamilies of living canids are in fact fairly generally recognized, all occurring in Africa though only two in the region with which this work deals. The third, the Otocyoninae comprising solely *Otocyon*, the bat-eared fox, is confined to southern Africa and the eastern side of the continent as far north as Ethiopia. The question as far as West Africa is concerned, therefore, reduces to the validity or otherwise of recognizing two subfamilies, and the distinction which may be drawn between them.

No one could mistake *Lycaon* for anything but a dog, though it is true that it differs slightly in minor matters of general appearance from the more typical members of the family, the jackals, foxes, wolves and so forth. However, on the score of its slightly simplified molars and its possession of only 4 digits on the forefoot it is retained herein as representing the subfamily Simocyoninae, though it is admittedly doubtful whether these and other minor distinctions should logically be accorded any greater than generic significance.

KEY TO THE SUBFAMILIES OF *CANIDAE*

(Previous key page 28)

Coat with varicoloured blotches; forefoot with only 4 digits; adult skull length about 200 mm; m^1 with little or no sign of lingual cusps; m^2 only about one-third or less of the size of m^1 . . . . **Simocyoninae** (*page* 75)

Coat sometimes grizzled or speckled, and often with splashes of black, but not a varicoloured patchwork; forefoot with 5 digits; adult skull length not more than about 130 mm; m^1 with two small internal cusps and a heel; m^2 about half as big as m^1 or more . . . **Caninae** (*page* 34)

Subfamily CANINAE Gill, 1872

TYPICAL DOGS

The Caninae are in distribution co-extensive with the family, of which they form by far the greater and more varied part. Eight genera are now recognized covering the wolves, jackals, coyotes, foxes and various other less familiar animals as well as the domestic dogs, the precise ancestry of which is in some dispute and is doubtless of a diverse nature. The general characters of the subfamily are those detailed above for the family with the exception mainly of the points brought out in the foregoing key.

KEY TO THE GENERA OF *CANINAE*

(Previous key page 34)

1. Size small, head & body length 350 to 400 mm; ears extremely large for the size of the body (about 90 mm); hindfoot about equal in length to the ear or not much longer; bullae very large, their length almost equal to the breadth across the back margins of m^2—m^2. . ***Fennecus*** (*page* 54)
   Size larger, usually at least 400 mm; ears moderate and the hindfoot appreciably more than their length; bullae not so large. 2
2. Back and/or flanks with at least some fairly definite and obvious splashes of black; of fairly large size, head & body measuring 590 mm or more, the tail less than half their length; maximum skull length over 130 mm; postorbital processes without any depression on their upper side ***Canis*** (*page* 35)
   Back and flanks without any definite black markings, though sometimes greyish in tone; size moderate, head & body generally measuring 400 mm or more, the tail well over half their length; skull under 120 mm; postorbital processes with a slight dorsal depression . ***Vulpes*** (*page* 62)

Genus **CANIS** Linnaeus, 1758

Canis Linnaeus, 1758, *Systema Naturae*, 10th ed. **1**: 38. Type species *Canis familiaris* Linnaeus, the domestic dog. *Canis* was the Latin word for a dog.

Thos Oken, 1816, *Lehrbuch der Naturgeschichte* **3**, 2: 1037. Type species *Thos vulgaris* Oken (*Canis aureus* Linnaeus). *Thos* was the Greek name for (probably) a jackal. Oken's work has been ruled to be taxonomically unavailable.

Lupus Oken, 1816, *Lehrbuch der Naturgeschichte* **3**, 2: 1039. Type species *Canis lupus* Linnaeus. *Lupus* was the Latin for a wolf. Unavailable.

Vulpicanis Blainville, 1837, *Annls Sci. nat., Zool.* **8**, 2: 279. Type species *Canis aureus* Linnaeus. This name was compounded from the Latin *vulpes* fox and *canis* dog.

Dieba Gray, 1869, *Catalogue of the Carnivorous, Pachydermatous and Edentate Mammalia in the British Museum*: 180. Type species *Canis anthus* F. Cuvier. The name is a Latinized form of *dieb*, a North African vernacular name for a jackal.

Schaeffia Hilzheimer, 1906, *Zool. Beob.* **47**: 364. Type species *Canis adustus* Sundevall. This was called after Dr. Ernst Schäff in recognition of his help in the investigation of jackals.

There is little doubt but that this genus has had a greater impact upon man than any other group of mammals with the possible exception of the ungulates; for apart from wild species which, despite greatly reduced numbers, in most parts of the world even today impinge considerably upon human activities, it has given rise to the millions of domestic dogs upon whose varied special abilities man is dependent in many spheres—without taking into any account a more intangible emotive intimacy, widespread though this last may be. The limits of the genus, taxonomically speaking, have altered a good deal through the years, *Canis* at one time being held to cover almost any species of dog-like appearance (exemplified in Mivart, 1890), and at others to be reasonably separable into a number of independent genera, as partly indicated by the above synonymic list, which includes only names of concern to West Africa. It is not a function of this present work to deal with domestic varieties, though it may be observed in passing that there are several different strains in West Africa whose appearances, attributes, origins and possible relationships merit some study and record. Of these, the small, black Ogbomosho hunting dog is, or was, amongst the most highly trained and skilled.

Wild species of *Canis* occur in Europe (wolf), Asia (wolf, golden jackal), North America (wolf, coyote), Africa (golden, side-striped and black-backed jackals), and Australia (dingo), this last probably a domestic form anciently introduced by man and subsequently gone feral. The foxes were at one time also considered appropriate to this genus but there is now fairly general agreement that they are best separated as *Vulpes*. Certainly the two genera, in the forms of the European fox and the domestic dog, though not infrequently in popular belief held to hybridize, have never, in fact, been shown to do so, even with artificial insemination (Gray, 1954). This leaves, therefore, only three true wild dogs of the genus *Canis* in Africa, of which two, *C. aureus* and *C. adustus*, the golden and side-striped jackals respectively, are known to occur within the limits herein dealt with. It will be appreciated that, with a range extending over much of the globe from Australia to the Arctic, there must be a good deal of variety of appearance and form in the genus. No useful purpose is served by attempting to provide a general diagnosis of it, the main characters of which can be sufficiently gathered from the descriptions of the two West African jackals which follow.

These two may be differentiated thus:

KEY TO THE GENUS *CANIS* IN WEST AFRICA

(previous key page 35)

Backs of the ears greyish; flank generally with a blackish longitudinal stripe beneath a white one; skull profile shallow, almost flat from the nasals to the frontals; the zygomatic arch shallowly curved in the vertical plane **adustus** (*page* 49)

Backs of the ears reddish; dorsal pelage often with irregular black patches; skull profile fairly arched and with a marked change of level about the middle of the nasals; the zygomatic arch strongly up-curved . . . **aureus** (*page* 36)

CANIS AUREUS Linnaeus Golden Jackal

Canis aureus Linnaeus, 1758, *Sytema Naturae* 10th ed. 1: 40. Benna Mts., Laristan, S. Persia (*fide* Thomas, 1911). The specific name is Latin for golden.

FIG. 3. Golden Jackal (*Canis aureus*)

(*Canis*) *anthus* F. Cuvier, 1820, in Geoffroy & Cuvier, *Histoire Naturelle des Mammifères*, pt. 17, pl. 173 and text. Senegal. *Anthus* was, in ancient Greece, the name of an Arcadian family of which, according to the Roman author Pliny (Book 8) a member was believed to be periodically chosen by lot to be metamorphosed into a wolf for a period of nine years.

Canis variegatus Cretzschmar, 1826, in Rüppell, *Atlas zu der Reise im Nördlichen Afrika, Säugethiere*: 31, pl. 10. Nubia and Upper Egypt. (Not *Canis familaris variegatus* Gmelin, 1788). The name *variegatus* is Latin meaning composed of various colours; given by reason of the pelage.

Canis riparius Hemprich & Ehrenberg, 1832, *Symbolae Physicae seu Icones et Descriptiones Mammalium . . .*, decas secunda. Coast of Abyssinia, near Arkiko.

Canis vulpes dorsalis Gray, 1838, *Proc. zool. Soc. Lond.* for 1837: 132. Senegal. (*Vide* Ellerman & Morrison-Scott, 1951: 224). This name is the mediaeval Latin adjective meaning pertaining to the back, probably given in reference to a distinctive dark saddle.

Thos senegalensis Hamilton Smith, 1839, Jardine's *Naturalist's Library*, **25** (of the series), **9** (of Mammals): 210, pl. 13. Senegal.

Canis anthus soudanicus Thomas, 1903, *Proc. zool. Soc. Lond.* **1**: 295. El Obeid, Kordofan, Sudan.

Canis doederleini Hilzheimer, 1906, *Zool. Anz.* **30**: 16. Upper Egypt. Named after Professor Dr. Döderlein.

Canis thooides Hilzheimer, 1906, *Zool. Beob.* **47** 364. Senaar. This name is compounded of the Greek *thos*, wolf, and the termination *-oeides* implying resemblance.

Thos aureus nubianus Cabrera, 1921, *Bol. Soc. esp. Hist. nat.* **21**: 264 This name was to replace *Canis variegatus* Cretzschmar, preoccupied.

Distribution and general. The golden jackal (fig. 3) is sometimes called the common jackal, but this may be a misleading term, certainly in West Africa. It is also frequently referred to as the Asiatic jackal since it is spread across much of that continent and was more commonly and better known from there than from Africa. Its range is, indeed, wide. In Africa it extends from Kenya and north-eastern Congo northwards and westwards to Senegal, Morocco and the countries bordering the Mediterranean. Thence the range continues across south-eastern Europe, the Arabian peninsula, and a good deal of southern Asia, including the whole of India and Ceylon, to as far east as Burma and Thailand.

From West Africa specimens exist in the British Museum from Takoukout (Damergou), Lake Chad, Tchsiderak, Manakaoki (Aïr) and (just extralimital, in Ahaggar) Tazerruk. The species has also been recorded from near Timbuctu, from Portuguese Guinea (Madina de Boé and Gabu), from Dahomey and from Cameroun; but it almost certainly occurs throughout the Sahel vegetation zone. This together with the Subdesert are its main habitat. It is replaced in the Sudan and Doka by the side-striped jackal, *C. adustus*.

Taxonomy. With this wide distribution it will be readily understood that a good deal of variation of colour and size occur and that, in consequence, a large number of local races has been described. Several attempts have been made to synonymize many of the proposed names; but the taxonomic position with regard to the golden jackal in Africa remains so confused and obscure that it is impossible to come to any precise conclusion. The reasons are twofold. Although jackals are, in suitable localities, common enough in the field, the collected study material is for the most part meagre and of scattered provenance. Yet more fundamentally frustrating than this is the plain fact that the early type descriptions on which alleged races are based are so inadequate as to be without any real meaning or ability to afford any proper criteria by which clearly to differentiate from others the animals to which they refer.

A glance at the above synonymic list, compiled from names which have at one time or another been associated, directly or indirectly, with West Africa, shows that of the 10 forms listed 6 were described before 1840, reliance being almost entirely on colour; one is simply a replacement name; leaving merely 3 dating from relatively recent times, the early days of this century. One only of these, *soudanicus*, has ever in a direct manner been held to occur within the area covered by this present account; and it alone furnished in its diagnosis cranial and dental data as well as external measurements.

Workers have thus for over a century been in the position of attempting to equate collectors' specimens with ill-defined taxonomically classical forms, partly by external appearance and partly according to locality. It is possible, and indeed probable, that certain African forms of *aureus* differ from Asiatic forms and from each other in colour and size sufficiently markedly and constantly as to merit trinominal distinction; but attempts to do this for West Africa on the basis of existing classical names and in the face of the lamentable deficiency of material is little more than an exercise in plausible ingenuity. Dependence upon pelage pattern is vitiated by the almost certainty of a high degree or individual variation, especially of the chief character taken into account, the amount of black in the coat, both dorsally and on the tail. There can be very little doubt indeed that within any one population or family this cannot help but be a matter of considerable variability and one upon which little sound argument can be based. This, to judge from British Museum specimens, would seem to apply to the amount of rufous colouring in the pelage make-up as well. Colour and pattern are also affected by age and moult. This is well-evidenced by two skins from Rio de Oro (extralimital), B.M. Nos. 5.9.1.1 and 5.9.1.2, one a fairly old animal with scarcely a trace of black, the other a youngish one, with a relatively large amount. Had they been collected at different times at slightly different places they might well have been given separate distinctive names.

It seems, indeed, very possible that the existence or form of black markings, often deduced from single specimens, or even from illustrations demonstrably wrong in other respects, have been credited with a constancy of occurrence and a taxonomic significance which they do not possess.

Skull character and size would appear to provide a sounder line of reasoning; but here, the material available is often so limited and of such scattered origin that, certainly as far as West Africa goes, it is scarcely possible to base any convincing argument upon the threadbare data it yields. *C. lupaster* skulls from Egypt are indisputably far larger than any others; but when it comes to the consideration of the remainder of alleged forms the position is not so clear-cut. That size is not always dependable, especially when only two or three skulls are taken into account, is demonstrated by a pair of apparently similar age from the Plain of Tokar (extralimital), one being 15 to 20 per cent larger all round than the other. It is true that one is male, the other female, but no such marked sexual disparity is evidenced elsewhere as sex-linked. The size and proportions of the teeth appear to be more reliable than the skull itself, but in these, as in other characters, it must be repeated that the material available from West Africa is so limited that it is scarcely possible to come to any precise conclusion; and in any case it is difficult, if not impossible, to relate cranial and dental measurements to corporeally diagnosed classic forms.

Before leaving the general aspect of this matter one factor contributory to racial obscurity must be mentioned. There can be little doubt about the wide-ranging capabilities of these wild dogs. Like their more domestic relatives they can cover considerable distances, untiringly and often, by human standards, at a fair speed. They may do this, without any marked impulse to return upon their tracks, in the chase, in response to sexual urge, seasonally as the result of the movement of game and other food supplies, or just by reason of a roving nature. There is, in the part of Africa under consideration, no vegetational or physical barrier to wide transcontinental movement; and dogs by their very nature, the wiry strength of their build, their stamina, their readiness and eager persistence in pursuit, and their ability to be self-supporting, are better able to take full advantage of this freedom than most. Thus, while species must always remain separate, the maintenance of discrete races under such circumstances would seem to be altogether another matter.

We must turn now from these general considerations to a more particular investigation of the reputed West African forms. The position can only be summarized; enough has been said to show that there is little profit in too searching an examination. The above synonymy shows that, basic species *aureus* apart, three forms have been specifically attributed to western Africa, *anthus*, *dorsalis* and *senegalensis*, all typically from Senegal. Considering these first, it may be said at once that *dorsalis*, described by Gray as a fox, is unquestionably a jackal, so juvenile as to be indeterminable but in all probability *aureus*. The other two forms at once plunge us into doubt. Cuvier described *anthus* as a species in its own right, differentiating it from *aureus* not very exactly in words and only slightly more clearly in pictures—which, however, tend to belie the meagre verbal diagnoses. There are other difficulties. Cuvier stressed the fact that the two jackals had been found in captivity to interbreed fertilely. This, if nothing else, seemed to make it improbable that two separate species were involved; and the modern view is that the golden jackal exists as a single species, *aureus*, spread across Asia and the more northerly part of Africa as described earlier on. If this is so, and there is little reason to doubt the correctness of the view, *anthus* can be regarded as nothing more than a race of *aureus*; and such is, in fact, the status universally accorded it today. Yet a complication remains. Cuvier indicated that the two reputed forms existed sympatrically; and as this could hardly be so with two races of one species—and especially since they had been demonstrated to interbreed—one is left wondering whether they do, in fact, occupy the same country or what his so-called *aureus*, with which he contrasted *anthus*, might be.

What, indeed, is *anthus*? No one seems very clear from Cuvier himself onwards. The original type specimen had been a female kept in captivity in Paris. Ten years later, Cuvier who, as indicated in the previous paragraph, had already laid the foundations of future doubts, further confused the issue by describing, and illustrating, as the male of *anthus* an animal which has since been pretty generally regarded as something quite different. Hilzheimer (1908) in a long monograph attempting to sort out the by then even more obscure position remarked on the confusion which, consequent upon the erection of *anthus*, the tendency to refer all North African jackals to this species had given rise to—a situation not least due to Cuvier himself. Oldfield Thomas, certainly, was never very clear regarding West African golden jackals. *C. anthus* was, by diagnosis, expressly related to Senegal; but no specimen from this area existed in the British Museum, and there was thus nothing which could with confidence and any justification be regarded as truly representing the form. In 1903 Thomas especially remarked on the value of the two specimens, mentioned earlier, newly received from Rio de Oro, "as being more nearly typical of the Senegal jackal described by F. Cuvier than the North African examples which have usually had to do duty as such". Rio de Oro is well north of Senegal, outside the Tropics and of a different vegetation. It may therefore be wondered how much more typical of the Senegal jackal they really were. This is the more so since, as mentioned in an earlier paragraph, they differ from one another totally in appearance and very much in age and size. The young one with its blackish back has more likeness to Cuvier's illustration of *anthus* than the older one, which bears no resemblance to this whatsoever; but it may here be remarked that no specimen of any kind in the British Museum shows any sign of the rufous colouring on the fore part of the belly which constitutes one of the clearest pelage distinctions, in Cuvier's illustrations, of *anthus* from *aureus*.

Thomas (1921) made only one other reference in literature to *anthus* when he attributed to this form a very much more heavily blackened specimen, B.M. No. 21.2.11.28, collected by Angus Buchanan at Takoukout (Damergou). This is, in fact, for all practical purposes indistinguishable from Buchanan's five later specimens from Aïr, which Thomas (1925) then named *riparius*, as recorded below. From all this it will be appreciated that there is very considerable uncertainty regarding the identity of *anthus*.

This brings us to the consideration of the third reputed West African form, *senegalensis*. Hamilton Smith devised this name for the second, male, jackal which had been described and figured by Cuvier as *anthus*, as mentioned above; because, as Smith wrote of Cuvier's two illustrations, "an artist seeing both would hardly admit more than the approximation of the two species". Smith's comment applies with incomparably greater force to his own picture of *senegalensis*, for this bears not the slightest resemblance to Cuvier's plate. His description is also largely at variance with Cuvier's; and, indeed, one is left in some doubt as to whether it really was the male rather than the female that he had in mind.

Part of the argument put forward in support of the various alleged forms lies in coat colouring, part in different size or build. Verbal description of all these three categories, in the type diagnoses now under review, is regrettably inadequate. In the matter of size, no account is taken of the possible influence of age; and the few measurements furnished are sometimes given in different forms or are in other cases not comparable. Cuvier, for example, gives his male as standing 17 inches (*pouces*) at the shoulder and 16 inches at the hindquarters, but his female as 15 inches at the mid-back. Hamilton Smith gives no actual measurements other than what is presumably an estimate from these figures, that one jackal is at least an inch higher at the shoulder than the other.

A good deal of the argument must necessarily depend upon the illustrations. It is extremely improbable that any direct comparison of the appearances of living animals can have been made, as Cuvier's female was described and illustrated in 1820, his male in 1830, and Hamilton Smith's *senegalensis* in 1839. This brings into prominence the considerable importance attaching to the circumstances of the making of the three illustrations involved: that is to say, the competence in draughtmanship and colour matching of the artists concerned; and whether the paintings were in fact executed from the living animals or from pelts and measurements made from them; or were reconstructions of build made in response to verbal prompting. In addition to this, the possibility of inaccuracy of reproduction of colour in printed books during the early days of the 19th century cannot be overlooked. How poor, in fact, Hamilton Smith's artist was can be gathered from a glance at his version of *Lycaon pictus*. The whole matter of description, both verbal and pictorial, of the animals with which we are here concerned is fraught with doubt.

Over the years many systematists have spent a good deal of effort and ink in attempts to establish exactly what Cuvier's *Canis anthus*, male and female, and Hamilton Smith's *senegalensis* might be. In view of the facts outlined above, the present writer regards such attempts as little more than a futile waste of time; and in this work it is proposed to draw no nomenclatural distinction beyond the specific name *aureus*. This is not to hold that West African golden jackals may not prove to be validly distinguishable from those of Asia or elsewhere in Africa. It is simply an expression of the opinion that to try to equate any existing inadequate material to these insufficiently and confusingly diagnosed forms, merely because they are classical and repeatedly and unquestioningly appear in literature as occurring in this area, is both misleading and unrelated to the reality of the situation. Nothing short of a wide-reaching review of the species based on first-hand comparison of very considerably broader study material than today exists can lay sound foundations of the subspeciation of *aureus* and justify categorical assertions regarding it. Anything else is frankly unhelpful.

Because of the transcontinental nature of the major ecological zones, certain forms named chiefly for Egypt and Sudan have been said to occur also in the west—as, in view of the uninterrupted nature of these biotopes and the absence of impassable physical barriers, they well might. A brief examination of the remaining names in the synonymic list must therefore be made. Cretzschmar's *variegatus*, though frequently mentioned in literature, is excluded by its prior use by Gmelin elsewhere in the genus. Cabrera therefore intended that it should be replaced by *nubianus*; but Schwarz (1936) thought that there was much to be said for identifying Thomas's *soudanicus* with *variegatus;* and if this is so—and there is good reason to support the view—*variegatus* must be replaced by *soudanicus* rather than by *nubianus* which it antedates.

Setzer (1956), following G. M. Allen (1939), further synonymizes *doederleini* and *thooides* with *soudanicus*; and though this may possibly not be justified, the two animals thus named by Hilzheimer appear to have little connexion with West Africa and are, in any case, antedated by *soudanicus*. There remains only *riparius*. Under the influence of Hilzheimer (1906), Thomas (1925) came to regard his *soudanicus* as identical with *riparius*, described much earlier by Hemprich & Ehrenberg from the "coast of

Abyssinia". Setzer (1956) by implication rejected this. The position is not easy to evaluate. When Thomas accepted Hilzheimer's view he had no skin or skull from the type locality of *riparius* on the Red Sea coast with which to make any kind of direct comparison of his *soudanicus*. On the face of it, the distribution of a single race between such an area and West Africa, with the Abyssinian mountains in between, seems unlikely; but the vegetation map (Keay *et al.*, 1939) shows that there are continuous vegetation zones passing around these from the east to the west coasts. The possibility of such a range is thus not so improbable as at first appears; and some of the available Ethiopian skins in fact agree well with the Aïr series. Of all the north-eastern specimens in the British Museum those which would seem to correspond in provenance most nearly to *riparius* are two from the Plain of Tokar, near the Red Sea. These correspond in appearance to West African skins, and also fairly closely in cranial and dental measurements, as the table on page 55 shows.

The table referred to at the end of the previous paragraph is chiefly concerned with mean cranial and dental measurements; for though some external data are provided they are not wholly reliable. It demonstrates a succession of specimens in the British Museum across the Sahel vegetation zone from Takoukout in Damergou to the Red Sea. Unfortunately nothing is available from further west, that is to say from Senegal; but the area generally implied by this geographical term, and especially in the early days of last century when *anthus* and *senegalensis* were described, lies in this same vegetation belt. To these Sahel specimens are added for comparison three skulls from the Saharan highlands of Aïr and Ahaggar, and also one from Rio de Oro, all these localities lying nominally in Subdesert, the rather more arid contiguous zone.

It will be seen that though there is some variation of size between the largest and the smallest there is a broad general agreement. It must be remembered that the means are derived from very limited numbers which fail to take into account the range of size normally occurring in the different populations. Only in one area are as many as five specimens involved. The size variation becomes very apparent when the skulls are laid out in order; but there is no regularity in this from which clinal or racial trends might be deduced. Given single specimens only, it would be difficult for any taxonomist to equate the relatively small Takoukout skull, a female, with its next, larger, neighbour from Lake Chad, a male; but two from Tokar, of equal age yet vastly different size, indicate that it would be unwise to lay too great a stress on apparent size difference argued from scant material. The smaller of these two, a female, matches the Takoukout animal; the larger, male, that from Chad. All but one of the skins embraced by the table bear a pretty close resemblance to each other; and it is probably justifiable to hold that, with one possible exception, all the animals in this transcontinental series could be assigned to a single race.

The possible exception is that from Rio de Oro. In this animal the upper carnassial, p^4, is appreciably larger than in the others and occupies nearly 26 per cent of the toothrow from c–m^2 as against about 23 per cent in the rest. This fact combined with the different appearance of the pelage, as recorded earlier, as well as its extra-tropical provenance, could indicate that we are in this dealing with a different, North

African, race. But, once again, it must not be overlooked that argument here is based on a single specimen alone; and also that the second, very much younger, of the Rio de Oro skins has the dorsal pelage sprinkled with black in the manner of the Sahel zone animals.

To sum up: from what has been said it seems likely that, in so far as present purely West African material is concerned, we are dealing with a single form; and such departures from a mean as occur are in all likelihood individual rather than racial, and fall within the limits of normal idiosyncratic variation. This applies to reputed differences of muzzle shape and length of leg as well as to marking and size. Further than this, without very greatly increased data, both morphological and biological, it does not seem justified to go.

Finally, in connexion with the question of races in general it is of interest to note that Dobroruka (1959 and 1963) has recorded a change of reputed race between young jackals born in captivity and their parents.

General description. A fully grown golden jackal weighs some 6·5 kg. All the West African skins available for study in the British Museum are sufficiently similar to merit a single description. The dorsal pelage is dense, long and rather harsh. It consists of a mixture of very long, wiry, terete bristle-hairs and shorter, finer, buff-coloured underfur, the general appearance being a mixture of buff and black. The bristles, about 65 mm long, are four-zoned alternate black and white, the base being white, the terminal portion black. This latter is of variable length. Where the black occupies only the tip the general buff colour is scarcely affected; where it is long it forms, in combination with contiguous hairs, a conspicuous element of the coat, giving rise to larger or smaller splashes of colour. Owing to the more or less regular length of the bristles these marks sometimes tend, in a greater or lesser degree, towards forming slight transverse patterns. But in general the black markings are scattered irregularly and vary in amount and pattern individually, with no taxonomic significance. Sometimes instead of the intensely pigmented terminal zone being sharply bounded it merges through a longer or shorter weakly pigmented zone into the white, the area of mild pigmentation being reddish, the underfur being also palely reddish. This gives rise to rufous areas in the pelage, often on the nape and mid-back, generally present in a minor degree, though sometimes very pronounced. There is insufficient study material to draw any firm taxonomic conclusions from this; but it is very possible that this, too, is a matter of simple individual variation.

The black speckling is carried on to the very long-haired bushy tail; but the hairs are only black-tipped, not banded. These terminal zones aggregate into a pronounced black mark, usually some 50 to 75 mm beyond the root of the tail; and at the end of the tail they become lengthy, jointly forming a conspicuous black tip.

The nose is rufous; the crown speckled buffy-grey; the ears golden-brown on their backs, with long white hairs on their inner face and a marginal bursa. The upper lips are white. The flanks are progressively less speckled than the back, the whole underside from chin to anus is generally buffy-white, though there is sometimes a little obscure speckling and colour on the throat. There is no sign in British Museum specimens of the rufous zone on the fore-part of the belly indicated in Cuvier's illustration of *anthus*,

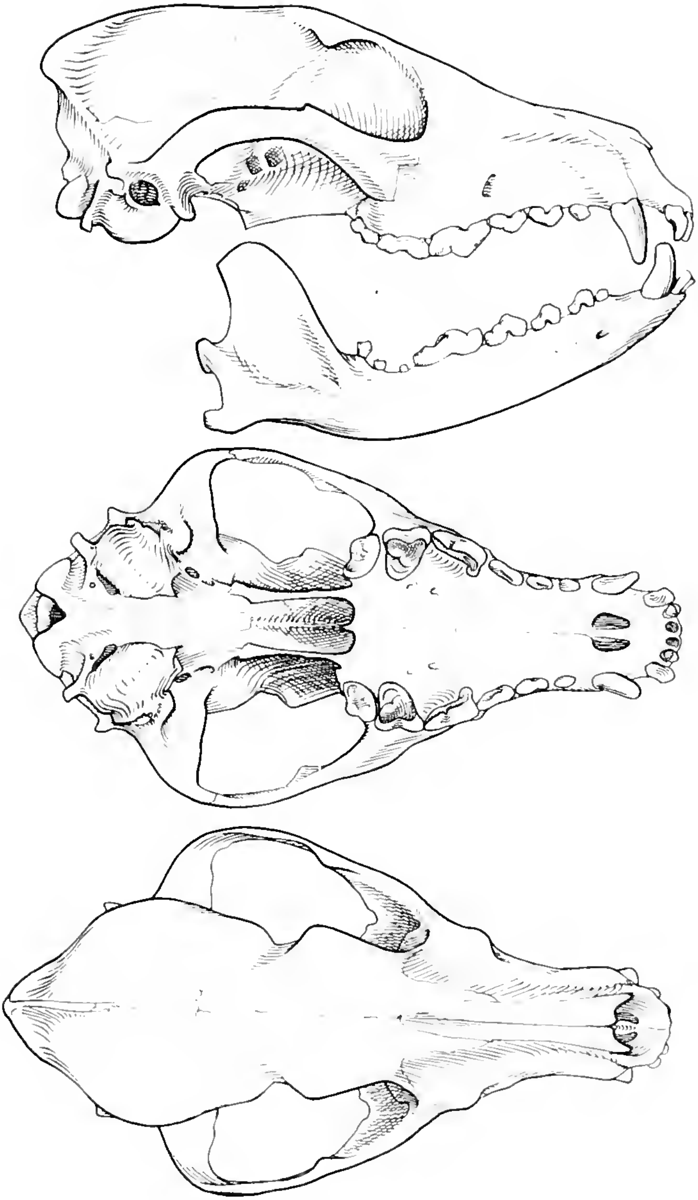


FIG. 4. *Canis aureus*: skull, B.M. No. 21.2.11.28, .

The legs, fore and hind, are palely red on their outer aspect; and the forelegs carry a longitudinal black streak to the wrist, sometimes clear, sometimes very much reduced.

Skull (fig. 4). In all West African skulls the profile shows a marked descent from the frontals to the nasals as opposed to the relatively flat outline of *adustus*. The zygomatic arch upcurves strongly, forming in some cases an almost semicircular outline. The sagittal crest is low over most of the braincase but becomes sharp and keel-like posteriorly and joins equally pronounced lambdoidal crests to form an acute pyramidal prominence. The rostrum is shorter, less tapering and slender than in *adustus*; the nasals are shorter. The mandible is more curved and rather more powerfully built than in *adustus*, the depth of the ramus being greater. The coronoid process, too, is broader, generally with an incurved hind-margin and a slight backward hook at the top, the front margin descending in a broad convex curve from this hook to the base. In *adustus* there is no hook, and both margins are almost perfectly straight.

The chief feature of the dentition is the relatively greater length of the carnassials. It will be seen from the table of measurements, page 55, that both p^4 and m_1 are longer than they are in *adustus*; and in addition to this the length from front to back of p^4 is at least 82 per cent of the length of $m^1 + m^2$, and that of m_1 is well over 130 per cent of $m_2 + m_3$.

Habits. Close studies of these animals in the field have been made in recent years by Wyman (1967) and Goodall (1970), and much of the following account is derived from these sources. Golden jackals are to be seen on the move by both day and night, especially if the latter is brightly moonlit. Like most dogs they can sleep or be active at a moment's notice as occasion demands; and though they do most of their feeding by day it is sometimes necessary to follow up kills made at night by lions or hyaenas even though they may probably, apart from a few hastily snatched mouthfuls, have to wait at a safe distance till well after sunrise before feeding can commence in earnest.

Often golden jackals are solitary animals; but at mating times and during the raising of a family they are always in pairs; and sometimes these or small family units hang together for extended periods. A. J. Hopson noted that they were frequently to be seen up to four in a party in the Sahel woodland and *Salvadora persica* (Salt Bush) thickets near Lake Chad (private communication). Their popular reputation is solely that of scavengers, cleaning up, in company of the vultures, when other larger carnivores have killed and eaten their fill. That they do this is true; but it is only part of the story. It is possibly their easiest way of procuring a full meal since it calls for little more than patience or the skill to see an opening and the agility to dash in, seize a few mouthfuls and nip quickly away before the heavier and slower-moving feeders can prevent them.

But, in fact, their dietary is much wider than this, and they do a good deal of killing on their own account. They mostly confine themselves to small prey, pouncing upon hares, rats, ground squirrels, cutting-grass (*Thryonomys*) and the like; they are known to take lizards and not infrequently to kill and eat snakes. Ground-haunting birds such as francolins and bustards fall prey to them. They also consume a surprisingly large amount of insects: dung beetles, larvae, termites, or grasshoppers, the last of which they may either pounce on or catch in flight. They also eat a good deal of fruit at the right season, fallen figs and the berries of *Zisyphus jujuba* (Hausa *magariya*) being said to be particularly welcome. Another sort of vegetable food they have been observed to eat is certain kinds of fungi. Like other medium- to large-size carnivores, golden jackals steal the more or less helpless young of antelopes unless the mother is by to fend off the attack; but even if she does make a determined defence it is unlikely to succeed if more than one jackal is concerned, since while she is dealing with one aggressor another leaps in and carries off her fawn. Adult gazelles, duikers, warthogs or anything else that would make a suitable meal and is incapacitated by wounding or sickness also fall prey to these predators. Further, it is not generally realized that golden jackals quite frequently themselves hunt and kill fully grown antelopes of the smaller kinds, duikers or gazelles; but this they do, for the most part, only if three or more jackals are working in concert. However, Goodall (1970) once saw a lone jackal chase a female gazelle for some 3 km, unsuccessfully, both animals being by then too exhausted to do more than trot. They are often held responsible for the theft of fowls, lambs, kids or even calves from domestic stock; and they are, hence, themselves ruthlessly hunted. Besides the varied articles of diet enumerated above golden jackals will mark down and follow the females of antelopes that have just given birth in order to be able to pick up the after-birth. They also readily eat fresh droppings from rhinos. Droppings of all kinds are, of course, a source of dung beetles.

When golden jackals hunt antelopes for themselves and succeed in making a capture they, like others of the dog tribe, make no deliberate attempt to kill their prey but rip open the belly and start eating the entrails. Smaller creatures, such as rats or snakes, they kill by shaking; but Goodall once saw a jackal eat a snake alive beginning from the tail end. These animals often carry away more food than they can consume and this surplus is then buried, usually in several different places. It is generally recovered from these within 24 hours; but the caches are sometimes robbed by hyaenas. It would appear that golden jackals can survive for long periods without drinking.

When at rest golden jackals curl up, like a domestic dog, and go to sleep. This they may do on the surface; but the lives of these smallish predators, unlike the far more nomadic hunting dog, are, at other times as well as at breeding periods, very much centred round a home burrow. These shelters—"earths"—may be dug out by the jackals themselves but are probably more usually enlargements of already existing, promising-looking holes made by other, smaller creatures; or adaptations of larger burrows previously the home of an aardvark or warthog. Not much has been done to explore and describe these earths; but there are reputedly one central chamber and two or three independent escape routes to the surface. These homes may be in a secluded spot or, sometimes, not far from those of other den-dwelling carnivores, hyaenas or hunting dogs. Golden jackals have rather loosely defined hunting ranges the defence of which is not very seriously undertaken and, according to Goodall, appears somewhat arbitrary, some intruders being driven back, others peacefully accepted. The area concerned also varies considerably in extent according to the circumstances of the environment. It may be only about 2½ square kilometres or, where game is more scattered and the chance of picking up a meal correspondingly reduced, as much as 20 square kilometres or more. That there is no meticulous insistence upon exclusive ownership is demonstrated by the not unusual presence at a lions' or hyaenas' kill of more than one pair, or one family, of jackals. Goodall once observed as many as 14 golden jackals at one such feast; but as only 6 of these were fully adult perhaps no more than three families were represented. The different nature of the receptions accorded to intruders upon the range may possibly be accounted for by those hostilely treated being complete strangers while those calmly admitted are erstwhile, though now independent, members of the family. The much more restricted territory around the burrow is quite a different matter. It is well defined, the boundaries being clearly demarcated by constant urination or the deposition of faeces, and it is hotly defended against trespass by other jackals. When there are young to be protected dangerous visitors of other kinds, such as hyaenas, are made very unwelcome.

Fights of a serious nature between golden jackals break out sometimes at kills, sometimes in the defence of territory. In these, which are accompanied by a good deal of snarling, the main object is to bite into the opponent's neck, or failing that the face. Hyaenas are driven off by snapping at their hindfeet and legs. The jackals are aided in this by their extreme nimbleness, being always very quick indeed in their movements which thus enable them to contend successfully with much stronger but more clumsy opponents. A swift movement employed by jackals in common with other members of the Canidae is a quick rotation of the body sideways, striking the opponent with the whole flank, thus knocking it off its stance. This would not, of course, be tried against an obviously bulkier opponent but is used amongst the jackals themselves and is an effective method of frightening vultures away from kills. The numbers of jackals must somehow be constantly kept in check. A full list of lethal enemies is not known; but possibly leopards and other large felids attack them. Certainly in their juvenile stages they are in danger from hyaenas and possibly hunting dogs as well as the cats and large birds of prey. Undoubtedly disease plays its part; Goodall observed the total demise of a litter of five weakly cubs in a period of a few days. Golden jackals are themselves, like all dogs, potential reservoirs and spreaders of rabies; an accurate knowledge of the extent to which they may be expected to range in search of mates or better feeding grounds is therefore of some importance.

Since golden jackals associate, most of the time, only in limited family groups there is obviously not the same scope for the development of a recognized social hierarchy as there is amongst animals which live in larger and more diverse packs. Nevertheless, Goodall (1970) observed clear indications of social order established amongst the cubs of a single litter. There is no question of the parents entering into this; but between themselves the male seems always to be dominant, and Wyman indicates, in a photograph, that he always feeds first. Goodall, on the other hand, clearly refers to the pair feeding together off their recently-made kill.

One of Wyman's most interesting observations is the existence of a behaviour pattern relating to the solicitation of food. This is a greeting ceremony primarily employed by the cubs when their elders return from foraging. They dance around the parent wagging their tails and laying their ears back but always keeping their muzzles to the corner of the mouth of the adult, who in response regurgitates chunks of meat upon which the youngsters then feed. Sometimes they regurgitate more than the cubs can cope with. The same ceremony, with a similar result, is used also by fully adult jackals, possibly of a previous litter, which have for some reason remained at the burrow instead of joining the hunt.

Courtship starts with periods of prolonged grooming of the other's fur by each prospective partner. As the time of actual coupling draws nearer the male makes more meaningful advances to the female with his tail stretched out horizontally, his head lowered and his ears laid forward. The female repels these advances with a bite. Coupling probably takes place in darkness. The mean period of gestation is 9 weeks but it may vary by as much as 5 days on either side of this. There may be from 1 to 5 cubs, 2 or 3 being common numbers in a litter. Their eyes open at about the 10th day. Their first pelage is very dark, almost black, and they do not assume their lighter, golden-grey colour until they are nearly a month old.

The cubs are milk fed for about three weeks and are thereafter gradually introduced to solid food For the first few days suckling takes place in the den; but when the cubs can move about they come to the mouth of the burrow in response to a whining call of the mother and are fed there or just outside the entrance. When they are strong enough suckling takes place in a standing position with the cubs on their hindlegs, their forefeet pressed against the mammae. They are fully weaned at about two months. Unlike the hunting dogs or hyaenas, golden jackal cubs are often left alone for long periods while both the parents are out hunting. When the parents return the cubs greet them by nibbling at their muzzles and ears; and ultimately when they are old enough they carry out the begging ceremony, as related above, and are fed by regurgitation.

The father as well as the mother takes part in the upbringing. When feeding is over the female carries out a good deal of grooming; and the pups themselves indulge in much boisterous play. Goodall observed a female to have a second litter within six months of having weaned the first. Another activity carried out as a family, fairly regularly morning and evening and sometimes at night, is howling, the head and ears laid back with nose stretched upwards to the sky, the mouth wide open. The sound is a high-pitched, two-toned "*oooo*". It is always answered by other families in the distance. A golden jackal has been known to live in captivity for about 16 years; but survival for as long as this in the wild is probably unusual.

CANIS ADUSTUS Sundevall — Side-striped Jackal

Canis adustus Sundevall, 1846, *Öfvers. VetenskAkad. Förh., Stockh.* **3**: 121. According to Sundevall, the interior of South Africa; given by Roberts (1951) as Magaliesberg, Transvaal. The name *adustus* is the Latin word for sunburnt or swarthy.

Canis adustus centralis Schwarz, 1915, *Jb. nassau. Ver. Naturk.* **68**. 60–62. Bate, near the Uham River, Cameroun. The Latin subspecific name was intended to indicate that the type came from the middle of Africa. Sometimes regarded as possibly covering all West African jackals of this species.

Distribution. The side-striped jackal (fig. 5) occurs from the Transvaal northwards to Ethiopia on the east and to Cameroun, Northern Nigeria, Dahomey, Guinea and upper Gambia on the west. It inhabits rather moister regions than the golden jackal, that is to say in West Africa the Sudan and Doka zones. Only two specimens exist from West Africa in the British Museum, one from near Gombe, Northern Nigeria, the other from Gambia, the exact locality unrecorded, the skin, but no skull, having been received from a zoo. It has also been reliably reported from the Shendam area of Nigeria, somewhat north of the Benue at about 8° 55 N, 9 28 E, in Doka woodland; and by G. S. Child who has found it and its dens in the Borgu Game Reserve in extreme western Nigeria.

Description. One of the distinguishing features generally cited between this species and the last is that the tail tip is white as contrasted with the black of *aureus*. While this is true of South African and many East African specimens it does not appear to hold for West African animals and certainly does not occur in the two examples from that region in the British Museum or those from the same vegetation belt as far east as Bahr-el-Ghazal. Another reputed distinction between the two species is that which gives the common name to *adustus*, a black stripe along the flank of this latter, lacking in the golden jackal. Such a mark certainly occurs in the majority of specimens, but it is not always easily discernible and often by no means as clear as it is made to appear in most illustrations. It is in some measure dependent upon individual idiosyncracy, in some upon moult, and in some upon the actual lie of the coat, which may emphasize or obscure it. It can, indeed, vary very much in distinctness on the two flanks of one jackal. This black flank-stripe is emphasized by the existence of a white band above it which divides it from the darkish, speckled back. Questions of set coat patterns apart, side-striped jackals are altogether much darker animals than golden jackals, partly because the black in the coat is more evenly distributed, seldom, except on the flanks, aggregating into black patches, and then only of small size. There is always one certain point of distinction between the two; the ears in *adustus* are grey on their backs, not golden-brown as in *aureus*.

Aside from gross differences of appearance the pelages of the two species are appreciably discrepant in detail. That of *adustus* is long but not quite so long and dense as in *aureus*; and it is possibly a trifle less harsh. It similarly consists of abundant fine underfur and very long, banded, terete bristle-hairs: the former being approximately 20 mm long as compared with about 30 mm in *aureus*; and the latter 50 to 60 mm compared with 70 to 80 mm in the other. When the coat is turned up backwards a sharp distinction between the two species becomes evident: *adustus* is seen to be largely pale reddish-brown in contrast to the buffish-white of *aureus*; and also, the white subterminal bands of the bristle-hairs, although very much shorter than in the latter species, show up far more conspicuously because of their greater contrast to the deeper-coloured lower part of the fur. The red of the underfur often pervades the dark speckled saddle-patch of the back, the extent to which it does this depending upon the state of moult and the consequent density of the bristle-hairs at the time.

The nose is red-brown; the crown of the head and the nape are speckled, the white subterminal bands to the short hairs covering these areas making a conspicuous "frosting". The upper lips are narrowly whitish but this pallidness scarcely spreads to the cheeks. The chin is grey, the throat mostly whitish or buffish but there is usually a speckled collar at its lower end. The rest of the underside is clothed with long hair

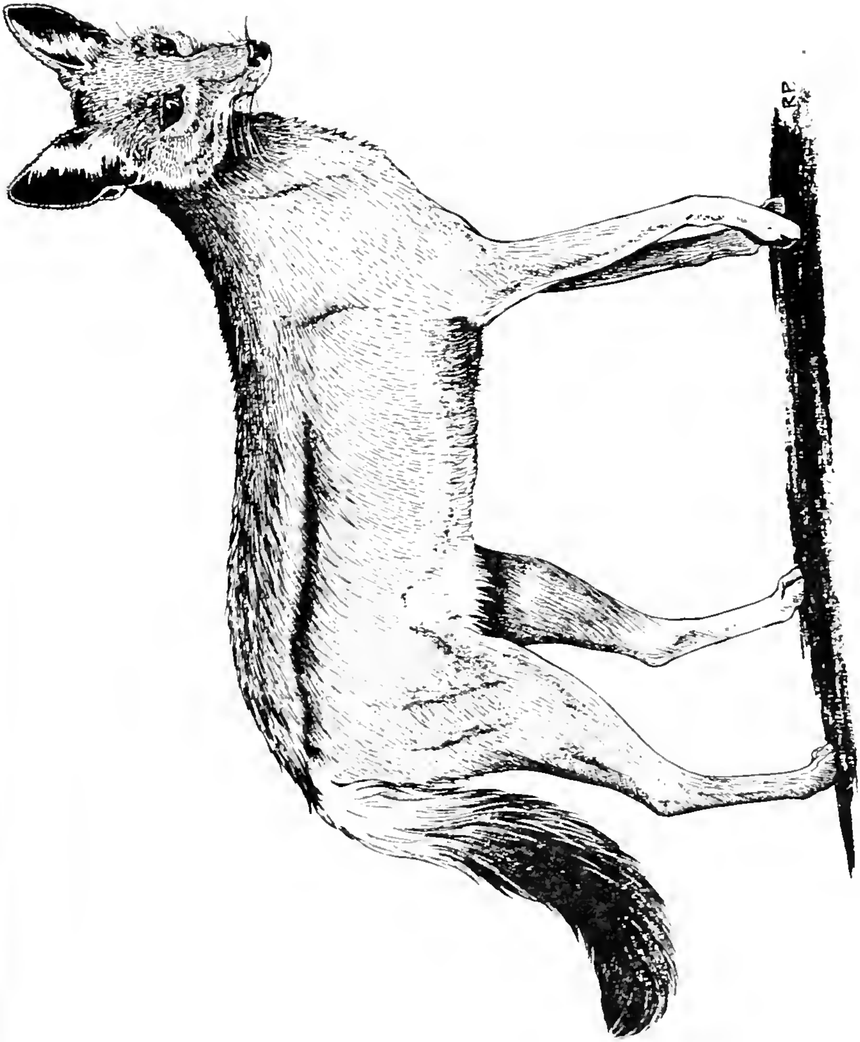


Fig. 5. Side-striped Jackal (*Canis adustus*)

having long buffish tips over a pale chocolate base. The limbs and feet are a deeper shade of red than in *aureus*; and there is often some sign of a black longitudinal line on the forelegs, but this is not always clear and is sometimes lacking. The bushy, very long-haired tail is basically buffish, often with a touch of red, but it always has a considerable amount of black on it, far more than in *aureus*. In West Africa the tip is black.

It is difficult to give any precise idea of the relative sizes of *adustus* and *aureus* since in the British Museum there are no external measurements relating to West Africa and very few from elsewhere. The figures for the usual four bodily measurements given in the table on page 55 are merely estimates compiled from a few extralimital data in conjunction with Schwarz's (1915) figures published for *centralis*—which themselves were derived from a dry skin. From these it would seem that there is not a great deal of difference in size except that the ear is possibly shorter in *adustus*. One animal from Bahr-el-Ghazal was said to weigh 7·7 kg, that is slightly more than *aureus*.

Skull (fig. 6). The first obvious difference between the skull of *adustus* and that of *aureus* lies in the former's longer rostrum, sloping evenly from the supraorbital region instead of markedly dipping below the frontal. The nasals are generally considerably longer in *adustus* and extend further forward over the anterior nares, which are thus less open dorsally. The skull is narrower all round; the zygomatic breadth, the braincase, the interorbital and postorbital widths are for the most part less. The supraoccipital crest viewed from the front is much less angular, almost semicircular in outline. The zygomatic arch is far less curved vertically than the subsemicircular arch of *aureus*. The mandible appears to be less powerfully built than in *aureus*. The ramus is not so deep and is only slightly curved, so that the angular process is not much elevated above the level of its lower margin. Both anterior and posterior edges of the coronoid process are practically straight, the process thus being of a truncated wedge-shape.

The carnassials are smaller than in *aureus* both in absolute terms and in their ratio to the molars. In this species p^4 is not much more than 70 per cent of the length of $m^1 + m^2$; and m_1 is well under 130 per cent of $m_2 + m_3$.

Taxonomy. The taxonomy of *adustus*, at least in so far as West Africa is concerned, is much less confused than that of *aureus*. As a species it was originally the subject of a perfectly clear diagnosis; and most of the nine races subsequently named have been fairly adequately described during the present century. Only one of these, *centralis*, probably came from within the limits set for this book; but it is difficult, or impossible now, to fix the type locality, Bate, with any certainty. It was said by Schwarz (1920) to lie on the Uham River on the German side of the Cameroun frontier; but this river does not appear to cross that boundary. The most likely position of Bate seems to be roughly 7° N, 15° E, that is in the Guinea woodland. The next nearest recorded specimens to the type of *centralis* seem to be those from Chak-Chak, Bahr-el-Ghazal (Doka woodland), which Setzer (1956) assigned to *bweha* Heller.

It is obvious that with the extremely limited material from West Africa available for study—two specimens only, of widely separated provenance and possibly different vegetation zones, and differing somewhat in appearance from each other—it is almost

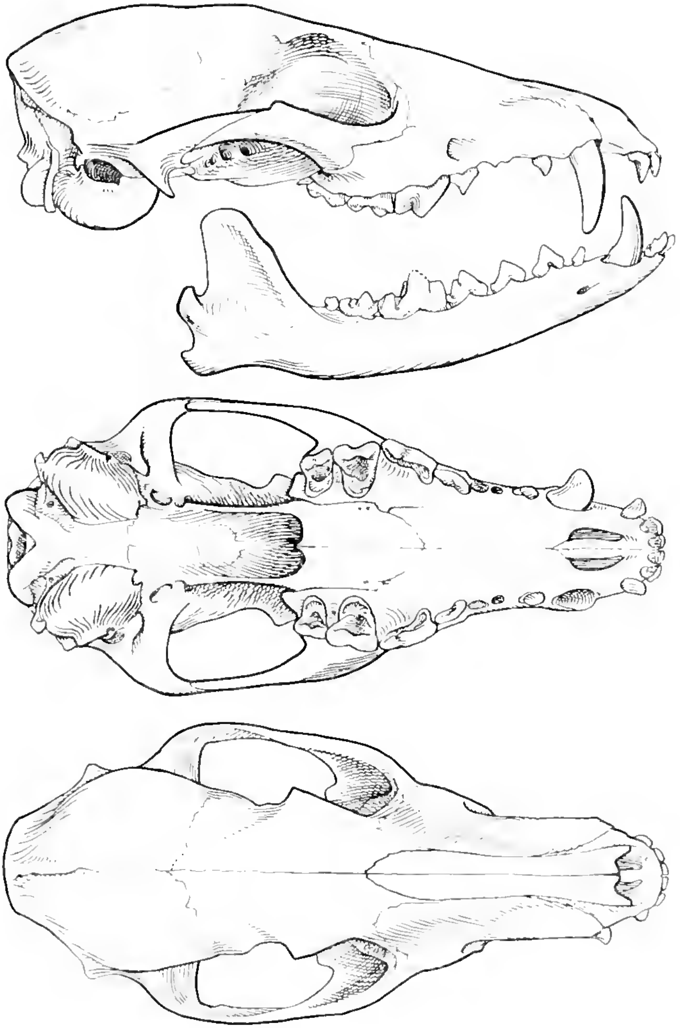


FIG. 6. *Canis adustus*: skull, B.M. No. 28.6.3.8, sex ?, × $\frac{5}{8}$

pointless to attempt reasonable comparison with descriptions of these races from further east in Africa. Neither West African specimen would seem to match Schwarz's diagnosis of *centralis*, described as noteworthy for its very light ground-colour. That from Gombe, on the other hand, is very similar to the British Museum specimens held by Setzer to be *bweha*. All, indeed, seem to be a rather closer match to this race than to *centralis*, though they fail to correspond wholly to Heller's description. There is very little to choose in size between any of the specimens referred to in this section except that the *bweha* type seems to be a little larger.

Much more material is needed before any useful purpose can be served by attempting to attach a third name to West African animals. Doubtless the issue of geographical races is obscured in all these wild dogs by a good deal of individual variation, the extent of which it is quite impossible to estimate from exiguous collections.

Habits. These are not very well recorded but do not seem to differ in their essentials very markedly from those of the golden jackal. Side-striped jackals are by preference nocturnal but, like *aureus*, are also to be seen on the move in the early morning or late evening. It must be remembered that this species is probably less often seen than the golden jackal because for most of the year in West Africa, except at the height of the dry-season when the grass has been burnt, it occupies vegetation, the Sudan and Doka zones, in which the ground-cover is considerably denser. At night these jackals make their presence known by sitting and uttering at intervals their sad yapping howl, a relatively slow *woo-woo-woo*. Feeding habits are in general very much those of the golden jackal, but *adustus* is reputed not to steal farm stock. It seems, indeed, to be a rather shyer, more timid and secretive animal, mostly solitary in its habits or accompanied by a mate at the right season, or by pups in due course.

This jackal, like the other, shelters and breeds in a hole in the ground. The period of gestation is similar to that of *aureus*, around 9 weeks but varying by 4 or 5 days on either side of this. As many as 7 pups have been recorded in a litter, but 3 or 4 is probably a common number. A side-striped jackal has been known to live in captivity for 10 years.

Table 1: Numerical data for species of *Canis*

	C. aureus							*C. adustus*		
	Takoukout	Lake Chad	Darfur	El Obeid (*soudanicus* type)	Plain of Tokar	Air	Rio de Oro	Gombe River	Bahr-el-Ghazal	Bate (*centralis* type)
Vegetation	Sahel	Sahel	Sahel	Sahel	?Sahel	Sub-desert	?Sub-desert	Sudan	Doka	?Guinea
Number in mean	1	2	5	1	2	3	1	1	2	1
Condylobasal length	137·0	154·4	151·4	143·1	143·8	149·1	(158·0)	140·3	148·2	140·0
Basilar length	126·0	141·5	140·4	132·5	133·0	137·3	138·0	131·1	137·7	134·0
Palatilar length	65·0	73·5	73·8	70·0	70·5	73·7	76·5	72·1	75·6	70·3
Zygomatic breadth	78·5	87·2	84·6	78·2	76·0	81·8	85·0	67·3	76·2	70·9
Upper cheekteeth breadth	44·5	50·5	47·8	45·5	42·7	48·8	50·2	46·0	46·1	45·7
Nasals, length	51·9	57·0	55·3	48·5	55·1	53·9	59·5	58·4	61·1	58·4
Interorbital breadth	27·5	29·6	26·2	25·8	25·9	26·9	29·1	25·0	26·9	25·2
Postorbital constriction	29·0	30·7	29·2	29·0	30·0	29·7	(34·5)	30·5	27·1	—
Braincase breadth	49·5	55·0	51·7	49·6	48·2	50·0	52·5	46·4	48·1	—
Toothrow ($c - m^2$)	61·5	70·0	68·0	64·2	65·5	69·0	72·5	63·5	65·5	—
p^4 length	14·2	15·9	15·4	14·7	14·6	16·3	18·7	13·7	13·3	13·0
$m^1 + m^2$ length	17·2	18·3	17·6	17·4	16·8	18·7	19·0	18·5	18·6	—
m^1 breadth	12·9	14·8	13·9	13·7	12·8	14·6	15·0	12·6	12·4	—
m_1 length	16·5	19·3	17·8	17·4	16·3	19·4	(19·0)	15·2	15·5	—
$m_2 + m_3$ length	12·0	13·7	12·6	11·5	11·2	14·4	10·5	12·2	12·8	—
Head & body	660	679	655	650	—	590	—	—	673	680
Tail	330	262	271	240	—	275	—	—	279	240
Hindfoot	140	155	148	140	126	148	—	—	182	140
Ear	85	86	95	80	81	83	—	—	70	60
RATIOS (per cent)										
Tail/head & body	50	39	41	37	—	47	—	—	41	35
Zygom. br./condylob. l.	57	56	56	55	53	55	(54)	48	51	51
Braincase/condylob. l.	36	36	34	35	34	33	(33)	33	32	—
Braincase/zygom. br.	63	63	61	63	63	61	62	69	63	—
Palatilar l./condylob. l.	47	48	49	49	49	49	(48)	51	51	50
Interorb./postorb.	95	96	90	89	86	90	(84)	82	99	—
$p^4/c - m^2$	23·1	22·7	22·6	22·9	22·3	23·6	25·8	21·6	20·3	—
$p^4/m^1 + m^2$	82·6	86·9	87·5	84·4	86·9	87·2	98·6	74·0	71·5	—
$m_1/m_2 + m_3$	137	141	141	151	145	135	(181)	124	121	—

Genus **FENNECUS** Desmarest, 1804

Fennecs

Fennecus Desmarest, A. G., 1804, *Nouveau Dictionnaire d'Histoire Naturelle*, 24, Tableau methodique des Mammifères: 18. Type species *Fennecus arabicus* Desmarest (= *Canis zerda* Zimmermann). The name is a Latinized form of the Moorish word for a fox, *fennec*.

Megalotis Illiger, 1811, *Prodromus systematis Mammalium et Avium* . . . : 131. Type species *Canis cerdo* Gmelin (= *Canis zerda* Zimmermann). This name was made up from the Greek words *megas* (*megal-*) large and *ous* (*otos*) ear.

This is a monospecific genus distributed over a small area of northern Africa from Morocco to Egypt, as far south only as Aïr and Sudan, and thence across to parts of Arabia. In other words, it is an animal of dry sandy deserts or subdeserts. Since there is only one species there is no point in entering into a generic description.

FENNECUS ZERDA (Zimmermann) Fennec

Vulpes minimus saarensis Skjöldebrand, 1777, *K. svenska VetenskAkad. Handl.* 38: 267, pl. 6. Algerian Sahara. This name is regarded as invalid because, as given to a species, not a subspecies, it was trinomial. The second name, *minimus*, is Latin for smallest, given because of this animal's diminutive size for a fox; the third name is a Latinization of Sahara.

Canis zerda Zimmermann, 1780, *Geographische Geschichte des Menschen und der vierfuszigen Thiere* 2 247-248. Sahara and North Africa behind the Atlas Mountains. The name was said by Zimmermann to be that used in "Barbary".

Canis cerdo Gmelin, 1788, Linnaeus' *Systema Naturae*, 13th ed. 1: 75. Sahara. This name is another spelling of *zerda*.

Viverra aurita Meyer, 1793, *Systematisch-summarische Uebersicht der neuesten zoologischen Entdeckungen in Neuholland und Afrika*: 91. Biskra etc., Algeria. The Latin adjective *aurita* means having large ears.

Fennecus arabicus Desmarest, A. G., 1804, *Nouveau Dictionnaire d'Histoire Naturelle*, 24, Tableau méthodique des Mammifères: 18. Barbary, Nubia, Abyssinia.

Megalotis cerda Illiger, 1811, *Prodromus systematis Mammalium et Avium* . . . : 131. The name is a variant of *zerda*.

Fennecus brucei Desmarest, A. G., 1820, *Encyclopédie Méthodique*, Mammalogie: 235. Libya, Tunis, Algeria, Senaar. James Bruce, after whom this was called, was a well-known explorer of northern Africa in the second half of the 18th century.

Canis fennecus Lesson, 1827, *Manuel de Mammalogie*: 168.

Vulpes denhami Boitard, 1842, *Le Jardin des Plantes*: 213. Interior of Africa. This was named in honour of Lt. Col. Dixon Denham, a famous traveller in the Sahara and explorer of Lake Chad in the early 19th century.

Distribution and general. The range of this essentially Saharan animal has already been given above. In suitable localities it is not uncommon and because of its small size and rather charming appearance it has for long been a favourite with writers on natural history, figuring far more copiously in literature than many more widely distributed and rather more important animals. In general appearance it is a miniature fox with a sandy coat, huge ears and a very bushy tail, and it is, indeed, often known as the fennec fox, though any really close relationship to the true foxes has been brought into question. It does not occur everywhere in the Desert and Subdesert zones because it must have soft sand into which to burrow. Sand dunes are therefore ideal, but not in utterly barren situations since food must, of course, be available in fair quantities.

Description. The fennec (Plate 1) has a head & body length of about 300 to 370 mm and a tail of 160 to 240 mm. It stands about 150 to 175 mm at the shoulder and weighs about 2 kg. The pelage is long and very soft, both above and below. Broadly speaking, dorsally it is sandy, but there is a certain amount of variation, some specimens being rather greyer, some rather redder. The same applies to a darker, richer coloured, band along the spine, almost absent from some, clear in others, especially on the hinder part of the back. In this area, in some skins, the bristles are dark-tipped with a pure white subterminal band, forming a very prettily-patterned patch. In others the pattern is more diffuse, the majority of specimens having fine bristles with long black tips thinly dispersed over the entire dorsal region. The pelage is so soft to the touch because it consists, apart from these scattered bristles, entirely of dense, very fine, very long, underfur. This, in the North African examples, is pale chocolate-grey in the basal half the extreme base being narrowly white; but in the western specimen from Aïr there is no trace of this basal tinting; while in the Dongola (Sudan) skin it is relatively pale. The West African examples, too, are much shorter-furred; but they are all youngish animals. The underparts and the insides of the limbs are pure white, the fur being abundant and soft, but only half the length of that of the back.

The tail, which is roughly half as long as the head & body, is very bushy, the very long hairs with which it is clothed being towards the tips a rather redder brown than the back. There is a deep blackish-brown mark not far from the root of the tail covering a scent gland; and the extreme tip is also blackish-brown.

The head, with a broad face and large eyes, comes rather abruptly to a narrow muzzle and is wholly dominated by the enormous, pointed ears which are broad as well as long. On their backs they are sandy-grey, but all around the marginal area on the inside there are dense long white hairs. The crown and front are sandy, but much of the rest of the face, surrounding the eyes, the rhinarium, the cheeks, and the upper lips, is pure white with the exception of two dark, reddish-brown lines descending from the inner corners of the eys to the lips. The upper parts of the limbs are, in the northern African specimens, reddish-sandy; but in the Aïr examples they are nearly white.

Skull (fig. 7). The skull tapers fairly sharply from a moderately broad braincase and enormous bullae to a very narrow rostrum. The profile dips appreciably just forward of the orbits to give this narrow and low muzzle. The braincase is rounded; the supraorbital ridges are well-pronounced but narrow and sharp, hollowed on their upper surfaces, in the manner of *Vulpes* rather than *Canis*. There is no very marked interorbital constriction. The distance across the zygomata is wide, the maxillary process broad, the slender arches sharply up-curved, the circumorbital ring widely open. There is little or no sagittal crest and only poorly developed supraoccipital ones. The bullae are extremely large. The palate is very broad between the carnassials but narrows abruptly and becomes practically parallel-sided anteriorly. Its hind margin is about level with the middle of m^2. There is nothing particularly remarkable about the lower jaw or the dentition apart from its very sharply cuspidate nature which probably facilitates an insectivorous diet (fig. 1).

Taxonomy. This, despite the multitude of names, actual and in permutation, by which this animal has been known to science, is pretty straightforward. It is true that in the early days Buffon (1776, Suppl. **3**: 148) referred to it as the anonymous animal, and that Lesson (1827) wrote of it (in translation) that perhaps no animal had more engaged naturalists than this; they have made of it by turns a dog, a galago, or the type of the genus *Fennec*.

The old confusion of naming has now been swept aside and fixed with apparent permanency as *Fennecus zerda*. But, at a very considerably narrower pitch than that indicated in the previous paragraph, some doubt of the animal's precise relationship still remains. The fennec has long and widely been regarded as a kind of fox, and is in fact very frequently referred to as the fennec fox; but the cytological researches of Matthey (1954) have shown that the chromosomes (diploid number, 2N = 64) indicate that the genus lies closer to the wolves (*Canis*) than to the foxes (*Vulpes*).

So far, no races have been described. The West African material from Aïr is poor in quality and meagre in amount and it is therefore not possible to draw any reasonable conclusions; but superficially the animals from this area seem somewhat paler and shorter haired than those from further north-east; but there is no significant difference of size so far as can be deduced from the mean measurements of three from the one area and of five from the other.

Habits. Accounts of these in the wild have been briefly given by several collectors and observers over a large number of years; but, in all, the information from these sources amounts to little beyond the most obvious facts of life in the desert. However, because of the fascination which this miniature "fox" of charming appearance has long exercised over human-beings, especially as a household pet, the fennec has been more closely studied in captivity than most carnivores. Good descriptions of its behaviour and disposition under these circumstances have been given in recent years by a number of writers of whom the following are the chief: Rensch (1950), Petter (1957), Volf (1957), Hill (1961), Saint Girons (1962), Vogel (1962) and Gauthier-Pilters (1966). Though these accounts concern animals in unnatural conditions they nevertheless cast important light on instinctive behaviours, the more convincing in that many traits are displayed in common by animals of different origins at different times and places. It is not possible in a work of the present nature to do more than glance briefly at some of the recorded facts, more especially those which most probably reveal the fennec's normal activities.

Fennecs are essentially nocturnal or crepuscular in their activity; yet though, like so many desert animals, they avoid the full force of the mid-day heat, they are not averse to sunning themselves for brief periods before the day is far advanced. But

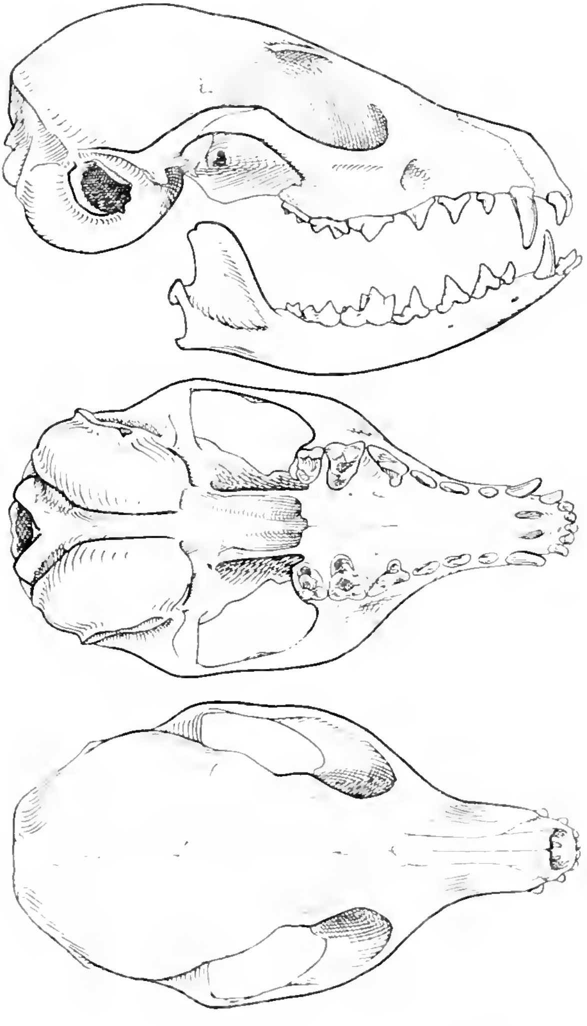


Fig. 7. *Fennecus zerda*: skull, B.M. No. 1939.1740, ♂, × 1

very little of this insolation suffices for their daily needs and they soon seek shade—though they may emerge for a second spell, a pattern that may be observed in many domestic dogs. The fennec's home is a hole in the ground, which it digs for itself, fairly deep probably to avoid overheating during the day. These "earths" are lined with soft material, and they have a number of different escape passages some of which are said occasionally to communicate with the homes of other fennecs, as these are sociable little animals which in suitable areas live amicably together in some numbers. The unit of these communities is almost certainly a small family group; and it would seem from indications, though it is not certainly known, that male and female hang closely together for long periods. Favourable localities for fennecs are characterized by soft sand into which burrowing can be carried out with ease. For this reason stable sand-dunes fixed by the roots of sparse vegetation are ideal, wholly barren desert having no attraction since food must be available in fair quantities. Given a soft soil such as exists in these sites, digging, carried out with the forepaws, is very rapid. All who have kept these animals refer to one habit that makes them difficult to tolerate as domestic pets: the constant and very noisy nocturnal scratching resulting from attempts to dig into unyielding wooden or concrete floors. That the instinct to hide is very strongly developed is illustrated by the fact that even in captivity fennecs always seek to shelter underneath furniture; or, if nothing more resembling an "earth" is available, by pulling over themselves such bedding as they may be provided with.

It has already been said that fennecs dislike intense heat, particularly direct insolation; but they very much appreciate warmth. They are, indeed, highly sensitive to cold, and this is another reason for the depth of the burrow so that a wholly equable temperature can be maintained. When above ground on the hunt for food, protection against the night cold that develops rapidly after sunset in sandy deserts is to some extent provided by the dense woolly pelage; but, to judge from behaviour in captivity, fennecs are intermittently active for short periods and this might be explained by the necessity, in nature, to return from time to time to the warmth of the home.

Another highly important reason for the avoidance of intense insolation and the frequent seeking of shelter in a deep burrow, in which the humidity probably remains at a high level, is the need to conserve water. It is unlikely that the majority of fennecs in the wild have easy access to standing water in order to drink, and very likely they obtain most of what they need from moisture in fruits and bulbous roots. Observations on drinking habits in captivity are curiously conflicting. Rensch found that his fennec drank little or nothing for the first two or three years except at the mating season; but later in life it drank daily. Vogel found much the same thing; but he noticed, in addition, that the animal was averse to drinking out of a bowl but readily lapped up drops spilled on the floor—so much so that it was observed, itself, to scatter water from the drinking vessel with its forepaws or nose. Rensch mentions his fennec as licking drops from a tap. This would seem to indicate that even if these animals had access to oases, or other pools, they would prefer to get what extra supplies they required beyond what is provided in fruit by licking small quantities from leaves or other surfaces moistened by dew or rare showers of rain. Schmidt-Nielsen (1964), in connexion with loss of bodily water, found that urine could attain a high concentration in the fennecs. When over-heated, fennecs can cool off to some extent, like dogs, by panting; but as this involves loss of essential moisture from the tongue it is not an operation that can commonly be engaged in.

Fennecs are seemingly almost omnivorous, and there is little difficulty in feeding them in captivity since they readily eat most things from roast beef to marmalade. In their natural surroundings they live on small rodents, such as gerbils and jerboas, lizards, insects, eggs, small birds and a good deal of vegetable matter, of which fruits and tuberous or bulbous roots form the main part. Vogel observed his fennec, like a domestic dog, to eat grass when opportunity offered. According to Professor Monod of Dakar quoted in Dekeyser (1955), fennecs are very fond of the bright yellow, leafless parasite *Cistanche phelypaea* Cout. often growing in fleshy clusters at ground level on the roots of, amongst others, the so-called salt bush, *Salvadora persica*, commonly occurring in the Sahel and Subdesert zones. Big pieces of food are consumed in a sitting posture; small ones are eaten while standing.

In many of their ways these little "desert foxes" reflect the manners of some domestic dogs: as, for example, in their inquisitiveness, evinced in sniffing at or quizzically regarding unfamiliar objects; in hiding away surplus tit-bits of food; in turning round three or four times before settling down. They particularly resemble poodles in their ability to stand and walk upright on their hindlegs, and in the way they stretch their hindlimbs after sleep, or lie flat on their bellies with both fore and hind legs stretched out. In other ways they are rather cat-like, particularly in their manner of cleaning themselves by licking their forepaws and "washing" their heads. The large ears are cleaned on their insides by the hindfeet. Like cats, too, fennecs are very competent jumpers, being able to accomplish a standing more or less vertical spring of 600 mm or more and a horizontal spring of 1200 mm. They also, at times, can purr something like a cat; and when they sit on their haunches they curve their tails sideways and forwards like a cat, sometimes even raising the tip off the ground as cats do. Fennecs, too, are very competent climbers and can ascend vertical obstructions that offer some sort of foothold. They can also squeeze through remarkably narrow crevices.

These animals scratch a shallow hole to defaecate and urinate in and they cover their droppings with sand, sometimes shovelling it over with the nose or, more often, flinging the earth backwards with a scraping action of the hindlegs, just as domestic dogs can often be seen to do. This latter ritual is performed automatically even when it is pointless on the hard wooden floor of a cage. Fennecs utter a variety of sounds from a low growl to a higher snarl; when content and being stroked or fondled they make a purring noise similar to that of a cat. They are given to yapping at night. There is an annual moult. Opinions differ as to whether these animals are ever completely tameable. As with almost any wild creature it is probably merely a matter of inbuilt temperament, varying from one individual to another. One fennec, at least, has shown itself to have a very long memory and to be able to recognize its owner with excited pleasure after many months of separation—and this at a distance by sight, the possibility of smell being eliminated by a glass front to the cage. These animals have a longevity of about 12 years. Schmidt-Nielsen records that the young are dug out of their nests, fattened up and marketed for eating.

Mating and breeding in captivity have been observed and recorded by Petter, Volf, and Saint Girons. After penetration the male turns round so that the two sexes face in opposite directions, and coition lasts 1¼ hours. There is apparently no attempt at subsequent copulation. The period of gestation is 50 or 51 days. Petter found that after mating the female continued to act normally but the male grew aggressive towards people whom he knew well; this became more pronounced after parturition and so he was separated from the mother. By then she was so upset that she kept transporting her newly born cub from place to place and ended by thus accidentally causing its death. Volf records very much the same sort of thing. From 1 to 3 cubs are born. Their eyes are closed, their ears free though giving no hint of their future huge size. The pelage is fine and short. Under natural conditions the young appear always to be born in March or, at the latest, the beginning of April.

Gauthier-Pilters (1966) has recorded in some detail her observations on play in the fennecs made on 21 animals over a period of 11 years, all born in the wild. Juvenile fennecs play with each other very like fox cubs or the puppies of domestic dogs, biting each other in the legs and neck and rolling each other over. They also shake small objects as if shaking a rat to death. From the age of about 6 weeks they indulge in racing play, chasing each other, the pursuer with ears erect and directed forwards, the pursued with them laid back, zigzagging or making abrupt changes of direction. This they will do even, if necessary, in a very confined space. Where opportunity offers they may play a kind of hide-and-seek. Should play become too rough and one of the participants get cornered, or for that matter at any time or any age when offensive or defensive posture seems necessary, the back becomes arched and the ears are laid back in a threatening attitude. Fennecs have no ability to raise their hackles like a dog, but instead, the black mark at the root of the tail is erected and displayed. Solitary play also takes place, using articles of food or substitute toys, tossing these in the air or shoving them about with foot or nose. Chasing their own tails is sometimes indulged in. Fennecs will play even with strange animals which they have only just met. Gauthier-Pilters (1966) records games between young fennecs, dogs and jackals; but cats appear unwelcome and frightening. Should other creatures fail they play willingly with human beings.

Inclination to play appears to vary with season, falling to a minimum at breeding time. This observer found the pattern of female behaviour with the male to differ before and after parturition, exhibiting in the first place elements of greeting behaviour and in the second of breeding behaviour, that is the bringing and offering of food—though the male was, in the event, never allowed to take it. Most play takes place at evening or at night. Indeed, with captive fennecs, to judge from the experiences recorded by Gauthier-Pilters, this can be somewhat of a trial for the owners of these nocturnally very active creatures, since they persistently play after dark for hours on end, preferably over and under beds, tables and chairs. This author records a 14-day trek with half-tamed fennecs which for safety had to be tied at night to her camp-bed and which, despite their thus restricted freedom, spent their time in romping or, at intervals, digging deep holes in the sand.

Such play activities, especially in the young, are recognizably related to behaviour exhibited in various situations regularly arising in later life, and for which they are, in effect, rehearsals, training and strengthening the necessary muscles and inculcating instinctive reaction on occasions demanding offence, defence, capture or killing.

Table 2: Numerical data for *Fennecus zerda*

	West Africa (Aïr) **means**	West Africa (Aïr) extremes	Sudan (Dongola) single specimen	Northern Africa **means**	Northern Africa extremes
Vegetation	Subdesert	—	Subdesert	Subdesert	—
Number in mean	3	—	1	5	—
Condylobasal length	83·2	82·8–83·7	82·3	83·8	78·7–86·7
Basilar length	77·9	77·4–78·2	76·5	78·2	73·6–80·4
Palatilar length	39·0	38·9–39·1	37·3	38·9	36·4–41·0
Zygomatic breadth	45·4	44·4–47·2	43·8	46·1	43·5–48·6
Upper cheekteeth breadth	24·2	23·3–25·4	24·0	25·0	23·2–25·9
Nasals, length	27·5	26·2–28·8	26·8	27·1	26·1–28·7
Interorbital breadth	16·5	16·0–17·0	15·8	16·2	15·5–17·0
Postorbital constriction	20·3	19·8–21·2	17·7	20·2	18·7–21·3
Braincase breadth	36·8	36·7–37·0	35·7	36·5	35·5–37·5
Toothrow (c—m^2)	35·1	33·6–36·0	35·3	35·4	32·4–36·4
p^4 length	7·4	7·2–7·6	7·0	7·6	7·4–7·8
$m^1 + m^2$ length	10·1	9·9–10·2	9·4	10·1	9·5–10·5
m_1 length	8·3	8·1–8·4	8·1	8·3	8·0–8·5
$m_2 + m_3$ length	8·0	(7·9)8·0	7·1	7·6	7·2–7·8
Head & body	355	350–360	360	371	333–395
Tail	170	160–180	190	147	125–187
Hindfoot	93	92–94	92	94	90–98
Ear	90	86–95	90	94	90–97
RATIOS (per cent)					
Tail/head & body	48		53	40	
Zygom. br./condylob. l.	55		53	55	
Braincase/condylob. l.	44		43	44	
Braincase/zygom. br.	81		81	79	
Palatilar l./condylob. l.	47		45	46	
Interorb./postorb.	81		89	80	
$p^4/c - m$	21·0		19·8	21·4	
$p^4/m^1 + m^2$	73·2		74·6	75·2	
$m_1/m_2 + m_3$	104		114	109	

Genus **VULPES** Fleming, 1822

True Foxes

Vulpes Frisch, 1775, *Das Natursystem der vierfüssigen Thiere*, 15. This work has been ruled to be unavailable by the International Commission on Zoological Nomenclature (Opinion No. 258 of 1954). The name is the Latin for a fox.

Vulpes Oken, 1816, *Lehrbuch der Naturgeschichte*, **3**, 2: 1033, 1034. Type species *Vulpes communis* Oken (= *Canis vulpes* Linnaeus). Oken's *Lehrbuch* is similarly unavailable (Opinion No. 417 of 1956).
Vulpes Fleming, 1822, The Philosophy of Zoology, **2**: 184. Type species *Canis vulpes* Linnaeus.
Cynalopex H. Smith, 1839, Jardine's *Naturalist's Library*, **25** (of the series), **9** (of Mammals): 222. Type species *Canis corsac* Linnaeus.

Distribution. This genus is spread throughout Europe, much of Asia and of North America, and over the more arid areas of Africa. The common red fox of Europe (*Vulpes vulpes*), in one form or another, occurs over a great part of this wide range with the exception of the more southerly parts of Asia and Africa south of the Mediterranean region—though its identity with the American red fox, frequently alternatively designated *V. fulva*, is disputed. Rather less than a dozen species in all are recognized, of which three occur in Africa south of the Sahara, two of them being found within our limits.

Foxes are small to moderate-sized carnivores, having a long, soft, dense, often very attractive coat and an outstandingly bushy tail—termed in hunting circles the "brush". This profusely haired tail in conjunction with a sharp face and prominent ears makes it difficult to differentiate foxes precisely from some of the typical (wild) dogs; and, indeed, this genus has often been synonymized with *Canis*. However, in general, in Africa, foxes are smaller and have shorter legs—they are much more able than dogs to slink along with their bellies almost in contact with the ground. Nevertheless, despite shortness of limb they can move very fast over long distances. A more positive character dividing the foxes from the typical dogs is that the tail in the former measures more than half the length of head & body, whereas in the latter the reverse is the case. In foxes the pupil of the eye is a vertical oval, rather in the style of a cat but with not so wide a range of expansion and contraction. Some, if not all, foxes have a scent gland on the top side of the tail about 50 to 60 mm beyond the root; this organ exists, according to Anderson (1902), in at least one of our West African species. There are five clawed digits on the forefoot but only four on the hindfoot; the soles of the feet in the African species are abundantly hairy between the pads, *rueppelli* yet more so than *pallida*.

Skull (fig. 8). No general description of the *Vulpes* skull is given here. Its form bears a close overall resemblance to that of *Canis*, differing, apart from a considerable disparity of size, in one minor point. This concerns the supraorbital ridges which in *Canis* are dorsally smoothly convex, whereas in *Vulpes* there is a slight concavity in the upper surface. It is this lack of any important cranial or dental disagreement that has made taxonomists sometimes doubtful of the validity of generic distinction between *Vulpes* and *Canis*.

Habits. Little enough is known of the lives of the majority of species apart from the fact that the palaearctic common red fox has been intensively observed and to some degree studied over a long period of time. This species is popularly regarded as exhibiting in its appearance and behaviour the acme of slyness and cunning, and its name has passed proverbially into European languages as the most apt and succinct expression of these attributes. It has, indisputably, other more admirable qualities: courage, determination, endurance. It is the combination of all these that has rendered this fox possibly the favourite and most exciting animal of the chase. And it is these characteristics, too, that have in large measure enabled these harmful predators to survive in considerable numbers in the face of human expansion and of intensive organized hunting over many centuries, when wolves, bears and other carnivores antagonistic to man's interests have tended towards extermination. In what degree, if at all, this craftiness and skill in self-preservation are shared by African species is unrecorded. But it is perhaps worth noting, from an historical point of view, that a Hunt in semi-English style existed some years ago at Zaria (Nigeria), its activities being directed against the sand fox inhabiting the neighbouring fields and hillsides in fair numbers. There is good reason to suppose that proximity to man so far from being distasteful is welcomed by foxes since any occasional danger arising from it is more than compensated by the ready availability for food of domestic animals and birds, more concentrated in amount than wild prey and less apt at defending themselves.

Most foxes are in large part nocturnal, but they are also commonly active during daylight hours, especially in the early morning or late evening. So far as is known, all species of *Vulpes* shelter and breed in self-constructed "earths" in the ground or, much more rarely, in the protection of holes formed by rocks. Some live only in small family units; others are more gregarious. Beyond these generalities it is difficult to go; for nothing appears to have been recorded for African species regarding the various aspects of breeding, and little about feeding habits. Concerning these latter, it may be safely assumed that African foxes take a wide diet, not only of flesh but of fruits and other vegetable matter as well. Their enemies are the more powerful carnivores, birds of prey, the larger snakes—and, of course, diseases. These last, and their possible impact upon man, have not been investigated for tropical African foxes.

Taxonomy. It has already been mentioned that opinion has differed in the past, from Linnaeus onwards, as to whether the foxes constitute a separate genus or should be regarded as wholly one with *Canis;* but the two are now generally looked upon as validly separable. There are no problems with regard to African species, though there has been at times a little confusion of thought—*vide* Thomas (1918), who cleared up points relating to *rueppelli* and *pallida* but fell into the trap of supposing that Gray's *Vulpes dorsalis* from Senegal was indeed a fox, whereas, as pointed out by Ellerman & Morrison-Scott (1951), it was in fact a jackal.

The two species that occur within our limits may be separated thus:

KEY TO THE WEST AFRICAN SPECIES OF *VULPES*

(previous key page 35)

Tail over 300 mm, tip white; dorsal pelage with a bright reddish spinal band flanked with greyish; ears over 80 mm long; breadth across the outside of the upper cheekteeth over 30 mm; c — m^2 over 45 mm **rueppelli** (*page 66*)

Tail under 300 mm, tip black; dorsal pelage darker medially but not bright red or flanked with grey; ears under 80 mm long; breadth across the upper cheekteeth under 30 mm; c — m^2 under 45 mm . . . **pallida** (*page 70*)

VULPES RUEPPELLI (Schinz) Rüppell's Fox

Canis ruppelii (sic) Schinz, 1825, *Cuvier's Thierreich . . . Aus dem Franzosischen frey ubersetzt . . .*, **4**: 508. Dongola. Eduard Rüppell, after whom this was named, explored and collected in various parts of north-eastern Africa for the Senckenberg Nature-research Society, Frankfort-on-Main.

Canis famelicus Cretzschmar, 1827, in Rüppell's *Atlas zu der Reise im nordlichen Afrika*, Säugethiere (dated 1826): 15; pl. 5. Nubian desert and Kordofan. The name *famelicus* is the Latin word for hungry or starved, given, apparently, in reference to the slender body and thin legs.

Canis sabbar Hemprich & Ehrenberg, 1833 *fide* a MS. note by Sherborn, *Symbolae Physicae, seu Icones et Descriptiones Mammalium . . .*, decas secunda, folio ff. Dongola. This was a vernacular name. (Not a synonym of *V. pallida*, as given in G. M. Allen, 1939).

Vulpes ruppelli caesia, Thomas & Hinton, 1921, *Novit. zool.* **28**: 5. South side of Mt. Baguezan, 1000 metres. Type in the British Museum, No. 21.2.11.26, ♂; skin good, and skull in good condition except for the left zygoma partly missing. The subspecific name is the Latin for bluish-grey and refers to the dorsal pelage. Of doubtful validity.

Distribution and general. Rüppell's fox (Plate 1) occurs from the Sahara in the west (Aïr, Hoggar mountains, Tibesti) to Libya and Eygpt in the north of the continent; and eastwardly in Africa to the shores of the Red Sea, and south to Berbera on the Gulf of Aden. From the Red Sea it ranges across the Arabian peninsula north to the Dead Sea and Iraq, and east as far as Baluchistan and Afghanistan. Throughout this wide area it confines itself to arid sites, often rocky or stony rather than sandy—the type of desertic terrain vernacularly termed *Hamada*.

In suitable localities these small foxes, with a head & body length of some 450 mm and tail about three-quarters of this, are fairly abundant. In fact, Petter (1952) characterizes them as one of the commonest carnivores of the Sahara. The species is plentifully represented in museum collections, though there are rarely sufficient specimens from any one locality or area to furnish adequate data.

Description. The overall impression of the coat of Rüppell's fox (Plate 1) is that of a speckled grey back with a broader or narrower not very clearly delimited speckled pale red band down the spine, usually from the neck to the root of the tail. The flanks are more creamy and, generally, relatively lightly speckled. This creamy colour encroaches towards the red median band in two patches just behind the shoulders. The underparts, with the exception of cases noted later, are pure white.

This change from a white belly, through grey, to a red dorsum is brought about in the following way. As in other members of the family the pelage consists of a dense mass of very fine, long and soft underfur amongst which are stout bristle-hairs, fairly widely scattered. In the majority of specimens the pelage below, both underfur and bristle-hairs, is pure white. On the flanks, the underfur in some specimens remains pure white; in others, even from the same area, it starts to become darkly pigmented; but in all cases some of the bristle-hairs develop a few millimetres of black tip, and some become black throughout their length. This accords to the flanks a varying degree of speckled greyness. Moving towards the mid-dorsal line the underfur acquires a deep mauvy-grey colour; and finally, in the spinal region, the terminal portion assumes a bright rufous colour. The underfur here is about 25 mm long. The bristles, about 35 to 40 mm long, also become dark basally but nearly all have a pure white

Sand Fox, *[illegible] pallida*. Fennec, *[illegible]*. Ruppell's Fox, *[illegible]*.

subterminal band and a narrow black tip. It is these white subterminal zones, each about 5 mm wide, that come to lie together and give the coat its highly frosted appearance. The bristle ends are subject to wear and to snapping, and when this happens the degree of frosting is correspondingly less marked.

Two specimens from the Hoggar Mountains have the belly and lower chest a very striking, intense mauvy-red, the pelage where this occurs being, in comparison with more normal specimens, both scanty and peculiarly close-lying. The same feature, but in a very much paler form, is found also in a specimen from Dongola (Sudan), B.M. No. 32.7.3.1. The reason for this is not apparent. It does not seem to be moult and the colour bears no resemblance to anything occurring elsewhere in the coat.

The neck and the crown of the head are pale reddish or sometimes buffy, the same colour extending down the front of the face to the rhinarium, being bordered by two very conspicuous dark brown bands descending from the eyes to just forward of the middle of the upper lips—which are, themselves, white. Something of the same dark colour actually encircles the eyes. The ears are pale red or buffy-red on their backs and have long white hairs around the margins of their inner sides. They are pointed and much larger than those of *Vulpes pallida*. The legs are pale red on their outer aspects, white inside. The extremely bushy tail is a mixture of buff and black-tipped hairs about 50 mm long, the total amount of black varying considerably with different specimens. The tip is always white. There is a gland on its dorsal surface, not far from the root, which according to Anderson (1902) clogs the surrounding fur with a yellow secretion that gives off an aromatic odour.

Skull (fig. 8). This is like a small version of *Canis adustus* without such well-developed occipital crests. The profile is much the same, having only a slight dip over the nasals to break the otherwise flat outline. The rostrum is relatively more slender. The braincase is rounded; the postorbital processes are blunt and narrow, their upper surface having the slight depression that differentiates *Vulpes* from *Canis*. There is very little constriction between the orbits. The zygomatic arches are strong, almost semicircularly upcurved in the manner of *C. aureus*. The bullae are relatively large; the palate usually terminates at about the mid-length of m^2 or sometimes anterior to this. There is nothing remarkable in the dentition; but the carnassials are of greater size in this species than in *pallida*, as Table 3 on page 74 demonstrates.

Habits. Little is known of this fox in the field. It has already been said that *rueppelli* often affects a more rocky, hilly terrain than *pallida* does. Buchanan noted on the label of the *caesia* type from Mount Baguezan that the species is locally held to occur only in the mountains and is never heard of at Agades in the plains a little further south. Petter (1952), however, writes of a specimen captured in the region of Agades. An example from Somalia is labelled as having been trapped on a hill; but the only other collector's note contradicts the idea of *rueppelli* being purely a fox of stony ground since the relevant specimen (from Wadi el Natrun near Cairo) was dug from a burrow in the sand. Indeed, it is known that the species does occur in the same areas as the sand-loving fennec. Rüppell's fox is reputed to be largely nocturnal; but like all foxes it is not infrequently to be seen on the move during the early and late hours of daylight.

Petter (1952) appears to be the only author to have given some account of the

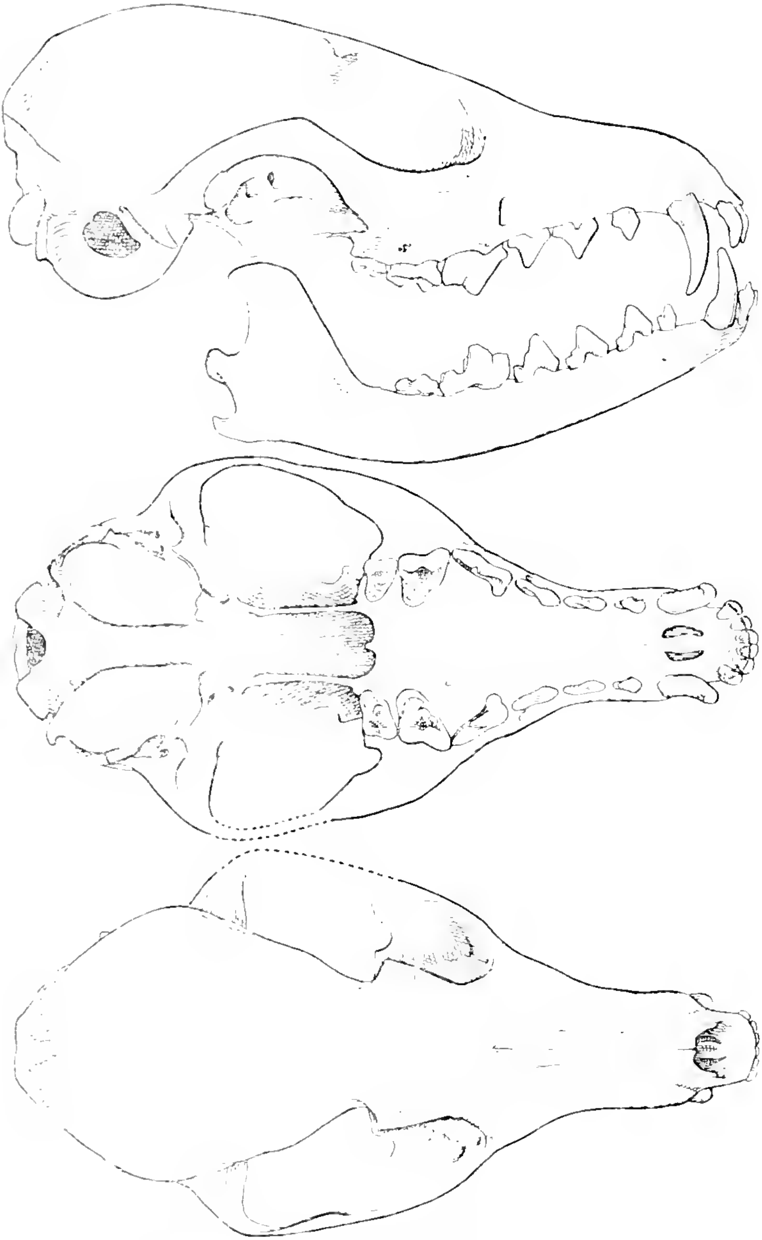


Fig. [illegible] *Vulpes rueppelli* skull, Type of *caesia*, B.M. No. 21.2.11.26, ♂. 1

living animal, chiefly in regard to a captive specimen in Paris. He noted it as having exceedingly keen sight and hearing, able to detect movement or an unusual sound at over 100 metres. This captive animal became very attached to the human beings with whom it had had close relations from an early age. It remained playful with advancing years; its joy at visits from well-known friends was expressed in sonorous cackles and long moans; it wagged its tail rapidly and would lie down for caresses with its ears laid back. On the other hand, with strangers it would growl and retreat, utter short barks and snap. Other specimens have, indeed, been known to possess quite different temperaments from this animal, being either aggressive or wholly indifferent.

Petter's fox thrived on a mixed diet, flesh and vegetable, but it never drank. This would accord with the sort of thing to be expected in the free state, where gerbils, insects, roots and fruits would be the kind of food taken, and where the opportunity to drink would be extremely rare. The captive animal only occasionally actually ate out of its dish; it preferred to fill its mouth with a large quantity of food which it then carried away and hid in its bedding straw, returning to repeat the action once or twice before settling down to actual eating. As in other canids it went through the motions of scratching earth over what it had hidden even though this, on wood, carpet or cement, was in fact pointless. If given live food it would play with it for a long time, over an hour, without injuring it.

Rüppell's fox does not have the ever-present strong, objectionable odour of the common red fox of the palaearctic regions; but it nevertheless has scent glands. Should anything threaten to rob it of food that it is in the process of consuming it presents its hindquarters to the presumed aggressor, makes small menacing noises, lowers it head and arches its back, separates its hindlegs, which are stretched to their maximum, holds up its tail and ejaculates towards the unwelcome visitor a malodorous secretion from the anal glands.

Almost nothing is known about breeding, the preferred period of the year, the duration of gestation or the size of the litter. Anderson (1902) records, for Egypt, a female with 3 newly born young which had their eyes and ears closed. This species does not appear to be so gregarious as *pallida*.

Taxonomy. Half-a-dozen races have been described. If extremes are selected—as an exceptionally dark skin from Somalia, B.M. No. 97.8.9.9, and a particularly red one from Arabia, B.M. No. 52.1487—there is a very marked difference of impression. Yet, this apart and despite the animal's wide east-westerly range, there is over all a considerable uniformity of appearance. Speckle-coated tropical mammals very frequently display appreciable variations of tone and pattern amongst the members of a single local population; and, given sufficient material, it is nearly always possible to pick out an individual which exhibits such variations to a degree that other specimens from the area demonstrate to be not properly representative. This is so in *rueppelli*. In complete contrast to the two very diverse skins just cited it would, without knowing their widely separated provenance, be difficult to find any significant distinction between B.M. No. 86.10.15.4 from Afghanistan and B.M. No. 34.8.2.10 from the Hoggar Mountains in the Sahara. The latter, together with two more from this area, have white undersides, while two others of the same series, all collected within 10 days, and irrespective of altitude, have intense red bellies. In view of these facts it is by no means sure that any real value is to be found in the attachment of subspecific names in *rueppelli.*

In regard to the reputed West African race *caesia*, Buchanan collected four skins within a limited area, about 25 miles across, on and around Mount Baguezan, all at about 1000 metres in Aïr. One of them is badly in moult (end of July) and need not be considered. The remainder differ amongst themselves. The type, said by Thomas & Hinton to be "distinguishable by the nearly complete disappearance of the ochraceous on the back, and its consequently more wholly grey colour", stands in this respect alone, the other two being good matches for the majority of specimens from Sudan to the east and the Hoggar Mountains to the north. The type not only has the breadth of the dorsal band reduced but the tone of its red also appreciably deeper than is usual; and the skin, in fact, very exactly matches that dark specimen from Somalia mentioned in an earlier paragraph. The type of *caesia* would therefore seem to be nothing more than an idiosyncratic exception and not, in respect of its lesser area of red, typical of a distinct race. If any case were to be made out for separating West African specimens racially it would seem to be more likely to stand on their rather more silvery appearance. But even this is marginal.

The table of measurements on page 74, admittedly derived from a most inadequate number of specimens, indicates that there is very little difference of any significance between specimens of *rueppelli* from various areas, with the possible exception of those from north-east Africa, which may prove to be very slightly smaller.

VULPES PALLIDA (Cretzschmar) Sand Fox

Canis pallidus Cretzschmar, 1827, in Rüppell's *Atlas zu der Reise im nordlichen Afrika*, Säugethiere (dated 1826): 33, pl. 11. Kordofan. The Latin *pallidus* means pale, referring to the light-coloured pelage.

Vulpes edwardsi Rochebrune, 1883, *Bull. Soc. philom., Paris* (7) **7**: 8. Cayor, Oualo, Gandiole, in forest of gum-trees (*Acacia*), Senegambia. This was named after Professor Alphonse Milne-Edwards of the Paris Natural History Museum.

Canis (*Cynalopex*) *pallidus oertzeni* Matschie, 1910, *Sber. Ges. naturf. Freunde Berl.*: 370–371. Dikwa, Cameroun. Type, No. A.165,10,1, ♂, in the Berlin Zoologisches Museum. Named after its collector Lieutenant von Oertzen.

Vulpes pallida harterti Thomas & Hinton, 1921, *Novit. zool.*, **28**: 4. Takoukout, Damergou (Niger), 1550 feet. Type in the British Museum, No. 21.2.11.23, ♂, skin, good, and skull, good except that *m*3 is missing on both sides. Called after Dr. E. Hartert who collected for Lord Rothschild's museum at Tring, England.

Canis pallidus (Mivart) Rüppell, subspecies *haterti* Zimara, 1935. *Sber. Akad. Wiss. Wien*, **144** (1): 9. Gourma-Bahrus. A *lapsus calami* for the above.

Distribution and general. The sand fox, sometimes called the pale fox or pallid fox (Plate 1), is roughly the same size as Rüppell's fox but has a relatively shorter, black-tipped tail and a smaller ear. The two alternative names, though apt in regard to Subdesert specimens, are not properly applicable to examples from moister biotopes where the pelage assumes deeper hues; and the term sand fox is also not altogether truly descriptive since this animal does not confine itself entirely to sandy places but is found also, some distance south of the Sahara, on other soils. However, it demands a soft, friable soil rather than a stony one and thus differs from Rüppell's fox. *V. pallida* is not of such wide distribution as *rueppelli*, being confined to the Saharan and sub-Saharan region of Africa between about 10° and 20° north, but having a considerable trans-continental range from Senegal to the Red Sea. It is most typically an inhabitant of the very dry zones, the Subdesert, Sahel and Sudan types of vegetation, but it also occurs, apparently more rarely, in the somewhat moister Doka woodland. West African specimens exist in the British Museum from Takoukout, Agades and Zinder (all Niger); and Gombe, Farniso, Kontagora and Zaria (all Nigeria). A. J. Hopson observes (*in litt.*) that the sand fox is common near Lake Chad and numerous colonies of up to 30 burrows are to be seen in *Acacia tortilis* var. *raddiana* woodland (*i.e.* Sahel) usually on the crests of sand dunes. Elsewhere it has been recorded from Kayes (Senegal), near Timbuctu and Gourma Rharus (Mali); and the neighbourhood of Fort Archambault (Chad). In the correct localities it is a fairly common animal. The species has usually been divided into five races; these are discussed later.

Description. By comparison with the strikingly coloured *rueppelli* this is a relatively dull, though elegant, little fox, with its finely speckled sandy coat and black-tipped tail (Plate 1). There is an appreciable range of colour from creamy-buff to pale red; but this will be dealt with in more detail later, the present section concerning itself only with a broad general description of the *pallida* pelage. All specimens have a broader or narrower, ill-defined, band of deeper tone running from neck to tail. The pelage is composed of the usual mixture of abundant fine long underfur and scattered stouter bristle-hairs. The former is from 15 to 20 mm long, the latter from 25 to 30 mm. In broad terms, the underfur is white-based; it then has a paler or deeper sepia zone, becoming finally in the terminal third buffish or reddish. The bristles are white-based, then medium-brown, succeeded by a brilliantly pure white band, which passes through a progressively deepening red-brown zone until it becomes, in most cases, black at the tip. It is the white bands and the dark tips of the bristle-hairs that impart the speckled pattern to the back. The intensity of colouring in the pigmented zones is considerably variable, giving rise to the different overall impressions that have led to the erection of races. The pelage becomes paler on the flanks and passes in the majority of cases without any very sharp line of demarcation into a pale underside, generally pure white or creamy.

The neck and the crown of the head are much the same as the back; the backs of the ears slightly darker in tone. The cheeks are pale to a very varying degree in different forms, pure white in those from the Sahel and Subdesert. The eye is surrounded by a dark ring, broadest at the inner corner, and continuing thence to the lip, sometimes rather indistinctly. The muzzle is sharp. The legs are lighter or darker red-brown on the outside, white on the inner faces. The tail, which is not so bushy as in *rueppelli* is the same basic colour as the back flecked to a greater or lesser degree with long black tips, which form the usual black mark not far from the root and come together terminally to form a very pronounced black tip. The live weight of an adult is about 1½ to 2 kilos.

Skull. This does not differ to any marked extent from that of *rueppelli* except that the bullae are slightly larger and the nasals appreciably longer. The most pronounced difference between the two species lies in the dentition. In *pallida* both carnassials top and bottom, are from 1 to 3 mm shorter than in *rueppelli;* and as the length of the posterior cheekteeth is much the same in the two species, the ratios which the carnassials bear to these are considerably less.

Habits. Although these little foxes are pretty common over a broad arid zone stretching for 6000 kilometres across the continent from east coast to west coast, little has been recorded of their way of life beyond the bare fact that they live a fairly social existence in soft open sandy wastes. Like all members of the genus they shelter in burrows, but no one has given any detailed account of these. Nor are there any known facts relating to breeding; but a specimen is noted as having lived for nearly three years in captivity. Petter (1952) noticed that these foxes do not emit the usual foxy odour. Rothschild & Wollaston (in de Winton, 1901) observed that they swim well and readily. Anderson (1902) records that Witherby found skulls of the species in the nest of a kite, near Khartoum.

Taxonomy. No question arises as to the standing of *pallida* and its complete independence from *rueppelli* or other species. The only point at issue is its subdivision into races. Three of these have been attributed to West Africa: *harterti* from the Sahel vegetation, *edwardsi* from the Sudan woodland, and *oertzeni* for the Doka. The nominate race was described from Kordofan (Sudan), its exact provenance lying possibly in Subdesert, possibly in Sahel vegetation.

The question of subspeciation in *pallida* is, as so often, a difficult one. It is not that appreciable differences do not exist between animals from different localities; there is, for example, a wide discrepancy of coloration between the type of *harterti*, B.M. No. 21.2.11.23, and skins from Gombe (Nigeria), B.M. Nos. 28.6.3.9 & 11. The trouble lies in drawing clear lines of distinction and in the danger, in the face of a good deal of variation, of entering into a complexity of rather meaningless nomenclature. In addition there is the usual paucity of material from which to draw conclusions. Evaluation of pelage character is rendered a little more difficult by the different setting of the skins, those that are flat, owing to the exposure of the flanks and part of the belly, giving a much paler impression than the colour of the actual dorsum warrants. The table on page 74 shows that there is not a great deal to choose in size between the few specimens of each reputed race; *harterti*, as represented solely by the type, seems to be a little smaller than the rest in nearly every respect.

Before considering other races the first thing is to determine the appearance of typical *pallida*. No precise type locality was named beyond the general description "Kordofan" and there is nothing in the British Museum actually so labelled, the most likely specimens to correspond to the original locality being those from Shendy, on the Nile below Khartoum. They do, in fact, agree very closely with Cretzschmar's plate. They are well matched dorsally by others from Suakin 300 miles to the north-east on the Red Sea, both localities reputedly in Subdesert vegetation (*vide* the map in Keay *et al.*, 1959). Anderson (1902) said that his specimens (presumably from Suakin) "agree exactly with the type of the species in Frankfort". Turning now to West Africa, a skin from Agades (Niger; Sahel vegetation) corresponds very closely to the

Shendy material, though with somewhat more white on the face. It might thus be regarded as representing typical *pallida* in West Africa. The type of *harterti*, from Takoukout, Sahel zone some 100 km to the south, is marginally paler and browner, but it seems scarcely worth while drawing a nominal distinction between the two. It is true that, as Thomas & Hinton pointed out, *harterti* seems to be smaller; but this conclusion is drawn from the measurements of a single example compared with equally or almost equally, inadequate data.

The skins from further south, at Zinder (Niger, near the edge of the Sahel/Sudan zones) and Farniso (Nigeria, well into the Sudan zone) are a close match for one another dorsally, being of a slightly warmer red-brown than those from nearer the desert. But there are differences below. The flanks of the two Zinder skins are paler than in that from Farniso, but one has a pale pinkish-ochraceous wash from throat to anus, the other being chiefly white with an extremely pale hint of pink in one axilla and over the belly. The Farniso underparts are greyish, but much of this is probably due to staining.

In the past these slightly warmer-coloured skins have been assigned to *edwardsi*. Rochebrune's description of this form is far from precise. Most of it would cover a range of *pallida* specimens; but he does state that the coat is grey below. This is unusual and only one specimen in the British Museum could possibly fit such a character and that is the Farniso skin, in which the grey colour is possibly extraneous. The only two measurements given by Rochebrune, for length and for height, are ill-defined and have no great significance. On the strength of the description furnished, his summing up of the case for *edwardsi* seems altogether too sweeping: "Confused with *Canis pallida* of Ruppell, this remarkable type differs from it in size, pelage and many anatomical characters". Whether the Zinder and Farniso animals really correspond to this Sahel form from Senegal is at least open to doubt.

There remains Matschie's *oertzeni* to consider. He described this as being "isabel" on the back; this is a somewhat disputed colour but usually reckoned as a dirty yellow and is depicted as such in Ridgway (1912). No British Museum specimen could be likened to this. However, Matschie described the underside as reddish, the throat rosy-white, in contrast to the usual pure white or near-white of most *pallida*. Specimens from Gombe, Nigeria, some 370 km to the south-west and in the same vegetation zone (Sudan) as the type locality, and especially B.M. No. 28.6.3.9, might be held to correspond to this. The mid-dorsal pelage is very much that of the Zinder and Farniso skins but the flanks are more brown, and the underside quite different from that found in any other London example of *pallida*. The overall impression is therefore that of a much more intensely coloured animal. Specimens from Kontagora and Zaria in the Doka zone of Nigeria have similar dorsal coloration but their bellies are mostly whitish.

It will thus be seen that there are appreciable differences between the various existing West African specimens, and especially between the extremes from Subdesert and Doka. But it would be difficult to say with conviction which, if any, correspond to present named races. Out of the 11 West African skins, in only three cases are there more than one example available from a given locality (Takoukout 3, Zinder and

Gombe each 2); and these show at least slight differences from each other. It would appear that the existing specimens are randomly taken samples from a cline; and no matter what proliferation of races were proposed it would remain impossible to say where one started and another finished. In these circumstances, and especially in view of the very limited material available, it would seem that no practical end is served by attempting to categorize specimens into hard and fast subspecies. The best that can be

Table 3: Numerical data for species of *Vulpes*

	rueppelli				*pallida*			
	North Africa	Sudan (Type area)	Aïr (*caesia*)	Hoggar	Sudan (*pallida*)	Takoukout (*harterti*)	Zinder, Farniso, Grombe (?*edwardsi*)	Kontagora, Zaria (?*oertzeni*)
Vegetation	?	Sub-desert	Sub-desert	Sub-desert	Sub-desert	Sahel	Sudan	Doka
Number in mean	3	3	4	6	2	1	2	1
Condylobasal length	98·5	102·9	105·5	106·0	92·6	91·4	99·6	101·2
Basilar length	91·4	96·4	101·0	98·8	90·8	85·0	93·1	93·8
Palatilar length	47·8	50·9	53·7	52·0	45·6	43·8	47·1	46·9
Zygomatic breadth	53·3	57·4	58·6	57·7	54·2	50·8	55·5	54·0
Upper cheekteeth breadth	30·9	30·6	31·4	31·1	28·2	26·7	28·6	27·7
Nasals, length	34·1	36·0	39·1	38·4	33·6	30·8	34·4	31·7
Interorbital breadth	18·8	20·3	20·2	20·4	19·5	17·1	19·5	17·2
Postorbital constriction	21·1	20·6	19·1	20·6	21·5	22·1	21·4	19·6
Braincase breadth	38·7	39·1	40·7	40·6	39·6	39·3	40·6	39·4
Toothrow ($c - m^2$)	46·1	47·8	50·4	49·6	43·4	41·6	42·2	44·3
p^4 length	10·3	10·2	10·6	10·5	8·5	7·7	8·3	8·8
$m^1 + m^2$ length	12·7	12·1	13·0	12·8	11·6	11·2	12·2	12·3
m_1 length	12·0	11·6	11·9	12·1	(9·8)	8·8	9·9	10·6
$m_2 + m_3$ length	8·0	8·9	9·4	9·0	9·0	(8·6)	9·4	8·9
Head & body	415	456	462	472	420	406	448	—
Tail	305	323	358	342	270	273	286	—
Hindfoot	97	106	113	114	108	89	100	—
Ear	87	90	97	95	70	64	66	—
RATIOS (per cent)								
Tail/head & body	74	71	77	72	64	67	64	—
Zygom. br./condylob. l.	54	56	56	55	59	56	56	53
Braincase/condylob. l.	39	38	39	38	43	43	41	39
Braincase/zygom. br.	73	68	69	70	73	77	73	73
Palatilar l./condylob. l.	49	50	51	49	49	48	47	46
Interorb./postorb.	89	99	106	100	91	77	91	88
$p^4/c - m^2$	22·4	21·4	21·1	21·2	19·6	18·5	19·7	19·8
$p^4/m^1 + m^2$	81·1	84·3	81·5	82·1	73·2	68·7	68·1	71·4
$m_1/m_2 + m_3$	150	130	127	134	108	102	105	110

done is to say of intensely coloured specimens with dark bellies "near *oertzeni*"; and to call pale Sahel and Subdesert animals "*p. pallida*"; *edwardsi* with its reputedly grey belly would seem either not to exist as such or to be applicable to a wide clinal range between the two extremes.

Subfamily **SIMOCYONINAE** Zittel, 1893

In this Subfamily the sole African genus, *Lycaon*, is rather doubtfully lumped together with two other living genera, *Speothos*, a South American dog, and *Cuon*, from Asia, to form a convenient taxonomic unit. Included with these is a large number of fossil genera, chiefly of interest as uniting the Canidae with the Ursidae, the bears. These matters are not pursued here and we proceed at once to consideration of the only genus of immediate relevance to West Africa. The name Simocyoninae is derived from the Greek *simos* flat nosed, and *kyon*, *kynos* a dog. It has no particular significance apart from the fact of the muzzle in *Lycaon* and *Speothos* being somewhat less sharp than in the jackals, foxes and wolves.

Genus **LYCAON** Brookes, 1827

Hunting Dogs

Lycaon Brookes, 1827, in Griffith's *Cuvier's Animal Kingdom* **5**: 151. Type species *Lycaon tricolor* Brookes (= *Hyaena picta* Temminck). Lycaon was a character in Greek mythology who was transformed into a wolf.

Cynhyaena F. Cuvier, 1829, *Dictionnaire des Sciences Naturelle* **59**: 454. Type species *Hyaena picta* Temminck. This name was formed from the Greek *kyon*, *kynos* dog coupled with the name *Hyaena*.

Hyenoides Boitard, 1842, *Le Jardin des Plantes:* 215. Type species *Hyaena picta* Temminck. This is the Greek termination *-oeides*, from *eidos* form, implying resemblance, added to the name *Hyaena*.

Hyaenoides Gervais, 1855, Histoire Naturelle des Mammifères **2**: 53. This is simply an academically more correct spelling of the above.

The hunting dogs are the sole African representatives of the Simocyoninae and are characterized in appearance by their varicoloured, mottled coats; and in structure by their feet, both fore and hind, having only four digits. In the skull, the posterior upper molar (m^2) is much reduced in size, being smaller than the antero-external cusp of the carnassial (p^4); and the palate is relatively broader than in the true canids.

Taxonomy. The rather doubtfully justifiable association of *Lycaon* with *Speothos* and *Cuon* has been referred to above; but though the relationship of these to each other is possibly not as close as a subfamily connexion would imply the group is a convenient one and could only be rationalized at the expense of creating a number of smaller not very meaningful units.

As regards the organization of the genus itself, Matschie (1915) erected a great many independent species, three of which were applicable to West Africa. The basis of all these was very slender, resting almost exclusively on variations in pelage pattern; and the modern view is that there is, in fact, only one valid species, *pictus*, throughout Africa, Matschie's creations ranking, if they have any validity at all, as no more than races of this.

LYCAON PICTUS (Temminck) Hunting Dog

Hyaena picta Temminck, 1820, *Annls gen. Sci. phys. Brux.* **3**: 54. Coast of Mozambique. The Latin word *picta* means painted or ornate and was applied to this animal because of its varicoloured coat.

Hyaena venatica Burchell, 1822, *Travels in the Interior of Southern Africa* **1**: 456; & 1823, **2**: 229. North-east of Asbestos Range, Griqualand West, South Africa. The specific name is Latin and means given to hunting.

Canis (Lycaon) tricolor Brookes, 1827, in Griffith's *Cuvier's Animal Kingdom* **5**: 151. Cape of Good Hope. The specific name is a combination of the Latin words *tri-* meaning three and *color* the colour of the skin, given in reference to the black, white and yellow pelage.

Lycaon typicus A. Smith, 1833, *S. Afr. Q. Jl* **2**: 91, (= "Burchell's Lycaon"). The specific name is Latin for typical.

Lycaon pictus sharicus Thomas & Wroughton, 1907, *Ann. Mag. nat. Hist.* (7) **19**: 375–376. Mani (*not* Maui), lower Shari River (Chad). Type in the British Museum, No. 7.7.8.74, ; skin and skull both in good condition. The racial name is a Latinized form of the type locality.

Lycaon manguensis Matschie, 1915, *Sber. Ges. naturf. Freunde Berl.*: 364–366. Near Djamaga, north of Sansanne Mangu, near the Oti River, Togo. The name is a Latinized form of the town Mangu from near which the animal came.

Lycaon mischlichi Matschie, 1915, *Sber. naturf. Freunde, Berl.*: 366–369. Northern part of the Kete Krachi district, Togo, probably near Bimbila, between the Oti and Daka Rivers. This was called after its collector, Professor Mischlich, a German government official.

Lycaon ebermaieri Matschie, 1915, *Sber. Ges. naturf. Freunde, Berl.*: 369–371. Lake Chad area, probably near Dikwa. This was named in honour of the German Governor of the Kamerun, Karl Ebermaier, who sent the living animal to the Berlin Zoo.

There is a further extensive 20th century synonymy, mostly erected by Matschie and mostly applying to southern and eastern Africa.

Distribution and general. The hunting dog, sometimes too restrictedly, and certainly today misleadingly, called the Cape hunting dog, is confined to Africa but has a very wide range throughout much of the continent from the Sahara to South Africa. In the former of these it is generally regarded as probably little more than an occasional rare visitor; but Heim de Balsac (1936) thinks there is good evidence in support of a distinct Saharan race. Two specimens were captured north of In Ouzzal (Adrar des Iforas) in 1927 (Lhote 1946); and it is said to occur in Tanezrouft, Tibesti and Ennedi.

South of the Sahara it is an animal of the more open kinds of grass-woodland but is erratic in its occurrence, the more so today as its numbers are, in general, becoming ever less and less owing to the widening settlement and use of the land by man and the consequent reduction of available food in the form of antelopes. A century ago it might at times be seen to hunt in packs of up to a hundred, or possibly even more, and those of thirty to forty were common. Now, and especially in West Africa, the packs tend to be smaller, sometimes only six or eight, and often less; but R. H. Kemp, of the Nigerian Federal Forest Research Department, saw a pack of at least 30 in April 1969 in Borgu (extreme western Nigeria), half of them pups estimated to be five or six months old (personal communication); and with general game protection in this Reserve it seems possible that it is there becoming again more numerous. There are records of occurrence from the north of the Ivory Coast, the upper Volta area, and across this belt to Sudan, Eritrea and Somalia. Thence the species ranges

Fig. 9. Hunting Dog (*Lycaon pictus*)

down the eastern half of the continent south to Transvaal and Portugese East Africa and across to Angola and South-west Africa. South of the Tropic of Capricorn, where it formerly dwelt in large numbers, it is now absent or only a very occasional wanderer. In the British Museum there exist from West Africa only one complete specimen, that from Mani (Lower Shari River, Chad), and two partial specimens, the one an unmeasured skin from Leri-n-duchi (Zaria, Nigeria), the other a skull from Lake Chad.

The hunting dog prefers open country where vision and pursuit of quarry are not much obstructed. It is therefore most commonly to be found in the Sudan and Sahel woodlands where the grass is fairly short and relatively sparse; and though it certainly occurs in the Guinea woodland this is probably for the most part during the dry-season when, as a result of the annual grass burn, this type of country becomes very open. During the rains, on the other hand, the ground cover in most places in this zone is both too dense and too high—2 metres or more—to make hunting in the manner of these dogs a practical possibility. This applies in a somewhat lesser degree to the Doka zone.

Description. *Lycaon* (fig. 9) is easily the bulkiest and most solidly built of West African canids, standing 61 to 66 cm at the shoulder, with a head & body length of about 114 cm and a bushy tail of 35·5 to 38 cm. The weight of a fully grown animal would be some 27 to 32 kg; but the average in a pack, is probably more in the nature of 20 kg. The Hunting Dog is quite unmistakeable with its short coat, blotched with black, yellow and (often) white, and its very conspicuously large and rounded ears. Though quite obviously a dog, it is, by the features just enumerated, very readily distinguishable from the jackals, which are much smaller and have pointed ears.

The pelage is harsh, of moderate length, close-lying and not at all dense; and it is, thus, vastly different from that typical of the jackals and foxes. It is, indeed, of entirely different composition since it consists solely of stiff, terete, bristle-hairs and has no underfur whatsoever. These bristles are, by comparison with the closely packed fur of the foxes, relatively widely spaced at their roots and emerge from the hair follicles mostly in pairs, occasionally in threes, rarely singly. Instead of the colour annulation common in the pelage of other canids these bristles are to all intents and purposes unicolorous from root to tip, pure white, blackish or pale yellowish-brown. These tints occur over sharply defined areas of the skin and result in a broad mottling of the pelage with little intergrading of one patch with the next, the fur thus exhibiting nothing of the intimate "pepper and salt" mixture common to so many mammalian coats. The proportion of one colour to the others varies very considerably, as do their relative positions on the body. Matschie (1915) tried to establish fixed patterns in relation to various geographical areas, the basis of his proposed specific naming. Not only were the data on which this supposition was founded mostly exiguous, but also, where in the British Museum collection more than one specimen exists from a given locality, constancy of pattern is seen to be non-existent. This is amply confirmed by photographs of packs taken by R. H. Kemp in the Borgu Game Reserve, Northern Nigeria, (Howell, 1968, and private communication); and also by those illustrating Kühme (1965b).

The chest and belly are mottled in the manner of the back but the hair is considerably shorter and yet more scanty, scarcely obscuring the skin. In the only two West African specimens available for study the chin and under the jaw are black; the throat and upper part of the chest white. The back of the neck and the top of the head to the forward level of the eyes are pale brown; and a broadening black stripe runs medially through this region over the crown and down the centre of the face to join the all-black muzzle. The posterior part of this line is sometimes faint or lacking. The muzzle itself is short, broad and heavy; the nostrils are well-separated and widely open. The large, rounded, ears, about 115 to 125 mm long, are black on their backs and to some extent on their anterior faces as well, though here there is also a white tuft situated over the lower part of the inner edge.

The legs are variegated with the same colours as the back. In this subfamily there are only four toes on each foot, the short claws being deep and powerful. The feet themselves are strongly built. The two middle toes are widely separated but joined by a narrow naked web (Pocock, 1914b). The proximal margins of the digital pads carry long fringes of stiff reddish hairs; but the rest of the sole between these and the plantar pad is scantily clad. The distance between the plantar and carpal pad is unusually long and narrow. The hindfeet are similar but narrower. The tail is short-haired in its basal third, and then has a longish-haired black and white bush, the terminal quarter being conspicuously pure white. The females usually have about 12 teats.

Skull (figs 10 and 11). The skull is very powerfully built, with strong ridges and arches and a massive dentition. As canid skulls in general go it is short and broad. The braincase, as in other members of the family, seems unexpectedly small; it is rounded but carries a pronounced, sharp sagittal crest which joins an equally prominent supra-occipital crest to form a backwardly-projecting pyramidal "helmet". The interorbital region is slightly constricted, the pointed, triangular, downwardly curving postorbital processes being well-developed, their hind margins continuing and converging posteriorly across the temporal region in a diamond outline to meet the forward end of the sagittal crest. The muzzle is noticeably short, wide and deep, the anterior nares very open.

The zygomatic arches are broad and strong, sharply upcurved, and since the pointed process on the upper margin of the jugal is not very distantly separated from the post-orbital process the orbit goes some way towards complete encirclement, but not quite so near as in the hyaenas. The palate is broad throughout, being particularly so between the carnassials, and shows little of that marked anterior narrowing between the premolars and canines that gives the more typical dogs their sharply pointed muzzles. Posteriorly the palate comes to an end about the level of the hind margin of m^2. The bullae, though prominent, can not, in comparison with the size of the skull and their relative development in the jackals and foxes, be characterized as large. The mandible is robustly built, with deep, solid rami and strong coronoid, condylar and angular processes.

The dentition is powerful, all the teeth being relatively broad and strongly cusped. But the posterior upper molar, m^2, is much reduced in size and is less in bulk than the antero-external cusp of the carnassial, p^4. As in the other West African canids the cheekteeth are $\frac{4.2}{4.3}$. The outer upper incisor (i^3) is much enlarged and caniniform in

FIG. 10. *Lycaon pictus*: skull, Type of *sharicus*, B.M. No. 7.7.8.74, , ½; lateral view

shape; the outer lower incisor ($i3$) is also enlarged but not to the same marked extent and not caniniform but flattish and bicusped like the rest.

Habits. The hunting dog has, over a long period of years, attracted a good deal of attention which has resulted in an abundant recording of the chief features of its mode of life. Some of its alleged habits, traditionally held and passed from writer to writer or by word of mouth from one naturalist to another, appear to have been directly contradicted by close and specialized study of the species made in the field in recent years. The most prolonged and concentrated investigations have been carried out by Kühme (1965a and b), Estes & Goddard (1967) and Goodall (1970), whose published observations contain a great deal of information relating to the daily and nightly habits of packs in the Serengeti plains and Ngorongoro crater (Tanzania), observed at close quarters over long periods. Much of what has been noted in these areas is doubtless, *mutatis mutandis*, also applicable to West Africa.

The interest and repute of hunting dogs rest, as their common English name indicates, on the way in which they secure their food; for, although solitary individuals are from time to time observed, these dogs generally live a highly communal existence and hunt, skilfully and persistently, in packs. These vary in number from an extended family unit of about half-a-dozen to a sizeable group of 30 or so. Anything larger than this is today, even in East Africa, relatively rare. Certainly in West Africa few packs of this magnitude are likely to be found, though one such has recently been observed. Probably a dozen dogs might well be regarded as constituting a more normal pack for this region. Concrete information of any kind relating to the area covered by this present work is, however, extremely scanty. In East Africa packs have often been found to show a predominance, in numbers, of males.

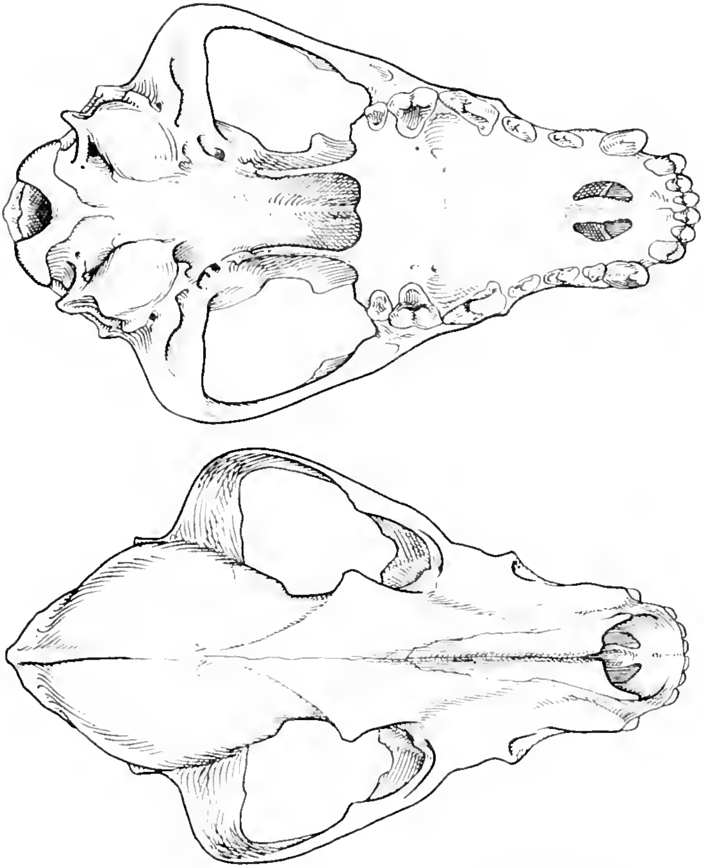


FIG. 11. *Lycaon pictus:* skull, Type of *sharicus*, B.M. No. 7.7.8.74, ♂, × ½; palatal & dorsal views

Hunting is normally engaged in regularly twice a day, in the early morning and late evening; but if the weather is deeply overcast, or for some other less apparent reason, it may as an exception be carried out during the intervening period. A chase has been known to be continued till after dark (Estes & Goddard, 1967); and moonlight hunts have also been recorded; but such nocturnal events in ill-lit conditions are relatively rare since *Lycaon* hunts by sight rather than by smell. According to Kühme's observations it would seem that what is acceptable as a meal may vary from day to day, a change of diet apparently being desirable, readily available prey of a kind that was one day willingly taken being passed by the next in the search for other flesh. Estes & Goddard, however, found that something in the nature of 69 per cent of the kills were Thomson's gazelle, and 18 per cent juvenile wildebeest. What is pursued is doubtless determined to some extent by the size of the pack, the more numerous this may be the greater the possibility of being able to overpower the larger sorts of antelopes. In West Africa it is unlikely that anything as bulky as a waterbuck or roan would ever be tackled, though attempts would certainly be made on their calves. On two occasions R. H. Kemp has found the kill in Nigeria to consist of a fully mature hartebeest in good condition. When a Land Rover stopped near one of these kills some of the pack made attempts to drag the hartebeest away and two dogs did, in fact, succeed in drawing it about 27 metres (personal communication). Probably the main sources of food in West Africa are gazelles, reedbuck, cob and hartebeest; but bushbuck, oribi and crowned duiker, though less gregarious than the others, may doubtless also be taken. A bushbuck killed by hunting dogs was in fact observed by David Brown in the Borgu Game Reserve (Nigeria). Warthog are from time to time hunted. Hunting dogs are, indeed, known to take much smaller fry such as cutting-grass (*Thryonomys*), giant Gambian rat (*Cricetomys*), hares (*Lepus*), ground squirrels (*Euxerus*) and so forth; but this they usually do as independent individuals, not as a pack though others may be present and all on the move in search of more satisfying prey.

A look must be taken at some of the long-held views regarding the method of hunting that have now been upset by close and continuous observation. Traditionally these dogs were believed to pursue their prey tirelessly and relentlessly over vast distances until the quarry faltered and fell from sheer exhaustion, the outcome of prolonged terror and physical effort. It was even said that in the case of the larger and stronger antelopes such a chase might extend over as much as 15 or 20 km and that during this the leading dog would be deliberately relieved from time to time by relays of others which were less fatigued. What in fact really happens is, to take the morning hunt, that soon after dawn the various dogs of the pack emerge from their sleeping quarters and wander slowly round defaecating and carrying out an extended greeting ceremony, each with every other member of the pack. This consists of poking the nose into the corner of the other dog's mouth and of licking the lips and face. If all are not present a not unmusical bell-like call is uttered to assemble distant members. Eventually, some half an hour or so after daybreak the pack moves off at a trot in more or less open formation to look for game. When suitable quarry has been sighted approach to it is made with some care, at a walk, in a slightly crouching attitude with head and tail both lowered.

In the past it has been commonly held that *Lycaon* strikes far more terror to the heart of the antelope population than does the presence of lions; and that not only would antelopes stampede at the first hint of danger but would actually entirely desert any district tainted by the mere existence of hunting dogs (Bere, 1956). Nevertheless, that antelopes do not, in fact, always recognise their danger is shown in E. M. Lang (1963) where a herd of gazelles is recorded as actually running inquisitively towards an approaching pack until they were no more than about 30 metres away before realizing that they were in grave peril. Kühme, in the papers cited above, also found that antelope herds were either not visibly wary of near-by hunting dogs or took flight only when an obviously actively hunting pack on the run towards them was within some two or three hundred metres, though Estes & Goddard estimated the alarm distance in these circumstances somewhat higher. It is, however, quite certain that a herd of antelopes instinctively knows when a pack means business, exhibiting no fear even though dogs may be at very close quarters but stationary, and but little alarm when a pack is merely walking or trotting. It is this that enables the dogs to approach fairly close before setting a herd in rapid retreat; or, in the calving season enables them to edge very near to a mother and her fawn before snatching the latter.

Once the prey has been set in motion the dogs break into a run and follow, still in more or less open order. If more than a single antelope is being chased there appears to be no deliberate selection of any particular victim from the start, choice of that which becomes the ultimate prey being as much a matter of chance as anything, resolving itself into a question of the slowest member of the herd. This is possibly a gravid female or the tardiest to abandon grazing for flight, most frequently a male. At the start of a chase every dog follows that beast which is most directly in front of it, and hence nearest, but they tend to switch to any one that is obviously less distant from its aggressor, until ultimately the hunt nearly always resolves itself into the pursuit of a single animal. There is no deliberate taking over the task of leading dog in relays, as in the past supposed. If change takes place it is probably most often due to the fact that the quarry, failing to escape on a direct course, starts to circle; and whereas the foremost dogs follow immediately on its heels others further in the rear can more easily follow the chord of the arc and so, pursuing a shorter line, gain ground over both the antelope and erstwhile leader. Yet this is not necessarily always the pattern; for Estes & Goddard (1967) found, in Ngorongoro, that the dominant dog of the pack selected the victim and led the pursuit. Nor does the hunt always resolve itself into a single kill. E. M. Lang (1963), for example, describes an incident where a pack divided into two.

The search for prey is carried out at a trot of about 11 km an hour; actual pursuit is at a steady 48 km an hour, a rate which can be maintained by healthy adult dogs over long distances. Short spurts can if necessary be made at about 56 km an hour. Not all the pack can keep up with this, and laggards or young dogs may still be 1 or 2 km in the rear at the time of the kill, not catching up till the leaders have already had 5 minutes or so at demolishing the victim. So far from the dogs patiently and steadily running an antelope to exhaustion before killing it, as popularly supposed, Kühme observed that the kill was preferably made as swiftly as possible. Prey given a leading start of 300 metres would be caught and overcome in a further 600 to 800 metres. This according to other observers is rather short. Estes & Goddard reckon the average chase to cover 1½ to 3 km and to last 3 to 5 minutes; and Goodall found that the hunt, if not successful, was abandoned after 4 to 5 km; but he did, nevertheless, follow one that fruitlessly covered somewhat more than this. Since, moreover, this pack had travelled 8 km in the preliminary search for suitable prey before it actually started to hunt it must in all have covered some 13 or 14 km.

The idea that these dogs lope untiringly behind a fleeing antelope until it drops from exhaustion must also be abandoned. The antelope is not always captured; and if the chase goes on past a certain distance the dogs, as Kühme observed, can get just as exhausted as their quarry. This is confirmed by Macintosh (1953) who writes of the finding of an exhausted gazelle, panting in the grass and just capable of staggering off, and some 350 metres or so away a hunting dog in a similar state. In such cases the pack rests for some 5 or 10 minutes and then forms up for a renewed hunt. Similarly, if a successful hunt should turn out to provide an insufficient meal for all or part of the pack, the late-arriving laggards for example, then a second hunt is almost immediately entered upon, at least by those with unsatisfied appetites.

Hunting is, to all intents and purposes, always by sight, not smell, and if the quarry, during the chase, is obscured by grass the hunting dogs make intermittent leaps to keep their prey in view, the white tail tip at these moments becoming very conspicuous to an onlooker. Opinions have differed regarding whether these dogs hunt mute or not. This is dealt with later. Eventually, in the normal hunt the foremost dogs after a while find themselves almost literally at the heels of their prey and they then repeatedly jump forward to snap at the hindquarters, flanks or belly, tearing away ribbons of skin or lumps of flesh. At length the animal is brought to a standstill or knocked down and the dogs leap upon it. There is no attempt to kill it outright. It is either literally torn apart by seizing the limbs and tugging in opposite directions, or eaten alive, starting by ripping open the belly and devouring the entrails. It is, of course, impossible to say for certain but there is some likelihood that the victim does not suffer so much in this as might at first seem, being in a daze and a merciful state of shock. All but the toughest parts—heads, horns, hoofs, and sometimes skin and leg bones—generally disappear with astonishing rapidity. It has been mentioned above that not all hunts end in a kill. There are widely diverse estimates of the success rate. Goodall (1970) records only 39 successful kills in 91 hunts, that is 43 per cent. Estes & Goddard (1967), on the other hand, analysing a much smaller number of hunts found a success rate of over twice this, 85 per cent.

However, success rate apart, hunts do not always result in a satisfactory meal, for other, stronger predators have to be taken into account. Lions are not above robbing hunting dogs of their legitimate kill, and they are too powerful for the dogs to be able to do anything about it, even as a pack. Spotted hyaenas are another matter. These too, of course, are bigger and stronger than hunting dogs but they lack proper pack co-operation; so that the outcome of attempts at superpredation by them depends very largely on the relative numbers of the two contenders for the meal. There is no doubt that hyaenas sometimes deliberately sit and watch hunting dogs, or wander in their vicinity eating their droppings, waiting for them, or at times even deliberately stimulating them, to set out on a hunt, in which they then follow them. If the chase ends with only one or two dogs in at the kill the hyaenas can then leap in, frighten the dogs off and snatch a hasty feed before the rest of the pack comes up and, by a reversal of power, establishes ownership. If the hyaenas do pluck up enough courage to sneak in again and seize part of the prey they are chased off (E. M. Lang, 1963), and they are reduced to waiting on the outskirts of the feeding pack until the dogs have finished and they can then safely close in and polish off the skin and bones or any other residue that may be left. There is, indeed, an odd sort of enmity between hunting dogs and spotted hyaenas. Sometimes the former tolerate the latter in close proximity; at other times they delight in mobbing a single hyaena, biting fiercely at its buttocks so that ultimately its only defence is to squat down and so protect its hindquarters while snapping at dogs that come too near. But there never seems to be any question of the dogs, even as a pack, killing a hyaena or even doing it much visible harm; and it eventually slinks off. Jackals, vultures and other birds of prey which almost invariably try to share in a kill are driven off and made to wait, though golden jackals, in their nimble fashion, often manage to dash in from time to time and secure a mouthful here and there.

Kühme estimated that the pack he observed occupied a living area of roughly 16 square kilometres and hunted over an area of between 100 and 200 square kilometres. It will be appreciated that it is thus not normally easy or possible for a casual observer to follow a hunt at close quarters from its inception to its end, the more so as it is carried out at a fairly high speed. Only if one chanced to be actually near at hand at the correct moment and suitably mounted was this possible in the past; and the finer details of what actually takes place during pursuit were therefore witnessed by relatively few people. This accounts for a good deal of supposition, of inaccurate observation or wrong interpretation of a pack's behaviour. The problem is lessened today by the existence of motor vehicles that can travel safely and easily across country; and this is the method of observation employed by Kühme and other modern field workers. Hunting dogs are little disturbed by the presence of a vehicle at a reasonable distance. R. H. Kemp (personal communication) twice found these animals to pay little attention whatsoever to his Land Rover, coming towards it and getting out of its way very slowly or, when it stopped, lying down in front of it. One stood on its hindlegs to get a better view. Nevertheless, Macintosh (1953) records the attack by a pack on the tyres and wings of a slowly moving car.

Lycaon, apart from its normally wide hunting range is, except at breeding times, by nature a rover and in the course of a year may cover an extremely wide stretch of country. It is driven to this wandering habit partly by the migratory nature of the antelopes on which it preys since these are pretty constantly on the move to fresh pastures. On the other hand, some limit may be set to unrestricted nomadism by the existence of other neighbouring packs, each claiming right over a more or less defined area, though there seems to be appreciably less insistance on strict territories in hunting dogs than with many other predators. Anyhow, some degree of boundary observance has been noted in East Africa where the large antelope population is sufficient to support numerous *Lycaon* packs; but in much of West Africa the herds of antelopes are comparatively small, the hunting dog being consequently of relatively rare occurrence and the territories over which the few packs can roam correspondingly large and probably, for this reason, less well defined. During three months of breeding and family upbringing the pattern of life is, of necessity, different since the interest of the entire pack is completely centred round the earth or earths in which the pups are being raised. It therefore, apart from brief daily sorties after food, becomes something of a sedentary unit. Such a pattern postulates a set breeding season for all females. Kühme's pack contained only two adult bitches, each with a recently born litter; it would be interesting to know what happens where there are several adult bitches breeding at different times.

It has already been mentioned that hunting dogs, though subsisting mainly on antelopes, apparently like to alternate from one species to another; and that when these are not conveniently available they turn their attention to other kinds of flesh. It is virtually certain that nothing would come amiss to them so long as it was readily obtainable; and they certainly do not hesitate to eat the dead of their own kind. In parts of Africa, and particularly in the past when they were in larger packs and of more common occurrence, they have shown themselves to be highly destructive of cattle, sheep and goats; and they have themselves been relentlessly hunted and shot or killed with poisoned bait on this account. It was probably their depredations amongst domestic flocks that chiefly earned for them the reputation of indiscriminately slaughtering far more than they could possibly eat; but here again Kühme's observations run counter to this widely held belief since he found that his small pack never killed more than was absolutely necessary to satisfy the 8 adults and 15 whelps. When the latter were very young and ate relatively sparingly the foragers regularly killed and brought home a single 30 kg antelope morning and evening; but when the pups had grown and become more demanding they doubled their twice-daily kill. This figure is, of course, nothing more than a rough estimate; but at the end of the rearing period when all 23 dogs might be assumed to eat practically adult meals this would work out at an average of something like 5 kg a day. On the other hand, Estes & Goddard (1967), working on a pack numbering 21, estimated that there was an average of 2·7 kg a day of meat available to each dog; this amount would however vary with the size of a pack between 2 and 4 kg, the smaller packs getting the larger amount. It is interesting to compare these estimates with the figure given for zoo animals of $1\frac{1}{2}$ kg of meat daily (Dekker, 1965). Such captive specimens would, of course, get relatively little exercise compared with those hunting for themselves in the field and their demand would be correspondingly less. It may here be noted that these zoo specimens were given an occasional whole chicken or whole pigeon, indicating that, in the wild, birds, such as francolins, may be included in the diet of *Lycaon*.

There is, however, some evidence in support of the charge that these animals kill more than they can eat. R. H. Kemp (personal communication) twice observed in Nigeria that the kill had scarcely been damaged except for one hindleg and the belly ripped open. At 8 a.m. in the Borgu Reserve he once observed about a dozen animals which had just made a kill; but the rallying hoot heard in the distance not only indicated that the pack was in fact larger but, strangely enough, served also to call away the dogs by ones and twos from their newly killed hartebeest, which still remained untouched at dusk. This must be unusual; but the commonest explanation of only partially eaten prey is probably that these corpses are the outcome of second hunts by unsatisfied members of a pack, too few in number to be able to consume all of their kill. Hunting dogs, unlike many other carnivores, never feed a second time from the same kill.

Kühme never observed his pack to drink, and it is to be presumed that much of the necessary water can be picked up from blood or from licking their coats when wet with dew, or from like sources; for it is known that these dogs can go for long periods without drinking. But they certainly do drink on occasion. Goodall says that they will do so daily if possible, and quite clearly deliberately seek out water-holes to this end.

Apart from their understandable fierceness in the pursuit and capture of their necessary prey, these animals seem by nature to be of an essentially friendly and sociable disposition amongst themselves. They do not seem to engage in the fierce protection of boundaries practised by the spotted hyaenas; they are not even aggressive towards other packs unless these approach too near to the breeding burrows (Goodall, 1970). There appear to be no records of any attack by hunting dogs on man; and in fact, they seem in nature to regard human beings with some indifference. They can, however, be successfully tamed but have an unwelcome drawback as a domestic pet in their strong odour. This is probably due to glandular exudation; but they have also attaching to them another smell that seems to permeate their very bones and persists for many years after their death. A cupboard containing thoroughly cleaned skulls of *Lycaon* has a particularly nauseating odour, shared, it is true, with hyaenas and some other flesh-eaters.

Amongst their own kind these wild dogs are playful and rarely quarrel, and then only briefly. They share the same shelters, even at breeding time, and peacefully look after each other's young. They have, according to Kühme (1965 a & b) developed a classless social system that involves the ready sharing of both food and labour. Such a view is diametrically opposed by Goodall (1970) who, while agreeing about the sharing of food and labour, finds that there is a recognized social order not only throughout the pack as a whole but in each of the sexes separately as well. This conclusion was reached as the result of long and close observation of a single pack, and was derived from the interpretation of submissive body postures. The pack was normally led in the hunt by an old male; but even when on one occasion this dog fell into fourth place he was still found to influence the direction taken by the leaders. Estes & Goddard (1967) found that there was a pack leader, either male or female, but no other rank order.

It has been noted earlier in this present work (on page 48) that Wyman (1967) observed a food-begging ritual amongst the jackals. An exactly similar ritual had previously been discovered in the hunting dogs by Kühme. That is to say that on the arrival home of the foraging party those dogs that have remained on guard, and those young which are of an age to require a full meat diet, excitedly thrust their noses at the lips of the returned hunters until these latter, in response, regurgitate some of the meat with which they have recently, and partly with this end in view, been filling their stomachs. This performance is repeated until those that have remained at home have received enough food to satisfy their hunger. The young, in their unrestrained impatience, often go beyond the mere ritual of nose-thrusting and become aggressive, actually biting the adults in their lips or legs. It is this voluntary sharing of food that enables labour also to be parcelled out between those that hunt and those that undertake the vitally important duty of guarding the helpless young against marauders. It is extremely interesting to note that the males take a tremendous part in the raising of the young. On their return from hunting they make a point of regurgitating food for them in preference to the females; and, it was observed in one pack, that when, through death, no adult females were left the feeding and bringing up of the orphan pups was willingly and successfully undertaken by the males alone (Estes & Goddard, 1967).

No mother, therefore, is essential after the first short period of milk feeding. Care of the young, both in the steps taken to guard them and in the matter of seeing that they are properly fed, seems to play a dominant role in pack behaviour; for later in life when the young dogs reach the point of accompanying their elders on the hunt they are given absolute priority over the kill, all the adults retiring until the pups have first fully satisfied themselves. This, according to Kühme, is the only kind of precedence recognized within the pack.

This begging ritual at the homecoming has been extended to a similar, but unrewarded, greeting ceremony carried out between adult members of the pack in the early morning and late afternoon before setting out on a hunt, and especially between those about to remain behind and those who sally forth after food. Any of the young who attempt to take part in this ritual in which the adults formally register with each other their fellowship of the community are snarled or snapped away; and it is not until they are accepted without protest at this twice-daily ceremony of mutual recognition that they can be reckoned as fully adult members of the society.

In the course of their hunting, feeding and the ripping of their still living prey to pieces these dogs become well splashed and smeared with blood; but they take good care later to lick themselves quite clean. This is, of course, easier with their short, sparse bristle-fur than it would be had they the dense tangle of long fine underfur possessed by the foxes. In this type of pelage, too, there is less shelter for fleas and other ectoparasites; but, nevertheless, a good deal of time is spent scratching at their fur.

Like other dogs, these utter a variety of sounds according to mood or circumstances. Their most famous note is the oft-repeated bell-like "*hooo-hooo*" used as an assembly call, either to gather the resting pack together for hunting or, when quartering for game, a find has been made and there is immediate need to concentrate all forces on the line of assault. It is also used should a dog find itself separated from the others. The cogency of this call is indicated by the observation made by R. H. Kemp, noted above, that it was sufficiently compelling to induce a dozen dogs to abandon a newly-made kill without feeding. Although it is soft and musical it carries a very long distance, 2 or 3 km.

It seems that most of a chase is carried out in silence, but the dogs break into guttural or raucous yelps when closing in for a kill and emotion rises to a pitch. This becomes an almost bird-like chirruping at the kill. This last sound is uttered also at other moments of high anticipatory excitement such as when about to set forth on a hunt, or when mobbing hyaenas. The normal cry of alarm at possible danger is a growl breaking into a short, deep, harsh bark which, however, is not really much like that of a domestic dog. A softer bark is used as a greeting; and there is a good deal of whining as an accompaniment to begging for food.

Commonly, hunting dogs, leading a nomadic life, lie about during the day or sleep at night simply curled up on the surface in whatever slight cover the vegetation affords; but when it is a question of breeding, the whole life of the pack becomes centred round a burrow or burrows made in the abandoned holes of aardvarks, giant pangolins or other excavators. These underground shelters have not been described in any detail but appear to be lined with grass. Though their main purpose is for parturition and the protection of the young they may also be used by any adult as an occasional refuge against the midday heat or inclement weather or for sleeping at night. Not infrequently two or more bitches litter in a single earth (Brand & Cullen, 1967) or in closely proximate holes, either without quarrelling or with at most minor disagreement. Indeed, as part of the communal life and communal sharing out of food and duties they look after, and even suckle, one another's young.

The absence of precedence within the pack appears to extend to the matter of mating, the males not contending for the females as they commonly do in other groups. Coition takes place several times over a matter of a couple of days. The period of gestation is from 69 to 73 days; and there may be any number between 2 and 19 pups in a litter (Goodall), probably 7 or 8 being an average size. The pups, which weigh 350 to 380 grammes at birth, are suckled for from 10 to 12 weeks, their eyes opening between the 10th and 14th days. This is a tricky period and should anything happen to disturb the mother she may, as has been found many times in captivity, eat her young. If she is upset or thinks them in danger she carries them in her mouth from place to place. The presence of the male seems to be necessary at the period immediately following birth (Cade, 1967; Crandall, 1964). Crandall found, indeed, that the mother did not clean the new-born puppies, this being done by the male, whose active duties in connexion with the litter were then over. But though the close presence of the father becomes for a period unwelcome he must remain within easy distance.

From the time of the opening of the eyes onwards the pups, though very much centred on the nest, quit it more and more frequently and for increasingly longer periods. Much of the suckling, if not all after the first couple of weeks, is carried out above ground, actually in or not far from the entrance to the earth. During this act, which may take place either at the direct vocal invitation of the mother or in response to whining requests from the young, she may either lie down or stand. In the latter case the pups stretch up on their hindlegs steadying themselves with their forefeet against the mother's belly. Suckling sessions last only from 2½ to 3 minutes (Goodall), in sharp contrast to the lengthy bouts indulged in by young spotted hyaenas.

Though breast feeding is continued for nearly 3 months the pups are in fact given meat after about a fortnight. This is specially prepared for them by the female chewing to small size some of the meat she has begged from the returned hunters and regurgitating it for the second time for her offspring. The male parent, too, may take some part in this, as he does, now, in the general care of the litter. Gradually in this way the young are weaned until they take large pieces of flesh for themselves, regurgitated by the hunters; for from this stage the entire pack evinces a lively interest in the welfare of their next generation; and, as has already been said, should, through accident, no adult female remain the males competently see to the upbringing of the litter. The whole process of raising a family to the point where the young dogs can take care of themselves and join in the hunting occupies about three months. Throughout this period the breeding-ground is never, or only exceptionally, left unprotected, a varying number of dogs and bitches always remaining on guard duty while those in search of food are absent. During the period of upbringing the site of the home burrow is changed, over a short distance, from time to time, especially if any danger has threatened.

To do this, in the early stages, the pups are carried in the mouth to the new site, other females besides the actual mother sometimes assisting.

It is interesting to note that in order to escape very pressing danger a hunting dog has been known seemingly to feign death with complete success though it is not clear whether this was, in fact, merely very convincing acting or an actual coma brought about by an attack of very powerful domestic dogs that had been so closely pressed home as to cause real death, by worrying, of a companion. The hunting dog in question maintained its apparent demise though dragged over the ground for some distance, and for some further time after its aggressors had gone away and left it lying. Nothing is definitely known of the expectancy of life of these animals in their natural environment but one has been known to live in captivity to an age of about 10 years.

Taxonomy. It has already been mentioned, in connexion with the general description of the *Lycaon* pelage, that Matschie (1915) used the differing proportions of colours and their varying situations on the body to create a large number of independent species. The material on which this study was based was extremely limited for each of the separate species proposed; and the characters on which these species were based, moreover, were such as might be suspected as intrinsically inconstant. Further, apparent differences of size cannot be ascribed to entire populations on the strength of single skulls possibly of varying ages and of unknown background. Holz (1965), as the result of statistical study, which embraced skull measurements, came to the conclusion that there was absolutely no foundation for Matschie's proposals at specific level, and that valid separation even at racial level was doubtful as any distinctions appeared to be clinal. It is, of course, possible that, at some future date, given a statistically significant number of specimens from each of a variety of localities, some valid racial separation may become evident. But any present attempt to maintain such distinction on the basis of the few, mostly single, specimens that now exist seems to pretend to an understanding of the situation that does not, in fact, exist, and is without real meaning or value. Subspecific names are therefore ignored in this present work.

The accompanying table shows the measurements of the only two British Museum West African specimens, together with those two of Matschie's proposed species for which measurement data are given in his paper.

Table 4: Numerical data for *Lycaon pictus*

	Mani (Shari River) Type of *sharicus*	Lake Chad B.M. No. 1937.7.10.1	Djannaga (Togo) Type of *manguensis*	Kete Krachi (Togo) Type of *mischichli*
Vegetation	Sahel	Sahel	Sudan	Guinea
Number in mean	1	1	1	1
Condylobasal length	189	210	—	—
Basilar length	173	192	c.190	—
Palatilar length	88	98	—	—
Zygomatic breadth	122	135	125	128
Upper cheekteeth breadth	68	77	72	74
Nasals, length	67	71	65	76
Interorbital breadth	37	46	49	49
Postorbital constriction	37	42	—	42
Braincase breadth	69	72	69	69
Toothrow ($c - m^2$)	77	89	82	87
p^4 length	19·4	22·2	—	—
$m^1 + m^2$ length	21·5	25·6	—	—
m_1 length	22·5	27·8	—	—
$m_2 + m_3$ length	14·9	16·2	—	—
Head & body	900[a]	—	1150[b]	1130[b]
Tail	325[a]	—	375	410
Hindfoot	220[a]	—	200	215
Ear	c.90	—	120	125
RATIOS (per cent)				
Tail/head & body	36	—	34	36
Zygom. br./condylob. l.	64	64	—	—
Braincase/condylob. l.	36	34	—	—
Braincase/zygom. br.	57	53	55	54
Palatilar l./condylob. l.	46	47	—	—
Interorb./postorb.	100	109	—	116
$p^4/c - m^2$	25·2	24·8	—	—
$p^4/m^1 + m^2$	90·0	87·0	—	—
$m_1/m_2 + m_3$	151	172	—	—

[a]. As given on the labels; Thomas's type diagnosis figures differ.
[b]. These appear to have been taken from the prepared skin.

Family **MUSTELIDAE** Swainson, 1835

Polecats, Weasels, Otters, etc.

General. The Mustelidae constitute an important family of very wide distribution throughout the world except in Australasia, Madagascar and the polar regions, being most common in the northern temperate belt. The family contains animals with such well-known English names as polecat, stoat, ferret, mink, marten, badger, ratel, skunk, weasel, otter and others. These are carnivores of from very small to medium size, often with strikingly patterned coats and mostly with a greater or lesser degree of objectionable odour, the secretion of special glands, in some cases involuntary and constant, in others deliberate as a defensive act.

The mustelids may be terrestrial, arboreal, riverine or lacustrine; and there is an extralimital genus that lives in the sea. In general they have long relatively slender bodies and markedly short legs for their size; there are five digits on each foot, webbed more or less deeply and armed with claws that are non-retractile. Progression is, in African mustelids, mostly digitigrade. In the Mustelidae as a whole development of an aural bursa is variable; but as far as all the West African representatives of the family are concerned it is always absent. By nature these animals are fierce hunters, being responsible for the destruction of large quantities of small mammals and birds, and in some cases a certain amount of insects. To the great majority of Mustelidae any kind of flesh is welcome, preferably freshly killed by themselves but they will consume that killed by others if it is readily available, and even carrion if they are hard pressed. The main prey is rodents, hares, shrews and birds—in Africa up to the size of a francolin or the young of larger breeds. Eggs, too, are welcome, and, less commonly, reptiles and amphibians. More exceptional diets are found in the river-haunting otters, which live on fish, and in the ratel, which often robs wild bees' nests for honey and grubs.

Skull. The rostrum is short and blunt; there is no alisphenoid canal. There may be 32, 34 or 36 teeth, each of these totals occurring in West Africa. This is due to the different arrangement of the cheekteeth in the subfamilies: $\frac{3\cdot1}{3\cdot1}$ or $\frac{3\cdot1}{3\cdot2}$ or $\frac{4\cdot1}{3\cdot2}$. There are always 3 incisors and 1 canine, top and bottom on each side.

Taxonomy. Five subfamilies are now generally recognised (Simpson, 1945). The position, however, is by no means as straightforward and clear-cut as this might imply. Palaeontological evidence of affinities and present structural morphology are both complex and in the past the family has been grouped and regrouped in a number of different ways. Pocock (1921c) gave a useful summary of the variously held opinions between Gray in 1869 and the time of his own paper. In this last he assessed the differing views, gave an account of what he regarded as relevant external characters and evolved yet another, virtually independent, classification in which he recognised no less than fifteen subfamilies in respect of living forms alone. Simpson (1945) once more reviewed the position, in the light of both living and extinct forms; and, regarding Pocock's treatment as "excessively inflated", reduced the subfamilies of extant mustelids to the five now widely accepted.

Only three of these subfamilies occur in West Africa, the two that do not exist there being the Melinae (true badgers) and the Mephitinae (skunks). The three subfamilies relevant to this present work may be distinguished by the following key.

KEY TO THE SUBFAMILIES OF MUSTELIDAE

(Previous key page 28)

1. Dorsal pelage very long and with a well-defined longitudinal pattern of black and white bands; total length of skull under 70 mm; cheekteeth $\frac{3\ 1}{3\ 2}$. **Mustelinae** (*page* 93)

   Not like this 2

2. Fur coarse, the upper side typically whitish or pale grey from the crown of the head to the root of the tail (but this area often reduced or, not infrequently, entirely black like the rest or the pelage); claws of the forefeet very long and powerful; ears with no free external shell; skull with very little interorbital or postorbital constriction; bullae large and subglobular; cheekteeth $\frac{3\ 1}{3\ 1}$ . . . . **Mellivorinae** (*page* 110)

   Fur soft and sheeny; postorbital constriction fairly marked; bullae rather flat and subtriangular; cheekteeth $\frac{4\ 1}{3\ 2}$ (but p^1 often missing). **Lutrinae** (*page* 128)

Subfamily **MUSTELINAE** Gill, 1872

Polecats, Weasels, etc.

General. This subfamily contains most of the smaller mustelids, fulfilling the important function of holding the rodent population in check. They, of course, kill other prey too, mostly birds, insects and some reptiles. Their bodies are often long, slender and lithe, the whole effect being added to by an unusually lengthy neck; but in the African species these features are not so pronounced as amongst the European and American forms. There is no bursa on the ear pinna. The tail is short to moderate, that is to say at most never quite as long as the body; and it is sometimes showy. The pelage is often striking; and in the case of the mink (*Mustela*, subgenus *Lutreola*) is so much sought after as the most luxurious of commercial furs that it has become the subject of a flourishing farming industry and of selective breeding experiments directed to the production of distinctive colourings. Some members of the subfamily inhabiting the colder northern regions undergo a pelage change in the winter, the brown coat becoming white; in the case of the stoat (*Mustela erminea*) the tip of the tail remains black and the fur is much sought after on this account, most notably as a decorative trimming to official robes. Another well-known member of the subfamily is the ferret, a domesticated, and often albino, form of the Asiatic polecat, bred, and to some extent trained, as a hunting animal to flush rabbits or other subterrestrial species from their burrows.

The genus *Mustela* penetrates into the Mediterranean region of northern Africa;

but in so far as the true Ethiopian region is concerned there are three African musteline genera, *Ictonyx*, *Poecilictis* and *Poecilogale*, of which only the first two are found within the area dealt with in this present account. *Poecilogale* is essentially a southern African genus but extends as far north as Tanzania and parts of the Congo and Uganda; and there seems no obvious reason why this animal, which closely resembles *Ictonyx* in external appearance except for a far more slender body, should not have spread further westwards across the continent. The two genera with which, however, we are here concerned may be distinguished as follows:

KEY TO THE GENERA OF MUSTELINAE
(Previous key page 93)

White marking on the face continuous across the front; tips of the ears only very slightly white; total length of skull under 50 mm . . . **Poecilictis** (*page* 104)

White facial marking broken above the eyes; tips of the ears conspicuously white; skull 55 mm or more . . . . **Ictonyx** (*page* 94)

Genus **ICTONYX** Kaup, 1835
African Polecats

Zorilla Oken, 1816, *Lehrbuch der Naturgeschichte*, **3**, Zool. pt. 2: 51. Oken's work has been ruled to be unavailable by the International Commission on Zoological Nomenclature, Opinion No. 417 of 1956. This name is the Spanish *zorilla*, a diminutive of *zorra* a fox.

Zorilla I. Geoffroy, 1826, *Dictionnaire classique d'Histoire Naturelle*, **10**: 215. This name has been suppressed by Opinion 818 of the International Commission on Zoological Nomenclature and placed on the Official Index of Rejected and Invalid Names in Zoology with the Number 1912. (*Bull. zool. Nomencl.* **24**: 153–154).

Ictonyx Kaup, 1835, *Das Thierreich* . . ., **1**: 352. By Opinion 818 of the International Commission this name has been placed on the Official List of Generic Names with the Name Number 1759. Type species, by monotypy, as recorded in the same Opinion, *Ictonyx capensis* Kaup (= *Bradypus striatus* Perry). The name was compounded from the Greek *iktis*, *iktidos*, a weasel, and *onyx* claw, the latter referring to the strongly clawed forefeet.

Rhabdogale Wiegmann, 1838, *Arch. Naturgesch.*, 4th year, pt. 1: 278, footnote. Type species *Bradypus striatus* Perry, selected in Ellerman, Morrison-Scott & Hayman, 1953: 111. The name is from the Greek *rhabdos*, rod or wand, *rhabdotos* striped, and *gale* a weasel, referring to the pelage.

Ictidonyx Agassiz, 1846, *Nomenclatoris Zoologici Index Universalis*: 558. An emendation of *Ictonyx* Kaup in accordance with the Greek from which it was derived.

Ictonys Roberts, 1936, *Ann. Transv. Mus.* **18**: 228. A *lapsus calami* for *Ictonyx*.

This is a monospecific genus the description of which is, thus, adequately furnished by the account of the species which immediately follows. There has been very considerable, and heated, argument in recent years over the question of whether the name *Ictonyx* should replace the commonly used *Zorilla*. The matter, now resolved by Opinion 818, was a highly complex one the various aspects of which can be found by those interested set out in China (1962, 1965 and 1966); Van Gelder (1966); and Hershkovitz (1963 and 1966).

ICTONYX STRIATUS (Perry) African Striped Polecat or Zorilla

Bradypus striatus Perry, 1810, *Arcana or the Museum of Natural History*, part 11, pl. (41) and text. Cape of Good Hope. A note on the validity of this name is given by Hollister (1915); and the name *striatus* Perry has now been placed on the Official List of Specific Names in Zoology with the Number 2202. The name *striatus* is the Latin adjective meaning marked with channels or bands, given in reference to the dorsal pelage. The generic name is from the Greek *bradys* slow, and *pous* foot, meaning slow-footed.

Mephitis capensis A. Smith, 1826, *A Descriptive Catalogue of the South African Museum*, pt. 1, Mammalia: 20. No locality named. This generic name is the Greek word for a disgusting smell, and refers to the body odour.

Mustela zorilla β. *senegalensis* J. B. Fischer, 1829, *Synopsis Mammalium*: 219. Senegal. The generic name is the Latin for a weasel.

Mustela zorilla Smuts, 1832, *Dissertatio Zoologica, enumerationem Mammalium Capensium continens*, 12. Not *Viverra zorilla* Schreber (= *Spilogale*).

Mephitis africana Lichtenstein, 1838, *Abh. preuss. Akad. Wiss.* for 1836: 284. Cape of Good Hope, Senegambia, Abyssinia, Barbary.

Rhabdogale mustelina Wagner, 1841, in Schreber's *Säugethiere*, Supplement, **2**: 219. Cape of Good Hope. The specific name is Latin for weasel-like.

Zorilla striata var. *senegalensis* Gray, 1865. Senegal. Type in the British Museum, No. 50.7.8.38, [illegible]; skin good except for the terminal part of the tail probably missing, skull good.

Distribution and general. The African striped polecat is very often, both in literature and speech, termed the zorilla or zorille, sometimes zoril, a Spanish name having no real application to *Ictonyx*. The steps by which this came about are involved: but reduced to their simplest terms the position stems from confusion arising in the early 19th century between the African polecats and the central American spotted skunk (*Spilogale*), of rather similar appearance and of which zorilla was the local Spanish-American name.

This is one of the most striking of small African mammals, with its conspicuously banded black and white coat; but it must not be confused with the closely similar, though very much smaller, striped weasel which may occur in the same locality. When the animal is at rest in grass or other cover this bold pattern doubtless serves to disrupt its form and conceal its true nature; but such coloration is just as likely, in the open into which the animal must often enter, to act as a warning to rapacious birds and other beasts of prey, cautioning them to avoid attacking a victim capable of emitting a nauseating fluid. Conspicuousness in these circumstances is added to by the absence from this entirely black-bellied animal of the usual protective counter-shading.

Ictonyx striatus ranges over the drier zones of Africa from the Cape northwards to Sudan and Ethopia on the east, and thence across to Senegal in the west. It also occurs in South-west Africa and parts of Angola. This is an animal chiefly of the drier open woodlands, mostly (as far as West Africa is concerned) the Sudan and Sahel, but penetrating also into the Doka zone. It would seem to be pretty common in the southern and eastern part of its range; Shortridge (1934) characterises *Ictonyx* as one of the most ubiquitous mammals in Southern Africa, in all kinds of vegetation, down to the sea coast and even in town gardens. It also occurs up to 2000 metres on mountains. It seems to be much less common in the area dealt with in this present account—though this apparent relative rarity in West Africa may be due merely to lack of collecting. Only 5 skins and 5 skulls exist in the British Museum from this area: from Senegal (2), Farniso, Nigeria (2) and Zaria (Nigeria).

Description. The African striped polecat (fig. 12) varies a good deal in size, and such differences have been used, at least in part, diagnostically in the erection of local races. The males are generally held to be appreciably larger than the females; but this distinction is not evident in the scant data available for West Africa—one male skull compared with four females. The pattern of the pelage is broadly the same throughout the animal's wide range but the proportions of its component elements, that is to say black and white, vary, seemingly from place to place and so commonly constitute the major basis of proposed subspeciation. The length and quality of the fur also vary. In West Africa this polecat attains a head & body length of between 320 and 350 mm, the narrowly bushy tail being some 250 to 280 mm. The body is fairly, but not markedly, slender, and the legs short, the animal standing about 115 to 130 mm at the shoulder. The weight of an adult may be about 1 kg or sometimes a little more.

The dorsal pelage is fairly long and dense but loose in texture. It generally has a sheen. The underparts are considerably shorter and often sparser, sometimes almost naked over the belly and chest. On the back it may be regarded, purely for convenience of description of West Africa specimens, as basically white marked with three highly conspicuous longitudinal black bands. (The converse of this probably more accurately expresses the true position). The centre one of these black bands, running along the spine, starts from the crown of the head; the two lateral ones originating a little short of this, at the fore part of the neck. These three lines are here narrow (roughly 5 mm or less broad) and they run approximately parallel to not quite the middle of the back. There the two outer ones broaden somewhat (to roughly 12 to 15 mm) and diverge, curving outwards to the top of the flanks and then in again to the root of the tail, where they meet or nearly meet, thus enclosing a regular elongated ellipse. The medial black line continues its path to the tail through this white ellipse but at about the midpoint broadens into a black blob, roughly of diamond shape and 30 mm wide at its broadest point, then narrows again posteriorly, meets the two outer bands and continues on to the basal part of the tail. The sides of the neck, the shoulders and the entire underparts, together with the legs and feet are wholly black. The long-haired but nevertheless rather narrow tail is an intimate mixture of black and white, the latter colour dominating in West Africa (except in the basal 70 mm) though not always elsewhere.

The pelage is composed of long fine underfur and considerably longer and stouter bristles. These elements are self-coloured throughout, either all-black or all-white; and, in general, the two colours occupy clearly defined areas of skin without intermixing. But there are exceptions. Here and there one or more isolated pure white bristles occur amongst black patches; and sometimes there are small islands of white in the black areas; and, more rarely, in some (extralimital) specimens or forms, bristles coloured at the base and arising in the black areas, become, against the prevailing character of pigmentation, white in their terminal half. Such aberrations, and especially

Fig. 12. African Striped Weasel (*Poecilictus libyca*)
African Striped Polecat (*Ictonyx striatus*)

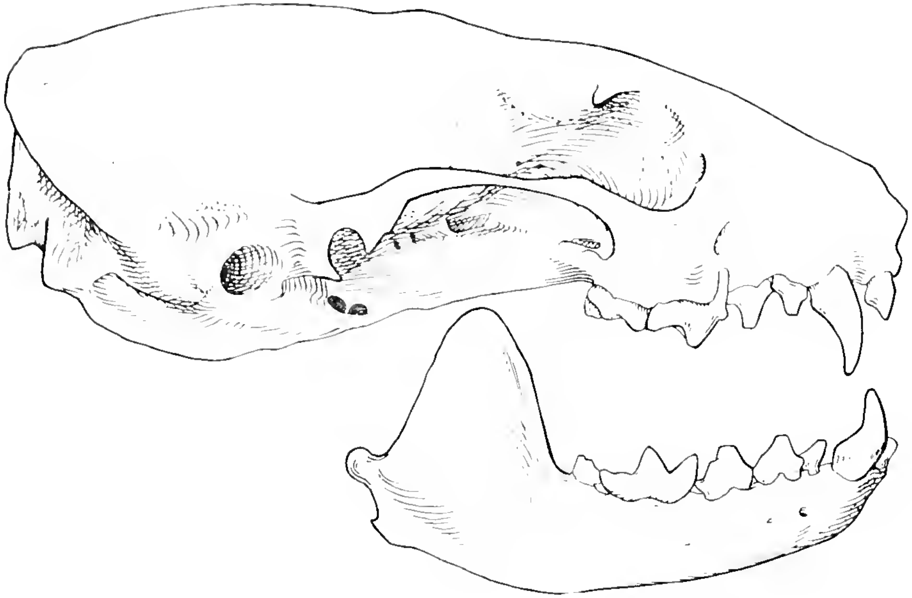


FIG. 13. *Ictonyx striatus senegalensis*: skull, Type, B.M. No. 50.7.8.38, ♂, 2: lateral view

this last, lead, in cases where they are more marked than others, to a certain blurring of colour and of marginal definition in the pattern. The five available West African skins are of uniform external appearance and can be distinguished from forms which occur elsewhere: and there would seem to be possibly a somewhat sounder foundation for local races in this species than is often the case. In West Africa the underfur is 18 to 22 mm long, the bristles 32 to 35 mm; but some of the solitary white bristles run up to 38 mm.

The head in this species is small for the general size of the body, shallow-skulled and narrow, the muzzle bluntly pointed. Basically, the whole face, chin and throat are black; but this is interrupted by very prominent white markings. These consist of a broad white patch which runs, on each side of the face from below the ears inwards to just above the outer corners of the eyes; separated from the inner limits of these is a central white frontal patch, lying between and backwards of the eyes. The separation, broader or narrower in different forms, is generally quite clear-cut; but in two West African specimens there is considerable tendency to unite—and thus, incidentally, obscure a distinguishing character between *Ictonyx* and *Poecilictis*. In some specimens the cheek patches spread below the ears a little onto the throat. The size and extent of the white facial markings have been used in racial diagnosis. The ears are small and semicircularly rounded, the top portion being narrowly but very conspicuously white. The forefeet are larger than the hind and are furnished with very long, deep, slightly

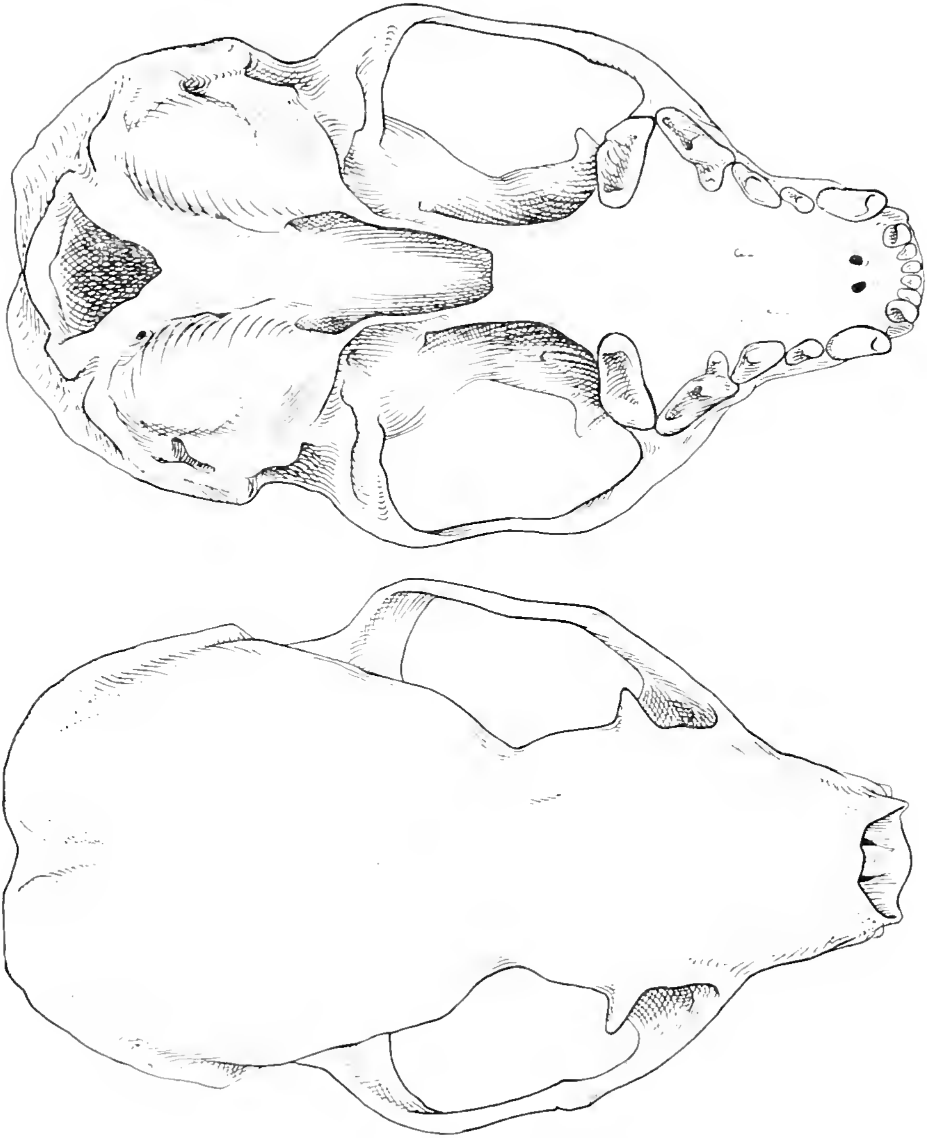


Fig. 14. *Ictonyx striatus senegalensis*: skull, Type, B.M. No. 50.7.8.38, × 2: palatal & dorsal views

curved claws about three times as big as those of the hindfeet. The soles of both fore and hindfeet are naked. Albinos are not uncommon.

Skull (figs. 13 and 14). This is very solidly built and it is rarely possible to detect, even in moderately young ones, any trace of the sutures since these become completely ossified from an early age. In form, the skull tapers from a fairly broad braincase to a remarkably short, blunt rostrum. There is very little or no sagittal crest but a well-developed supraoccipital one, often prominently framing the whole posterior part of the skull. There are narrow, sharply pointed postorbital processes, and there is a distinct postorbital constriction; but from this point forward there is relatively very little narrowing of the skull up to the widely open nares. The zygomatic arch is strong at both its anterior and posterior roots but decreases centrally to an unexpectedly slender, weak jugal. The palate is very broad between the carnassials and extends, after a sudden contraction, narrowly far beyond the toothrows. The bullae are, like the rest of the skull, very strongly built, long but relatively shallow, considerably strengthened posteriorly by overgrowths of the mastoids and paroccipital processes, and connected in front to the pterygoids by slender processes. The palatal foramina are small.

The dentition is reduced but compact and powerful. In the upper jaw the six incisors, deep from front to back, are closely set in a more or less straight transverse row, the outer one on each side larger than the middle four. The canines are not very tall but are strong. There are only three premolars on each side with no space between them or even slightly imbricate; p^2 is about half the size of p^3; p^4, the carnassial, is well-cusped, having also a small anterior hook on the cingulum. There is only one molar m^1; this is very narrow laterally but extends almost parallel-sided, well into the palatal region. In the manner of this subfamily it is deeply excavated between the outer and inner edges.

The mandible matches the upper jaw in its shortness and extreme strength of build, the rami being deep, solid and curved. There is very little angular process; but the condylar process appears unusually wide and strong. The straightly transverse incisors reflect those of the upper jaw in the compact solidity of their setting. There are three premolars and two molars. Of the latter, the carnassial, m_1, is very sharply cusped but m_2 is greatly reduced in size and is scarcely as big as the anterior cusp of m_1. It is, in fact, more or less functionless since on occlusion it lies posterior to the upper dentition, its front edge barely touching the rear margin of m^1. The dental formula is thus $\frac{3.1.3.1}{3.1.3.2}$ 34.

Habits. Considering how common *Ictonyx* is, at least in parts of its range, and how often it has been kept as a zoo exhibit or a domestic pet it is strange that so little is known of its way of life beyond the broad outlines. This is in some measure due to the fact that the striped polecat is mainly nocturnal, though it may sometimes be observed at dusk or dawn. During the day it lies up in holes in the ground, which it excavates itself with the aid of the long and strong claws of the forefeet. It also digs to get at sheltering rodents, such as gerbils, or at large insects. Besides subterranean burrows, *Ictonyx* takes advantage of naturally occurring shelters amongst boulders; and, in South Africa, it is well-known to live in, or in holes beneath, farm outhouses.

Striped polecats seem to live more or less solitary lives except at mating time when pairs are seen together. They live on rodents, hares, ground-squirrels and other small mammals, insects of the larger sorts, birds, eggs and probably lizards and frogs. They are said to be deadly enemies of even large snakes. Roberts (1951) records that these carnivores sometimes prove a nuisance to the field naturalist by following the line of his traps and consuming all the rodent specimens that have been caught. They not infrequently take up residence near villages or farms and then sometimes become persistent fowl thieves. However, they appear to be very easily trapped (Thomas & Hinton, 1923). The normal gait is a trot with the back slightly hunched; but observers differ as to whether the tail is held up or out. When chased by a dog the striped polecat can run fast. Though mostly terrestrial it can also climb into trees; and it is said to be able to swim well if forced to.

But *Ictonyx* does not always take to flight, or only for a short distance to where it may reach a rock, log or tree affording a slight eminence whence it may with greater advantage against a larger enemy bring into play its best known response to fright or attack. This is to present the rear quarters to the source of danger, lift the tail vertically and ejaculate fluid from the anal glands into the face of the enemy. This is not only nauseating in its smell but also very persistent and difficult to eradicate from fur or clothes even with washing. Roberts (1951) records having received a discharge full in the face. Apart from the sickening stink, this caused a painful burning in the eyes. He found that the application of benzine quickly neutralized the offensive fluid except, of course, in the eyes to which he was unable to apply the remedy. It gradually oozed from these throughout the night causing a continual renewal of the stench. This defensive action has, understandably, been most commonly observed as a reaction to chasing by dogs. These do not seem to be much put off at the time though it is said that once one has experienced the polecat's ejection it becomes chary of going into attack on future occasions. Such an effect is the essence of warning coloration.

All observers are agreed that as well as being, like most of its close relations, a very fierce hunter and killer, *Ictonyx* is correspondingly stout-hearted and tough in its own defence. It utters angry shrill screams and erects its hairs thereby doubling its apparent size. When pressed to its limit, and threats or anal glands have failed to deter the attacker, it feigns death, for half an hour or more, until it judges that the danger is past, when it gets up and trots off. There is an interesting manuscript note made by Sir Andrew Smith in his own interleaved copy of his Catalogue (1826) in the British Museum: "This is also called by the Farmers Duckatongat in consequence of the size of the anus—It is extremely tenaceous (*sic*) of life and will often after being bitten and shook by dogs for a long time and left apparently nearly dead recover and run about in a few hours as well as ever".

It may be added that after such an encounter the dogs would be completely unfit for admission to a house since they would inevitably be unbearably smelly. The coat of the polecat, too, would from force of circumstances be in a similar condition; but normally these animals are entirely without smell. Further, they are easily tamed, even if nearly full-grown when captured; and it is a remarkable fact that they then, under domestic circumstances, rarely if ever use their defensive odour. They become not only tame but actively friendly.

Despite their one-time common appearance in zoos few accurate observations seem to have been recorded of mating, gestation, number of young, and general behaviour in relation to bringing up a litter. It is said that there are generally 2 to 3 young at a birth, born naked and blind. A. J. Hopson (in a letter) thinks that in the Lake Chad area, where it is occasionally seen, the species may breed during the rains since young ones are to be observed from September to November. It is recorded that one lived for almost 5½ years in the London Zoo. A malarial parasite (*Plasmodium*) was recorded from one of five specimens caught in traps in Senegal (Leger & Bedier, 1923).

Taxonomy. It was stated above, in the opening of the account of the genus, that *Ictonyx* is monospecific; yet Roberts (1951) was convinced that there were four recognisable species in South Africa alone. He arrived at this conclusion largely from a consideration of the coloration of the tail: two, of differing but overlapping sizes, with the tail wholly white; one with the tail wholly black; and one with a white tipped black tail. These were further divided into races, twelve in all for southern Africa, on such characters as the relative widths of the black and white stripes, or whether the black stripes reached as far forward as the neck or the back of the forehead. It is doubtful whether the character of tail coloration is of a specific nature; and, indeed, Ellerman, Morrison-Scott & Hayman (1953) rejected it, suggesting that it was of no greater significance than the well-known phasal occurrence of black or white tails in the mongoose *Ichneumia albicauda*. They likewise attached no taxonomic importance to the alleged size difference, concluding that the genus consisted of a single species, *striatus* alone. These are matters extralimital to this present work, cited to show that the sailing in *Ictonyx* is not as plain as it might seem and that complete unanimity of opinion does not necessarily exist. In as far as they concern West Africa it may be said that the five specimens from this region in the British Museum do, in fact, correspond to Robert's external diagnosis of *striatus* and, in large measure, to the skull sizes he quotes for this.

The question of the validity of subspecies is quite another matter. It has already been said earlier that variety of pattern certainly exists, though it lies within fairly narrow limits; and though unquestionably a good deal of minor individual variation occurs some overall constancy seems to attach, at least broadly, to series from different regions. Significant differences of size also seem to occur. There, therefore, appear to be rather more satisfactory grounds for the recognition of local races in *I. striatus* than is the case with many other genera. A practical stumbling-block exists in the difficulty, the inexactness and the general inadequacy of verbal description. Such expressions as "much whiter above" or "black lines less clearly defined" convey little of positive value to either museum taxonomist or field worker devoid of a range of study material. A plate of comparative photographs is about the only really satisfactory answer to this difficulty.

One described race certainly and one possibly concern West Africa. Fischer's diagnosis of the first of these, *senegalensis*—half-a-dozen Latin words amounting to "with white marks, especially above, almost confluent with the flanks"—is an extreme illustration of the inadequacy of verbal description in relation to variations of such a pattern as characterises *striata*. Gray's (1865b) description of his *senegalensis* (in comparison with the South African form) is not much better: "White streaks broader leaving only very narrow dark dorsal ones; tail whiter." Nevertheless, it can be taken that a form conveniently identifiable as *senegalensis* does exist in West Africa from Senegal to at least Lake Chad; but whether some of the more easterly animals validly differ from it in pattern, though they possibly do in size, is open to question.

The second possible West African race, *sudanicus*, was described by Thomas & Hinton (1923) a male from Jebel Marra at 1200 metres, the pelage being noticeably longer than in *senegalensis*, the pattern, though broadly a good match, rather less intensely black, with the three parallel dark lines over the neck yet slimmer and far less distinct. It has been suggested (Dekeyser, 1955) that possibly this form may reach

Table 5: Numerical data for *Ictonyx striatus*

	senegalensis (West Africa)			*sudanicus* (Jebel Marra)
	♂	♀ means	Total range	♂
Vegetation	Sudan and Doka			?Sahel
Number in mean	1	4	5	1
Condylobasal length	64·8	62·6	59·7–66·2	66·5
Basilar length	58·2	54·1	53·1–58·2	60·0
Palatilar length	30·3	29·2	26·0–30·3	30·7
Zygomatic breadth	37·7	37·2	35·3–40·7	38·8
Upper cheekteeth breadth	23·2	24·0	21·7–25·2	21·9
Nasals, length	—	—	—	13·6
Interorbital breadth	17·0	17·3	16·0–19·0	17·8
Postorbital constriction	14·0	15·2	14·0–16·7	16·1
Braincase breadth	29·9	29·5	28·2–31·0	30·1
Toothrow (c—m^1)	20·3	19·8	19·2–20·3	20·0
p^4 length	7·2	7·0	6·9–7·2	6·5
m^1 length	3·5	3·1	2·3–3·7	2·9
m_1 length	7·8	7·3	7·0–7·8	7·2
m_2 length	2·3	2·6	2·3–3·2	2·8
Head & body	—	323	320–327	355
Tail	—	262	248–277	255
Hindfoot	—	51	50–53	58
Ear	—	25	24–25	24
RATIOS (per cent)				
Tail/head & body	—	81	—	72
Zygom. br./condylob. l.	58	59	—	58
Braincase/condylob. l.	46	47	—	45
Braincase/zygom. br.	79	79	—	78
Palatilar l./condylob. l.	47	47	—	46
Interorb./postorb.	121	114	—	110
p^4/c—m^1	35·5	35·3	—	33·0
p^4/m^1	206	226	—	228
m_1/m_2	339	281	—	257

from Jebel Marra as far west as Lake Chad; but in all probability it owes its shagginess of coat to its high altitude habitat and is therefore absent from the low-lying country between its type locality and Nigeria, and thus cannot be looked upon as being a contiguous form to *senegalensis*. It is omitted from the checklist of known West African forms given on page 1; but it might none the less turn up, discontinuously, on some of the West African highlands. The size of the only known specimen, the type in the British Museum, is not markedly different from *senegalensis*, as shown in the table on page 103. A slight difficulty exists over the comparison of sizes in this genus; the males are generally reckoned as appreciably larger than the females. There is only one male of *senegalensis* to compare with other reputed forms or with the four females in the British Museum. This last reveals no significant sexual difference, the type, a female, being almost as large as, or in some respects larger than, the male. This is shown in Table 5.

Ictonyx striatus senegalensis (Fischer) Senegal Striped Polecat

The description of this form may be taken as that given on pages 96 to 100. Specimens exist in London from Senegal (Thiès and unspecified), and from Nigeria (Farniso and Zaria).

Genus **POECILICTIS** Thomas & Hinton 1920

Striped Weasels

Poecilictis Thomas & Hinton, 1920, *Ann. Mag. nat. Hist.* (9) **5**: 367–368. Type species *Poecilictis libyca* (Hemprich & Ehrenberg) (*Mustela libyca* Hemprich & Ehrenberg) from Libya. This name is from the Greek *poikilos* vari-coloured or pied and *ictis* weasel, in reference to the black and white pelage.

Distribution and general. The striped weasels are, at least in West Africa, very closely similar in external appearance to the striped polecats though of much smaller size. For a long time the two were, indeed, regarded as congeneric; but there are certain small external and cranial differences which led Thomas & Hinton to erect for the weasels a separate genus. Seven species have at one time or another been named but these are all now regarded as either synonyms or merely forms of a single species *libyca*. The range of this, and hence of the genus, is restricted purely to the northern portion of Africa, from about 12° North, that is within the Sudan woodland zone, to a little short of the north coast from Morocco to Libya and lower Egypt. *Poecilictis* is thus essentially a dry or very dry country animal, about half-a-dozen local races being recognised. The general generic diagnosis and the points which distinguish *Poecilictis* from *Ictonyx* can be sufficiently gathered from the description of *libyca* which follows.

Taxonomy. Whether *Poecilictis* merits separate recognition from *Ictonyx* as a genus is open to doubt. There are a few small external differences of pattern and of such minor matters as hairy or naked soles. Thomas & Hinton, who erected the genus, characterised the *Poecilictis* skull as truncated, greatly expanded across the mastoids, and having hypertrophied bullae. Very little support for the first two of these is afforded by comparative measurement of the two genera. The bullae are indisputably larger in *Poecilictis;* but this alone cannot justify a genus or even a subgenus. Since its creation in 1920 *Poecilictis* has been accepted by most authors, including Simpson (1945) and Ellerman & Morrison-Scott (1951). However, Dekeyser (1955) rejects it—probably justifiably, though this course has not, in fact been adopted in this present work.

POECILICTIS LIBYCA (Hemprich & Ehrenberg) Striped Weasel

Mustela libyca Hemprich & Ehrenberg, 1833, *Symbolae Physicae seu Icones et Descriptiones Mammalium . . .*, decas secunda, folio k *verso*. Libya. *Mustela* was the Latin name for a weasel.

Rhabdogale multivittata Wagner, 1841, in Schreber's *Die Säugethiere*, Supplementband **2**: 221 f.n.; Supplementband **3**, pl. 133B. Upper Nile. The specific name is from the Latin *multum* much, many and *vitta* a band, with reference to the striped pelage. Valid as a race.

Ictonyx frenata Sundevall, 1843, *K. svenska VetenskAkad. Handl.* for 1842: 212, pl. 4 f.1. Senaar. The specific name is Latin for bridled, given in fanciful resemblance of the pelage pattern to a horse's harness.

Poecilictis rothschildi Thomas & Hinton, 1920, *Novit. zool.* **27**: 316. Farniso, Kano, Northern Nigeria. Type in the British Museum, No. 21.2.11.29, ♀; skin only, in good condition. This was named after Lord Rothschild under whose patronage and for whose museum at Tring this and many other specimens were collected by Captain Angus Buchanan. The skull, which was originally believed to exist, has never come to light.

Distribution and general. The little striped weasel (fig. 12) is not as wide-spread and is apparently much less common than its bigger relative the striped polecat. So far as is known its distribution is restricted to the edges of the Sahara and the contiguous arid zones from Senegal and Morocco in the west to the Red Sea coast in the east, but nowhere further south than about the 12th parallel. Both *Ictonyx* and *Poecilictis* occur in the same area—witness the British Museum specimens of each, caught at Farniso on the same day. Although, to judge from museum collections, the weasel is much less abundant than the polecat it is apparently locally common. Six of the eight West African specimens came from Farniso, five of them caught on the same day or almost the same day.

Description. Although the pelage pattern in *Poecilictis* is fundamentally the same throughout the species there is a wide difference of detail between forms from different localities. The description which immediately follows is therefore couched in broad terms, the finer points of diagnosis of West African animals being reserved for the later account of the race *multivittata*.

The striped weasel has a head & body length of from 200 to 280 mm and a long-haired, more or less bushy, tail of from 100 to 170 mm. It stands some 60 or 70 mm at the shoulder; but the fluffing out of the fur in excitement makes a good deal of difference of appearance in size. The pelage, which is composed of dense, fine, fairly straight underfur and abundant, much longer, stouter bristle-hairs, is of very diverse lengths in the various races, from moderately long to very long. The dorsal pattern is of dark blackish-brown and white. In West Africa it consists clearly of alternating longitudinal dark and white bands, closely recalling that of *Ictonyx*; but, though this is doubtless the basic pattern throughout the species, some of the extralimital forms have it so broken up into irregular spots and patches, and the dark so much overlain by the lengthy white hairs, that the resemblance to the striped polecat becomes relatively remote. In most cases the dark element is not so black as in *Ictonyx*. The underparts and legs, as in that genus, are very largely blackish, but there are generally a few rather isolated white spots, especially on the belly.

The facial markings offer a fairly constant distinction between *Poecilictis* and *Ictonyx*. In the former the white patch that runs across the front is continuous as a broad band from ear to ear instead of being interrupted above each eye as in the latter. (In one *Poecilictis* skin there is a very narrow interruption; and in a few *Ictonyx* there is a narrow connexion between the medial frontal spot and the lateral patches). In *Poecilictis* this white band is continued below the ears onto the chin where it forms a, usually, very conspicuous forwardly-pointing V. The upper lips in this genus are always more or less white; but the upper rim of the ears, unlike the polecat, has only very little white on it.

The tail is whitish, being covered with very long bristles which are broadly white at both base and terminal third, the medial band being dark brown. The claws of the forefeet are only slightly longer than those of the hindfeet, and thus offer no close resemblance to the long, strong claws of *Ictonyx*. The soles of the feet, too, differ from that genus in being hairy between the pads. There are well-developed anal glands capable of ejecting a malodorous fluid.

Skull (fig. 15). This, though in most cases of markedly smaller size, bears a very close overall resemblance to that of *Ictonyx*. The bullae are relatively larger, being somewhat more domed and, in absolute terms, almost as long as those of the larger animal.

Habits. Even less is known of this animal than of *Ictonyx*. Petter (1959) seems to be the only author to have observed and recorded these small carnivores in captivity. There are no field notes of any kind on collectors' labels. The general habits would appear to be quite similar to those of the polecat; the weasel is nocturnal, lives on small rodents, insects, eggs, young ground birds, and lizards; and it shelters throughout daylight hours in subterranean burrows. These it digs for itself in soft sand, either down into level surfaces, or straight into the sides of dunes. They are of very simple form, and for the purposes of breeding consist of a single gallery ending in a chamber which has been dug deep enough to reach compact soil. This chamber is left unlined, the young being deposited directly on the soil itself.

Once these refuges have been detected it is easy enough to dig out the inhabitants; but there is, in northern Africa, a strong prejudice against doing this because of the virtual certainty of being subjected to the ejaculation of nauseating fluid from the anal glands. Unlike the polecat the weasel stinks at all times without remission, a characteristic which places it in quite a different category as a domestic pet. Moreover, according to Petter its temper is quite unlike that of the friendly polecat; for, although living peaceably with others of its kind, his captive specimens proved aggressive to anyone who disturbed them. Handling was therefore difficult except that it was found possible to do so when the animals went to sleep since they took some time to wake up again. When angry, striped weasels erect their fur and growl or hiss.

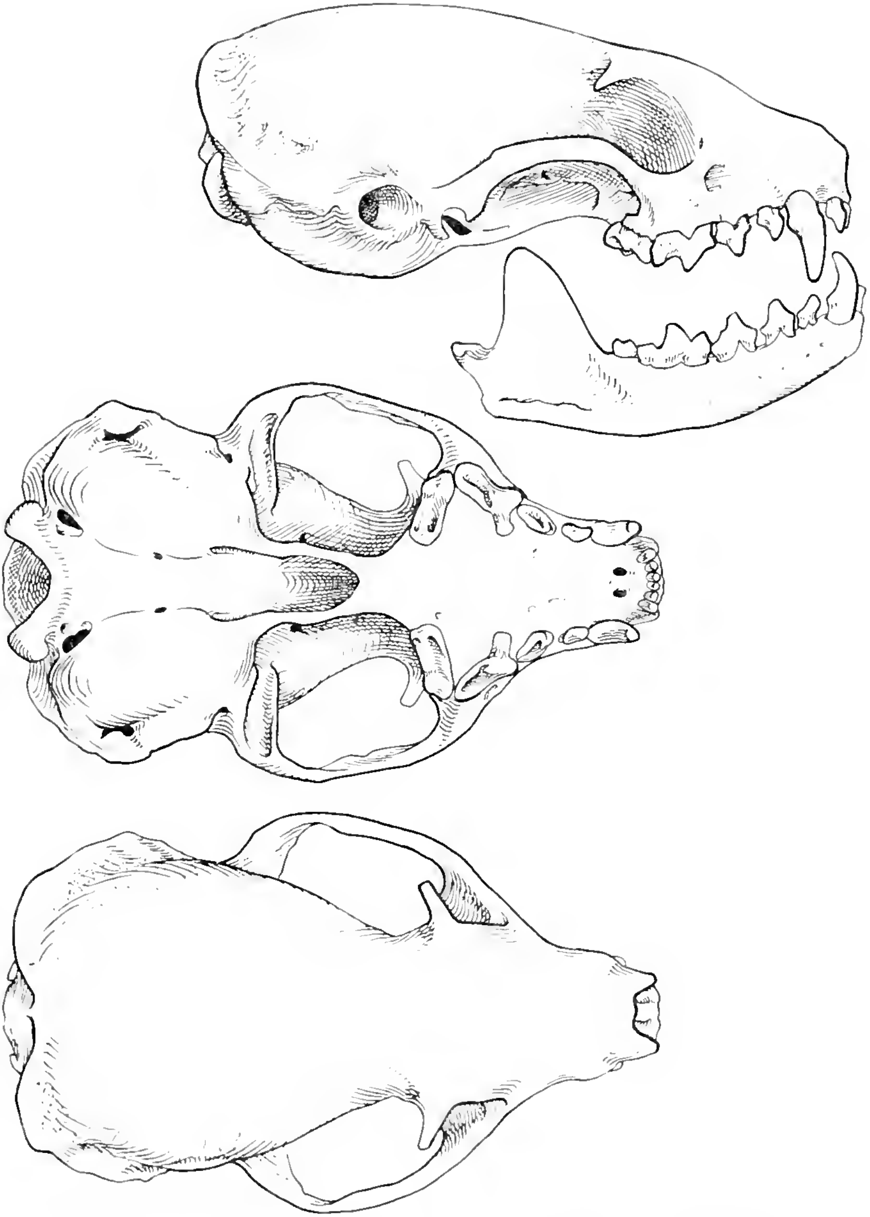


FIG. 15. *Poecilictis libyca*: skull, Type of *rothschildi*, B.M. No. 25.5.12.26, ♂, × 2

So far as is known, there are generally two or three young in a litter. It would seem that the period of gestation might be as little as 37 days, a remarkably short period, unique in carnivores; but this is by no means certain, and as Petter, to whom this observation is due, points out it might be as long as about 11 weeks. The young are born blind but their ears are not sealed down. They are not absolutely naked but are covered, except at the shoulders, with very short (1·5 mm) hair. Some very young weasels brought to Petter in Morocco were entirely covered with white hair, the skin being invisible. The dark pattern developed at about 3 weeks. It seems that the eyes open at about 3½ weeks. As so often happens when breeding conditions are not exactly right in captivity, the three young born to Petter's specimens were unceasingly carried from place to place by the mother until they died from this treatment. The adults, however, were still alive at the end of five years or more.

Taxonomy. Although all the forms now included in *Poecilictis* were originally described as independent species the genus has long been regarded by taxonomists as monospecific. There is a vast difference in size between North African skulls, from Morocco and Tunis, and the normal run of *libyca*. The same applies in a rather lesser degree to those from the Red Sea coast at Suakin; and there would seem to be a strong probability that two, if not three species are really involved, that is *libyca*, *vaillanti* Loche and *oralis* Thomas & Hinton. However, it is accepted here that West African specimens without doubt belong to the first of these.

Of the 7 named subspecies one, *rothschildi*, was created from West African material; and the 7 British Museum skins, all from practically the same restricted area, all clearly accord with Thomas & Hinton's diagnosis. But whether *rothschildi* differs validly, or indeed in any significant respect, from Wagner's *multivittata* is another matter. These authors do not make clear with what reputed *multivittata* specimens they made comparison for the purpose of their diagnosis; but it would seem fairly clear, from their references to the length and colour of the pelage, that they must have taken examples from the lower Nile as representing this race rather than from the upper Nile, whence Wagner had described it. For present purposes comparison has been made with three Sudanese specimens from Omdurman, Tuli Island (Khartoum) and Jebel Hadoza—those three specimens, in fact, which Setzer (1956) took as typical of *multivittata*. From these the West African specimens differ most obviously in one minor point: that in six out of the seven specimens there is a small, sometimes very small, black mark on the tail tip; whereas in the Sudan animals this, though detectable, is reduced to the blackening of the extreme tips of a few hairs. The frontal white band in Sudanese examples may be a trifle narrower; and possibly there is somewhat less white on the upper lips. But these differences are so slight and, with more material, may well prove inconstant that it scarcely seems worth while retaining two races. The table on page 110 shows that there is very little divergence of size between the West African and Sudanese specimens. This present account therefore rejects *rothschildi*.

According to Hoogstraal (1964) it seems likely that some races are less widespread than they used to be, and are even, through lack of adaptation to more severe competition, either extinct or on the way to becoming so.

Poecilictis libyca multivittata (Wagner) Southerly Striped Weasel

This form is found over a zone stretching from Senegal to the Nile, covering for the most part the Sudan and Sahel vegetation zones but extending a little south into the Doka woodland in Nigeria and a little north into the Subdesert in Sudan. How continuous its distribution is throughout this belt is unknown; but it must be locally common since Buchanan obtained four adult specimens on a single day at Farniso and another three days later. At the eastern end of the range specimens exist in the British Museum from Omdurman, Tuli Island (Khartoum) and Jebel Hadoza; while in the west there are 6 specimens from Farniso (near Kano), one from about 150 kilometres further north-west at Dan Kabba, and one (a skull only) from an unspecified locality, all these places lying in Nigeria. Dekeyser (1955) records the race from Aïr and the region of Timbuctu. It has been reported verbally as plentiful at Sokoto (Nigeria); but whether correct distinction was made between *Poecilictis* and *Ictonyx* is not certain.

This is a small form, the head & body some 200 to 220 mm, the tail about 100 to 130 mm. The pelage is of moderate length, but not nearly so long and loose as in Egyptian specimens. The underfur is about 10 to 14 mm long, the bristle-hairs some 15 to 25 mm, some of the very longest white ones running to 30 mm or more. The pattern of blackish-brown bands on white is very distinct. Starting from the back of the neck there are, as in *Ictonyx*, three parallel dark lines, separated, except sometimes in the case of the middle stripe, from the dark band extending across the crown. These dark lines are not so clearly defined as in *Ictonyx* and are, indeed, often confluent and always somewhat broader than those of *I. striatus*. At just before the mid-back they begin to diverge, as in that species, the outer ones in a very similar fashion, but sometimes broken up, curving in again to the root of the tail. But the middle one is quite different from *Ictonyx* since it divides into three, the median portion continuing in a direct line down the spine to the root of the tail, the two outer ones describing an ellipse roughly parallel to the two extreme outside stripes, joining together again about the level of the thighs. There are thus, at the small of the back, five dark bands alternating with white, not three as in *Ictonyx*. The dark colour is continued from the median stripe on to the base of the tail the rest of the tail being whitish, though obviously overlying a dark colour. This is due to the banding of the constituent bristle-hairs as described earlier. The tip has a narrow black mark, some 30 to 40 mm long, often much smaller, along one side.

The top of the head is blackish; the white band which runs across the face from side to side above the eyes is about 10 mm broad. It continues under the corners of the jaw forward across the throat to meet at a sharp angle at the chin. The upper lips are fairly broadly white, especially near the rhinarium; the lower lips narrowly so. The ears have only small white tufts at their extreme apices. The limbs are totally black; and so is most of the underside except for small irregular spots of white on the belly.

In some specimens the dark pattern is considerably overlaid by long white bristle-hairs so that it becomes greyed and relatively obscured.

Table 6: Numerical data for *Poecilictis libyca*

	"rothschildi" (West Africa)			*multivittata* (Sudan)	
	♂ means		Total range	♂ means	Range
Vegetation		Sudan		?Subdesert	
Number in mean	6	1	—	3	—
Condylobasal length	48·0	47·5	46·0–49·8	46·7	46·0–47·2
Basilar length	43·2	43·6	41·2–44·8	42·0	41·2–42·6
Palatilar length	20·2	21·0	19·3–21·6	19·5	19·0–20·1
Zygomatic breadth	29·2	27·9	27·7–29·8	26·2	26·1–26·4
Upper cheekteeth breadth	17·2	18·4	16·5–18·4	16·5	16·3–16·9
Nasals, length	—	—	—	9·7	8·2–10·9
Interorbital breadth	12·8	12·7	12·1–14·0	11·4	11·3–11·5
Postorbital constriction	11·1	11·0	10·3–11·7	10·2	9·6–10·8
Braincase breadth	22·4	22·6	21·9–22·8	22·3	21·8–23·0
Toothrow (c—m^1)	15·5	16·3	15·0–16·3	15·3	15·1–15·6
p^4 length	5·4	5·5	5·0–5·8	5·3	5·2–5·4
m^1 length	2·6	2·7	2·5–2·9	2·4	2·2–2·6
m_1 length	5·5	5·5	5·2–5·8	5·6	5·6
m_2 length	2·0	2·2	1·8–2·2	2·0	1·7–2·1
Head & body	200	215	204–222	210	—
Tail	105	121	96–127	135	—
Hindfoot	29	28	27–32	30	—
Ear	18	17	17–20	15	—
RATIOS (per cent)					
Tail/head & body	50	56		64	—
Zygom. br./condylob. l.	61	59		56	—
Braincase/condylob. l.	47	48	—	48	—
Braincase/zygom. br.	77	81	—	85	—
Palatilar l./condylob. l.	42	44	—	42	—
Interorb./postorb.	115	115	—	112	—
p^4/c—m^1	34·8	33·8	—	34·7	—
p^4/m^1	208	202	—	221	—
m_1/m_2	275	250	—	280	—

Subfamily **MELLIVORINAE** Gill, 1872

Ratels

This subfamily consists of a single living genus containing a single species; there is therefore little need to give any separate account of it. Further, only one fossil genus has so far been included here. However, at one time the ratel was, together with the striped polecat and striped weasel, included in the same subfamily as the skunks and the common European badger, the Melinae; but it is now generally recognised that there are obvious differences which are of more than generic standing. As far as the three African subfamilies are concerned it is easy to differentiate between the fairly bulky, stocky, harsh-furred animal now to be dealt with and the small, loose-furred, striped animals of the Mustelinae on the one hand and the sleek, aquatic Lutrinae on the other.

Genus **MELLIVORA** Storr, 1780

Ratels

Mellivora Storr, 1780, *Prodromus methodi Mammalium* . . . : 34 and Tab. A, Mamm. Type species *Viverra ratel* Sparrman (= *Viverra capensis* Schreber). This name is from the Latin *mel* honey, and *voro* to devour.

Ratellus Gray, 1827, in Griffith's *Cuvier's Animal Kingdom*, **5**: 118. Type species *Viverra capensis* Schreber. A Latinization of the Africaans name.

Ratelus Bennett, 1830, *The Gardens and Menagerie of the Zoological Society*, Quadrupeds: 13. Type species *Ratelus mellivorus* Bennett. A variant spelling of *Ratellus* Gray.

Ursitaxus Hodgson, 1836, *Asiatic Researches*, **19**, 1: 61. Type species *Ursitaxus inauritus* Hodgson, an Indian race. The name is from the Latin for a bear, *ursus*, and for a badger, *taxus*.

Melitoryx Gloger, 1841, *Gemeinnützige Hand- und Hilfsbuch der Naturgeschichte*, **1**: 57. Type species (as selected by Pocock, 1941, *The Fauna of British India* . . . : 454) *Viverra capensis* Schreber. The name is compounded of the Greek *meli*, *melitos* honey, and *oryx* a tool for digging, referring to the animal's habits.

Lipotus Sundevall, 1842, *K. svenska VetensAkad. Handl.*: 211–212. Type species *Ursus mellivorus* Cuvier (= *Viverra capensis* Schreber). This name is formed from the Greek *leipo* to be wanting, and *ous*, *otos* ear, with reference to the almost complete absence of any ear conch.

The range of the ratel is very wide: from Sierra Leone, upper Senegal and the southern fringe of the Sahara in the west, throughout most of the Ethiopian region to the extreme south of the continent; and across the Arabian peninsula and Iran to as far east as central India. Though most commonly an open-woodland animal it is known to occur from the high forest to the subdesert. Despite the vast area and variety of vegetation, climate and terraine involved in this, *Mellivora* is generally reckoned as monospecific: the characters of the genus, therefore, are implicit in the following account of this single species.

MELLIVORA CAPENSIS (Schreber) Ratel or Honey Badger

Viverra capensis Schreber, 1776, *Säugethiere*, pl. 125; and 1777, **3**: 450 and 588. Cape of Good Hope.

Viverra ratel Sparrman, 1777, *K. svenska VetensAkad. Handl.* **38**: 147. Cape of Good Hope. *Ratel* was the Africaans name.

Ursus mellivorus G. Cuvier, 1798, *Tableau élémentaire de l'histoire naturelle des Animaux*: 112. Cape of Good Hope. *Ursus* is the Latin for a bear; the specific name was derived from the Latin *mel* honey, and *voro* to devour.

Ratellus typicus A. Smith, 1833, *S. Afr. Q. Jl*, **2**: 83. South Africa.

Mellivora leuconota P. L.Sclater, 1867, *Proc. zool. Soc. Lond.*: 98, pl. 8. West Africa. The specific name is from the Greek *leucos* white, and *noton* the back, in reference to the striking pelage pattern.

Mellivora cottoni Lydekker, 1906, *Proc. zool. Soc. Lond.*: 112, pl. 7. Ituri forest, Congo. This was called after Major P. H. G. Powell-Cotton who secured the specimen.

Mellivora concisa Thomas & Wroughton, 1907, *Ann. Mag. nat. Hist.* (7) **19**: 376. Type in the British Museum, No. 7.7.8.62, ♂; skin and skull, both good. The specific name is the Latin adjective for cut off or short, given because the grey colour of the back does not extend as far as usual.

Mellivora signata Pocock, 1909, *Proc. zool. Soc. Lond.*: 394, pl. 61. Type in the British Museum, No. 9.7.19.1, sex ?; skin, good, and skull, good except for one nasal missing. The name is from the Latin *signo* to mark out, probably with reference to the white head and neck, contrasting with the rest of the pelage.

Mellivora buchanani Thomas, 1925, *Ann. Mag. nat. Hist.* (9) **16**: 190–191. Type in the British Museum, No. 25.8.12.27, ♂, juvenile; skin and skull, both good. This was named in honour of the collector, Captain Angus Buchanan.

Distribution and general. The ratel (fig. 18) is unique amongst African carnivores both in appearance and habits. As regards the former, it exactly reverses the usual mammalian colouring of dark on the back and pale beneath; and as concerns the second, it is the only flesh-eater that regularly sets out to procure honey as a major part of its diet. The extreme looseness and toughness of its skin are also out of the ordinary. This animal has therefore excited a good deal of interest in the past 200 years since accounts were first given of its habits. The distribution from extreme western Africa to India as a single species is also exceptional, almost rivalling that of the leopard. The often-used alternative name honey badger is not, like so many common English names, altogether inappropriate; for in its thick-set, short-legged body, its lumbering, flat-footed trot and burrowing habit it quite closely recalls the true badger of Europe.

Mellivora is a not uncommon animal especially in the more easterly and southerly part of its range. T. S. Jones (personal communication) characterises it as rare or rarely seen in Sierra Leone. In 14 years he never came across a skin; but he did, however, see a living animal crossing a road in car headlights about 50 km south of Njola in invasive woodland; and was told of other sight records at Bo and Mano. The ratel, indeed, is not often seen in the wild. This is because it is to a large extent nocturnal; and though it is sometimes active during daylight hours it seems to be pretty wary in this respect and generally to avoid exposing itself near human habitation. Nevertheless, in its commonest forms it is a striking animal even by moonlight, its silver-grey back picking up and reflecting the pale moonshine, the rest of the body being an indistinguishable shadow. This, of course, does not apply to the all-black animals which exist in the high forest, especially in West Africa. Whether these are representatives of a valid race or simply melanos is not clear and will be discussed later.

Description. Indeed, the animal could be regarded as fundamentally black, this colour being relieved by the intrusion of white over a greater or smaller area of the dorsal surface. In what is generally looked upon as the most typical form the whole upper surface from the forehead, just above the eyes, to the root of the tail is pale grey or even, at times, pure white. This pale colour extends as a broad parallel-sided band, the width of the head, across the crown and the top of the neck as far as the shoulders; it there broadens and curves down deeply over the flanks, narrowing again above the thighs, terminating at the rump or actually extending onto the tail. There is a sharp line of demarcation between this dorsal patch and the black, the latter covering the front and sides of the face, the forelegs, shoulders, lower flank, hindlegs and thighs. The entire underside is also clad with black hairs; but, except sometimes for the throat, so sparsely that the skin is clearly visible. However, this general picture is liable to a good deal of variation. Even at its most "typical" the colour is generally more intensely white over the head and neck, becoming more and more adulterated with black posteriorly. It is the diminishing of the white influence, always progressively from crown to tail, that gives rise to different "forms". Sometimes in these dorsal variations the divison between black and white is more or less clear-cut; in other cases the black is "frosted" with white, very lightly over the hindquarters, more densely over the shoulders and neck.

The pelage, though conforming throughout the species to an overall basic pattern, nevertheless exhibits some variety in the finer details of its composition. Two elements are present: abundant long, strong, straight, flat bristle-hairs, which dominate the pelage; and much finer, curly, terete underfur. Both are most commonly either all-black or all-white. The white bristle-hairs are approximately 0·15 mm in width, their length varying between 22 and 30 mm; the black are a trifle less broad, about 0·13 mm, but their length is generally somewhat greater and may, indeed, reach as much as 38 to 40 mm, especially on the lower back. There is, in fact, some tendency for the fur to lengthen from neck to rump. The underfur is conspicuously finer though, at 0·04 mm diameter, still pretty coarse by comparison with softer-furred carnivores. In the majority of cases bristle-hairs and underfur are of one colour throughout their lengths—all-black or all-white; but *signata* is exceptional in that some of the white bristle-hairs have black tips and some of the black bristle-hairs a white subterminal band, not sharply defined but about 5 mm broad.

The white areas of pelage may consist purely of white bristle-hairs and white underfur; but quite commonly the latter is black though, since it is short and well overlain by the white bristle-hairs it has little or no effect on the overall colour. However, when such an area is invaded by black bristle-hairs as well, the total effect is grey. The black areas are generally pure black; but sometimes there are scattered white bristle-hairs amongst it. The underfur is normally about 18 to 20 mm long and is generally relatively sparse and so plays little part in the overall texture or appearance of the fur; but in some cases it is distinctly more abundant, more undulate and much longer, reaching 24 to 27 mm. In the form known as *signata* the basal portion of the bristle-hairs, as well as the underfur, tends to curliness.

The body of the ratel is fairly long—some 60 to 70 cm—but distinctly thick-set and broad across the back. The skin appears to be remarkably loose; and many field observers have maintained that it almost seems as though it were independent of the body and that the latter could turn and twist freely inside it. The head, for this bulky body, is unqestionably small, rather flat, and with a short muzzle, the whole front of the face being black. The eyes are not very large; and the ears, though shaped and folded rather in the manner of human ears, have no independence of the head but appear as little more than ridges of skin. They have no bursa. The legs are short and sturdy, the animal standing some 23 to 28 cm at the shoulder. The feet have 5 toes each, armed with very strong claws, those of the hindfeet short, but those of the front remarkably long, the central three of much the same length (25 to 30 mm) and forming a unit connected by short webs, the 1st and 5th digits lying posterior to these. The soles are thickly padded and naked to the wrist, the posture being semi-plantigrade. The tail is short, naked below at the base but clad with long hairs for the rest, though narrow in form since these are fairly close-lying. The circumanal region is hairless; there are two very large scent glands situated within the anus and these according to Pocock

FIG. 16. *Mellivora capensis*: skull, B.M. No. 26.8.7.1, ♂, × ¾; lateral view

(1920) "discharge copiously a suffocating fluid exactly as in the Skunks . . ." There are two pairs of abdominal mammae in the females.

Skull (figs. 16 and 17). The specimens in the British Museum show, irrespective of age, a wide range of size and some variety of detail. All, however, are very solidly built; the sutures fuse at an early age, and in fully adult skulls quite literally leave absolutely no trace of independent bone structure. The braincase is relatively rather broader than in the dogs. There are slight, pointed postorbital processes but little in the way of interorbital constriction and usually not much postorbital narrowing, the frontal aspect running almost parallel-sided from the temporal region to the rostrum. The last is very short and broad, the nares widely open. The same applies to the posterior nares, the intervening nasal structure being finely complex indicating a highly developed sense of smell. The zygomatic arch is strong, the glenoid fossa deep. In fully mature skulls there is a slight sagittal crest which joins a very marked, though shallow, supraoccipital crest. The whole posterior aspect of the skull is one of firm solidity of build, including the foramen magnum and its adjacent condyles. The anterior palate is short and broad; posteriorly it continues, parallel-sided, well back of the toothrows. The bullae are large though not highly domed, and like the rest of the skull extremely strongly built, being fused posteriorly to large paroccipital processes. The mastoids are well-developed and prominent.

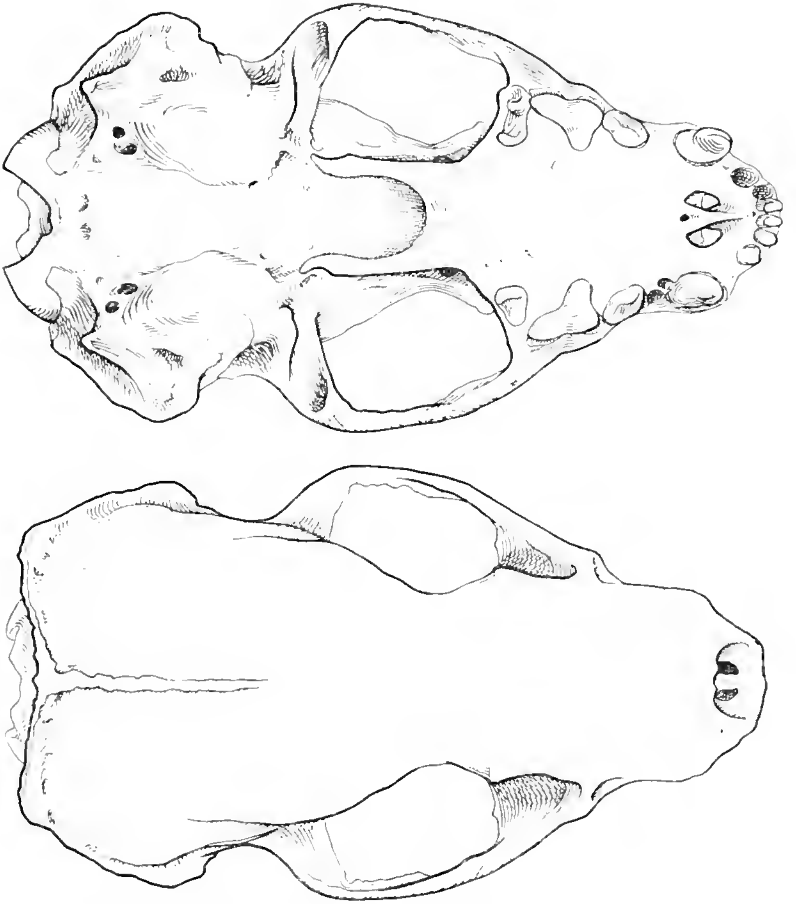


FIG. 17. *Mellivora capensis*: skull, B.M. No. 26.8.7.1, ♂, $\frac{1}{1}$; palatal & dorsal views

The dental formula is $\frac{3.1.3.1}{3.1.3.1} = 32$. The teeth seem often of rather irregular development, one or more being exceptionally small, set at an unusual angle, or lacking. The type of *signata* has a second lower molar on the left side but not the right. The carnassials appear to be slow to erupt; and in several skulls, even with well-ossified sutures, two sets of teeth exist, what is presumably a very adult-looking milk dentition being replaced by the final set. The cheekteeth are in the young skull very sharply cuspid; but, for an animal reputed to live to a great extent on relatively soft food, all the teeth seem to wear very badly. The incisors are often pretty irregular; but when properly developed form, top and bottom, a very compact, strong cutting unit, the upper ones being considerably larger than the lower, the outer pair in each case being somewhat bigger than the others. Though it is not always detectable, in the lower jaw i_1 is bifid, i_2 trifid, and i_3 generally unnotched, though it occasionally shows faint traces of trifidy. The canines are stout but, for carnivores, relatively short.

Habits. One of the foremost characteristics of the ratel is its extreme bravery and general toughness. It appears to be quite without fear, and when flight seems of no avail will turn savagely to attack man or any other creature. It can take any amount of punishment and is so tireless in combat that it has been known to exhaust and overcome far larger animals. Indeed, one is said to have killed a buffalo in the Kruger National Park. One of the things that makes it so difficult for dogs or anything else to deal with is the extraordinary toughness and looseness of its skin. The first makes it well nigh impossible for teeth to penetrate; the second enables the ratel, in spite of being held, to twist and turn so readily that it can inflict a fierce bite on any aggressor that has seized it in hand or mouth. Sikes (1963) found that the only safe grip was by the skin on the back of the head; anywhere else, including the scruff of the neck, was highly dangerous. How impenetrable the skin is is illustrated by an account given by T. Rawson-Shaw (in Fleetwood, 1958) in which he relates that blows from a matchet "which would have cut any other animal of that size in half merely bounced off, leaving a shallow gash on his hide, and it took about ten of these and four .22 bullets to kill it".

Others have found much the same; and it is commonly held that a direct shot in the head from a fairly powerful rifle is the only certain way of killing a honey badger. In the Bauchi area of Northern Nigeria it was well known that arrows and spears were almost useless and that the best, indeed reputedly only, way of certainly killing one of these animals was to club it over the back of the head. As opposed to these views the plain fact remains that though a few are damaged a very high proportion of the skulls in the British Museum have perfect craniums. In tussles with dogs it is usually the ratel that succeeds in sinking its teeth into its opponent, hanging on tirelessly, with jaws clenched like a vice, despite being banged on the ground or against trees or rocks, and finally, when the dog is completely exhausted, making off apparently none the worse for the experience. Sikes (1964a) found that, in play, a captive ratel being swung round hanging on to a sack actually appeared to enjoy being bumped roughly up and down on the ground.

Caught young, in fact, these animals take very kindly to captivity and become not only docile but actively friendly (Sikes, 1963 and 1964a; Hoesch, 1964). They are affectionate and very playful, even inventing games (Sikes, 1963). They recognise friends and voices, distinguishing various tones in summons, command, warning or reprimand. Hoesch's pet used to nibble in a restrained fashion at hands or clothes in friendship. But in captivity, as in the wild, ratels can with some abruptness work themselves up into an ecstatic fury. During such a bout the hair stands on end, the animal foams at the mouth and becomes almost literally blind to any external calming influence. Such moods, however, quickly vanish. Sikes (1964a) supposed that these rages, which of course are an invaluable reaction to aggression in the wild, were brought on or augmented by unusually large releases of adrenalin into the blood stream. Hoesch (1964) found his captive animal to be clean in its habits. Sikes (1964a) observed hers to urinate or defaecate into a suitable hole, which if not of approved size or shape would be industriously altered. The droppings were rarely covered. The scent emitted by ratels affects different people in different ways, some finding it extremely repulsive, others (Sikes) after a time not unpleasant. All agree that it differs from the ordinary musky smell of other mustelids.

Ratels are mostly solitary animals but may at mating time hunt in couples, or a mother may be seen with her two young ones. When not active in the search for food they shelter in holes, either in the ground, in tree trunks or logs, or amongst boulders or, in suitable country, in a cave. Earthen burrows may be dug by themselves, this being one of the functions of their powerfully clawed forefeet; but, like so many other subterranean dwellers, they make full use of aardvark holes, warthog dens or termite mounds. No account has been given of the extent or nature of these underground homes, whether they have side passages or any kind of lining. No one appears ever to have attempted to dig out a ratel; and, indeed, it can be gathered from the previous paragraphs that this might well prove a hazardous undertaking.

The ratel is generally recorded as being purely nocturnal, a reputation doubtless deduced from many a midnight raid on fowl houses and the fact that it seems to be relatively rarely encountered by day. However, not unusually it is active at dusk or at dawn; and in certain conditions it is undoubtedly on the move in full daylight. Probably these animals suit their habits to prevailing circumstances. In areas where they are liable to be much harassed by man they make constant use of the cover afforded by darkness; but in remote districts of low human population they probably become bolder. Certainly, captive in zoos, they find no difficulty in adopting a fully diurnal habit; and their known behaviour in connexion with honey seeking, detailed later, would seem to postulate pretty regular daylight activity.

When on the hunt ratels move at a steady jog-trot with the fore toes characteristically turned in. This at best is not so fast as a young man can run, and it has been often said that they can keep this pace up tirelessly; but this is nothing more than a guess hazarded on the leisurely nature of the gait and of the known general stamina of the animal. No one has, in fact, ever followed a ratel very far; as soon as it becomes aware of being chased, as it soon must on open ground where it can itself be seen, it makes for cover in undergrowth in which it is quite impossible to keep track of its direction. Nor have any experiments been carried out with marked animals to determine, without continuous observation, how far they travel. During the course of its hunting or other excursions a ratel defines or redefines its territory by means of its scent glands, squatting at intervals to press its anal region on the ground or against strategic trees or rocks. As no specific field investigation of the ratel has as yet been carried out the extent of the hunting range is unknown.

Despite the name honey badger these animals are by nature essentially carnivores, and the pursuit of food therefore concerns itself a good deal with flesh of various kinds. Almost certainly a hungry ratel would take any sort that came conveniently to hand, including carrion; but its normal range of food embraces small rodents, birds, eggs, insects, lizards, tortoises and frogs. Some, at least, of the rodents it may dig out from their burrows—gerbils, ground-squirrels and others; the birds are such as dwell and nest upon the ground or pay it frequent visits: francolins, bustards, plovers, quail, doves and so forth. Frogs, too, are sometimes dug up: Angus Buchanan (1926: 251), writing of the race of *Mellivora* from Aïr named after him refers to "a regular warren of holes scooped out in the night by a ratel in search of dormant frogs buried in the sand a foot or two beneath the surface".

Ratels have sharp, backwardly-pointing papillae on their tongues which enable them to deal effectively with tough foods. Tortoises present no difficulty to this animal which can readily crush the shells with its very powerful jaws. Snakes also are taken, including highly poisonous ones; and that they are not always of small size is shown by an extraordinary record in *African Wild Life*, 1964, **18** : 37 which tells of a ratel fighting, killing and feeding on a python some 10 or 11 feet long. The beginning of this exceedingly noisy and energetic combat was not seen, but the battle must have continued for some half an hour, at the end of which the snake "was so mutilated that it looked as if it had been run over by a train". The ratel has, at the Asiatic end of its range, earned a reputation for excavating yet another kind of food: inadequately buried human corpses. Though doubt has often been cast upon this, Pocock (1941 : 465) says that the truth of the belief has been proved beyond doubt. Like other small carnivores ratels welcome vegetable food such as berries and other fruits, roots and bulbs as a regular part of its diet. They inquisitively lift stones or tear flaking bark from trees.

The ratel's partiality for birds very often leads it into becoming a pest in farmyards or private compounds where domestic fowls are kept. Such is its strength and persistence that it is difficult to keep out. It has been recorded (Fleetwood, 1958) as ripping thick planks from a strongly built hen-house, or burrowing beneath stone foundations. A ratel is known to have climbed the mud wall of a hen-house to a small window covered with wire netting fastened down with staples, ripping this obstruction aside to gain entry. Another, unable to get in in any other way, tunnelled under the wall and up through the floor, which was paved with large stones set in mud mortar. The sturdy, muscular legs and long, strong claws of the forefeet enable tunnelling to be effected speedily even in hard ground. Once entrance has been effected to a fowl-house it often happens that everything inside is slaughtered and eaten, nothing beyond a few scattered feathers remaining. In one episode recorded by Fleetwood (1958) 17 Muscovy ducks were lost, and in another 36 half-grown pullets; and the same sort of thing has happened to many others. Rawson-Shaw, to whom these figures are due, reached the conclusion that a ratel may have an ancillary following of other carnivores, such as civets and jackals. For just as the lion's kill may soon be made use of by a waiting band of scavengers, so other less adventurous and able carnivores may well be at hand to take advantage of the courage, strength and determination of this pioneer burglar. It should perhaps be made clear that in many such cases it has been quite definitely proved, by shooting, trapping or other means, that it was indeed a ratel responsible for the entry and at least initial damage. It must be added that visits may be repeated on successive nights either until there is no further attraction or the raider has been killed. Sikes (1963) found that in captivity a young ratel would eat a whole dove, but that

FIG. 18. Ratel or Honey Badger (*Mellivora capensis*)

an adult requires a full-grown fowl. Skin, hair, feathers and bones of a victim are all eaten as well as the flesh. The food is held down by the forepaws.

But the food and the robbery for which *Mellivora* is most widely famed concern honey and wild bees' nests. Since about the middle of the 16th century, when a missionary priest wrote an account of Portuguese East Africa, one of the travellers' tales that must have circulated in Europe was of a bird that for its own ultimate benefit deliberately guided men, by song and a clapping of the wings, to stores of wild honey. It was not until some 200 years later, however, that this story was extended to include the ratel as possibly the bird's chief medium for breaking open the nests and laying bare mutually beneficial supplies of honey, wax and grubs. The story of this strange cooperation, if not symbiosis, between animals of otherwise quite different ways of life, and which set the natural history world wondering for two centuries, was due to the writings of a Swedish naturalist, Sparrman (1786, 2 : 180–181) who accompanied Captain Cook on his second voyage to the south seas and explored the interior of South Africa on the way back. His historic, though certainly not reliable, account make both amusing reading and a good starting point for the examination of this reputed partnership:

"The *ratel*, a sort of weasel or badger, by nature destined to be the adversary of the bees, and the unwelcome visitor of their habitations, is likewise endued with a particular faculty for discovering and attacking them within their entrenchments. His long claws, besides assisting him in digging the dark subterraneous passages which serve him for an asylum, are likewise of use to him in the occupation he is frequently employed in of undermining whole colonies of bees. Now, as a man placed at the mast-head can easiest descry a sail or land at a great distance about sun-set, so probably this time of the day is the most convenient for the ratel to look out for his supper; for he is likewise said to be particularly attentive to his business about sun-set, when he will sit and hold one of his paws before his eyes, in order to modify the rays of the sun, so as to render them inoffensive to his organs of sight, and at the same time to have a distinct view of the object of his pursuit; and when, in consequence of peering in this manner on each side of his paw opposite to the sun, he sees any bees fly, he knows that at this time they are going strait forward to their own habitation, and consequently takes care to keep in the same direction as that in which they fly, in order to find them. He has besides, as well as the Hottentots, the Caffres, and the peasants of the Cape, the sagacity to follow a little bird, which flies on by degrees with the alluring note of *cherr, cherr, cherr*, and guides its followers to the bees' nest . . .

"Those bees' nests which are built up in trees, are in no danger whatever from the ratel. In the first transports of his rage at having sought after these bees in vain, he uses to bite or gnaw the trunk of these trees; and these bites are sure marks for the Hottentots, that a bees nest is to be found up that tree. I should myself have entertained many doubts concerning all these properties attributed to the ratel, had I not obtained various accounts of this curious animal, entirely corresponding with each other, from many experienced farmers and Hottentots living in different parts of the country".

The bird to which Sparrman made reference is known as the greater honey guide (*Indicator indicator* Sparrman), a representative of a family, the Indicatoridae, comprising four genera, largely African but extending their range to Malaya and the East Indies. Nearly all of the eleven species are known to eat wax as part of their diet; and all, so far as is known, are parasitic, laying their eggs cuckoo-fashion in the nests of other birds. Some two or three species without question seem to guide, or to attempt to guide, men to bees' nests; but whether similar behaviour could in truth be related to ratels as well, as Sparrman had asserted, was not so clear. It so often happens in natural history that early held beliefs or superstitions, especially when they concern the unusual, are copied from work to work, year after year, without closer inquiry. They make good reading. Like others, the story of the ratel and the honey guide was incessantly repeated, both verbally and in written accounts; yet critical enquiry showed it to be nothing more than hearsay, no wholly reliable and competent observer ever having openly laid claim to actually witnessing the alleged behaviour. The story, in fact, might have been on a par with the pelican pecking its breast or the porcupine shooting its quills.

At length, however, Friedmann (1955), Curator of Birds in the United States National Museum, spent many years making an extremely interesting and detailed study of the Indicatoridae and their habits. He came to the conclusion that while Sparrman's account was in many respects inaccurate, the reputed association of the ratel with the honey guide was true. He arrived at this opinion only as the result of a great deal of sifting of old records and circumstantial evidence. No one has, in fact, ever witnessed a complete sequence of events from the initial attraction by the bird of a ratel's attention, through the stages of guiding, to the discovery and breaking open of a nest. It is merely that *Mellivora* and *Indicator* have been seen together in a number of isolated circumstances that are capable of being joined together into a coherent series of events. Whether the behaviour, either in its observed parts or presumed whole, has been correctly interpreted is altogether another matter.

Briefly, what takes place, with a ratel as with humans, is that the bird, perched not very high up on a tree, utters a great deal of unceasing chatter, *churra, churra, churra*, to attract attention; and having achieved this end flies, still chattering, a few yards ahead and settles on another perch. The ratel responds to this chatter with occasional grunts or growls. This is continued until within sound of a bees' nest the bird becomes quite silent. Such a course may cover a few yards or half a mile or more; and, correspondingly, a few seconds to half an hour. The route taken, except when extremely short, is never direct but circuitous, meandering or even criss-cross. Having arrived in the vicinity of a bees' nest the honey guide will remain silently perched quite patiently for a very long time until the store of honey has been laid bare and pieces of comb are left lying about to feed on.

This is no place to discuss in any detail the alleged guiding habits of *Indicator* except in so far as may be necessary to draw attention to the fact that the apparent co-operation between bird and mammal is not to be lightly accepted at its face value. The uncritical animal lover may all too easily follow others into a trap. When this apparent partnership was first reported it seemed to be nothing other than a case of an intelligent and hungry bird discovering a store of honey, seeking out a better equipped ally, and deliberately exciting this essential participant to curiosity and leading him or it to the mutually desirable spoil. All of this is very much open to question. It has been amply shown that hunger is not the operative excitant since birds exercise the guiding ritual even with full stomachs. It is very possible that there is, indeed, no deliberate seeking out of a helper but merely that the chance sight of certain animals leads to an agitated reaction in the birds. The complex path taken to reach an apparent goal suggests that no specific goal was actually in sight at the commencement but that by criss-crossing the bush over a sufficient distance a nest is eventually hit upon. It is a common fact that in much of the African woodlands there are plenty of wild bees of one kind or another and that by quartering the bush it is not excessively difficult even for a human being to discover some sign of a nest in a tree or a bank. There may, therefore, be no true guiding, the expedition being, in fact, little more than a voyage of mutual discovery.

If the bird stimulates the ratel to action with its chatter, the ratel in its turn keeps the bird in a state of excitement by responding from time to time with its deep growling grunt. African hunters who know this utter the same sound with a view to keeping the bird interested. Guiding does not necessarily take place to a nest well stocked with honey; it may be to an almost new one; and it is known that a long-deserted nest containing good stores of honey holds no attraction for the honey guide. It is the sight or sound of numerous bees that brings the bird to a halt and causes its chatter to cease. This is in the vicinity of, rather than actually at, the nest; but the assertion that the bird will, if necessary to an unintelligent helper slow in detecting the desired honey, go further and point to it with its bill is, as might be expected, nothing more than a picturesque embellishment.

These are some of the many aspects of so-called guiding brought out by Friedmann's classic study, which make it clear that it is not the simple purposeful act that early naturalists assumed it to be. A few other points may be glanced at in conclusion. Firstly, it is interesting to speculate on how this partnership between bird and beast evolved; what can have been the original stimulus, and the route by which it came to its present state. The co-operation serves no vitally essential purpose as it does in true symbiosis; honey badger and honey guide can each flourish without the assistance of the other. There are, indeed, signs that the habit is, from force of changing circumstances in modern Africa, on the decline. We are, in this present work, strictly concerned only with the habits of *Indicator indicator* in relation to the ratel; but it may be briefly added that it is possible that the bird occasionally leads baboons to honey, and may make, apparently wholly unsuccessful, attempts to interest other animals. A caution should perhaps be given that the course taken by the bird may not always lead the follower profitably to a bees' nest; for more than one man has found himself suddenly face to face with a dangerous animal. Such an occurrence, once regarded as deliberate on the part of the bird, is most probably a purely accidental outcome of quartering the bush in its search for a concentration of bees. Finally, for those who may find themselves in proximity to a noisily excited bird in the grass-woodlands, the greater honey guide is of moderate size, some 120 to 150 mm long with an additional tail of about 60 to 80 mm. Its coloration is variable with age, sex and other factors but in general is dark drabby or olive brown above, the wing coverts and some of the tail feathers white-edged, and with a small chrome-yellow bar on the shoulder. In the young the breast is bright yellow.

Sparrman asserted that the ratel was quite unable to climb and that bees' nests in trees were therefore unattainable. This is not strictly true. A ratel may not be able to climb up a surface that offers no foothold, or very far up a vertical smooth-barked trunk; but given a reasonably rough surface, and particularly one at a slight slope, such as so many open-woodland trees have, it is a pretty competent climber. A mud wall or a coarse-barked tree can be scaled with some ease; and any African bee farmer who fails to set his hive sufficiently high and along a sufficiently narrow branch is liable to find it robbed. Since a fair proportion of wild bees' nests are made in hollow trees this ability to climb is useful if not important. Ratels can climb wire-netting or expanded metal without difficulty, bite through wire, scratch and gnaw to pieces strong posts, and burrow through hard earthen or wooden floors so that a cage to retain a captive animal must be of very solid construction.

Little is known of mating or breeding despite the many specimens which have been kept in zoos. The gestation period, not very accurately determined, is said to be about six months. There are commonly two young at a birth, born blind. They are moved from place to place if necessary in the mother's mouth. They utter a plaintive whine. Details of development are unknown; but there are two or three records of ratels having lived in captivity for approximately 24 years. Hoesch (1964) found his tame animal to drink only rarely; but it used its drinking bowl for keeping cool.

Taxonomy. Since its first alleged variant was described in 1792 *M. capensis* has been something of a favorite for the naming of subspecies. G. M. Allen (1939) lists 11 currently recognised for Africa, and Ellerman & Morrison-Scott (1951) 5 more for Asia. No less than 5 races are, indeed, said to occur in West Africa. The points which have been taken into consideration in the diagnosis of races are the extent of the pale dorsal colour; its degree of whiteness of greyness; the annulation of, or absence of it from, the hairs; general size. Differences based on these are often clear enough in single specimens; but whether a variation has any constancy throughout a population and hence constitutes a valid local subspecific distinction can be established only by the existence of adequate material. Of the 12 West African specimens available in London from which to confirm the validity of 5 reputed races, 2 have no skins and are therefore racially indeterminable; and of the 10 remaining, only in three cases (Aïr, Tarkwa and Abenasi) is there more than a single specimen from a given locality. Of the 8 specimens which have skulls, only 4 can be regarded as mature; and of these, 2 are badly mutilated and incomplete. From such material it is quite impossible to reach any unequivocal conclusion.

In the matter of pelage pattern, it is difficult to believe that Thomas & Wroughton's *concisa*, with merely a small area of the white lacking from the lower back, is anything but a minor individual variation, the more so as signs of a comparable reduction is to be seen amongst skins from other regions. The possibility, though unlikelihood, of this occurred to the authors; but they held, if such did prove to be the case, that its smaller size was alone sufficient justification for their proposed race. As the type of *concisa* is a young male with quite unworn teeth, the sutures not fully ossified, and no development of crests, size comparison is scarcely a reasonable basis for argument. Size plays the major role, too, in Thomas's *buchanani;* but the type of this is quite juvenile, with unfused sutures, teeth not fully erupted with some of the milk dentition still in place. It is true that Thomas cited a paratype which, though described as a fully adult female with worn teeth, has skull measurements (as given by Thomas since this skull is no longer available for assessment) that differ only minutely from those of the juvenile type, as shown in the table on page 127. It is, of course, possible that the ratels of the inhospitable Subdesert, feeding largely on frogs and lizards, are truly of a smaller size; but argument based on present study material is not altogether convincing.

It is tempting, and not entirely unreasonable, to suppose that differences in the grey dorsal patch have little to do with locality and are nothing more than the sort of individual variation that one might expect in a pelage of this kind. But, looking outside West Africa to districts from which a much wider range of study material exists, there does often seem to be a strong overall uniformity in pelage coloration from a single area—as, for example, in the dozen skins from Somaliland. The argument, however, is weakened by the frequent ability to match patterns from widely separated regions, a striking example of this being a skin from Suakin on the Red Sea (No. 4.8.2.27) having a very distinctive pure white flank stripe precisely similar to one from Namaqualand in South-west Africa (No. 4.2.3.54). The *buchanani* skins vary somewhat amongst themselves; and when the reputedly mature female is put with the Somaliland specimens it is seen to differ very little from them except for size.

The situation might be explicable by the postulation of ecological rather than geographical races. This brings us to the consideration of *cottoni*, the all-black form. It has been suggested, and is very possible, that this is nothing other than a melano which, in the nature of these things, might turn up in any population. Yet the fact that the only 5 known *Mellivora* skins from Ghana are all of this type might suggest that the black coloration has some kind of racial connotation rather than that of an occasional mutant. The form was originally described from the Ituri forest, over 3000 kilometres away on the other side of the continent; and it is also known from Cameroun. The factor which these three regions have in common is high forest; and it would seem that *cottoni* might, indeed, be an ecological form typical of wet, closed-forest conditions. Yet this, too, would appear to be negatived by the fact that of Bates's 4 Cameroun specimens, 2 are all-black and 2 have very white backs presumably typical of *leuconota*. It is true that only one of these four specimens, a white one, is associated with a definite locality, Bitye; but practically all of Bates's mammalogical collecting was carried out in a restricted area of high forest. It is recorded also (J. A. Allen, 1924) that partly white forms (which, incidentally, appear from photographs to be excellent matches for the West African *signata*) occur in the Congo in the same region as the black form.

Age, too, may play its part in the question of blackness. The three black Ghana skins accompanied by skulls are all very old animals with extremely worn teeth; and Pitman, quoted in Shortridge (1934), expressed the opinion that "As the Ratel gets older the white patch on the back becomes gradually darker, until in some very old males it is only just distinguishable". On the other hand, if this were so one would have supposed that attention would have been drawn to the fact in connexion with the several specimens known to have lived in zoos to a ripe age.

The situation, therefore, is confused. The present writer is of the opinion that many of the variations of pelage are purely individual and may turn up in widely separated places though there is possibly a tendency for some to be commoner in certain ecological conditions than others. They are, thus, rather "varieties" than regional or truly ecological races. They are retained herein as such and described below for what they are worth.

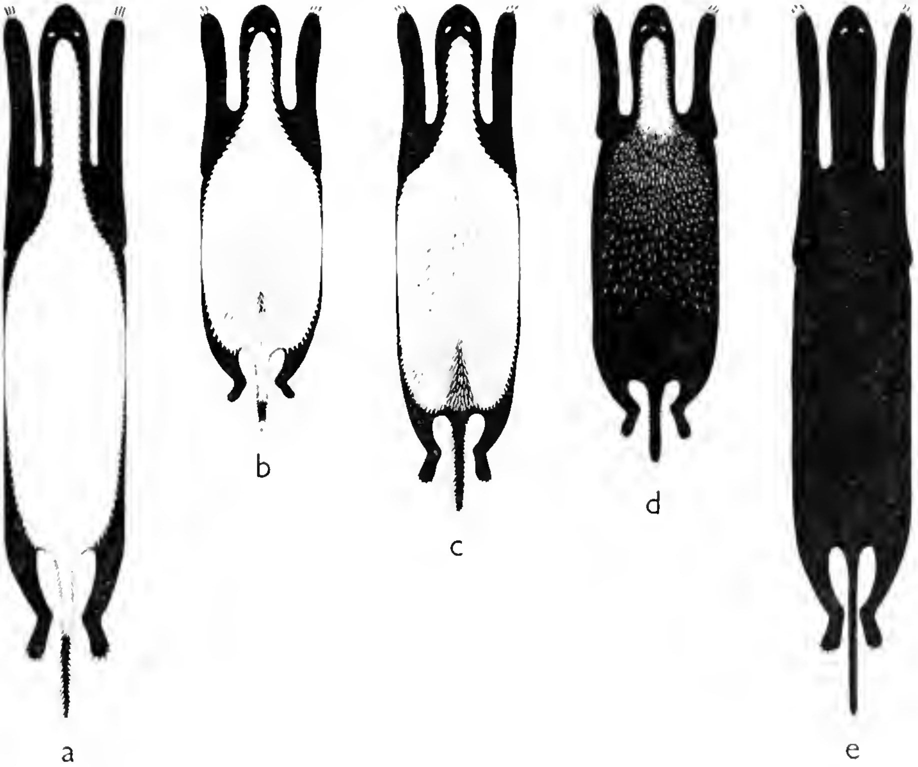


FIG. 19. *Mellivora capensis*: dorsal coat patterns, showing the extent of white in the various forms: a. *leuconota*, b. *buchanani*, c. *concisa*, d. *signata*, e. *cottoni*

A table showing such measurements as are available for West African specimens will be found on page 127; but since for the reasons given above these figures necessarily embrace a mixture of ages from juvenile to very old they are not reliably comparative. The diagrams in fig. 19 will aid in the identification of the different forms; but there seems no reason why all manner of intermediate patterns should not turn up.

Mellivora capensis leuconota P. L. Sclater White-backed Ratel

This was originally said to come from "West Africa" without closer definition; but it has since been held (e.g. G. M. Allen, 1939) to range from southern Morocco to the former French Congo. No specimen definitely identified as *leuconota* occurs in the British Museum; but it is to be assumed that two of Bates's Cameroun specimens, one from Bitye, are this form. Though only the apparently smaller of the two has external measurements (given on page 127) it appears to rank among the largest of all ratels.

In this form the entire upper side from the face to half way along the tail is pure creamy white with a minimal and almost undetectable admixture of black hairs. The white hairs may have narrow black tips, but these, again, are almost invisible.

Mellivora capensis cottoni Lydekker Black Ratel

This form occurs in the high forest, or at its edge, in various parts from at least Ghana to the north-eastern Congo. The known West African specimens all come from Ghana: Tarkwa, Abenasi and Oda.

As its name implies this form is typically entirely black though some skins have an extremely small number of scattered white bristle-hairs only detectable on close inspection. But there is one exceptional partial skin from Abenasi in which there is an even scattering of white or white-tipped bristle-hairs throughout the whole of the deep brown, rather than black, dorsum. The coat is thin and harsh, but the whitish hairs become rather denser over the top of the head.

Mellivora capensis concisa Thomas & Wroughton Lake Chad Ratel

Only one specimen of this is known, from Lake Chad, but it is almost certainly only a minor variant of the ratel that occurs eastwards throughout the Sahel and Sudan zones, as far as Somaliland and there called *brockmani* Wroughton & Cheesman. The dorsal coat consists of a preponderance of very long pure white bristle-hairs amongst long fine black underfur and a minority of black bristle-hairs. The feature which is held to distinguish *concisa* is the fact that, for all practical purposes, the white bristle-hairs are entirely lacking from an area starting on the spine at about the small of the back and broadening a little to the tail, which is also all black.

Mellivora capensis signata Pocock Speckled Ratel

The type, from an unspecified locality in Sierra Leone, via the London Zoo, is the only specimen known in the British Museum; but according to Monard (1940) the race occurs at Catio, Portuguese Guinea. The characteristics of the type are that although the pelage is the normal dense white over the crown, the pale colour starts to thin out over the neck and shoulders, and continues thence to the rump only as scattered white "ticking" amongst essentially black fur; and also that the white in this part of the coat is not due to wholly white bristle-hairs, as in other forms of ratel, but to subterminal white annulation of otherwise black bristle-hairs. The "ticking", already scanty, fades out entirely just forward of the rump, the whole hindquarters and tail being completely black. The skull has an extra lower molar (m_2) on the left side.

Mellivora capensis buchanani Thomas — Aïr Ratel

The question of the small size of this form, known only by three specimens from Elmeki River and Tarrare River in Aïr (Subdesert), has been discussed above. Apart from this matter of size it is doubtful whether this form differs essentially from the Sahel and Sudan zone ratels referred to above under *concisa*. It is a little whiter over the head but this may be due to the young age of the specimens now to hand. For the rest, it is essentially a grey-backed form, the pelage being an intimate mixture of long pure white bristle-hairs amongst fine long black underfur and a fair proportion of black bristle-hairs. The white mixture spreads to the basal part of the tail, one of the specimens having a small white tip as well.

Table 7: Numerical data for *Mellivora capensis*

Vegetation	*leuconota* (Bitye) Forest	*cottoni* (Ghana) Forest	*concisa* (Type: Lake Chad) Sahel	*signata* (Type: Sierra Leone) ?Forest	*buchanani* (Type & paratype: Aïr) Subdesert
Number in mean	1	3	1	1	2
Condylobasal length	—	142·3	134·8	125·8	108·5
Basilar length	—	129·8	120·7	120·1	97·2
Palatilar length	(67)	59·1	57·5	52·2	46·3
Zygomatic breadth	87·0	81·1	71·0	66·7	62·3
Upper cheekteeth breadth	49·1	49·2	42·9	44·0	38·6
Nasals, length	25·2	—	23·4	23·7	21·6
Interorbital breadth	36·7	35·6	30·5	29·6	29·2
Postorbital constriction	30·3	30·5	32·1	28·5	30·2
Braincase breadth	—	66·3	58·1	58·5	52·8
Toothrow (c—m^1)	41·8	40·7	38·8	33·5	32·5
p^4 length	14·4	13·5	12·6	13·0	11·0
m^1 length	4·3	4·1	4·3	4·2	4·2
m_1 length	15·4	(13·9)	14·4	13·0	12·1
Head & body	840	736	590	—	489
Tail	240	240	156	—	140
Hindfoot	135	120	95	—	85
Ear	40	35	19	—	29
RATIOS (per cent)					
Tail/head & body	29	33	26	—	29
Zygom. br./condylob. l.	—	57	53	53	57
Braincase/condylob. l.	—	47	43	47	49
Braincase/zygom. br.	—	82	82	88	85
Palatilar l./condylob. l.	—	42	42	42	43
Interorb./postorb.	121	116	95	103	97
p^1/c—m^1	34·4	33·1	32·5	38·8	33·8
p^4/m^1	335	329	294	310	262

This is one of the few specimens with any field notes: according to Buchanan it burrows for deeply buried frogs, the stomach being found to contain remains of these and of lizards.

Subfamily **LUTRINAE** Baird, 1857

Otters

Distribution and general. The third and last West African subfamily of the Mustelidae has a wide distribution not only throughout much of Africa but also in North and South America, and in Asia to southern China, Japan and some of the larger East India islands. Five or six genera, covering a score of species, are recognised, all of them at least semi-aquatic, mostly riverine or lacustrine, but one, *Enhydra* Fleming, marine in the northern Pacific Ocean. Two of these genera occur in Africa, including the region dealt with in this work.

Vegetation is of little moment to the otters. They occur in all kinds, their main criterion for existence being the availability of ample stretches of water harbouring adequate supplies of fish and other food materials, and preferably fringed with enough plant growth to afford secure cover. This last, however, is not absolutely essential, for they are sometimes found along relatively open stream-banks. Otters, thus, mainly frequent rivers, lakes, swamps and, since they do not object to brackish water, estuaries and tidal creeks. This does not mean that they are to be found everywhere in such situations; for they are for the most part shy, generally confining themselves to quiet localities little frequented by humans. For this reason there are large stretches of potentially suitable water quite devoid of these animals. In West Africa otters are known to range from Senegal to Cameroun and from Lake Chad to the mangrove swamps. They appear to be commonest in the rain-forest, but there are not a great many study specimens from which to draw more than very general conclusions regarding either abundance or distribution. More than one species may exist in a single locality.

Yet though they are largely associated with and mainly dependent upon water it must not be thought that they are in any sense wholly aquatic. Otters, indeed, spend a good deal of their lives on dry land, coming ashore to eat, to sleep, to defaecate or urinate, to breed or merely to indulge in play. More surprisingly, they occasionally, and for no very obvious reason, travel long distances overland and may be unexpectedly come across many miles from water, sometimes at night picked up by the headlamps of a car.

Description. Otters vary a good deal in size. In West Africa they may range from a weight of about 3½ kg to one of five or six times as much. Similarly the head & body length may range from some 60 cm to nearly 100 cm with, in addition, a tail of roughly half these lengths. But even the largest of these is small in comparison with some extralimital species, one from the Amazon basin being said to attain a weight of nearly 35 kg. The very short-legged body is long and beautifully streamlined in shape, increasing gradually in diameter from head to hips. It is intensely muscular and solidly built but extremely lithe. Indeed, the extent to which an otter can, and regularly does, flex its body in all directions must be seen to be believed.

The head is broad, short-muzzled and markedly flat; the neck of approximately equivalent diameter. The facial vibrissae are an extremely pronounced feature, long, strong and abundant. There is a tuft below the chin and particularly large tufts on the lower cheeks. The rhinarium differs in size and shape in the various species, being quite diagnostic (Pocock, 1921b); the nostrils are usually widely flared on land but are capable of closure on submersion. The roundish eyes are of moderate or even small size; yet, by their wide-open brilliance and large round pupils, they contrive to be a very conspicuous feature, even at night when they pick up and reflect light from the *tapetum lucidum*—in varying colours, ruby-red, emerald-green or amber according to species (Harris, 1968). The oval ears are small, set well down and back on the side of the head, and are devoid of any bursa. They, too, can be sealed by the closure of two lips during diving. The tail, in hunting circles usually termed the "pole" or "rudder", is a very notable structure. It is roughly half the length of head & body, often rather more or sometimes slightly less, highly muscular, thick and compressed dorso-ventrally at its base but tapering thence continuously to a narrow tip, thus completing the overall streamlining. The short legs are powerful, the paws terminating in five digits, both front and rear. These are webbed to a greater or less extent, in some species to the extreme tips of the digits, in others to only about half-way or less. In the most typical otters the toes are armed with fairly powerful, sharp, non-retractile claws; but in a few, including two of the West African species, the so-called clawless otters, there is nothing beyond small vestigial nails, and even these are absent from the majority of the digits. The palmar and plantar pads are various in shape, sometimes rather poorly developed (Pocock, 1921b). The hind feet are always larger than the forefeet.

On the underside of the tail, near the root, there are paired scent glands which abundantly exude a quantity of milky fluid with a powerful musky odour but not so repulsive as that of some other mustelids such as the polecat. Their purpose seems to be rather for recognition and the demarcation of territory than for defence. Females may have, at most, three pairs of mammae, abdominal and latero-pectoral, but some of these are often lacking or obscure.

Otters are noted for the character of their pelage. The fact that this is dense and handsome has given it some commercial value, both locally and in the world fur trade, with consequent adverse effects upon the survival of various species. The colour differs, of course, in the different species but in general is, dorsally, lighter or darker sepia-brown, though it is in some cases distinctly pallid, and pure white areas occur in others. Albinos are known. The dorsal fur is sometimes slightly "frosted"; and it always, even when quite dry, has a sparkling sheen. This is due to the composition of the pelage, which is remarkably constant throughout the genus. It is short, of unusually uniform length over the entire body, as much below as above; very soft to the touch and exceedingly dense. The hairs are of two kinds. The short, crinkled underfur, about 8 mm in length, is extremely closely packed and is of outstanding slenderness, being, at 0·01 mm diameter, amongst the finest of all hair. Despite this, its surface, seen under high magnification, is rough with long and relatively coarse scales. In the majority of cases it is white for most of its length but becomes lighter or darker brown near the tips, so that if an otter's coat is rubbed up the wrong way it is seen to be white-based – rather surprisingly since the extreme density of the fur normally completely obscures what lies below the closely-packed tips.

Mixed amongst this crowded underfur stand much longer hairs, by comparison widely spaced yet in sum forming a continuous coat that entirely overlays and conceals what lies beneath. These bristle-hairs, which are 16 to 18 mm long, are very slender and whitish in the basal half so that they are there indistinguishable by eye from the underfur; but beyond the reach of this latter they expand into a thick, usually densely pigmented blade. This is not concavely guttered as in some mammals but has a slightly convexly oblong section; and though by comparison with the rest of the fur relatively broad, it is, in fact, only about 0·1 mm wide with a length of some 6 or 7 mm, tapering terminally to a sharp tip. It is these blades that glisten and give the coat its characteristic sheen. Because of their long slender stalks the hairs have nothing harshly bristly about them. In the newly-born otter, at least in so far as the West African *Lutra maculicollis* is concerned, the pelage is quite different. There is no sign at all of dense underfur, the coat being almost entirely composed of long, straight, rather wiry hairs. A somewhat older specimen of *Aonyx capensis* shows the development of the dense coat well under way but the ultimate outer cover of glossy bristles only beginning to be visible amongst the, as yet longer, wiry baby hair. It is possible that the reluctance of young otters to take to the water may be due to the inadequacy of their protection against cold.

The composition of the belly fur is precisely similar to that of the back; and, what is more unusual, so is that of the tail too. It has been said that this pelage is waterproof; but though this is not absolutely true, it is a fact that the tightly packed underfur renders its penetration by water extremely difficult, and the hard, glossy bristle-hairs, though they bunch together when wet, are very rapidly dried out. An otter gets rid of the water in its coat not so much by vigorous shaking, as a dog does, but more by rolling or rubbing against a dry surface. This is possibly because its legs are too short to give itself a really effective shake. It may be added that the skin of an otter is tough, rather like that of a ratel; and similarly it is also pretty loose so that the animal can twist and turn dangerously if held by it.

Skull (figs. 20, 21, 23 and 24). There is some difference of style as well as of size between the three otters with which this book is primarily concerned. There are also variations due to age and sex, chiefly to do with development of the crests. Detailed description is reserved for the accounts of the different animals given later, the following being some of the more general features of the lutrine skull.

The typical otter skull has a broad, flat braincase which contrasts strongly with the narrow, often parallel-sided interorbital-intertemporal region. The muzzle region, situated anterior to the orbits, is extremely short, being even more abruptly truncated than in *Mellivora*, the anterior nares widely open. In the most typical otter skulls there are prominent sharp postorbital processes, the posterior ridges of which join the sagittal crest, helping to outline in this interorbital area a fairly well defined pentagonal plate. In fully developed males of most species there is a well-developed, sharp sagittal crest extending from the postorbital region to the equally pronounced, upcurved supraoccipital crest, which continues as sharp ridges round the sides of the braincase forward to the very large mastoids. In females, though the supraoccipital crests may be present, the sagittal line generally carries nothing more than a very low ridge which in really old skulls may rise to a brief crest posteriorly. The zygomatic arches are broad and strong; the maxillary zygomatic process divides clearly into two branches which enclose an exceptionally open infraorbital canal, obviously transmitting muscle as well as nerve, nothing at all similar occurring in other West African Canoidea. The palate is continued, parallel-sided, well beyond the back of the toothrows; the bullae are unusually flat and elongated, relatively insignificant. The bone structure of old animals is dense and solid, fusion of the sutures leaving little or no trace of original independence.

The dentition is often very irregular through the loss, or whole or partial failure to develop, of a number of cheekteeth. These, when all are present, are $\frac{4\ 1}{3\cdot 2}$, giving a total for the whole mouth of 36 teeth; but this not uncommon deviation from normal should be kept in mind since it may give rise to some doubt or difficulty in the recognition of lutrine skulls. The most frequent tooth to be lacking is the very small anterior upper premolar (p^1), which, when not missing is generally sited in close proximity to the inside face of the canine. p^2 may also be in contact with the canine, as though, through the great shortening of the muzzle, there is becoming less and less room to accommodate these teeth and they are in the course of being eliminated. The exterior upper incisor (i^3) is much larger than the two interior ones (i^1 and i^2); in the lower jaw the distinction is not so marked and the incisors as a whole are often irregular and not in line.

Habits. Otters in Europe, since they are the subjects of regular organized hunting for sport, have been under close observation for many centuries; and, the world over, they have commonly been kept as domestic, and often very intimate, pets. Many books and articles have been written on this latter aspect, especially in recent years, and a good deal, therefore, is known of the behaviour in captivity of several different kinds of otter. Yet there are often unwelcome gaps in field knowledge of the more hidden aspects of daily or yearly life; and this is particularly true of the three African species dealt with in this work, one of which, indeed, is scarcely known except for skulls. But even in the less secret matters of everyday biology the views of specialists are sometimes strangely at odds about such things as senses of sight, hearing and smell, body odour, the use of glands, or readiness of the young to swim. Nevertheless, there remains wide agreement regarding broad general behaviour; and doubtless individual otters differ from one another in their physical and mental attributes, as other animals do, and care must be taken in assuming the general from the particular. So much, indeed, has been written of specific individuals in relation to sometimes rather unreal circumstances that one difficulty is to know what, in a brief account, can be taken as representative of the class as a whole in its purely natural environment. The most comprehensive account of otters in general, with descriptions of all the species, together with their habits in so far as they are known, is to be found in Harris (1968). It must be emphasized here that though in all likelihood most of the account of habits that follows is applicable to African species these last have, in fact, been relatively little studied in detail in the field and therefore it may be discovered that behaviour in the three species with which this book is primarily concerned differs in certain aspects from the general picture given. This may be especially so as regards breeding. Doubtless the three species differ amongst themselves in this as in other respects; and it is, indeed, vaguely recognised that the only two of the three that have been observed in life do live somewhat differently, though this is more a matter of general impression rather than of firmly established fact.

Otters are active by day or by night depending to some extent upon local circumstances as well as preference. If there is much danger of human interference they become rather careful of exposing themselves to view and are more inclined to forage nocturnally, particularly on moonlit nights. In any case their hunting tends to be more especially an early morning or late afternoon occupation. However, both species and individuals of them differ somewhat in their degree of shyness, and otters have been known to come into towns at night or to raise families in drains near or under houses; and once, even, beneath the floor-boards of a living room.

For the most part otters dwell near water, most commonly fresh, that is to say rivers, lakes or inland marshes; but they are by no means averse to brackish or even salt water and so not infrequently are to be found in creeks or estuaries or along the coast. They sometimes travel overland to a considerable distance from water, but there is no evidence that they spend long in such situations. Though they like to live near it they do not pass all, or even the major part, of their lives in water; they mostly take to it primarily for the business of seeking food, but this vital business, as will be seen later, is tempered with a good deal of sportive activity. Sleeping, breeding, defaecation, urination, and nearly always feeding are essentially dry-land occupations, as well as extensive periods of out-of-water play, and it will thus be seen that, though some species are more aquatic than others, otters in general spend at least as much time ashore as they do in the water. It is customary to refer to the males as "dogs" and the females as "bitches"; but in spite of this analogy with dogs the young are generally spoken of as "cubs", not "pups", though the term "whelps" is sometimes used.

On shore, an otter centres itself on a set shelter for the purpose of sleep or breeding. This is nearly always subterranean but may occasionally be in dense vegetation. These dens, or "holts" as they are technically termed, may be self-constructed or taken over from other animals or adapted from naturally-occurring holes such as those amongst riverine tree roots, amongst boulders, or even in a cave. Generally they have an underwater entrance—but extremely little is known of the exact nature of these homes in Africa. It at least seems highly likely that the African clawless otters would find some difficulty in digging except in the softest of swampy mud. The shelters are situated well above flood or seepage level and are frequently lined to some extent with vegetable matter, grass, leaves, reeds or moss; for, although they spend a good deal of time in water, otters like very much to be warm and dry. Drying off of the outer coat, by rolling or rubbing, is in fact one of an otter's first urges on leaving water. Custom in nest-lining, however, varies; possibly when the soil itself is of a warm and dry nature no nest lining is called for. Such conditions would seem to exist over much of tropical Africa, except possibly in the forest belt at the height of the rains.

Holts are occupied sometimes by a lone otter, sometimes by a family party. Such parties usually consist of a bitch and her offspring up to the subadult stage; the dog otter is, as far as the holt is concerned, generally kept at a distance, and occupies a separate, though neighbouring, shelter.

Some observers have maintained that otters combine and co-operate in fishing parties; but it is doubtful whether such collaboration, if it exists at all, ever extends beyond the immediate family. Most otters are by no means gregarious creatures and holts are generally fairly widely separated; and it would seem probable that each unit has its own recognised stretch of water, especially when one remembers the powerful scent-glands which otters possess and their probable use for demarcating territory. Yet a fixed territory implies some degree of permanence, and otters have a considerable reputation as wanderers, never dwelling long, perhaps only a night or two, in one place except at actual breeding time. Such nomadism or semi-nomadism may be for safety; or it may be that after a while a given stretch of water begins to become exhausted of food, or the fish, by constant hunting, accentuatedly wary. Whatever its motive, this continual moving renders the field study of otters a matter of some difficulty except at breeding times since the observer often does not know where to find his animals from one day to the next.

It is commonly thought that otters feed solely upon fish but this is far from true. Fish may form a large or even the major part of the diet but a good many other things living in or around the water are eaten, such as crabs, crayfish, prawns, mussels, snails, large water-beetles, and, on land, ground-birds, water-fowl, eggs, rodents and possibly other small mammals, lizards, including geckos, snakes, frogs, toads, grasshoppers, crickets, mole-crickets and other large insects. These are generalities, for each species has its preferences and each locality a differing availability of food materials. For example, it would seem that the two commonest West African otters differ in their feeding demands, *Lutra maculicollis* being predominantly a fish eater, *Aonyx capensis* consuming more crabs. But no set work has been done on this or on the kinds of fish preferred by each species in West Africa, though it is known that the latter species, at least, consumes, in Lake Victoria, a fair number of Lungfish (*Protopterus*) and probably clariid catfish as well. Eels, which form a considerable part of the food of otters in Europe, do not occur in the rivers of West Africa except possibly in estuarine waters. These considerations are of some importance since it has been held in Europe and elsewhere that otters cause a great deal of economic harm both in fish-hatcheries and amongst the more valuable "game" fish. Farmers join with fishermen in their condemnation, saddling otters with poultry thefts of which, often, they are not guilty. Such charges have, on the other hand been strongly denied; and there is a growing appreciation that otters may, in sum, effect far more good than harm in many ways, not least by getting rid of much fish that is diseased or otherwise undesirable.

Small articles of food taken in the water, such as snails, mussels and other mollusca, are then and there swallowed with a bite; small fish may be eaten in an upright position while the otter is treading water with head and neck above the surface, or while the otter is floating on its back; but anything large is brought ashore to be consumed. It may, if really large, be held down by the paws and eaten thus on the ground; but moderate-sized fish are held up to the mouth between the hands and eaten gradually from end to end. It has often been asserted that a start is always made at the tail end, the head finally being discarded; but this is by no means always so. Food is invariably eaten fresh at once or discarded, never stored, and, in fact, otters are usually believed not to eat anything but the food they have just caught; but Stephens (1957) records an opinion that, at any rate in Europe, they will, and regularly do, consume a large amount of carrion.

Ability to catch fish implies a superior ability to swim. The adult otter is certainly a past master in this art. On the surface, with the head partly above water, an otter progresses in a rather leisurely fashion, using its feet alone in a sort of dog-paddle; but once it has dived in earnest the whole demeanour immediately changes and the animal becomes a lively and remarkably dexterous hunter. Propulsion is mainly by powerful thrusts of the hindlegs, used as a pair, aided sometimes by a sinuous and rhythmic up-and-down movement of the body. The forelegs are occasionally but not always held back against the belly. The tail acts as a rudder. In this way a moderate speed is achieved over a short distance; but it is rather the otter's facility, with its supple body, to equal or outdo its prey in swiftness of turn that makes escape for the fish a matter of some hazard. None the less, it seems that otters as a rule prefer to go after the slower moving kinds of fish; and certainly the two categories mentioned earlier as being commonly eaten in Africa are both sluggish.

The eyes are kept open during submergence and probably function more efficiently under water than on land. The ears and nostrils are sealed; but no one seems to have determined how, when an otter opens its mouth to seize a fish, it avoids its lungs being swamped with water. Otters swim on their backs as well as on their bellies, and they sometimes float thus idly as though half asleep. How faultlessly streamlined the body is is well demonstrated not only by the easy progress of the submerged animal in rapid pursuit but, as well, by the manner in which an otter habitually slides into the water with scarcely any disturbance of the surface and consequent alarm for the fish. To all intents and purposes the only sign of an otter's diving lies in the trail of rising bubbles, probably from air trapped in the fur.

Otters, being mammals, must, of course, come up from time to time to breathe otherwise they would drown. Normally they remain submerged for a matter of a few seconds; Mortimer (1963), observing the speckle-throated otter in Zambia, found the commonest time to be from 10 to 15 seconds, and he never witnessed a dive lasting for more than 45 seconds, and that only on one occasion. But when they so wish or it is necessary they can remain under water for some four or five minutes; and Maxwell (1961) timed an Asian otter for just on six. This, in human estimation, is a very long time though it is brief in comparison with some other aquatic animals—a quarter of an hour for a manatee or a seal, and an hour or even two for some of the whales. Though no investigation appears to have been carried out on submersion actually in the otters it would seem likely that the mechanism by which prolonged abstention from breathing can be achieved is much that found amongst other groups. This, in brief, is a marked reduction of oxygen consumption brought about firstly by a very considerable slowing down of the heart-beat, and secondly by a constriction of the blood vessels in less important areas of the body while maintaining a full flow to the brain. There are contributory mechanisms such as, during preliminary breathing, a nearly complete change of air in the lungs, a greater ability in the blood to hold oxygen and less sensitivity of the respiratory nerve centre to increased concentration of carbon dioxide. Ability to stay under water has nothing whatsoever to do with extra lung capacity which, indeed, by increasing buoyancy would be more of a hindrance to diving than a help. Harris (1968) suggests that because of this adaptation to prolonged submersion otters are difficult to anaesthetize; but Stephens (1957) refers to two cases within her experience without hint of trouble. In one, morphia and chloroform were used; in the other, nembutal.

Whatever the precise mechanism an otter can, in five minutes, swim a long distance under water; and though fishing and other underwater foraging is most commonly carried out at shallow depths it has been shown, by the capture of otters in traps, that at times dives of at least 18 metres are undertaken. Ability to remain below water is to some extent dependent upon age, young otters being incapable of as long periods of submersion as adults. Despite outstanding mastery of water it is, indeed, generally held that young otters are most unwilling to enter it and, if they do, prove themselves to be nervous and highly inept swimmers. There seems little doubt, from numerous eye-witness accounts, that in most cases the mother has to teach her young both how to swim and how to catch fish. To judge from Maxwell (1961) it would seem as if this might well apply also to the clawless otter which occurs in West Africa; but doubtless idiosyncrasy plays its part in this as in other matters, for Mockford (1967) found two young captive otters of this species to take to water quite naturally and easily at an age estimated to be no more than six or seven weeks. This is the more remarkable in that *Aonyx* is increasingly regarded as markedly less aquatic than other species.

It seems likely that the exceptional development of the facial vibrissae may assist in the avoidance of rocks and other obstacles in cloudy water; and, by their sensitivity to the currents produced by even slight disturbances, aid in the detection of moving fish. Though both ears and nostrils are closed under water, hearing and smell nevertheless probably play their part too; certainly on dry land both these senses are fairly acute, smell, to judge from the complex internal nasal structure in comparison with the poorly developed auditory bullae, much more so than hearing. Odours, indeed, must play a constant role in the otter's life, as in those of most mustelids. Signals are constantly being left on rocks or on deliberately gathered bunches of vegetation; and the odour left by otters in normal passage over the ground is strong and very persistent, it being well known to those who hunt these animals in Europe that hounds may often be deceived into picking up a trail already a day or two old. The faeces, doubtless, have their own particular odour and convey their message to others. Otter droppings, which are most commonly black, rather liquid and slimy, are technically termed "spraints"; and it is well known in Europe that set sprainting places are used, sometimes over a period of very many years. Whether this applies to the same extent in Africa is not recorded; but Mockford (1967) found young *Aonyx* in captivity always to use definite spots and, therefore, to be scrupulously clean. Eyre (1963), on the other hand, found an otter of this species awkward to keep about the house since it persisted in registering ownership in this way. Experience of those who have kept otters as pets, as well as the abundance of spraints in the wild, indicates that defaecation, always simultaneously accompanied by urination, is frequent; and there is good evidence, from observation and from examination of the intestines, that digestion and passage of food through the gut are rapid. However, the spraints always contain some indication of the food taken, in the form of undigested fish bones and scales, or chitinous fragments from crustacea. Excretion is performed with straddled hindlegs and tail erect, and is accompanied by a constant dancing movement.

Though otters so obviously, in nature, thus constantly leave traces of their presence or passage it is a remarkable fact that no one of the very many who have kept them as pets has ever expressed objection to their smell, despite the animals' sometimes habitual use of carpets, chairs and often beds. In fact, otters have been recorded as having no smell at all unless kept out of water for several days; and some have described the faint odour of the dense fur as very pleasant.

Besides the evidence of their spraints otters frequently leave indications of their existence in an area in the form of rejected or discarded portions of food. Feeding, except of small, readily consumed objects, always takes place on shore and very often at definite sites such as a secluded strip of river bank or a conveniently flat rock. Such favorite feeding spots are often littered with the heads or tails of fish, or even whole bodies with a single bite out of them, for otters are sometimes wanton killers of more than they need. One of the most frequent signs in Africa is the remains of crab shells or claws, since *Aonyx* appears to have a preference for these arthropods above fish. Another sign of the recent presence of an otter is the footprints in soft sand or mud. These, amongst those who specialize in hunting otters, are known as "seals", a technical term that has been in use for at least three centuries. These tracks differ amongst the West African otters, since some feet are clawed, others are without them; some are webbed between the digits, others not.

Although they are fundamentally land animals otters are not there so completely adept as they are in water. Their walk, though brisk enough, is a kind of slight waddle from one side to the other with head low and back humped. Yet some are known to cover considerable distances, up to 20 or 25 kilometres, at this pace, and apparently without tiring. When put to it they can gallop moderately fast, "humping" along forefeet and hindfeet alternately. However, apart from their not very expert gait they still remain highly flexible, swift and versatile in movement, rolling, twisting, turning, scrambling over rocks, logs and other obstacles. They can climb to a certain extent, and, in fact, have been recorded (Stephens, 1957) as sometimes sleeping up in low trees. They often stand upright on their hindfeet, using their tails as a third support.

Otters have several different sorts of call or other vocal sounds according to circumstances. Animal noises are always difficult to express in writing; moreover, they differ quite a lot in the various kinds of otter and are not very well recorded for the species occurring in West Africa, if at all. Not much, therefore, can be said on this subject. The shrill nocturnal whistle of the European otter is, apparently, never uttered by African species. Harris (1968) describes the sound made by *Aonyx* when suddenly alarmed as "a strongly aspirated and explosive '*Hah!*' ". The same author says that this species uses "a querulous moaning wail" to express anguish, apprehension or, sometimes, greeting. Shortridge (1934) says he has frequently heard African otters "barking"; and, quoting Stevenson Hamilton, gives the sound made by *Aonyx* at bay as a throaty "*Kwa-a-a, kwa-a-a*". Young otters, as those of so many other kinds of mammals, continually utter bird-like twitterings and plaintive squeaks.

Though otters may occasionally idle in water they do not often do so, wakingly, on land. Unless they are actually asleep in their shelters they are generally busily active and rarely, like so many other animals, lie merely basking in the sun. When they are not engaged in eating or excreting they inquisitively examine all the details of their surroundings; or when this eager inspection palls they indulge in play, either alone or with others of their family. Otters have earned a remarkably wide reputation for play; and they are, without doubt, amongst the most dedicatedly playful of all animals, their activities in this field having every mark of real play and utter enjoyment without hint of anything more purposeful behind it. The stories of those who have had the good fortune to watch young otters in nature or who have kept them as pets are endless and are pervaded by a bewitching charm that is, at best, no more than palely reflected in even the most persuasive accounts of other animals of any kind. This is no place to record these, and only brief generalities of behaviour can be given.

Play takes place equally in water and on dry land, and as much by a lone otter as between two or three. It not infrequently involves the deliberate selection and use of a toy, and the otter's capacity for deriving continuing amusement from the simplest of sources is a matter for some amazement. In water, play may consist of delighted and quite aimless gambolling in the form of dives, twists and turns, or of endless rapid revolution about the longitudinal axis. It may consist of dropping a stone and diving to catch it in its descent; or it may be a walk on the bottom, shuffling a shellfish along with its nose. One otter is recorded (Maxwell, 1961) as taking a ping-pong ball down to the water to enjoy, and expertly appreciate, for lengthy periods its lively antics when released at a depth. A ball has its fascination also on land, being struck along with the nose or dribbled football fashion with the feet or flung from the mouth over the shoulder. In nature stones are used for this exercise in place of a ball; and an otter may occupy itself with a smooth pebble for a long time. The young may sometimes play a species of "tig" with one another. One of the pastimes for which otters are most widely famous, either alone or in company, is sliding. This is easily done in winter in cold climates on snow or ice, set slides being deliberately made and repeatedly used; but when or where these elements do not exist mud slides down steep river banks are made. These are by no means uncommon in Europe, but whether such slides exist anywhere in Africa seems never to have been definitely recorded. Water-chutes are similarly used for play where rivers fall over flat rocks in rapids.

The amusing and interesting things that otters can do in the artificial surroundings of a human habitation cannot be gone into very deeply here, the more so as circumstances must differ in every case. But it may be recorded that the otter's forepaws, which are so fashioned that they are expert at holding things, are rarely idle, exploring the possibilities and uses of anything within reach. This is particularly so with the West African *Aonyx* in which the fingers are unhampered by claws and the structure is not unlike, in appearance and manageability, a monkey's paw. So dexterous are these hands that *Aonyx* can open tins or bottles (Eyre, 1963) or peel hard boiled eggs, and amongst other things has shown itself to be an expert pickpocket. When indulging in such an operation, or on the rare occasions when they may attempt slyly to rob a companion of some tit-bit, these otters have the engaging habit of distracting attention from their act by turning their heads away and gazing abstractedly into the opposite direction.

It may be added here that otters have proved themselves to have most excellent memories both for persons and situations, recognising friends after prolonged absence (Pitt, 1938). They are long-lived, one being recorded as existing for 22 years in captivity.

There is no doubt that otters, caught young, make highly intelligent, enchanting, and indeed lovable, pets, being not only extremely entertaining but affectionate and loyal as well. Nevertheless, a warning must be given. They are certainly not for everyone or for those who like to preserve a well-equipped and tidy house. Their insatiable inquisitiveness, their sense of play resulting in mischief or destruction, their determination to get their own way, and their constant liability to soak clothes, furniture and beds calls for an even temperament and a forbearance not possessed by all. Add to this, occasional lapses into bad temper resulting in painful and sometimes serious bites, and it will be seen that the care of a baby otter is not a task to be entered upon lightly, especially if it is accompanied by admission to the house.

Something must now be said of breeding, though remarkably little that is definite is known of this even as regards the long-observed European otters. Copulation takes place in the water, lasts an hour or more and is repeated several times over the course of a day or two. The period of gestation is very much in dispute. Probably it is normally in the nature of 9 weeks or a day or two less, but this period may be very much lengthened by delayed implantation of the fertilized ova in the womb. There may be anything between 1 and 5 cubs at a birth; but both these extreme figures are unusual and the normal expectancy is 2 or 3. The newly-born cubs are covered with fine, short fur but the eyes are closed and appear to remain so for a matter of 5 weeks, though opinions differ largely as to this. Probably all the figures here given for these matters will be found to be only approximately correct for species in West Africa. The young are, if necessary for safety, carried from place to place by the bitch using the loose skin at the back of the neck. They are even said, still as blind juveniles, to be transported thus actually under water from one river bank to another; which would appear to indicate that not only do the nostrils and ears close reflexly but that, also, the oxygen-conserving submersion mechanism described on page 134 comes automatically into operation at a very early age.

It has been said (Stephens, 1957) that the young are born toothless; but two juvenile skulls of West African *Lutra* and *Aonyx* in the British Museum are both well supplied with teeth. Otter bitches make very good mothers, caring for their litters assiduously and protecting them fiercely. They alone bring up the family, at least in the initial stages, the dog otter not being allowed to come near the nest though he remains in the vicinity, occupying a holt of his own. The cubs seem to develop fairly slowly and do not leave the nest for several weeks. Thereafter they have still to be taught swimming and diving and to acquire proper proficiency in hunting. At this stage the father may return and take part in the training. The cubs probably remain with the mother until they are sexually mature, which is after about two years. There seems to be generally at most one litter a year, possibly less. Even in the diversely seasonal climate of Europe litters may occur in any month of the year, winter as well as summer; in the tropics it would seem that season, for water-haunting animals, must matter even less.

Otters have been found to harbour a number of different kinds of internal parasites, both in the gut and the bloodstream, of all the usual groups of worms, flukes and protozoa; but nothing is known of this in connexion with African species. They have also been recorded as carrying ticks, and it has long been believed that otters visit the sea from time to time in order that the salt water should rid their coats of these and other ectoparasites. In the normal course of events otters spend some time cleaning their fur by scratching, rolling, rubbing, biting and possibly licking. The last does not seem to be a common habit; but as otter fur is at times a constituent of the droppings (Stephens, 1957) they must at least occasionally clean themselves, or their cubs, in this way. Nevertheless, external parasites seem to be less common than on some animals, possibly, sea-cleansing apart, because the extreme density of the underfur makes life amongst it and passage through it difficult. The hazard of drowning, too, must always exist.

Apart from disease otters have two main enemies, man being the chief. There is, indeed, reason to believe that the otter population of the world, and especially of newly expanding areas such as Africa, is markedly decreasing, partly by direct persecution and partly because their once quiet haunts are more and more being invaded and diverted into economic use. The other enemy, in tropical waters, is crocodiles. Otters have often been observed in places infested with these reptiles and though they show no visible awareness or signs of fear it is obvious that they must continually be on the alert, ready to make a swift avoiding turn or to flee to the bank. They may also be aware that a crocodile's periods of entry to the water have something of a set daily rhythm dictated by the demands of their cold-bloodedness and virtual lack of bodily heat control except by alternate sunning and immersion. It is possible, also, in the tropics that pythons find their way into otters' holts; and though an adult dog or bitch would give a good account of itself in a fight with such a snake—though it might well be hampered in a restricted space—juveniles would easily be taken. And there is always the danger, on land, of being surprised and sprung upon by a leopard or other of the larger felines.

Taxonomy. The position of the Lutrinae as a distinct and valid subfamily of the Mustelidae has never been brought into question since Gray (1865) first suggested this classification. Within the subfamily itself the genera are fairly clear except that *Paraonyx* is often regarded as no more than a subgenus of *Aonyx* since it was so treated by Ellerman, Morrison-Scott & Hayman (1953). This course is adopted here. Some of the characters picked on by Hinton in the type as diagnostic of *Paraonyx* are seen not to be valid in other and better skins; and while there is, indeed, a remarkable difference in the teeth it is one of size rather than of anything phylogenetically more fundamental; and the rest of the characters, both cranial and external, denote an undeniably close affinity with *Aonyx*.

The second West African genus is the almost world-wide *Lutra*, which ranges over much of Europe, Asia, Africa and America. In consequence there have almost inevitably been attempts to subdivide it either into independent genera or at least subgenera. The sole African species of this genus, *maculicollis*, was first generically separated from the others by Gray as *Hydrogale*. This name was later found to be preoccupied and the proposed genus was eventually restyled *Hydrictis* by Pocock who, by reason of a number of small differences, both cranial and external, supported Gray's interpretation of the position. Once again, the distinctions drawn appear too minor to warrant full generic separation and *Hydrictis* has commonly been reduced to the status of a subgenus. It is so dealt with herein; but see page 141 for further comments on this.

The fullest study of the taxonomy of the Lutrinae is a long monograph by Pohle (1920) dealing with all the genera, species and races. Pocock (1921b) described some aspects of external characters.

The two West African genera may be told apart thus:

KEY TO THE GENERA OF LUTRINAE

(previous key page 93)

Cheeks, lips, throat, sides of the neck and the entire chest wholly white or cream; forefeet without long claws and with only slight webs; skull length more than 115 mm; mastoid projecting very prominently behind the aural orifice **Aonyx** (*page* 148)

White or cream area confined to the mid-throat and upper chest, and then to a greater or less degree irregularly blotched with the normal dark pelage colour; a similar spotted patch often on the after part of the belly; forefeet with well-developed claws and webs; skull less than 115 mm; mastoid not remarkably prominent . . . . **Lutra** (*page* 140)

Genus LUTRA Brisson, 1762

Typical Otters

Lutra Brisson, 1762, *Regnum Animale in classes IX distributum* . . ., 2nd edit.: 13. Type species *Mustela lutra* Linnaeus, Sweden. *Lutra* was the Latin name for an otter. (It is doubtful whether Brisson's *Regnum Animale* is properly available under the International Code; but certain of his names, including *Lutra*, were proposed to the Commission for validation, see Ellerman & Morrison-Scott, 1951: 3, though no action has been taken on this and the matter has been dropped. Even in the case of rejection the name still stands as of Brünnich.)

Lutra Brünnich, 1771, *Zoologiae fundamenta* . . . *Grunde i Dyrelaeren*. Type species *Mustela lutra* Linnaeus.

Hydrogale Gray, 1865, *Proc. zool. Soc. Lond.*: 131. Type species *Lutra maculicollis* Lichtenstein, South Africa. This name was preoccupied having already been used twice, by Kaup, 1829, and by Pomel, 1848, in each case for a shrew. It is derived from the Greek *hydor*, *hydr-*, water, and *gale*, a weasel.

Hydrictis Pocock, 1921, *Proc. zool. Soc. Lond.*: 543. Type species *Lutra maculicollis* Lichtenstein. The name was compounded from the Greek words *hydor*, *hydr-*, water and *ictis*, a weasel. Valid as a subgenus.

There is further synonymy of little concern in African literature.

General. As already stated above, the typical otters are widely spread over a good deal of four continents. Many of the chief characters and habits of the genus have been given in the general introduction to the subfamily and there is no need to elaborate further what has been said there; the more important distinctions between it and *Aonyx* are set forth in the key just given and will become more apparent in the detailed descriptions which follow. It remains only to consider briefly in what characters the African section *Hydrictis* differs from the most typical, Palaearctic, members of the genus, which, beyond this, are of no other taxonomic concern to this work.

Hydrictis was, following Gray, proposed by Pocock as generically separable from *Lutra* on the grounds of a reduction in the size of the rhinarium and a simplification of the external ear; larger, more fully webbed and hairy-soled feet, the palmar and plantar pads being less well developed. The skull was distinguished by "many cranial characters, especially the shortness of the muzzle, length of the orbital floor, and the generally immature aspect of the skull owing to the feeble development of constrictions, crests and prominences". This last is a very apt description, and even the oldest *Hydrictis* skulls are in no way so robustly built as those of *Lutra lutra*. The most noticeable feature is the narrowness of the interorbital region and complete absence of postorbital processes, as shown in figure 21, and the consequent lack of the usual lutrine interorbital pentagonal plateau, observable in figure 24 of *Aonyx*. The sagittal and occipital crests are relatively insignificant; the mandible and its condylar structure weaker. There is, indeed, quite a strong case for regarding *Hydrictis* as valid at full generic level.

Subgenus **HYDRICTIS** Pocock, 1921

African Long-clawed Otters

Since *Hydrictis* consists of a single species, *maculicollis*, no description of the subgenus is called for beyond the differential characters just given above and the account of the species which follows.

LUTRA MACULICOLLIS Lichtenstein — Speckle-throated Otter

Lutra maculicollis Lichtenstein, 1835, *Arch. Naturgesch.* **1**: 89–92, pl. 2, f. 1. South Africa (Bamboos Mountains). The specific name was derived from the Latin words *macula*, a spot, and *collum*, the neck, in reference to the markings on the throat.

Lutra grayii Gerrard, 1862, *Catalogue of the Bones of Mammalia in the . . . British Museum*: 101. Port Natal (= Durban), South Africa. A *nomen nudum*. This was named after Dr. J. E. Gray of the British Museum.

Lutra matschiei Cabrera, 1903, *Boln R. Soc. esp. Hist. nat.*, **3**: 182. Rio Muni. Named after Professor Matschie, German zoologist. Possibly subspecifically applicable in West Africa.

Lutra maculicollis nilotica Thomas, 1911, *Ann. Mag. nat. Hist.* (8) **8**: 726. Malek, upper Nile, Sudan. Possibly applicable in West Africa.

Distribution and general. The name speckle-throated otter is that most generally accepted for this animal; but it is a little misleading in that the picture conjured up by "speckling" is of a much finer order than that occurring in this animal For that reason it has sometimes been termed the spotted-necked otter. This, though in one respect more accurately descriptive is in another less so since the back and sides of the neck have no markings. The most correct name would be spotted-throated; but this has never been used—possibly because it is less euphonious than the term most commonly applied.

The speckle-throated otter is widely spread throughout Africa from near the Cape northwards to Ethopia in the east and Liberia in the west. Specimens have been recorded from most West African territories but in the British Museum exist only from Sierra Leone (Waterloo, and near Kenema); Nigeria (Oban, Maiduguri); and Cameroun (?Ndop); six skins only, two of them juvenile, and two skulls, one alone of which is adult. Nevertheless, *maculicollis* is thought to be not uncommon in suitable localities though, being secretive and wary, it is not often come across by collectors. A. J. Hopson observed it to be frequent on the shores of Lake Chad. It is also plentiful around Lake Victoria (Proctor, 1963); and it is possible that the species is more at home in lakes and similar wide expanses of water than in rivers. Skins are not commonly seen on sale in local markets. Indeed, T. S. Jones (personal communication) thinks that, at any rate as far as Sierra Leone is concerned, this is a much scarcer species than *Aonyx*. Amongst about 30 otter skins he examined during his years in that country only one was *Lutra*—that cited above from Kenema. Kuhn (1965) gives this species as occurring in the following places in Liberia: Farmington River, Gbanga, Kpeaple, Biadatou, Deaple, Harbel, Kahnple, Siron, Tappita, Towaitown and Zwedru.

About 10 different races have at one time or another been named, 6 of them recognised in G. M. Allen's Checklist (1939). None of these is actually from the area dealt with in this book, but it is possible that *matschiei* Cabrera described from lower Cameroun applies to otters of this species from the forest belt of Nigeria; while *nilotica* Thomas may cover specimens from the Sahel zone. The position, however, is by no means clear. Harris, indeed, cites Liberia, Nigeria and Cameroun as countries of occurrence of the nominate race though these areas are, of course, geographically, and probably ecologically, most distantly separated from the type locality.

Description. *Lutra maculicollis* (Plate 2) is the smallest of our three otters, with a head & body length of about 65 cm and a tail which is rather more than half this. The full-grown weight is about 4·5 kg for a dog otter or 3·5 kg for a bitch (Mortimer, 1963). These figures are the outcome of actual weighings of living animals; the often quoted "not more than 20 lb (9·1 kg)" sems to be nothing more than a visual estimate.

The pelage of the speckle-throated otter is almost entirely a deep rich red brown—intense sepia—both above and below. The base of the fur is, as in all otters, white. The only exception to this deep brown lies on the throat and sometimes the chin, the fore part of the chest and the after part of the belly which are white, spotted or blotched with the normal dark ground colour. The size of these mottled areas varies a great deal from individual to individual, being sometimes very much reduced or, particularly as regards the belly patch, lacking. The upper lips are also narrowly white, but this is not very noticeable. It is the extent of these white markings which best serves as a means of field recognition; for although the other two West African otters are bulkier and have a rather paler pelage, age may affect size, and wetness the apparent colour of the fur. In the species now under discussion the white is very strictly confined to the lower surface of the body, whereas in both *Aonyx* and *Paraonyx* it uninterruptedly covers a much larger area, rising to the level of the eyes and the sides of the neck and is thus

Speckle-throated Otter *L*[illegible] Cape Clawless Otter [illegible]

readily observable in various postures and at a distance. Albinos or partial albinos are known to occur.

Other external features by which *maculicollis* differs from *Aonyx* are only detectable in the dead animal, or at least at very close quarters. One of these is the rhinarium, which is much narrower than in the clawless otter, consisting virtually of two narrow wings enclosing the nostrils without any broad central, dog-like, dorsal area. The second lies in the feet, which, unlike those of *Aonyx*, have short but very distinct, sharp claws on each of the five digits of both fore and hindfeet, and the toes fully webbed practically to the tip. The palmar pad is a small four-lobed structure confined to the proximal part of the foot; the plantar pad is poorly defined and consists of three narrow lobes (Pocock, 1921b). The undersides of the digits have long hairs; the webs, sparse hairs. The eye is orange-red in adults (Proctor, 1963).

For the description of an unusual skin see the taxonomy section below.

Skull. As only one adult skull, and that broken and of a not fully mature animal, exists from within the boundaries set for this work, the following description is compiled largely from extralimital material. The *Lutra* (*Hydrictis*) skull (figs. 20 and 21) is not only much smaller than those of the other West African otters but also of an altogether less robust build. The braincase is ovoid, either without any trace of a sagittal crest, or in fully adult males a low one, often more in the nature of a ridge than a crest. Only the oldest females have anything of this kind at all; and it is, in fact, so unusual amongst a wide range of specimens as to raise doubts about the accuracy of the sexing in these few cases. Much the same applies to the supraoccipital crest, which even in the oldest males is not very prominent and only rarely markedly upcurved.

The braincase narrows sharply anteriorly, and forward of this the intertemporal-interorbital reigon becomes very conspicuously narrow and roughly parallel-sided to the deeply depressed, sharply truncate rostrum. Very noticeably absent are any signs of postorbital processes; and it is this peculiarity which most clearly separates *Hydrictis* from *Lutra sensu stricto*. The anterior nares are very wide. The zygomatic arch is fairly slender but none the less strong, its anterior root widely divided to form a large oval infraorbital foramen. There is a sharp clearly-defined spur on the upper margin of the jugal marking the lower posterior limit of the orbit. The palate is continued well beyond the toothrows. The bullae are of moderate size and rather less flattened than in other otters, including the typical European *Lutra*; the mastoids are not very pronounced—as they are in *Aonyx* and *Paraonyx*. The mandible is moderately strongly built. In mature skulls the sutures fuse leaving no trace.

The dentition is initially sharply cuspidate and, in fact, retains some of this character even in old skulls. The compact toothrow is crowded towards the canine, both p^1 and p^2 being closely approximated to this tooth; the former of these very small and sometimes deciduous, though much more rarely so than in other species. The incisors, both top and bottom, form two straightly transverse rows, tightly packed and strong. The size and form of the posterior cheekteeth in relation to those of the other African species are shown in figure 22.

Habits. There is not a great deal of particular application to this species to add to the general review of otter habits already given. Detailed studies have been made of

L[illegible] by Procter (1963) in the field in Tanzania, and by Mortimer (1963) in Zambia, mostly on a domesticated female. Both accounts tend to show that the speckle-throated otter corresponds in habits and behaviour fairly closely to other *Lutra* species in other parts of the world.

Fishing may take place at any hour of the day, or sometimes night, although on the relatively undisturbed shores of Lake Victoria the species appears to be chiefly diurnal: it is commonest soon after sunrise; but the otters may actually already have been swimming about for some time before this in the semi-darkness. From Procter's account it would seem that *maculicollis* is markedly more social than most. He records that parties of from 1 to 6 are fairly common, larger numbers than this getting progressively rarer, but he once observed a school totalling about a score. Small parties are mostly bitches; the larger ones dog-otters, often young. The two sexes are mostly difficult to distinguish apart in the water, though full-grown males are appreciably more heavily built than females. On shore, identification is easier, particularly at times of excretion since in the dogs the urine is projected forwards, in the bitches towards the rear. Defaecation is invariably accompanied by urination, but not *vice versa*; and, as in other otters, there are recognised spraining places. The spraints are mostly of the common, blackish slimy, otter type; but drier faeces of arthropod shells and fish scales are also dropped. In excretion the body crouches low, almost touching the ground; a bitch holds the tail out stiff horizontally, the dog vertically. Passage of food through the gut may be extremely rapid. House-cleanliness is evident in captive specimens.

Fig. 2[illegible]. *Lutra maculicollis*: skull, B.M. No. 23.1.22.44, sex ?, × 1, lateral view

Like other otters, *maculicollis* indulges in play both in and out of water. Amongst other things it is not infrequently given to teasing its prey, flinging fish back and forth from land to water and pursuing it, sometimes giving it a slight nip to disable it partially and slow down its movements. Crabs and such like are butted about with the nose. Procter, during long observation of the speckle-throated otter around the shores of Lake Victoria never saw mud-slides like those recorded as made elsewhere by other species; but Mortimer noticed what might well have been one of these, the more so as there were otter tracks around it. Incidentally, the tracks ("seals") left by this otter can be readily distinguished from those of the two other West African species by the clear presence of claw marks and, on very soft mud or sand, the faint imprint of webs reaching to the ends of the digits.

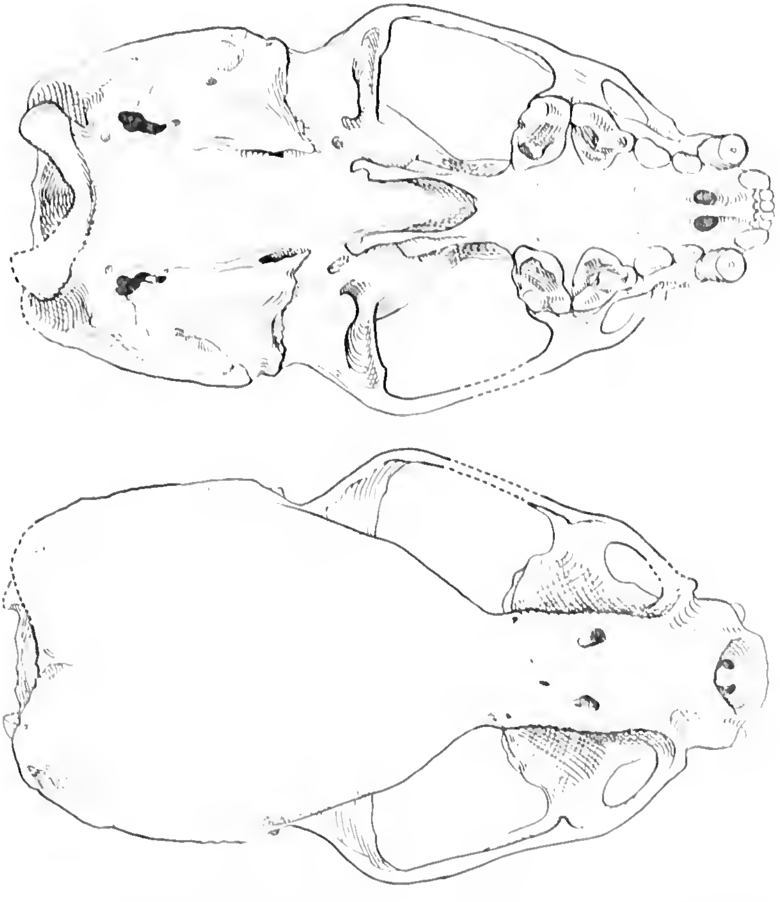


FIG. 21. *Lutra maculicollis*; skull, B.M. No. 23.1.22.44, sex ?, × 1; palatal & dorsal views

When diving to fish, the body is arched almost clear of the water and the subsequent dive is nearly vertical. This otter, as other species, exhibits astonishing grace and agility, especially in the rapidity of its turns; but there is not much actual speed in swimming. Mortimer gives measured figures for short distances which indicate a rate of progress through the water of only about 4 km an hour. Both fore and hindlegs are used in swimming, the main thrust coming from a vigorous use of the latter. Apart from swimming, diving is also graceful and skilled, being carried out from heights of up to 6 feet, leaving scarcely a ripple on the water. One of these otters, however, is not above an ungainly scramble into the water with a large splash when suddenly alarmed.

On land the gait is rather awkward but progress somewhat faster. For ordinary purposes a rather clumsy walk is used in which the feet are moved alternately or the hindlegs as a pair—this latter a gait sometimes used by domestic dogs as an alternative to the normal trot. A faster speed can be achieved by a run, the legs moving alternately. Mortimer's measured speed for this is about 5.2 km an hour; and finally there is a sort of gallop, the animal "humping" along, moving fore and hindfeet in pairs alternately. This was found by Mortimer to be at the rate of about 7·2 km an hour, though it is, said that over a short distance one of these otters can keep up with a running man, which would be at least twice as fast as this. Mortimer's experience with a young tame otter made him doubtful whether this species could travel long distances overland as this one, at least, appeared to become very soon overheated. Clambering up and over rocks is effected without difficulty; and Procter observed that a jump of at least one metre could be made across a gap.

Although various foods, including crabs and molluscs, are taken fish seem to constitute the chief diet in this species. Procter found *Haplochromis* of from 10 to 20 cm to be a favourite on Lake Victoria, a genus that occurs, but much more rarely, in West Africa. *Tilapia* is readily acceptable but often proves too fast to catch. Mortimer observed that a number of fish would be landed before the meal was actually commenced; but this is certainly not always so. His fully-grown bitch ate from 4·1 to 4·7 kg a week; and, as often popularly held for other species, invariably started at the tail end. Smaller fish or molluscs are eaten in the water, either upright while treading water or while the otter is floating on its back. Vegetable food seems not only acceptable but desirable; for Procter observed one of these otters to eat a small quantity of sedge, and Mortimer's tame one deliberately robbed the garden of carrots, beans, potatoes and peas.

When not in the water these otters spend a good deal of time grooming their fur. On emergence from the water the head is shaken but not the body, the drying of which is aided by the usual otter practice of rolling or rubbing. Vision on land is obviously only good over very short distances; hearing and smell are better developed. Mortimer observed the latter to make immediate response to seemingly quite insignificant quantities of water in flower vases or other small vessels. A pungent musky smell is emitted as a reaction to fright, in young animals at least. The sounds uttered are various. Procter describes four. The commonest call is "a shrill chikkering", used when playing or scolding. The second is "a prolonged mewing *ya-a-a-a*", probably a challenge. Another is "a squealing whistle", made when excited, as in play-fighting; and he once heard an "*ie-yang*" call but never anything resembling a bark. Mortimer described the commonest sound uttered by his *maculicollis* as a high-pitched squeak which, in certain circumstances, changed to a high-pitched trill.

Very little has been found out about breeding in the speckle-throated otter. It would seem that a litter of 3 is a common number. Procter thought the period of gestation might be a little over 2 months. Mortimer, who observed and recorded growth over a period of nearly two years, found the weight of his female to be 1·36 kg at 1½ months; 2·5 kg at 5 months; 3·3 kg at 6½ months; and 3·5 kg at 7½ months, at which time it was apparently full grown, for the weight thereafter remained stationary at this figure, at least up to 20 months when the weighing ceased. The body length, too, remained unaltered. Teeth were still being cut at 6 months.

Taxonomy. Nine forms have been named from different parts of Africa, six of them currently recognised in G. M. Allen's Checklist (1939). These have been diagnosed, often as independent species rather than races, on the characters of size or colour or markings, and mostly from single specimens or otherwise quite inadequate material. Colour is notoriously unreliable and in *maculicollis* is known to change with age (Procter, 1963). The same author indicates that the spotted white underside markings are even more undependable since even among the limited population on Lake Victoria "there is a very great individual variation in the amount of white on the throat. Every gradation is seen from no white spotting at all to the whole throat, chest, belly, front and sides of the fore-limbs and part of the hind-limbs being almost completely white". It has been suggested that both *matschiei* Cabrera, from Spanish Guinea with very dark pelage and relatively large teeth, and *nilotica* Thomas from Sudan, reputedly of yet larger size with larger teeth, may occur, in their respective habitats, in West Africa. But it will be obvious that, even if these races should prove to be valid, it is impossible to tell from existing West African material—one broken subadult skull and no skin furnished with measurements—whether this is so.

The anterior half of a very interesting skin exists in the British Museum, No. 34.9.16.1 from Maiduguri in the Sudan woodland of Nigeria. This is dorsally of a golden-brown colour rather lighter in tone than the usual run of rich chocolate *maculicollis* pelage; but the chief interest lies in the throat and chest area, normally pure white spotted with ground-colour. In this case it is merely a lighter golden colour without the least indication of any spotting; and, moreover, this paler area reaches higher than is usual in *maculicollis*, in fact to about the level of the eye and ear, the side of the neck and shoulder much as in *Aonyx*. Indeed, the specimen, which is a flat one, at first glance gives the impression of being an *Aonyx* skin that has been smoked and so discoloured; and it is in this and other respects not far removed from the type of Waterhouse's *Aonyx poensis*, No. 55.12.24.414. But it is not smoked; and the only foot now remaining on this partial skin, the left foreleg, bears three distinct claws, proving it incontrovertibly to be *Lutra*.

The measurements in the table on page 159 are derived from extralimital specimens of Bates's together with the young adult skull from Oban, south-east Nigeria.

Genus **AONYX** Lesson, 1827

African Clawless Otters

Aonyx Lesson, 1827. *Manuel de mammalogie, ou histoire naturelle des mammifères*: 157. Type species *Aonyx delalandi* Lesson (= *Lutra capensis* Schinz), from the Cape of Good Hope. The name is the two Greek words *a* without, and *onyx* claw, with reference to the feet.

Anahyster Murray, 1860, *Proc. R. phys. Soc. Edinb.* **2**: 157. Type species *Anahyster calabaricus* Murray (= *Lutra capensis* Schinz) from Calabar, Nigeria. This name is given by Murray himself as meaning belonging to an estuary, since Calabar lies in the estuary of the Cross and Calabar Rivers, but whence such a meaning was derived is not clear.

Paraonyx Hinton, 1921, *Ann. Mag. nat. Hist.* (9) **7**: 194–196. Type species *Paraonyx philippsi* Hinton, Uganda. The name is a compound of *Aonyx* with the Greek prefix *para* meaning near. Valid as a subgenus.

There are two groups of clawless otters, one wholly African, the other wholly Asian; the former are assigned to the genus *Aonyx*, the latter to *Amblonyx*, either as a

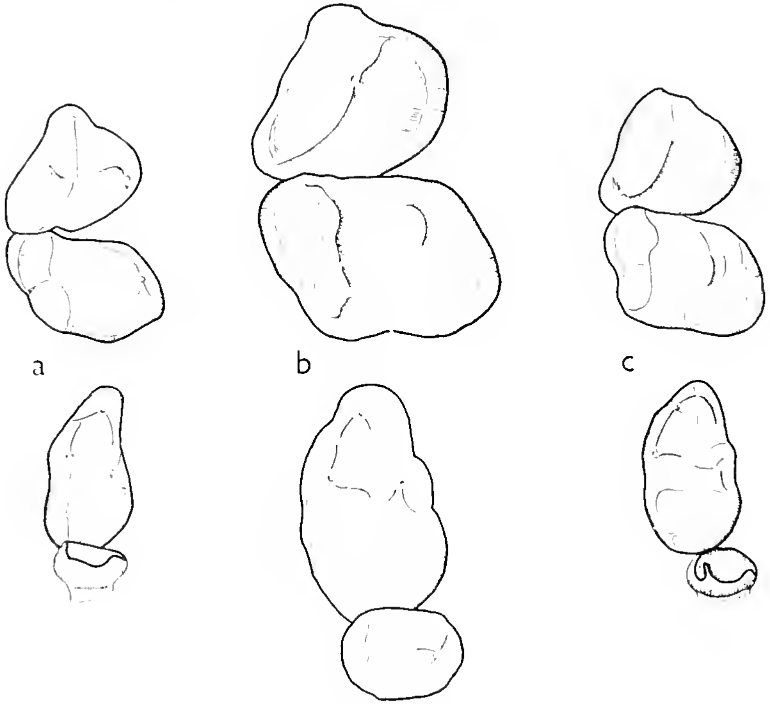


FIG. 22. Lutrinae: posterior cheekteeth; top row, right upper p^4 and m^1; bottom row, left lower m_1 and m_2, × 2: a. *Lutra maculicollis*, B.M. No. 23.1.22.44; b. *Aonyx capensis*, B.M. No. 10.11.25.2; c. *Aonyx* (*Paraonyx*) *congica*, B.M. No. 1938.9.29.8

full genus (Pocock, 1941; Simpson, 1945) or as a subgenus of *Aonyx* (Ellerman & Morrison-Scott, 1951). The Asian animals are much smaller than the African and have their feet webbed to the ends of the digits, whereas the African ones fall short of this. The African clawless otters are themselves divided into two groups, once considered to be distinct genera but now usually dealt with as one, though split into two pretty clear subgenera. These two sections have many points in common; but in spite of this it seems best to proceed at once to their separate consideration. The important diagnostic character lies in the dentition but the two subgenera may be told apart thus:

KEY TO THE SUBGENERA OF *AONYX*

(previous key page 140)

Dorsal pelage only slightly "frosted"; the crown width of m^1 about 13 to 15 mm, and of m_1 10 mm or over . . . . . . **Aonyx** (*page* 149)
Head and shoulders often with a well "frosted" mantle; the crown width of m^1 about 9·5 to 10·5 mm, and of m_1 6·5 to 7·5 mm . . **Paraonyx** (*page* 154)

Subgenus **AONYX** Lesson, 1827

Typical African Clawless Otters

Aonyx comprises a single species, *capensis* Schinz, and is sufficiently differentiated from its companion subgenus in the above key, and no further subgeneric details are here necessary.

AONYX CAPENSIS Schinz — Cape Clawless Otter

Lutra capensis Schinz, 1821, in Cuvier's *Das Thierreich . . . aus dem Franzosichen frey übersetzt* . . . **1**: 214. Cape of Good Hope.

Lutra inunguis F. Cuvier, 1823, *Dictionnaire des Sciences naturelle* . . ., **27**: 247–249. Cape of Good Hope. The specific name is the Latin for without a claw.

Aonyx delalandi Lesson, 1827, *Manuel de mammalogie ou histoire naturelle des mammifères*: 157. Cape of Good Hope. This was called after Mons. Delalande, who provided the information on which the species was founded.

Lutra poensis Waterhouse, 1838, *Proc. zool. Soc. Lond.*: 60. Fernando Póo. Type in the British Museum, No. 55.12.24.414, sex?; skin only, in poorish condition.

Anahyster calabaricus Murray, 1860, *Proc. R. phys. Soc. Edinb.* **2**: 157–158. Calabar, Nigeria. Type in the British Museum, No. 63.12.17.5, ♀; skull only, in fair condition but 3 upper incisors, the right m^1, and m_2 from both sides missing. The original B.M. number was 836b.

Lutra gambianus Gray. This was listed as a synonym by Gray himself under *Aonyx lalandii* in *Proc. zool. Soc. Lond.* for 1865: 130, as having been published in "Gray, Cat. Mamm. B.M. 111 (skull, B.M.)". In Gray's own handwriting in a MS. catalogue the reference appears as "Lutra Gambianus Gray Ost. Cat. p. 141, 1847". Both references appear to be quite untraceable, and no diagnosis seems, in fact, ever to have been published. The undescribed intended type, however, is in the British Museum, No. 46.11.2.12, ♂, (original No. 836a); skull only, in moderate condition, partly broken and with a number of teeth missing.

Lutra lenoiri Rochebrune, 1888, *Vert. Nouv. Afr. Occid.*, ser. 3, p. 9 (according to Trouessart, 1897, *Cat. Mamm. Viv. Foss.* ed. 1, pt. 2, p. 285); but this reference has not been traced—nor, seemingly, was it by G. M. Allen (Checklist, 1939) either.

Distribution and general. This is possibly the most widespread, if not the commonest, otter in Africa. Most otter accounts, both of wild and domesticated animals, seem to concern this species rather than *Lutra*. Described originally from the Cape of Good Hope, and hence somewhat misleadingly today referred to as the Cape clawless otter, it has since been collected or reported from a large number of places in most countries from South Africa northwards to Ethiopia in the east and Senegal in the west. It is as much a forest animal as one of the more open and arid woodlands; and it is known to occur on mountains at over 2000 metres. G. S. Child (private communication) records it from Kainji Lake and the Borgu Game Reserve in the Doka bush of extreme western Nigeria. It is said to inhabit, sometimes, the same localities as *Lutra*; and its unmistakeable tracks have certainly been observed by A. J. Hopson in the sand some 350 metres from the shores of Lake Chad, on which *maculicollis* is known to be fairly common. Moreover, skins of *Aonyx* are frequently exposed for sale in Malamfatori market, not far from the lake. In Sierra Leone *Aonyx* is, according to T. S. Jones (personal communication), plentiful in all areas, being frequent in the mangrove swamps. Skins are, there also, commonly offered for public sale. It seems possible that *Aonyx sensu stricto* is entirely replaced in certain areas by the subgenus *Paraonyx*.

Nine West African specimens exist in the British Museum from: an unspecified locality in Fernando Póo; Calabar (forest belt), Zaria (Doka woodland) and Maiduguri (Sudan woodland), all Nigeria; Ashanti and Asikumi near Oda (both forest) in Ghana; Sierra Leone, Bonthe and an unspecified locality but almost certainly forest; Bolama Island, Portuguese Guinea (mangrove); and Gambia, locality unknown. Two are complete juveniles; of the remainder only two have skulls, and there are no external measurements whatsoever.

Description. The Cape clawless otter (Plate 2) is a bulky animal. At 16 to 20 kg it is far larger than *L. maculicollis*; and even bigger specimens than this have been recorded in South Africa, up to nearly 30 kg. The head & body length is from about 750 to 925 mm and the tail about 410 to 550 mm, but precise measurements for West Africa do not exist. Indeed, of all the *Aonyx* skins in the British Museum only three have measurements, one from Kenya and two from Ethopia. The coat is variable in colour from a deep red-brown, almost as dark as *L. maculicollis*, to a distinctly paler mid-brown, the spinal zone being a little darker than the sides. In some cases the hairs have pale tips, particularly over the shoulders and neck, but these are not so white as in *Paraonyx* and the overall effect not nearly so "frosted". The feature which, apart from size, visually distinguishes this otter from *maculicollis* is the wholly white or cream, quite unspotted, chin, throat, upper chest, side of the neck and of the face to the level of eye and ear. The margins of the very small ears are white.

It is the feet, however, that constitute the most important difference between *Aonyx* and *Lutra*. They are quite devoid of the usual carnivore long, sharp claws though in some cases furnished with rudiments. These last are to be found only on the hindfoot, usually as tiny flattish nails on the 3rd and 4th digits. The digits themselves are finger-like in appearance; and, indeed, the whole paw is very similar to a small hand, the more so as the interdigital webs are much reduced on the forefoot. The structure is, in fact, used for grasping much in the manner of a hand and is far more deft than the usual mammalian structure apart from the primates. The palmar and plantar pads are better developed into a united central pad than in *Lutra*. The rhinarium is broad and rather dog-like.

Skull. The mature *Aonyx* skull is an incomparably larger, stronger and more rugged structure than that of *Lutra maculicollis*. The rather flat braincase is not only broader but has also, in the males, a sharp, deep sagittal crest and pronounced, upturned supra-occipital crest which continues round the sides of the braincase to exaggeratedly large and prominent mastoid processes. There are also large, slender paroccipital crests. In the females this cresting is not so highly developed; while in the young of both sexes the cranium is rounded and quite smooth.

The long intertemporal and short interorbital regions are abruptly narrow and more or less parallel-sided; there are sharp postorbital processes and slight ridges joining them to the sagittal crest, thus marking out the pentagonal plate usual in this subfamily. The arches are strong with well-developed jugal hooks reaching up towards the post-orbital processes. The rostrum is extremely short and falls away almost vertically; the anterior nares very large. The palate is rather narrow and continues, parallel-sided, well to the rear of the toothrows. The bullae are small and flat. The condylar hinge is deep and strong; the mandible very powerfully built, with a tall coronoid process, much excavated at its base in the ramus to accommodate a large muscle.

The dentition is powerful. The incisors of the upper jaw form a nearly straight, serried transverse row, those of the mandible being often a little more irregular. The canines are exceptionally long and sharp, suited to penetrating deeply and holding securely a peculiarly slippery and active prey; the first three premolars, above and below, are relatively small, p^1, when not lacking, and often p^2 as well, being practically in contact with the inner face of the canine. The result of the smallness of these teeth is that, though there is not strictly what is technically known as a postcanine gap (see page 18), there is enough space between the two toothrows anteriorly to accommodate a fair amount of flesh and thus increase the firmness of the canines' hold on a fish. The cheekteeth as a whole form a short compact series; the upper carnassial has one long pointed cusp, the lower three, set in equilateral fashion, but soon wearing down and together with the very broad posterior molars forming more of a crushing than sectorial unit, well suited to dealing with the soft flesh of fish and molluscs. In spite of the general impression of strength the teeth as a whole seem very liable to both wear and damage. It is the great breadth of the posterior cheekteeth which chiefly serves to differentiate *Aonyx sensu stricto* from the subgenus *Paraonyx* (fig. 22). The maximum crown width of m^1 in the former is of the order 13 to 15 mm as contrasted with 9·5 to 10·5 mm in the latter.

Habits. *Aonyx* has often been kept in captivity, and if procured at a sufficiently early age makes an agreeable, interesting and amusing pet, friendly to both human beings and other animals. Its behaviour in domestication has therefore been well observed and corresponds closely to that of other otters in similar rather artificial circumstances. But its way of life in nature is a different matter. Although the species has often been written about most of these accounts consist, in fact, of a good deal of surmise and generalities and remarkably little that is actually positive. Statements, indeed, seem sometimes to be diametrically opposed; as when (*fide* Shortridge, 1934) Lancaster says that *Aonyx capensis* is solitary as a rule, while Moseley asserts that it hunts in small companies. Both, of course, may be true, the latter applying, as in any other otter species, to a bitch and her young.

The African clawless otter may, in remote streams, lakes or swamps, sometimes be come across fishing or sporting in the water at high noon; but where it has reason to fear man it confines its activities to the early and late parts of the day, and possibly becomes largely nocturnal. A great drawback of having to adopt a nocturnal existence must lie in the increased difficulty of detecting and capturing fish in the dark. Possibly crabs are easier. *Aonyx* is always held to be much less of a fish eater and more of a crab eater than *Lutra maculicollis*. It is a fact that the spraints contain a good deal of crab shell, and the feeding sites, constantly revisited, are littered with claws and other remains of these crustaceans. The species is said to take, also, the usual list of other foods—molluscs, lizards, small rodents, birds and so forth. Eyre's tame *Aonyx* greatly appreciated freshly-killed moles. It has in southern Africa a great reputation as a fowl and egg thief; but no clear evidence of this seems to be forthcoming and any such robbery might as well prove to be the work of a ratel. Certainly any interest in eggs does not appear to lie in their attraction as food; for Eyre (1963) records an occasion when a domesticated otter, having of itself discovered two dozen eggs in a cupboard, instead of treating them as a desirable meal, hurled them, presumably one by one for amusement in the usual otter fashion of dealing with a pebble, all over the floor. Zammarano (1930), as the result of first-hand experience in the field, decided that the clawless otters were endowed with very acute senses, and he characterized them as cautious and cunning in the highest degree and the hunting of them, consequently, as anything but easy. The species has often been observed on the sea coast; it is, or was some years ago, to be seen in the large lagoons, not far from the sea, between Tiko and Douala (Cameroun). T. S. Jones obtained a specimen in a comparable situation of mangrove and sea at Bonthe (Sierra Leone).

Clawless otters make good pets if taken young and brought up on the bottle. In captivity these animals, though demanding in time and patience, exert considerable charm. They display quite unexpected intelligence, solving problems which they would not come up against in nature such as opening tins, bottles and cupboards with amazingly dexterous fingers. The paws are used almost as hands, not only holding things but also to throw small articles (Eyre, 1963). This author describes a variety of sounds made; a high-pitched squeak, demanding attention; a purring growl with a warble in it when pleased; a whine of frustration; a hiss and a growl when frightened; and a "most unearthly scream, most frightening, when he is in a temper". The explosive "*Hah*!" uttered by *Aonyx* in the wild has already been referred to in the general observations.

Nothing definite appears to have been recorded of breeding. The normal litter seems to be 2 or 3, but as many as 5 has been estimated from a field observation of a bitch and cubs. T. S. Jones (personal communication) had numbers of young brought to him in Sierra Leone and from these the litter size appeared to be invariably 2. The period of gestation is unknown but has been guessed at as about 2 months. There is probably no set breeding season in West Africa but T. S. Jones reckons that it is normally between September and October, the whelps being born in a hole in the bank. On the 5th October he obtained a very young animal which had its eyes open but which he thought was still being suckled.The skull of this specimen is, in fact, very thin and there is no sign of the permanent dentition. The skin has the correct adult coloration though the fur, as noted earlier, has not its final composition. On the other hand, two newly-born specimens exist, both wholly white, above and below. Eyre (1963) says that in a young animal the round eyes are a deep navy blue. As with other otters, the young have to be taught to swim by their parents—a fact that must be borne in mind with captive whelps. They are often somewhat reluctant.

Taxonomy. In spite of the very wide range of this otter there is little doubt of there being but a single species of *Aonyx* in its restricted, subgeneric, sense. The question of races is more obscure. Pohle (1919) recognised four, with *poensis* Waterhouse in addition as a separate species; G. M. Allen (1939) six, none of them from West Africa. There have, however, been four attempts to relate special forms to this region, three of the proposed types resting in the British Museum. In 1838 Waterhouse named *poensis* from a skin which, from its size and the nature of the pelage, appears to be that of a young animal. The diagnostic characters given, largely colour, are without much value; the skin has no feet and it is therefore not absolutely certain that it is *Aonyx* at all. In fact both Thomas (1889) and Lönnberg (1910) considered it to belong to *Lutra maculicollis*. However, the throat, neck and sides of the face follow the pale, unspotted, pattern of *Aonyx*, but instead of being white or creamy they are, as Waterhouse described them, "of a rich deep golden yellow with a faint brownish hue"—though in the past 130 years this has become obscured by London grime. Pohle (1919), disagreeing in respect of synonymy with Gray, Trouessart, Thomas and Lönnberg, accepted this unusual colouring as having full specific validity. He further entirely rejected Thomas's and Lönnberg's opinions regarding the genus of this specimen on the grounds that the throat was unspotted, a character that never occurred in the *maculicollis* group. That Pohle himself seems to have been wrong in this is demonstrated by the *maculicollis* skin, B.M. No. 34.9.16.1, with indisputable claws on a forefoot but without spots, and not very dissimilar from the specimen now under discussion. The possibility therefore yet remains that the *poensis* type is, in fact, a *Lutra*; and nothing further can be decided regarding its generic, specific or subspecific standing until more and better material emerges from Fernando Póo.

The next proposed form, *calabaricus* Murray from Calabar in south-eastern Nigeria, was founded on a skull very poorly diagnosed by Murray, not only as a species but as the type of a distinct new genus as well because it had one fewer premolar in the upper jaw than *Lutra vulgaris* of Europe. This absence of p^1 is now known to be a not unusual dental variant, and J. A. Allen (1924) regarded the species as "practically indeterminable" from Murray's diagnosis. The skull, now in the British Museum, appears to differ in no material respect, except possibly its slighter size, from other typical *capensis*. Next, never referred to in literature except by Gray himself, comes his *gambianus*, of no date but prior to 1865. The skull of this reputed species also is in the British Museum and, apart from its somewhat larger size, does not differ from typical *capensis*. The name is a *nomen nudum*; no description of the species seems ever to have been attempted and it appears, with untraceable references, merely in the list of synonyms of *Aonyx lalandii* Lesson given in Gray 1865: 130 and Gray 1869: 109.

Finally there is Rochebrune's supposed *lenoiri* from Senegal. The work in which this is reputed to have been described is said (Thomas, 1889: 196) to have been privately printed and hence never validly published. However, he apparently actually examined Rochebrune's description and remarked, in a footnote, that the so-called "diagnosis" suffered the usual lack of all diagnostic characters. This, therefore, is also a *nomen nudum*; and in this case there is, moreover, no known existing specimen of the reputed species whatsoever (Lönnberg, 1910: 3).

Whether or not there are forms that might constitute valid West African races is quite indeterminable from the study material at present available. In the erection of such races considerable caution would be called for in view of the known idiosyncratic variation that occurs in otters—illustrated earlier in this account by Procter's observations of *Lutra maculicollis*. The situation, in fact, has changed very little in the half-century since J. A. Allen (1924), with commendable understanding and restraint, wrote of the then reputed forms of *Aonyx capensis*: "As these five forms appear to have been described in each case from a single specimen, without flesh measurements and in some instances from poorly prepared material, none of them can be said to rest on a very satisfactory basis. The differences in coloration indicated by the descriptions of these forms are more than covered by the range of variation in the present Lang-Chapin series of some twenty specimens from a single locality (Faradje), while the individual difference in size is more than covered by the twelve adults. The status of these various forms should be held more or less in abeyance until a good series from each type locality has been studied and compared. Under such circumstances, it seems better not to add another name to the list . . . ."

Such skull measurements as are derivable from the present very poor West African material in the British Museum are given in the table on page 159. There are no external data.

Subgenus **PARAONYX** Hinton, 1921

Small-toothed Clawless Otters

The chief characters which distinguish this subgenus from *Aonyx sensu stricto* are sufficiently shown in the key on page 149. The main point of difference certainly lies in the dentition, the contrast in size of the posterior cheekteeth being so marked, as shown in figure 22, that in spite of the otherwise strong overall general resemblance of the skulls it is easy to tell the two subgenera apart at a glance.

Three species have been described: *congica* Lönnberg from lower Congo, *philippsi* Hinton from Uganda, and *microdon* Pohle originally from lower Cameroun but subsequently reported also within the limits set for this account. These have been pretty generally accepted as independent species; but it appears to the present writer that the evidence in support of this, based as it is on insinifigcant differences of size argued for the most part from single skulls, is very slender indeed. The three "species" can at most be reckoned as races; and the value of even such a reduced status is, on the few data now available, of doubtful worth or validity. Lönnberg's description of *congica*, the earliest form now assigned to *Paraonyx*, was based largely on a broken skull from which very limited measurements could be taken. Because of this, Pohle, in later erecting *microdon*, was able to make only three cranial comparisons, though in respect of teeth he made ten. None of the differences he cites seems to have much importance. Hinton in diagnosing *philippsi* as the type species of his new genus *Paraonyx* appears to have been quite unaware of Pohle's earlier creation. The three forms are here treated as a single species, *congica*.

AONYX CONGICA Lönnberg Small-toothed Clawless Otter

Aonyx capensis congica Lönnberg, 1910, *Ark. Zool.* **7**, No. 9: 1–8. Lower Congo.

Aonyx microdon Pohle, 1920, *Arch. Naturgesch.* for 1919, sect. A, pt. 9, **85**: 145–147. Bomse, Nana River, Cameroun. The specific name is from the Greek *micros* small, and *odon* tooth.

Paraonyx philippsi Hinton, 1921, *Ann. Mag. nat. Hist.* (9) **7**: 196–200. Lake Bunyonyi, British Ruanda (= Uganda). Type in the British Museum, No. 21.1.22.1; skin in good condition, skull with the arches broken and partly missing. Called after Captain J. E. Phillipps, M.C., District Commissioner at Kigezi.

Distribution and general. No specimen actually assigned to *congica* or emanating from the Congo exists in the British Museum; but there are four skulls and five skins of *philippsi*, all from Uganda. The position as regards the form most closely associated with western Africa, *microdon*, is in some ways the best. The existence of *Paraonyx* in West Africa itself was not suspected until in 1938 Dr. M. D. W. Jeffreys obtained several skulls from the Nun marshes. Two others were procured later by the present writer from the same area, so that there are now 9 skulls and a skin in the British Museum collection, a much better representation than there is of the other forms and of the more widely distributed *Aonyx capensis*.

It seems impossible today to fix with precision the whereabouts of the village of Bomse whence *microdon* was originally described; but it was probably at about 5°55N., 15°15E. The Nana River is a tributary of the Sangha and flows eventually into the Congo. It is thus just extralimital to the area covered by this present work. The Nun, or Noun, River flows into the Sanaga and thus lies well outside the Congo basin to the north. Its upper reaches pass through the Ndop plain and are there extensively marshy, the centre of this swampy area being at about 5°55N., 10°25E., that is to say some 40 km directly east of Bamenda. The surrounding area is today open country with scattered trees of a rather Guinea woodland type, though in the past it was very probably closed forest, relicts of this yet remaining. The altitude of the Ndop plain, though lower than that of the surrounding mountains, is probably still of the order 1300 metres.

No specimens assigned to *microdon* from elsewhere in the area herein treated as West Africa seem ever to have been recorded; but Pohle cites a number of localities of occurrence in lower Cameroun. These, however, are for skins unsupported by skulls, and their identification as what we now call *Paraonyx* rather than as typical *Aonyx* is, as Pohle himself pointed out, somewhat uncertain.

Through the courtesy of Dr. P. J. H. van Bree of the Zoologisch Museum Amsterdam it has been possible to examine a skull procured by him from Loa-Loa near Makokou, North-east Gaboon. This lies in a geographical situation distinct from those of the other specimens under consideration, since it is neither in the Shari and Niger drainage systems, taken in this work as constituting the major part of West Africa, nor in the Congo basin but in the westwardly sloping area emptying into the Atlantic via the Ogowe River. The locality is some 700 km south of the Nun marshes. Dr. van Bree's specimen differs in certain respects from the *microdon* material from this last area; but it is less toothworn, and the basisphenoid suture is still detectable, as it is not in the British Museum material. Moreover, it is a female, whereas none of the London examples is sexed. These facts may account in some measure for the differences which are apparent: there is no sagittal crest, no sharp supraorbital processes, the rostrum at the level of the canines is appreciably narrower, the mastoid processes are far less bulky, and the coronoid process more slender. But even if these distinctions held for further specimens from this area they are racial rather than specific.

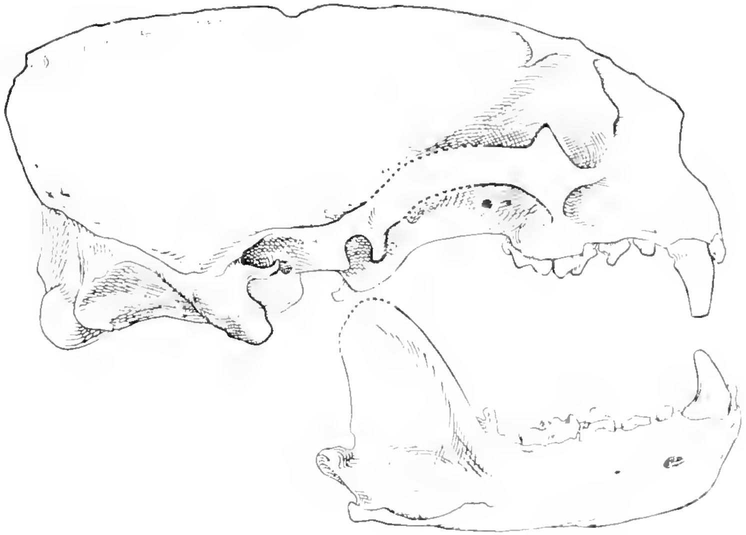


FIG. 23. *Aonyx* (*Paraonyx*) *congica*: skull, B.M. No, 1938.9.29.4, sex ?, × $\frac{4}{5}$; lateral view

FIG. 24. *Aonyx (Paraonyx) congica*: skull, B.M. No. 1938.9.29.4, sex ?, × $\frac{4}{5}$; palatal & dorsal views

Description. In general overall appearance *Paraonyx* is extremely similar to *Aonyx*. The body build is much the same, possibly a little larger; the pelage colour and pattern basically the same, that is to say deep sepia-brown on back and belly but the chin, throat, cheeks and chest wholly creamy-white without spots. The most obvious external difference lies in the "frosting" of the head, neck and shoulders due to the bristle-hairs being white-tipped. A little of this may be present in *A. capensis* but it is usually either lacking or not very marked; in *A. congica*, on the other hand, it forms a conspicuous feature extending from just back of the eyes to a little past the shoulders. In some cases it is pretty concentrated, in others well diffuse but none the less obvious. The margins of the small ears, too, are more conspicuously white. The forefeet are unwebbed; the hindfeet only to the second joint. Hinton said that the facial vibrissae were weakly developed in comparison with *capensis*; but there is not much evidence that this is so except possibly in so far as those situated above the eyes are concerned.

Skull (figs. 23 and 24). Apart from the dentition, which is comparatively shown in figure 22, there is not much to distinguish the mature *Paraonyx* skull from mature *Aonyx* except for a rather broader interorbital and intertemporal breadth. The rami, instead of being more or less straight-sided, curve in towards one another.

Attention has already been abundantly drawn to the relatively small size of the posterior cheekteeth, the most important diagnostic feature of the subgenus; the average crown width of m^1 is only about $9\frac{1}{2}$ mm as contrasted with at least 50 per cent more in *capensis*. The canines are rather shorter and slighter; and in 8 out of 13 skulls p^1 was never developed.

Habits. Absolutely nothing is known of the habits of *Paraonyx*. Lönnberg (1910) and Hinton (1921), however, both made some interesting surmises from the nature of the feet and the reduced size of the posterior cheekteeth, supposing from the one that this species would probably prove to be yet more terrestrial than *capensis*; and from the other that it was not well adapted to dealing with hard-shelled crustacea but rather with small terrestrial vertebrates and eggs. In this connexion it is of interest to note that the Ndop plain, which *microdon* inhabits, has numerous small streams and other water-courses but no largish rivers such as otters normally like to frequent and swim in and which would be much better stocked with fish. The swampy nature of the terrain makes it ideal for amphibian life, and it would thus certainly seem possible that this otter consumes a high proportion of frogs and relatively little fish.

Taxonomy. Something has already been said of this. There seems to be no good reason to suppose that three independent species exist. The question boils down to whether the named forms do in truth constitute valid races. The data are slender and a little confused. There is no specimen of *congica* in the British Museum from which to make direct measurements and comparisons; in respect of this, then, there exist only Lönnberg's figures from a broken skull (incidentally, misquoted in Hinton, 1921). On this very flimsy evidence it does, however, seem to be slightly the largest. The table on page 159 gives the impression that *microdon* is a little larger than *philippsi*; but the 3 skulls of the latter are all females; the *microdon* skulls are unsexed but from the appearance of the sagittal crest nearly all seem to be males. The evidence, therefore, is quite inconclusive and a third name is, at any rate for the time being, best omitted.

Table 8: Numerical data for subfamily *Lutrinae*

		Aonyx capensis		*A.* (*Paraonyx congica*	
	Lutra	*calabaricus*	*gambianus*		
	maculicollis	Type	Type	*microdon*	*philippsi*
Vegetation	Various	Forest	?Guinea	?Guinea	?Sudan type
Number in mean	4	1	1	9	3
Condylobasal length	105·7	(130)	(140)	125·0	118·0
Basilar length	94·4	114·4	125·1	113·2	104·9
Palatilar length	41·4	59·0	65·4	54·1	50·2
Zygomatic breadth	62·0	86·7	93·8	93·4	84·2
Upper cheekteeth breadth	32·6	(47)	(49)	39·5	36·6
Interorbital breadth	16·0	26·3	32·3	32·1	26·6
Postorbital constriction	16·6	24·5	26·1	31·9	29·4
Braincase breadth	51·1	66·5	69·0	70·2	66·7
Toothrow (c—m^1)	33·0	42·4	46·6	37·9	34·9
p^4 length	11·7	14·4	(14·7)	9·8	9·2
m^1 length	8·1	13·2	13·3	8·6	7·4
m^1 breadth	9·5	14·5	15·6	10·3	8·3
m_1 length	13·3	19·8	19·1	12·4	11·8
m_2 length	4·5	(6·6)	6·2	4·1	3·8
Head & body	648	—	—	—	—
Tail	378	—	—	—	—
Hindfoot	109	—	—	—	—
Ear	18	—	—	—	—
RATIOS (per cent)					
Tail/head & body	58	—	—	—	—
Zygom. br./condylob. l.	59	(67)	(67)	75	71
Braincase/condylob. l.	48	(51)	(49)	56	62
Braincase/zygom. br.	83	77	74	75	79
Palatilar l./condylob. l.	39	(45)	(47)	43	43
Interorb./postorb.	96	107	123	101	91
p^4/c—m^1	35·5	34·0	31·5	25·8	26·4
p^4/m^1	144	109	110	114	124
m_1/m_2	296	(300)	308	302	310

Superfamily **FELOIDEA** Simpson, 1931

The morphological distinctions between this group and the corresponding superfamily Canoidea have already been set out and discussed on page 29. Superficially the Feloidea are a somewhat less heterogeneous assemblage. There are only three families, all well represented in West Africa. The Felidae, or cats, may be taken as most typical of the group and, large or small, are of uniform and unmistakable appearance. A major section of the second family, the Viverridae, though with certain very obvious differences, bears in many respects a sufficient overall external resemblance to the Felidae to have earned the widely used general designation "bush cats"; though another section, the Herpestinae or mongooses, stands fairly clearly apart. The third family, the Hyaenidae, provides for the layman something of a mystery in that these animals which bear considerable external resemblance to dogs should, in fact, be grouped systematically with the cats. However, the fossil record shows them to be closely connected with the Viverridae, of which they are a late offshoot (Simpson, 1945).

As already made clear in connexion with the Canoidea there is no single character that indubitably defines this superfamily other than the septate bulla; and that, as will later be seen, is deceptive in the case of the hyaenas, as Pocock (1916c) made clear.

The three families, as they occur in West Africa, may be separated by the following key:

KEY TO THE FAMILIES OF THE FELOIDEA

(previous key page 27)

1. Cat-like in form; head roundish with a short muzzle; ears (except in *F. libyca*) wholly or partly black on their backs; skull with the rostrum abruptly deflected and short; braincase mostly rather rounded but sometimes with a low, abrupt sagittal crest and well developed supraoccipital crests; cheekteeth only $\frac{2\ 1}{2\ 1}$ or $\frac{3\ 1}{2\ 1}$ . . . . ***Felidae*** (*page* 373)
2. Somewhat dog-like in form with long legs but the back sloping downwards from shoulder to rump; muzzle long but blunt, the jaws very powerful; braincase long and remarkably narrow, merging gradually into a sharp sagittal crest but with a poorly developed supraoccipital crest; rostrum long; cheekteeth $\frac{4\ 1}{3\ 1}$ or $\frac{4\ 0}{3\ 1}$. . . . . . ***Hyaenidae*** (*page* 341)
3. Usually of small or smallish size, legs short, muzzle pointed; coat often spotted or speckled; braincase long and oval, with a pronounced supraoccipital crest but at most a low sagittal ridge; rostrum long; premolars $\frac{3 \text{ or } 4}{3 \text{ or } 4}$, molars $\frac{1 \text{ or } 2}{2}$ . . . . ***Viverridae*** (*page* 161)

Family **VIVERRIDAE** Gray, 1821

Civets, Genets, Mongooses etc.

Distribution and general. The Viverridae are a large family divided into 6 subfamilies and about 35 genera covering roughly 75 species. They are to be found in Asia, Africa and in a limited fashion, to the extent of one mongoose and one genet, in Europe. They are in a way specially associated with the island of Madagascar in that 4 of the 6 subfamilies occur there, 2 of them, embracing one-fifth of the viverrid genera, being endemic to the island and, indeed, the only wild carnivores there. Three subfamilies appear in West Africa; and in these there are 13 genera containing 23 species.

Most of the Viverridae are of smallish size; but in West Africa the civet is a relatively bulky creature running to as much, sometimes, as 14 or 15 kg. They live in all kinds of terrain from rain-forest to near-desert and up to an altitude of about 1800 metres. Some are wholly terrestrial, some largely arboreal; none is wholly aquatic but some live near streams or swamps and swim well. Most of them are, except at mating time, of a solitary nature; but some of the smaller mongooses hunt in parties. Some are in a small and mostly local way valued for their skins; one, the civet, has over the centuries played a more important and widespread commercial role in providing a basic ingredient of many perfumes; but all in an indirect way exert an influence upon civilization and the balance of nature in general by reason of their impact upon rodents, reptiles, amphibians and other creatures that man regards as pests and which would, in fact, get out of hand without the constant controlling influence of these small carnivores.

Description. In general, the Viverridae have long, slender, somewhat cylindrical and often cat-like sinewy bodies, but there are a few of rather heavier build. The tails are mostly long or very long, sometimes highly mobile, always well-haired and often bushy. In some it is conspicuously ringed; but never, except in one extralimital genus, prehensile. The pelage is of varying length, generally rather on the short side but always dense, spotted, striped, speckled or, in rare cases, black. The legs are short, the feet, in African species, mostly digitigrade, the sole pads being highly characteristic. In West Africa there are with one exception always five digits on each foot (though this is not so elsewhere) and the claws in the genets and palm civets are partly retractile. The head is small, the muzzle long and sharp, the eyes large or small, and the ears sometimes, if not large at least very prominent, sometimes inconspicuous. A bursa may or may not be present on the outer rim of the pinna according to subfamily. The females have 2 to 3 pairs of abdominally situated mammae; in all, scent glands are well developed especially the so-called anal ones; but there may be others in the perineal region, between the base of the penis and the scrotum in the male, or between the vulva and anus in the female.

Skull. The skull is elongate, with a braincase that is much longer than broad, ovoid in shape, smooth except sometimes for a low sagittal crest, and always with a prominent upcurved, sharp supraoccipital crest. There are marked, pointed postorbital processes which in some genera are short but which in others nearly approach or in some cases join the jugal process to form a complete circumorbital ring. The postorbital constriction is generally marked. The zygomatic arch is moderately stoutly built, the maxillary process being very short and penetrated by a fair, but not large, infraorbital canal. The rostrum is usually long, but less so in the Herpestinae; the anterior nares wide. The palate is mostly rather narrow but broadens somewhat posteriorly and is continued in a narrow parallel-sided extension considerably to the rear of the toothrows. The bullae are large and bulbous, showing anteriorly a more or less clear constriction indicating the internal septum dividing the structure into two chambers; but *Nandinia* is extremely unusual in having the posterior one of these merely cartilaginous and thus disappearing from all but very carefully prepared skulls. The paroccipital processes are sometimes virtually absent or indistinct, but are mostly well developed and closely adherent to the posterior aspect of the bullae. In old skulls the fusion of all sutures is very complete.

Flower & Lydekker (1891) wrote that the second lower incisor was raised above the level of the first and third; but, at least as far as West Africa is concerned, this is wholly untrue. The six incisors of both jaws form a compact more or less straight transverse row, the outer ones being somewhat or pronouncedly larger than the others; in some cases the lower incisors are bilobed. The premolars are of the usual form; the upper carnassial has an anterior lobe despite Flower & Lydekker's assertion to the contrary, though mostly small and sometimes, with wear, indistinct. The upper molars are mostly narrowly transverse and are usually markedly smaller than this tooth, but in some of the mongooses m^1 does approach p^4 in size; m^2, when present, is generally much smaller, and in *Nandinia* is reduced to a peg. The dental formula is very variable even within a single subfamily, the total number of teeth being 36, 38 or 40. Since the incisors and canines are always $\frac{3\ 1}{3\ 1}$ this is due to diversity in the premolars and molars of both jaws, these cheekteeth numbering $\frac{4\ 2}{4\ 2}$, $\frac{4\ 2}{3\ 2}$, $\frac{4\ 1}{4\ 2}$, or $\frac{3\ 2}{3\ 2}$.

Habits. Since these are vastly different in the different subfamilies, or even genera, little that is of general application to the family can be said here. The Viverridae are by nature fierce, both in the pursuit of their prey and in self-defence; but some of them if captured at an early age prove themselves to be interesting if not charming pets. Many people have kept, and have derived pleasure and even benefit from, the civet, genets and several different kinds of mongoose; but some of these, if not all, exhibit far more independence of their homes and keepers than members of the Canoidea or even of the Felidae or true cats.

The Viverridae are nearly all essentially nocturnal or crepuscular but some of the mongooses can be come across by day. They are all basically carnivorous, consuming various kinds of smaller creatures, rodents, birds, reptiles, amphibians, myriapods, crabs and insects; but many, if not all, also consume fruits. They mostly live in small holes or crevices; but, in fact, extremely little beyond broad generalities is known of the way of life of the majority of them.

Locomotion in certain African viverrids has been photographically investigated, analysed and sometimes figured by Taylor (1970) in relation to these species occurring in West Africa: *Civettictis civetta, Genetta spp., Nandinia binotata, Atilax paludinosus. Herpestes ichneumon, Galerella sanguinea, Ichneumia albicauda,* and *Mungos mungo.* The motions studied are walking, trotting, running, galloping, jumping, climbing, swimming and burrowing. He found that the only form of locomotion common to all was walking; trotting is the gait most usual to the bigger open-country viverrids, probably in association with the larger territories there customary.

Taxonomy. Of the three major groups into which the Feloidea are traditionally divided there is little disagreement regarding the clearly separate identity of the Felidae and the Hyaenidae and, at the same time, the close affinity existing between the animals of which each of these families is composed. The Viverridae, however, are more open to doubt. The six apparently natural groups of animals, comprising nearly 40 genera, therein lumped together may seem a somewhat heterogeneous collection to form a single family. Pocock, basing his ideas largely on external characters, gradually veered away from the standard conception of the Viverridae as a close-knit unit and came ultimately to elevate several of its six subfamilies to full family rank. All three West African groups were concerned in this more disassociated conception of Pocock's, the civets and genets becoming the Viverridae in a restricted sense, the mongooses the Herpestidae (originally Mungotidae), and the West African palm-civet the Nandiniidae, independent of the Asiatic palm-civets with which it had previously been associated.

Simpson's (1945) classification, however, rejects this and retains the wider conception of the Viverridae; and this grouping is adopted herein. It has a long history of acceptance by taxonomists, dating back, to all intents and purposes, a century and a half to Gray. During this period the majority of systematic mammalogists, no matter what their renaming or rearrangement of major cadres may have been, have seen little to disagree with in the close association with one another of all the small carnivores under discussion.

As regards the taxonomy of the Viverridae in general it must be added that Dücker (1957) from observations on instinct and behaviour reached the quite divergent conclusion that the Herpestinae are, in fact, related rather to the Canoidea than to the Feloidea, and most particularly to the primitive Mustelidae.

The three subfamilies may be separated by the following key, external distinction being easy but cranial differentiation more difficult.

KEY TO THE SUBFAMILIES OF VIVERRIDAE

(previous key page 160)

1. Coat speckled, or unicolorous blackish, sometimes with a transverse pattern of bands, but never spotted; tail bushy but never ringed; posterior part of the bulla with one exception (*Galerella*) much more inflated than the anterior part and subglobular or rather taller than it is long; auditory meatus with posterior and anterior lips which meet below in a horizontal V, thus forming a narrow gap which often extends as a slit into the floor

of the bulla; postorbital and jugal processes long and nearly or actually joining to form a complete circumorbital ring . ***Herpestinae*** (*page* 239)

Coat spotted or blotched, tail at least partially ringed; the whole bulla inflated, oval and longer than it is tall; or (*Paradoxurinae*) partly cartilaginous and usually mostly missing in prepared skulls; the auditory meatus a shallow ring without projecting bony lips; postorbital processes short (except *Paradoxurinae*) and far removed from a very short jugal process, leaving a widely incomplete circumorbital ring 3

3\. Two pale spots on the shoulders (sometimes indistinct); coat colour deep reddish brown; bulla cartilaginous or missing; postorbital process well developed . . . . ***Paradoxurinae*** (*page* 229)

No pale shoulder spots; coat reddish but not deep; bulla normal; postorbital process short . . . . ***Viverrinae*** (*page* 164)

Subfamily **VIVERRINAE** Gill, 1872

Civet, Genets, Linsangs

Distribution. The first of the three subfamilies to be dealt with in this work contains 8 genera. These are divided by G. G. Simpson (1945) into 2 tribes, the Viverrini and the Prionodontini, of which only the former is of West African interest, the latter, with 2 genera, being wholly Asiatic. The Viverrini also comprise 2 genera that are wholly Asiatic, besides 3 wholly African and one that occurs in both continents and extends its range into extreme south-western Europe as well. These figures, however, are subject to dispute according to the breadth of conception of some of the genera. Very considerable doubt and controversy exist also in regard to speciation in *Genetta*: but in this present account the 3 relevant genera of the subfamily are held to cover a total of 12 species.

There are a few apparently very rare and extremely local viverrines but the majority of the genera are common; and no part of West Africa, from coast to Subdesert, is without some representative of the subfamily. Extralimitally the group is widespread throughout the whole continent.

General characters. The West African animals included in the Viverrinae are very diverse in size, ranging from the bulky civet, scaling perhaps 17 kg, to the slender linsang, which can scarcely weigh more than 2 kg at most. All members of the subfamily dealt with herein have a prominent spotted or blotched pattern to their coats, never being merely speckled like the Herpestinae; and their mostly long or very long tails are at least partly ringed, and with few exceptions more or less cylindrical in form. The face is sharp, the ears mostly fairly large, rounded and conspicuously upstanding above the level of the crown—in this, as in many other ways, the subfamily differing clearly from the Herpestinae. The ears differ further in always possessing a marginal bursa on the pinna. The limbs are short or shortish, ending in 5 digits armed with curved claws that are mostly to some extent retractile but in the civet scarcely at all. With the exception of the pads, and sometimes the area immediately around them, the soles of the feet are hairy to the heel. The pelage is composed of fine underfur, often very dense, and of bristle-hairs of round or very slightly flat section, which in some genera are very long and dominate the coat, in others of subordinate importance.

The scent glands in the Viverrinae are perineal, situated between the scrotum and the prepuce in the male, and between the anus and the vulva in the female. They are, besides being of different form, thus quite differently sited from those of each of the two other West African subfamilies. The glands open externally into a medial pocket or pockets; and in one case, *Civittictis*, the waxy secretion collecting therein has been commercially exploited for many centuries.

Skulls. The skulls are narrow; even in the case of the very large and in some ways exceptional *Civettictis* the braincase is little broader than that of markedly smaller herpestines. The rostrum is long and narrow, very distinctly longer and narrower than that of any mongoose except *Liberiictis*. The orbital ring is far from complete, the postorbital processes being short, the jugal processes often little more than rudimentary. The postdental palate is short, nowhere near so long as it is broad. The large bullae are long and ovoid; the anterior chamber well-inflated, not depressed and reduced in size as in almost all Herpestinae.

There may be 38 or 40 teeth, the cheekteeth numbering $\frac{4\ 2}{4\cdot 2}$ or $\frac{4\ 1}{4\cdot 2}$. Again with the exception of *Civettictis* the dentition is by comparison with the mongooses relatively light, the anterior premolars being narrow, almost linear. It is clearly of a sectorial nature, not of an insectivorous type found in many members of the other subfamily.

Habits. Although nearly all the Viverrinae are common animals their lives in the wild have not been much observed. This is because they are nocturnal, solitary and secretive, spending much of their time in trees or dense undergrowth. All but the civet are arboreal, though they often come down to the ground to hunt. They are basically mainly carnivorous, the genets fairly strictly so, probably preferring small mammals and birds to other things; but the civet at least, and possibly genets too, consume reptiles, eggs, termites, beetle grubs and so forth if opportunity offers. They also from time to time eat fallen fruits.

So far as is known all viverrines are hole-dwellers, either on the ground or in trees. Breeding habits and periods vary and the little that is known of them will be found under the different genera, below. Both the civet and the genets have been kept as pets; but while they tolerate domestication during early life they remain more aloof than the mongooses and soon seek their independence in the wild.

Taxonomy. There is little doubt of the distinctness of the Viverrinae from the Paradoxurinae and Herpestinae, though the relationship with the former is much closer than with the latter. In fact, as explained later in the introduction to the Herpestinae, it is open to considerable doubt whether the two groups are really as close to each other as G. G. Simpson's classification puts them. General form, pelage, feet, claws, scent glands, skull characters and teeth are all quite distinctly different.

Within the subfamily the genera are clear, and there has not been that confusion which arose in the Herpestinae. But there is argument regarding the closeness of affinity between African and Asiatic representatives of the subfamily which affects two of the three genera covered by this present account, *Civettictis* and *Poiana*. The former is widely held to be synonymous with or at most a subgenus of the Indian *Viverra*; and the latter to be closely allied to the Asiatic linsangs, *Prionodon* and *Pardictis*. The present author follows Pocock in considering *Civettictis* to merit generic standing of its own for reasons given later in the account of this genus; and he further believes superficial resemblances between African and Asiatic linsangs to be misleading and probably more the outcome of convergence than of particularly close relationship.

KEY TO THE GENERA OF VIVERRINAE

(previous key page 163)

1. Size large, head & body about 800 mm; tail only about half as long; a white or pale patch, sometimes obscure, bordered with black on the side of the neck, and a black mask across the face from cheek to cheek. Adult skull about 140 mm; postorbital constriction not marked; dentition powerful . . . . **Civettictis** (*page* 167)

   Size much smaller, head & body not more than 550 mm, often much less; tail at least three-quarters as long as, or longer than, head & body; no conspicuous black and white pattern on the side of the neck or mask across the face. Adult skull rarely as much as 100 mm, mostly much less; postorbital constriction well marked; dentition light 2

2. Very slender; head & body about 380 mm; fur very short and velvety; mostly without any clear dark spinal stripe; spots always small; tail often with faint intermediate rings. Adult skull about 70 mm; cheekteeth $\frac{4 \cdot 1}{4 \cdot 2}$, the posterior lower molar being minute . . . . **Poiana** (*page* 219)

   Of heavier build and mostly larger size, head & body 400 to 550 mm; pelage longer and coarser, often with a distinct dark spinal stripe; the markings may be small spots but are more frequently larger blotches; tail without intermediate rings. Skull 75 to 90 mm; cheekteeth $\frac{4 \cdot 2}{4 \cdot 2}$ **Genetta** (*page* 177)

Genus **CIVETTICTIS** Pocock, 1915

African Civets

Viverra Linnaeus, 1758, *Systema Naturae*, 10th ed., 1. 43; in part, of various authors, especially before 1915. Type species ("both by elimination and selection", Thomas, 1911) *Viverra zibetha* Linnaeus, Bengal. *Viverra* was the Latin name for a ferret.

Civettictis Pocock, 1915, *Proc. zool. Soc. Lond.*: 134. Type species *Viverra civetta* Schreber, Guinea. The name is a compound of the specific name *civetta*, *q.v.*, with the Greek *ictis*, a weasel.

Distribution and general. Civets are sometimes referred to more fully, but misleadingly, as civet cats because of the superficial resemblance of their colour and markings to certain domestic cats. Actually, their much larger size and pointed muzzles might be thought to justify rather more the description often bestowed on them by country-bred Africans as bush dogs. Neither, of course, has any shadow of accuracy, though the relationship, as members of the superfamily Feloidea, is somewhat closer to the cats than to the dogs. They occur only in the Old World between western Africa and eastern Asia.

Two other, relatively minor, genera apart, the civets proper all belong to the two cited above in the synonymy, the former of these being wholly Asiatic, the latter wholly African. Until 1915 the two geographical groups were regarded as congeneric; and this is not infrequently still the case (*e.g.* Ellerman, Morrison-Scott & Hayman, 1953), the African civets being looked upon as little more than specifically different from the Oriental—a question of which something more is said below in the taxonomic section. Understood in this broadest sense, civets occur, in Asia, from the east coast of southern China to the Indian peninsula; and, in Africa, south of the Sahara from Senegal to central Angola and the northern parts of South Africa. The range is, thus, discontinuous, with a gap of something in the nature of 4000 kilometres separating the civets of Africa from those of Asia.

In the area dealt with in this present account, African civets are known to occur from Senegal to Cameroun. They are equally at home in forest or open country, at least as far inland as the Sudan woodland; but possibly do not exist in the Sahel, and certainly not in the Subdesert. T. S. Jones has noted them at an altitude of about 1000 metres on Bintamane Mountain, Sierra Leone. African civets are pretty abundant on the ground, except at the extreme inland vegetational limit of their range. As there is only one species, the matters of description and habits will be dealt with under the specific head; but a brief glance must be taken at the taxonomy of the genus.

Taxonomy. *Civettictis* is grouped by Simpson (1945) in the viverrine tribe Viverrini together with the three other African genera *Genetta, Poiana* and *Osbornictis*, and the two Asiatic genera *Viverra* and *Viverricula*. Distinctions between it and the first two are indisputable and are made clear in this present work; *Osbornictis* J. A. Allen, 1919, the so-called water civet or aquatic civet is recorded only as a very rare animal from eastern Congo and differs from all other known viverrines in its plain, unspotted, pelage. It is the separation of *Civettictis* from the Asian *Viverra* that is most commonly open to question and, consequently, of chief interest to West Africa.

Pocock, who as Superintendent for many years of the London Zoo had exceptional opportunities for the careful and comparative examination of deceased as well as living animals from different parts of the world, carried out detailed studies of many external features that had hitherto received scant attention or none at all. On these he based a number of taxonomic conclusions, including the generic disseverance of the African civets from those of the Orient. This last, though not wholly rejected by Hollister (1918: 116) was considered by him as better regarded as subgeneric until such time as further confirmatory evidence was available; and, following this, Ellerman, Morrison-Scott & Hayman (1953) expressed the positive view that Pocock's characters could not, at most, be rated higher than of subgeneric value.

The differential characters cited by Pocock were: firstly a marked distinction between the forms of the perineal scent glands; secondly, clear differences in the feet, the soles, apart from the actual pads, being entirely hairy in the Asiatic forms but naked anterior to the central pads in the African. In these latter, also, there is a metatarsal pad, absent from the former; and the claws are long and, more significantly, only slightly retractable as compared with short and more fully retractile in the Oriental civets. He cited, as well, other more minor points concerning the form of the plantar and palmar pads and also of the rhinarium. Pocock was well aware of the considerable tendency that exists to depreciate the taxonomic significance of external characters, and "since most contemporary mammalogists will probably consider cranial and dental characters of more value in the discrimination of genera than the external features here made use of . . ." he added supporting differences to be observed in the skull and teeth. In regard to the former he claimed that the bullae and the partially enfolding paroccipital processes were more prominent in *Civettictis* than in *Viverra*. This, however, is not always clearly so. On the other hand, his dental distinctions are manifest in that m^1, m^2 and m_2 are always of a very much greater size in the African species than in *Viverra*. To this he might have added that the lower carnassial in *Civettictis* is of a type appreciably further evolved from the basic sectorial form, being far broader and somewhat more complex posteriorly to bear on the enlarged inner section of m^1. The present author goes along with Pocock in regarding all these points as justifying generic distinction between the African and Oriental civets. G. Petter (1969) reached, from dental considerations alone, the same conclusion.

CIVETTICTIS CIVETTA (Schreber) African Civet

Viverra civetta Schreber, 1776, *Säugethiere*, pl. 111; 1777, text 3: 419–420. Guinea; but Congo, Cape of Good Hope and Aethiopia are also mentioned. The specific name is a Latinization of the French *civette*, itself derived from the Arabic *zabād* for one of these animals.

Distribution and general. The African civet (fig. 25) is distributed over most of the continent south of the Sahara, in the west from Senegal to central Angola, and in the east from Sudan to central Mozambique, that is to say roughly between about 15° North and about 18° South. This area covers a variety of vegetation from rainforest to open grass-woodlands, certainly as far inland as the Yobe Valley, near Yo, Lake Chad in the Sahel zone (A. J. Hopson, private communication). There seems little point in recording the names of the large number of places throughout West Africa from which civets are known; they are pretty common animals, more especially in the moister parts of their range, though they have also been reported as plentiful at Macina on the upper Niger, Sudan zone.

Description. These are easily the bulkiest representatives of the Viverridae in West Africa, weighing 10 to 17 kilogrammes and with a shoulder height of around 380 mm, that is to say over twice the size of a large genet. Civets are, nevertheless, for their size short-legged animals, their bellies not far off the ground. When on the hunt they trot purposefully through the bush, their long-faced, somewhat canine heads pointed straight before them and their relatively rather short, shaggy tails stretched out, but slightly drooping, behind. The impression is that of a bulky, greyish, heavily spotted, somewhat dog-like animal with a black tail.

FIG. 25. African Civet (*Civettictis civetta*)

The dorsal pelage is coarse and rather wiry; it varies in length, being in some specimens fairly long and in others unexpectedly short. It is composed of rather undulate and tangled underfur in which are mixed fairly abundant, very slightly flat bristle-hairs, strong distally but tapering basally. These bristles are markedly longer than the underfur, which they dominate not only by reason of this but because, also, of their much greater diameter throughout most of their length. They average about 40 mm in length but sometimes attain 50 mm, the underfur measuring only some 20 to 30 mm; and they may be wholly black, or white with longer or shorter black tips. Along the mid-dorsal line of the back from the shoulders or the hinder part of the neck to the root of the tail runs a long, black, erectile crest, the stout bristles of which are everywhere appreciably longer than the main pelage but increase in length posteriorly where, in the region of the hindquarters, they may attain 100 mm or more. These spinal bristles are dark throughout most of their length but always have longer or shorter glossy jet-black terminal portions. When, in anger or alarm, this crest is erected the animal assumes an appearance of even greater size than it really has.

The coloration of the African civet is widely variable. The dorsal ground-colour ranges between near-white, through creamy, to a slightly reddish-buff. On this is superimposed a pattern of dark spots or blotches, sometimes deep-brown but generally black. The size, shape and independence of these markings vary. Most typically the spots are large, of rather irregular roundish or quadrate shape, clear-cut, and nearly all separate from each other. They are not set in more or less regular longitudinal lines, as in some of the genets, but something in the nature of half-a-dozen rows can be made out on either side of the spinal crest. Occasionally the spots, especially those near the medial line, tend to coalesce into longitudinal bands; but in some specimens they display a tendency to run together laterally; and in some they are relatively ill-defined. Over the forequarters the bold spotted pattern fades out and the pelage becomes an intimate mixture of light and dark hairs, any maculation in this area being very obscure apart from a number of spots low on the shoulder.

On the side of the neck is a pronounced longitudinal black band which is separated below by a conspicuous white band from a second black one which broadens and passes below across the throat. The underparts are somewhat variable, the chest being always black or blackish; but the belly may be white, or blackish, or a mixture of the two. The face is strikingly marked with a black mask which crosses from cheek to cheek and just encloses the eyes. It is bounded anteriorly by a white area around the rhinarium and on the lips, and posteriorly by a whitish frontal area between the eyes and the ears. The continuity of the mark across the face is interrupted in some specimens, though rarely, by a medial whitish band joining the anterior white to the frontal grey area. The ears are rounded, low but none the less conspicuous with their white rims. A bursa is always present; its convex posterior flap is continuous above and below with the rim of the pinna; its anterior flap is widely but not deeply emarginate.

The upper portions of both fore and hind limbs are obscurely spotted; but the lower parts and feet are wholly black. There are five digits on each foot, the claws fairly long and only moderately curved, and very slightly retractile. In both feet the central plantar pad has the small pollical lobe separate from the main body of the pad

(Pocock, 1915a). In the forefoot the metacarpal pad is bilobed and is joined, in most cases, by two narrow strips of naked skin to the anterior naked sole area that lies between the central and the subdigital pads. The hindfoot, also, has this anterior sole area naked. The tail is little more than half the length of head & body. Dorsally it is wholly black; but the basal half has about 5 partial white rings, passing from side to side below. The tail is coarse-haired with very long bristles.

The perineal glands have been dissected, figured and described by Chatin (1874) and Pocock (1915a). Since these two accounts differ somewhat in their details the following is founded mainly on that of Pocock. He characterized the organs of the male and female as "tolerably similar". The glands are situated between the scrotum and the prepuce in the former, and between the anus and the vulva in the latter. Externally they appear as paired swellings separated medially by a slit-like orifice about 25 mm in length. When these two glandular lobes are drawn apart a moderately large oval orifice can be discerned on the inner face of each, and this leads into a large hair-lined sac or pouch which extends forwards, backwards and upwards within the gland. The inner walls of these two sacs secrete into them a very thick whitish or yellowish substance with a powerful musky odour, the "civet" of the perfumery trade; and this then makes its way through the two oval orifices into the intervening space between the two glandular lobes, which thus becomes a storage reservoir communicating with the outside world by the slit-like orifice first mentioned. Besides these perineal glands there is a pair of anal glands situated on the wall of the rectum. These secrete a foetid yellow liquid which imparts to the faeces a characteristic odour which may be of service in the demarcation of territory but, in view of the regular defaecation habit mentioned later, is more likely to be of defensive significance, as in the case of other small carnivores.

Completely black specimens are recorded from time to time; and in these it is impossible to detect any trace of the basic pattern, at any incidence of light, as one is often able to do in other melanos. One British Museum skin, referred to by Sanderson (1940), is quite different in its coloration from all the rest. In this, the ground-colour of the entire pelage, including the normally white areas of the neck and face, is a bright ochre-red. This may, of course, be natural, due to some form of erythrism; and if it is it is, indeed, remarkable. But the skin is obviously a locally prepared one, and Sanderson thought its unique appearance probably due to its having been cured in smoke, a not uncommon practice. The colour, actually, is not so much that yellowish tone produced by smoke as, rather, one which could be caused by steeping in palm-oil. This would have been a not improbable proceeding in the area from which the specimen came (Ogoja, extreme eastern Nigeria); and the soft pliability of the skin, as contrasted with the usual brittle stiffness of African sun-dried pelts, lends some support to this idea. The fur would, of course, have been subsequently washed to rid it of oil, but the residual red-dyeing effect of the palm-oil in the unpigmented hairs would resist this. Against all this is another fact: that though the long glossy black crest and tail are quite typical, the spots are smaller and more obscure than usual, as if there were something fundamentally exceptional about the whole skin.

Skull (figs. 26 and 27). The skull is strongly built, long and rather narrow, with a

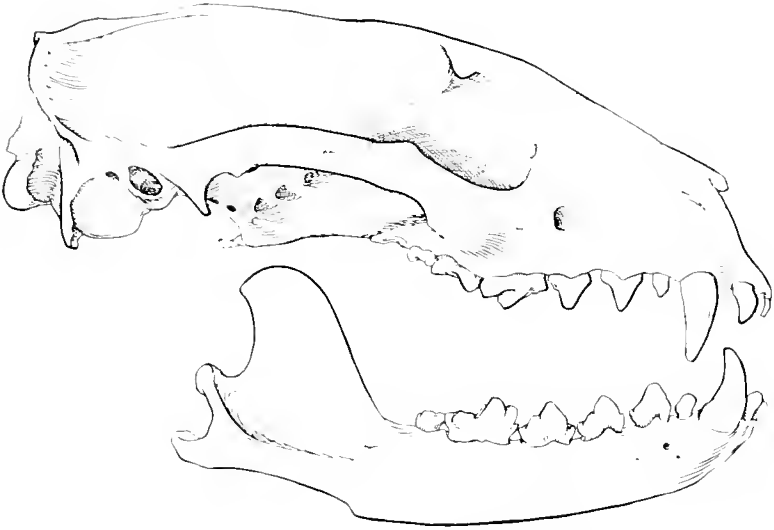


FIG. 26. *Civettictis civetta*: skull, B.M. No. 59.941, [illegible], $\frac{4}{5}$; lateral view

long ovoid braincase and not very marked interorbital and intertemporal constrictions. The supraorbital processes, though clear, are blunt, deflected, and not very extensive. All adult skulls, male and female, have a well-developed sagittal crest, joining a sharp, flange-like supraoccipital crest posteriorly in a T. The zygomatic arch is strong, the jugal process pronounced but blunt and short. The bullae are moderately large and oval, the posterior section far exceeding in size the anterior. The paroccipital processes are closely applied to the whole posterior aspect of the bullae and extend ventrally beyond their limit in long, strong points. The mandible has deep, strongly built rami; and, indeed, the whole skull and dentition constitute an instrument fashioned for powerful biting.

The dental formula is $\frac{3\ 1\ 4\ 2}{3\ 1\ 4\ 2} = 40$. The incisors are strong and set in a transverse curve; in both jaws the outer ones are larger than the inner; but this is most pronounced in the upper jaw, where i^3 is separated from the others by a small gap, is considerably larger and, being pointed and curved, begins to resemble a small canine rather than the normal chisel-edged incisor. The canines themselves, though strong, are not particularly large, and their outer faces lack the fine, shallow furrows characteristic of the other West African viverrids. All the cheekteeth, from p^1 to m^2 and p_1 to m_2, are strongly built; m^1 and m^2 are particularly large for this subfamily; m_1 is exceptionally broad posteriorly, and the whole tooth has more of a crushing than sectorial function. The posterior lower molar, also, is uncommonly well-developed, with a flat, far less acutely cuspidate, grinding surface than is usual.

One British Museum skull, No. 10.6.19.1 from Okigwi, eastern Nigeria, has an extra, large, premolar on each side of the lower jaw, set between p_4 and m_1.

Habits. Everyone is agreed that the African civet is an extremely secretive animal. This fact combined with its more or less strict nocturnal habits is responsible for the almost complete lack of field observations. It may seem strange that this should be so in a species that is pretty common in museum collections and which fairly regularly appears in zoos; but it is a not very intelligent animal and one that is readily trapped; and so, though not often observed in nature, becomes easily killed or captured. Sometimes a civet may be seen trotting up the road in the headlights of a car; and occasionally in the very early morning one may dart swiftly across a path, possibly disturbed by a

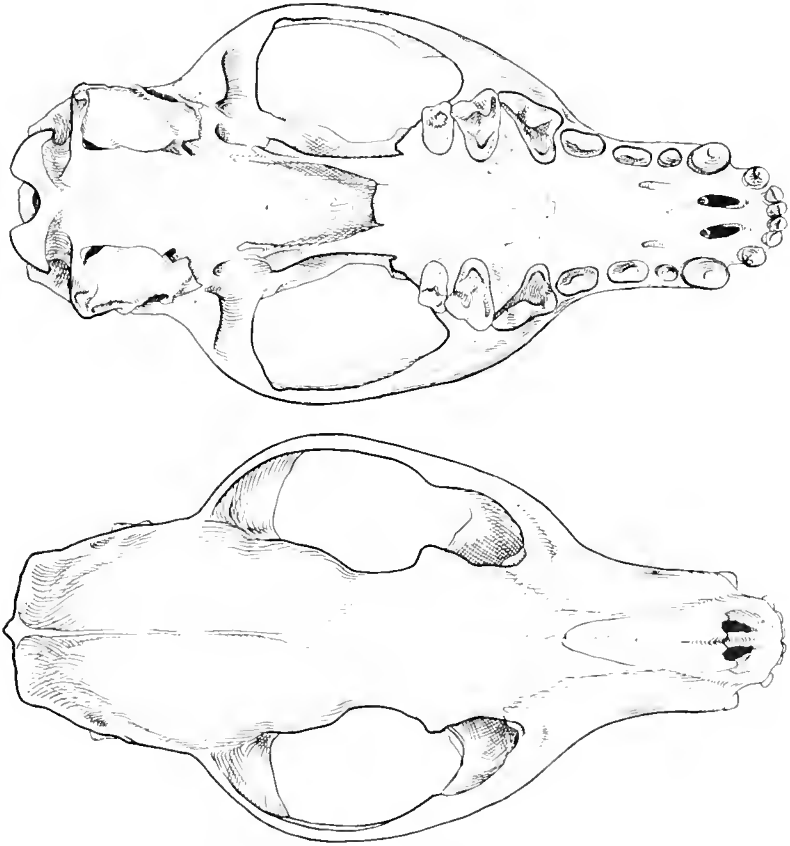


Fig. 27. *Civettictis civetta*: skull, B.M. No. 59.941, , ½; palatal & dorsal views

dog from its temporary resting place in the thick undergrowth. But civets can also walk stealthily; and even if one should be about in the half-light it is not easy to detect its grey spotted coat against checkered vegetation. With so little known about their habits it is impossible to be certain, but civets are generally believed to lead entirely solitary lives except at breeding time. They are certainly almost completely terrestrial, their shape and feet being little adapted to climbing in the manner of cats, though where there are positive footholds they can scramble up short distances, particularly before they have attained their adult bulk. They are said to be able swimmers, not afraid of taking to the water. Normally, during daylight hours they lie curled up in a temporary "form" in any dense vegetation; but when breeding they use a fixed nest, usually a hole in the ground made by some other animal, or amongst tangled roots. It seems probable that such nests are not lined in any way.

When it comes to the question of food, information is rather more certain because of the data yielded by droppings, stomach contents, and behaviour in captivity. African civets seem to be more or less omnivorous. Antelope meat, cane rat, guinea-fowl, eggshell, carrion, termites, beetles, grass and leaves have been found in stomachs (Bothma, 1965), carrion being predominant. But they are also said to eat other kinds of insects and their grubs; rats, snakes, lizards, frogs, crabs and millipedes. T. S. Jones, in a private communication, says that civets not uncommonly hunt in mangrove swamps, presumably to obtain crabs and mud-skippers. He has trapped them with stock-fish or dead rats; and Verheyen (1951), indeed, gives them almost the character of complete scavengers. At the right seasons they consume an exceptional quantity of berries and other fruits. T. S. Jones observed that they caused a good deal of trouble amongst young low palms just starting to fruit at Njala (Sierra Leone) by gnawing off the oily mesocarp. Astley Maberly (1955) records that they commonly eat the fruits of *Bridelia* and *Zizyphus*; and since civets mostly deposit their droppings in one fixed spot until they form a heap, such places often abound in dense seedling growths of these trees. Verheyen (1951) found one such excremental pile to measure 60 cm in diameter and 8 to 15 cm thick. Civets, like other viverrids, are known to raid poultry houses at night; and Shortridge (1934) recorded that they sometimes killed young lambs. The widely catholic tastes in food of African civets, and their partiality to fruit, has been well demonstrated in captivity; specimens, within the present writer's knowledge, consuming almost anything put down for them, including bowls of pawpaw and banana. That some food should have excitant properties is of interest: Mallinson (1968) records that it has been found inadvisable to feed freshly killed chicken or rabbit to viverrids with newly born young; female civets, and others, so fed have been found to become highly excited and subsequently to turn on and kill their litters. Some of the older writers on natural history stated that the amount of "civet" secreted by animals maintained in captivity for this purpose depended on the richness and abundance of food given.

The African civet can become very tame and docile in captivity if caught young enough; but Menzies (1966) found those of 6 weeks old already savage and to remain quite intractable. However, without question, reaction to attempts at domestication will vary with different individuals. One pet civet kept, or at least encouraged, about the house used to follow its owners like a dog for evening walks; and at dinner time would circulate round and under the table giving unsuspecting guests playful nips in their fingers should they by chance hold their hands down. Eventually, as sexual maturity is reached, civets, like so many unconfined pets, disappear into the bush never to return. An African civet has been known to live for almost 14 years in captivity.

Civets make a variety of sounds. They hiss when alarmed and utter a deep warning growl when they feel they are likely to be attacked. If they do get into a fight with one another there is a great deal of excited growling and yapping very like a dog-fight. Some years ago residents in the environs of Lagos often heard such quarrels at night, being sometimes awakened by the tremendous caterwauling and yapping.

There is little positive information with regard to breeding; but Mallinson (1968) has recently published a few facts gathered from animals in captivity. From two observed copulations he deduced that the period of gestation might be either 45 or 60 days. Nine births, covering 20 young, showed the litter size to lie between 1 and 4, the commonest being 2. The mothers frequently killed, and sometimes ate, their new-born young; and it was found less worrying for the female and less likely to lead to tragedy if the father were removed. Walker (1964) stated that there are generally two litters a year; but Mallinson, on the contrary, found with 5 females that the average interval between litters was approximately 12 months, and never less than 288 days. Immature specimens in the British Museum suggest that there is no favoured season for breeding in West Africa since very juvenile animals have been taken, in the forest belt, in mid-October, December and January, that is to say the beginning and middle of the dry-season; and also in mid-June and early July, well into the rains. According to Verheyen (1951) the newly-born young remain only about a week in the nest.

For many centuries the civets have been chiefly famous as the source of a widely-used ingredient of perfumes. This is an off-white or yellowish, very thick, greasy substance with a powerful musky odour secreted into the perineal pouch as already explained earlier in this account. Like many other basic materials, vegetable as well as animal, employed in the production of scents "civet" in concentrated form is apt to be nauseating or even highly repulsive; but when used in minute traces becomes not only tolerable but attractive. The trade, which was once extensive in Europe, North Africa, the near and middle East, has now considerably diminished, at least in Europe; but formerly African civets were kept under cruel conditions in very small cages in which they could not turn round, so that the animal could be easily controlled and was constantly available for the product to be scraped, with little effort, from the glandular pocket. This took place about twice a week, the animal being forced back against the back of the cage and its tail and hindlegs seized and held through the bars while the "civet" was collected, using a small spoon. The yield was about 2 or 3 grammes a time. Abyssinia was recently the chief source of supply, the substance being exported packed in hollow antelope horns; but earlier, Amsterdam was the centre of a big trade, both for the import of the substance to Europe and for its production on the spot by captive animals. The Dutch trader William Bosman, who was resident in

Table 9: Numerical data for *Civettictis civetta*

	West Africa general
Vegetation	Various
Number in mean	12
Condylobasal length	145
Basilar length	134
Palatilar length	73·6
Zygomatic breadth	77·1
Upper cheekteeth breadth	47·4
Interorbital breadth	29·2
Postorbital constriction	24·0
Braincase breadth	43·0
Toothrow ($c-m^2$)	57·7
p^4 length	13·0
m^1 breadth	13·7
m_1 length	13·5
m_2 length	8·2
Head & body	826
Tail	432
Hindfoot	123
Ear	57
RATIOS (per cent)	
Tail/head & body	52
Zygom. br./condylob. l.	53
Braincase/condylob. l.	30
Braincase/zygom. br.	56
Palatilar l./condylob. l.	51
Interorb./postorb.	122
$p^4/c-m^2$	22·5
m_1/m_2+m_3	165

West Africa towards the end of the 17th century and wrote a number of letters describing the various countries, their customs and animals, had, in translation, this to say of the civet "at present so well known in Holland that I need only acquaint you that they are brought to be sold to us very young, and then we give about eight or nine Shillings sterling for one. A large share of Trouble and careful Attendance is requisite to breed them up: Their Food is Pap boiled or made of Millet, with a little Flesh or Fish. They produce Civet when even very young; of which that of the Males is better than that of the Females, because the latter cannot avoid urining into the Civet Bag, which spoils it".

Besides its obvious worth to the scent trade, "civet" was also formerly much valued for a wide variety of reputed, but now long discredited, medicinal properties. It was employed as a diaphoretic; or as an emollient in such eruptive skin conditions as smallpox, measles and scabies; as a balm against apoplexy; as either a soporific or an aphrodisiac; or even as an ingredient of tooth powder.

Taxonomy. Other races besides the nominate one have been named, G. M. Allen (1939) recognising two, *congica* Cabrera, from north-eastern Congo, and *schwarzi* Cabrera, from eastern Africa. If these are accepted, then the correct citation of the West African civet must be *Civettictis civetta civetta* (Schreber). But the species shows such a degree of individual variation that there is a tendency today amongst authors to be sceptical of the existence of identifiable races.

Genus **GENETTA** G. Cuvier, 1816

Genets

Genetta Oken, 1816, *Lehrbuch der Naturgeschichte*, **3**, 2: 1010. Type species *Viverra genetta* Linnaeus. Oken's *Lehrbuch* is ruled to be unavailable by Opinion No. 417 of 1956 of the International Commission on Zoological Nomenclature. This name is a Latinization of the Old French *genette*, itself derived from the Arabic name for these animals, *jarnait*.

Genetta G. Cuvier, 1816 (*fide* Sherborn), Le Regne Animale, **1**: 156. Type species *Viverra genetta* Linnaeus.

Distribution and general. Genet is a simple enough name; nevertheless it is one that is not often used by English-speaking people in West Africa, who usually refer to these animals as bush cats. Not that the average person often, or ever, sees one of these nocturnal creatures in the flesh; but he may sometimes become aware of them through a raid on the fowlhouse, or occasionally through being brought a motherless baby for sale as a pet. Genets are, none the less, widespread and fairly common, occurring through practically the whole of Africa except the Sahara, and, in the region dealt with in this book, ranging from the Subdesert to the coast. They are known to occur at high altitudes in eastern Africa but were not taken at any great height on the Cameroun Mountain by Eisentraut (1963).

Genets, though all conforming to a general easily-recognisable pattern, occur in a wide number of different forms. How many of these, and indeed how many basic species, are valid is a much-disputed question. In this present work nine different species are described but, as will be gathered from the taxonomic section which follows later, some of these may not be valid or, as the outcome of a greatly-needed pan-African review of the genus, may eventually be shown to be merely western representatives of other, extralimital, species.

General description. The genets (Plates 3 and 4) are all smallish mammals with pointed muzzles and large ovoid ears in which a large bursa seems to be always present in West African species. The posterior flap of this arises, both above and below, behind the pinna, the shape of the anterior flap being variable in the different species. The slender, spotted body is some 450 to 550 mm long, the ringed tail somewhat shorter. Genets stand about 120 to 150 mm at the shoulder. An average weight of an adult is around 2 kg. The pelage, both of the body and the tail, consists of a mixture of terete or slightly flat-sectioned bristle-hairs and fine woolly underfur, the absolute and relative lengths of these varying from form to form. There is often, but not always, a medial dorsal stripe from about the shoulders to the root of the tail, dark, mostly black, consisting of somewhat, or much, longer bristles than the rest of the dorsal pelage, and apparently erectile. On either side of this spinal stripe run more or less parallel rows of spots, the number of such rows varying from 4 to about 7, though the lines are apt to become confused on the flanks and difficult to count precisely. The spots themselves vary in number from comparatively few to many; their spacing from relatively wide to close. They range considerably in size from fairly large to pretty small; in shape from quadrate to oval or rounded; and from full independence of one another to longitudinal coalescence into longer or shorter bands, more or less parallel to the mid-dorsal crest. Such concurrence usually concerns only the line or two lines nearest the spine, and commonly only the region of the lower back. The spots may be wholly of one colour, black or some shade of reddish-brown; or they may be annulate, having black margins with larger or smaller brown centres.

The back of the neck is basically marked with 5 more or less parallel longitudinal lines; a fine central one which posteriorly becomes the mid-dorsal stripe; on either side of this a slightly broader, but still narrow, line which joins the innermost series of spots; and, on the outside of these, two broader, and often very pronounced lines which posteriorly curl round and down over the shoulders. But some or all of these nuchal lines may, in certain specimens, become wholly or partly obscure. The belly is usually paler than the dorsal ground-colour and may be almost white, well-spotted or with very few spots. The thighs are spotted, the upper part of the foreleg often so; the lower parts of both legs may carry small spots or be practically plain. They may be light or almost black, this, at least as far as the forelegs are concerned, being often idiosyncratic and hence taxonomically unreliable, although in the past it has often been assumed to be diagnostic. There are five toes on each foot, digit 1 being separated from the others; each is armed with arcuate, fine, very sharp claws, which are retractile but not so completely as in the cats. Beneath each digit is a naked hemispherical or ovoid pad; a larger, composite one surrounding a central depression is situated in the middle of the foot; and another posterior to this, very long and bifurcate on the hindfoot. The face carries certain general markings, sometimes very clear, sometimes obscure though almost always detectable. The most prominent is a pale, often white, spot below the eyes; this is separated by a dark patch from a similar pale or whitish region on the upper lips around the rhinarium. There is a pale area between the eyes, parted medially by a dark line; and another pale spot above each eye.

The tails, though subject to some individual variation, are more constant in their basic characters than the dorsal markings are, and sufficiently distinctive to form the easiest and most dependable diagnostic character. The nature of the tail derives firstly from the actual length of the hair with which it is clothed and secondly from the relative length of the bristle hairs and underfur. In *genetta*, for example, the former are not only very long in themselves but also far exceed in length the underfur, which plays a very secondary role, the whole structure being of relatively rough appearance. In *servalina*, on the other hand, the bristles are short, and the abundant underfur only a little shorter, playing a major role in producing a soft, smooth, subcylindrical structure. In addition to this, the number and nature of the annulations are usefully diagnostic, though by no means so unswervingly constant as was formerly thought.

Genets are furnished with scent glands secreting a musky odour. These are situated in the male between the scrotum and prepuce, or in the female between the anus and vulva. Pocock (1915a) furnished a full description of these, both external and internal. Briefly, in his own words, they "consist of two elongated eminences covered with hair both externally and internally. When undisturbed the two lobes are closely apposed, their line of contact being marked by a longitudinal sulcus which is Y-shaped anteriorly, that is to say, just behind the vulva or prepuce". Internally, the glands are mostly tripartite, being imperfectly divided into three compartments by transverse ridges of integument. This description applies to the males of *tigrina*, *pardina*, *rubiginosa*, *genetta*, *dongolana* (= *senegalensis*) and *felina*, and to the females of the first three; but the females of the second three have a simpler, undivided pouch. Pocock regarded this as indicating two groupings of relationship within the genus.

Skull. Unfortunately *Genetta* skulls and teeth exhibit very little constant differences of shape and so are not a great deal of help in distinguishing forms. Some of the characters picked upon by Schwarz (1930) are misleading, being not certainly applicable to all members of a species-group.

The *Genetta* skull in general (fig. 29) is long in comparison with its zygomatic breadth, with a long, ovoid braincase, and pronounced postorbital processes separating marked intertemporal and interorbital constrictions. Yet though the whole skull is long and tapering the actual rostrum itself is remarkably short. Posteriorly, in the fashion common to the Feloidea, the braincase contracts and curves broadly out again to meet a very well-developed, flange-like supraoccipital crest. There may or may not be a sagittal crest over the main body of the cranium; but there is always a well-developed, sharp posterior portion joining the supraoccipital crest in a T. The forward continuation or absence of this over the braincase has been regarded as a valid specific character (Schwarz, 1930); the evidence from 29 mature West African skulls in the British Museum indicates that this may be broadly so but that its development is a function of age, and its absence save from really old specimens thus possibly misleading. There is, for West Africa, no evidence relating to sex, comparison being impossible since there are no old female skulls of *pardina*, in which species the crest is normally present in old males. A superficial look at some dozens of *Genetta* skulls from other regions revealed only three reputed females with developed crest. The bullae are fairly large, long ovoidal in shape. There is some evidence pointing to different relative developments of the anterior and posterior portions in different species, the anterior chamber around the meatus being largest in *genetta* and *thierryi*, less in *pardina* and least in *cristata* (fig. 28).

The ratio of the postorbital constriction to the interorbital breadth is fairly reliably diagnostic but not absolutely constant. In *genettoides* 19 skulls had the former appreciably less than the latter; but in 2 skulls the breadths were subequal. The *servalina* group also has the postorbital width less, one externally quite typical *cristata* specimen, No. 10.6.1.2 (Oban, Nigeria) alone having it greater. In a few exceptional cases the postorbital constriction is extremely marked. In one *genettoides* specimen, No. 46.397 (Oda, Ghana), it is as little as 8·4 mm in contrast to a mean of 11·5 mm; the difference between it and the interorbital breadth being about 6 mm as compared with a mean of the

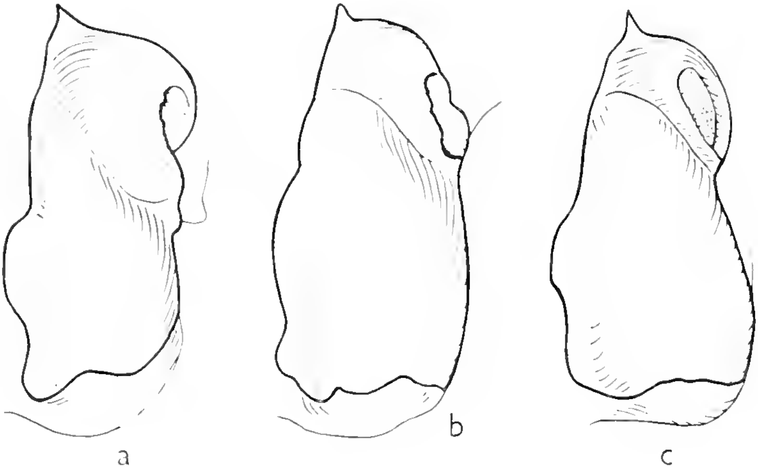


FIG. 28. *Genetta*: left bullae, × 3. a. *G. genetta* (? *afra*), B.M. No. 9.11.2.34, ♂; b. *G. genettoides*, B.M. No. 46.397, ♂; c. *G. cristata*, B.M. No. 30.323, ♀

order of 2 mm. For such atypical measurements there is no apparent explanation. The postorbital constriction is wider than the interorbital breadth in the *genetta* group and *thierryi*. Citing the postorbital processes as diagnostic Schwarz stated that they were absent or slight in *servalina*; this assertion would appear to be wholly untrue, except of juveniles, in both *servalina* and *cristata*.

The dental formula is $\frac{3\,1\,4\,2}{3\,1\,4\,2} = 40$. The incisors form tightly packed transverse rows, the outer teeth, both above and below, appreciably larger than the others, the cutting edges of the lower set being slightly bifid or trifid. The canines are strong and are chiefly notable for bearing very narrow, shallow, longitudinal striations on their outer faces. The lower canines are abruptly curved in the middle of their posterior faces and thus have the appearance of being bent upwards. The premolars are of the usual form except that p^3 in some cases has an additional cusp at the base of its inner face. When present it is, most commonly, well developed and quite obvious; but it is sometimes reduced in size. This feature is in some measure diagnostic but is not completely reliable: in 16 adult *genettoides* skulls this supplementary cusp was present and large in 9, small in 3, and absent from 4. Other species show something of the same irregularity of occurrence except *thierryi* where the cusp occurred in all 6 available skulls. There is nothing especially remarkable about the remainder of the teeth except that m^2 is always the smallest in the two jaws and may sometimes be very much reduced. Thomas & Wroughton (1910), writing of *stuhlmanni*, detected a marked sexual difference in the size of the upper carnassials, the females being 1 mm or more less in length. The comparative material from West Africa available in the British

Museum is too sparse to furnish reliable data relating to this; but such as it is it tends to confirm these authors' findings.

Habits. With the confusion that has existed over the different species of *Genetta* it is not practicable to relate the few field observations that exist precisely to named forms, and the general account which follows, a compilation from various sources, must take the place of the individual notes normally appropriate to specific sections. It can fairly safely be assumed that all genets are broadly similar in their habits except for such differences of detail as may arise from dissimilarity of habitat, high-forest species being possibly rather more arboreal in their way of life than those from more arid inland vegetation. It is, in some way, curious that so widespread and not uncommon creatures should have had so little recorded of them in nature. This is partly due to their secretive nocturnal lives; but they have long been kept in zoos and, within the present writer's experience, as domestic pets; yet though there are fairly plentiful records of their littering nothing beyond the most meagre observations on other aspects of their behaviour and way of life has, apparently, ever appeared in print.

Although exceptions, of course, always occur genets are pretty strictly nocturnal and are therefore rarely seen except in the headlights of a car by or those who range the bush at night with lamps. That they are from time to time seen and shot by local hunters is obvious; and they may occasionally be accidentally flushed from some daytime resting place in a tree or dense undergrowth; but the general run of skins and skulls in the British Museum gives the impression that the animals must for the most part have been taken in traps rather than killed by gun-fire. Experience with animals maintained about the house shows that they do, under these circumstances, put in an appearance about dusk; but even should they happen to be on the move in the forest while there is still daylight their excellently disruptive coloration combined with their stealthy caution would nearly always render them exceedingly difficult to detect.

Since authentic first-hand records of these animals in the wild are almost entirely lacking it is virtually impossible to make definite assertions. However, they appear to be rather solitary creatures except possibly at mating periods, when they doubtless forage in pairs. Even, at a later stage, the mother and her young do not openly associate for long, as they do in many other animals; for young genets, once past the early helpless state that confines them to the nest, quickly become capable of leading an independent existence.

Genets are to a fairly considerable extent arboreal, their sharp, curved claws being almost as well adapted as those of cats to scrambling up tree trunks. Some of their foraging is regularly carried out in trees, for birds, possibly their eggs and certainly their fledglings, for arboreal rodents, bats or the helpless young of larger tree-living species. They are commonly found in oil palms. However, a good deal, possibly even the major part, of their hunting is on the ground for ground rodents and reptiles. Like any other animals endowed with the power of swift climbing, genets take to trees as a ready and dependable means of escape from threat on the ground. Yet it would seem that, the first instinctive urge apart, they appear on reflection to feel safer, and with wider chances of escape, on the ground rather than limited to the trunk and branches of a single tree; for after their first hurried rush up the bole they frequently make for the ground again. Sanderson (1940) records that he only once saw a genet (*cristata*) in a low tree; alarmed at his presence it returned to the ground in an attempt to make its escape. He formed the opinion that the species was quite definitely terrestrial. Stevenson-Hamilton (1947), too, said of a South African species that when pursued it almost invariably took to a tree but on being approached generally leapt to the ground again to make off with bounds of remarkable length. He cited an instance of a genet leaping from a height of 5 metres and landing 7 metres away.

In consonance with their at least partial arboreal existence they have been recorded as sheltering or breeding in hollow trees or holes in trees. Loveridge (in Lawrence & Loveridge, 1953) tells of shooting a genet in Mozambique "as it lay curled up beside a hole high up on the trunk of a great baobab". Nevertheless, the majority of breeding observations—and they are not many—refer, rather, to holes in the ground. Possibly this may be due to the greater likelihood of accidentally coming across a nesting place in or on the ground than at some distance up a tree. Yet it is strange that those collectors who have spent a considerable time in West Africa "smoking out" or felling hollow tree stems in the search for bats or flying-squirrels seem never to have recorded the incidental discovery of genets. Possibly the sort of restricted holes that might appeal to genets as favourable breeding sites, such as small natural cavities where branches have fallen away, or woodpecker borings, or hornbill nests, are overlooked. The technique of smoking nevertheless commonly succeeds in South Africa (Stevenson-Hamilton, 1947).

However, holes are not always essential and, in the dry-season at least, nests may sometimes be exterior. One such was come across in February by an agricultural labourer near Freetown and described to T. S. Jones as "a bundle of sticks". From this a female genet had made her escape carrying one of her young in her mouth; the second baby was then captured in the nest and subsequently successfully reared. That such a breeding shelter was constructed by the genet itself seems improbable, and it is most likely to have been a fortuitous conglomeration of rubbish or, very possibly, a deserted squirrel drey. Jones also came across another unusual off-the-ground refuge, namely the roof of a house in Samaru (north Nigeria) from which he observed a family of 4 or 5 genets make its exit down a verandah post when it was nearly dark. This he was told happened every evening and that an adult pair dwelt permanently in the roof (private communication). This home would appear to have been naturally discovered and occupied by genuinely wild genets; but the present writer knew a more domesticated single animal that, having been captured young and hand fed, also discovered the roof as a warm shelter and spent its days concealed in a corner of the grass thatch, descending regularly at dusk to the sitting-room to be fed.

Genets, then, at least sometimes, occupy holes in trees; and according to Stevenson-Hamilton they may rest stretched out along a branch. But the majority of records refer to sleeping or breeding quarters on the ground; and in observations made on captive genets in which they were afforded a choice of sleeping quarters Carpenter (1970) certainly found them to prefer a hollowed out ant-heap on the ground to a covered box fixed high up. In suitable terrain terrestrial shelters may be amongst rocks; but they are more usually in the smaller kinds of "earths", either naturally occurring holes or those made or improved by other animals—ground squirrels, giant rats, porcupines, termites and so forth. They are almost certainly never self-constructed, the genet legs and paws being ill-adapted to excavation. Besides earthen holes, those amongst tree roots, or actually in rotted bases of trunks, or fallen, hollow logs are used; and temporary sleeping sites, though probably not breeding quarters, are made in thick grass, reeds or other dense low vegetation. The only actual first-hand description of a nest appears to be that of Loveridge (1922) who came across one in a hole in the ground consisting of a circular chamber with two bolt holes, unlined but perfectly clean.

If events in captivity can be used as a guide, breeding takes place pretty regularly twice a year. This, according to Verheyen (1951) is probably at the beginning and end of the rains—a supposition that is to a certain extent confirmed by juvenile West African specimens of *genettoides* in the British Museum collected in March, April, June, July, September and early December. The usual litter size is 2 or 3; but 1 is not uncommon, and 4 have been noted on several occasions, having occurred in no less than three successive births in the Duisburg Zoo in Germany (Remy & Condé, 1962). These latter authors have gathered together a considerable number of records, chiefly relating to the European genet; but the longest-continued observations of living animals are those made by Volf (1959 and 1964) in the Prague Zoo. He records that a single female genet (*genetta*) produced 32 young in 7½ years, of which 20 were born in the last 4 years of her life, the litters being almost without exception two a year. This animal attained sexual maturity at the age of about 4 years and died, of old age, at 13 years Such an age for genets in captivity is not uncommon, the record being about two months short of 15 years (Crandall, 1964).

The period of gestation has been put at 10 to 11 weeks (Volf, 1959); but Remy & Condé (1962) mention an American figure (Smithsonian) of only a little over 8 weeks. A well-authenticated period observed in Paris was 68 days, that is, just on 10 weeks. The young are born blind and with the auditory meatus covered; Volf (1959) observed the ears to open on the 5th day and the eyes on the 8th. According to the same author the newly-born kittens are well-haired though this covering is of a deeper, wholly greyish, hue than that of adults, to whose rather paler and warmer colouring they do not approximate until after the second month. In the British Museum there is a very dark, almost melanistic juvenile of *genettoides*. Writing of the European genet Volf said that at birth there are only 3 rings near the base of the tail, the whole dorsal aspect of the tail being dark, the underside paler. With advancing growth the pale colour encroaches on the dark and at the same time forms more rings, which reach 6 in number at three weeks. Weight at birth in this species is from 61 to 82 grams. This increases very rapidly, especially in the first few days, doubling itself in 12 days and quadrupling in a month. The growth curve is more or less a straight line; and at two years the fully adult weight is of the order of 2 kilograms. This may increase slightly with greater maturity. It has been found in captivity that immediately after birth the male must be removed for two or three weeks as he may otherwise kill the young. But according to Verheyen (1951) in the wild the male actually provides food for the resting and nursing mother. Killings of their newly-born kittens are, for unknown reasons, not infrequently carried out by the females.

Volf (1959) provides data for the eruption of teeth, given below. It is, however, not clear whether reference is to milk or permanent dentition; it may be presumed to be the former, yet the premolars which emerge subsequently to the molars on the 44th and 51st days would seem to be replacements of an earlier milk set. Volf observed the upper incisors to appear on the 23rd day, at which date, also, crawling commenced and the ability to raise the head. All the incisors and both upper and lower canines erupted by the 30th day; the molars appeared on the 37th day; the upper premolars on the 44th, and the lower premolars on the 51st. The young animals attempted at 5 weeks to defend themselves by spitting; and after 8 weeks by biting. At this age they were fully active and weaning took place, and they were capable of taking care of themselves. A certain amount of solid food is in fact accepted from about 6 weeks. Loveridge (1922) found that a baby he attempted to bring up would not look at meat but only drank milk sweetened with sugar to the consistency of treacle; and it became very fond of jam and would eat egg, after shelling. Mrs. Sonia Jeffrey (private communication) found that a baby genet could be successfully reared on tinned unsweetened milk with an occasional mixed vitamin tablet. This animal showed an interest in red meat when it weighed 255 grammes and ate its first mouse three weeks later when it weighed 310 grammes.

Although the shift to solid food normally takes place at about 2 months, young genets, if given the opportunity may continue to suck up to the age of 6 months. In captivity, Volf records, the young of one litter were usually removed from the mother before her next pregnancy. Where this, on one occasion, was not done the mother, through over-long continued suckling, reached a state of exhaustion in which the foetuses failed to develop properly and the young were either still-born or died soon after birth. It is interesting to note that although Volf estimated that the *genetta* female which mothered 32 young must have been about 4 years old before she became sexually mature, he found the offspring to attain this state after about only 2 years.

It has sometimes been held that genets, unlike many other flesh-eaters, are very strictly carnivorous in their diet, firmly rejecting all kinds of vegetable foods. This is not so. Dr. Gordon Corbet shot a genet in Kenya that had its whole intestine crammed with a mass of orange-coloured berries, besides the remains of a spider and insects (private communication). From the description it would seem that the fruits were almost certainly those of the so-called Jujube Tree, *Ziziphus mauritiana* Lam., widely spread in the more arid woodlands of tropical Africa. Another very interesting observation concerning feeding on vegetable material has recently been made by Sonia Jeffrey in Ghana (private communication). She found that something like 70 per cent of the contents of one stomach consisted of rotten wood, some of the pieces being up to 18 mm long. She supposed that this indicated that the animal had really been after some more tasty delicacy buried in the wood. Such an explanation is very possible since beetle grubs, sometimes of large size, frequently abound in dead trees, as woodpeckers well know. The fact that genets are often connected with palm trees leads to the speculation that they may, at least sometimes, be attracted not only by the fruits but also by the very large grubs of the giant palm-weevil found in decaying stems.

As concerns the more usual, carnivorous, foods Shortridge (1934) wrote that genets prefer fresh meat; but Loveridge found tinned corned beef to be quite acceptable; and Stevenson-Hamilton (1947) says they are partial to carrion and readily enter baited traps. Besides rats, gerbils, squirrels and hares they take insects, especially locusts and beetles, and will tackle birds of the size of guinea-fowl and domestic breeds. They also eat lizards; while Loveridge (in Lawrence & Loveridge, 1953) found the remains of a burrowing snake and a large yellow scorpion in the stomach of one. Whether they eat amphibians and molluscs seems to be unrecorded. They reputedly eat shrews; but Sonia Jeffrey kept a young genet that would eat most kinds of meat but would not look at a shrew. Although one of her captive specimens would not touch a freshly killed snake another one readily ate them. Stomach contents of genets examined by her included the legs of skinks and insects, and orthoptera wings; and one contained two mice which may, from the red colour of the fur, have been *Lophuromys sikapusi*. One of her live specimens pounced on and ate a bird that flew into the house.

In their attacks on fowl-runs they show, according to Stevenson-Hamilton, considerable cunning, generally taking a single bird at a time, returning for another when this has been consumed. A bird of this size is attacked at the throat, the blood sucked, and then the upper part of the breast taken. Carpenter (1970) found some evidence that males were more often poultry thieves than females; and that once a genet had acquired a taste for domestic fowls it tended to disregard more natural prey. In the absence of such an acquired taste rodents were nearly always preferred as food to birds, being pounced upon and killed forthwith, while birds were only killed and taken later if the rodent supply were insufficient. On two widely separate occasions Carpenter found genets to capture bats in roofs, the genera concerned being *Eptesicus*, *Scotophilus* and *Rhinolophus*. Over a period of five nights one genet took an average of six bats a night.

Genets are not normally offensive; but when alarmed spit and bare their teeth, and if hard-pressed can give a severe bite. Like other animals they vary a good deal in temperament and it is difficult to generalize. They can be tamed, especially when captured very young; and some become fairly trusting and even milldy friendly, though never to the extent of mongooses and other small mammals. They seem to be very much one-man pets and to resent strangers. The majority, at least under conditions of semi-freedom in Africa, as a rule soon manifest independence; and though they may appear in the evening to take what food is offered they mostly remain rather coldly self-sufficient, exhibiting the aloofness of a cat with none of its friendly domesticity. Genets are also doubtful assets; for while it is true that they may keep the house free of rats and possibly snakes they have no loyalty when it comes to a question of robbing their owners of meat from the pantry or effecting a midnight entry to the fowl-house.

Genets emit a musky odour, though not so strong as that of some other viverrines. Gray (1830), in his description of *maculata* as a living animal in the Tower of London menagerie, said that it had an exceedingly strong musky smell and was continually placing its two hindlegs against the wall of its cage, and pressing the subanal glands against it, leaving two chocolate brown musky streaks. These were far larger than those of a similarly captive common civet, which performed the same action; and it seemed, therefore, that more secretion was emitted by the genet than by the bigger animal. Both were obviously attempting to demarcate their territories; and it may be assumed that something of this sort is regularly carried out under natural conditions, though, in the wild, urination and defaecation are probably the most usual method and adequate to the purpose. Genets have not usually been reckoned amongst the animals that use fixed latrine sites but Carpenter (1970), working in Natal, found these to be not uncommon, generally in dry river beds or thick bush, some of them obviously in use for a considerable time. As regards territorial behaviour and the instinct and ability to return to the home range the same author has made some very interesting observations and deductions in relation to the rusty-spotted genet in South Africa. From these it would appear that females are more attached to a given territory than males, which are more inclined to wander. By repeated trapping and marking, these genets have been shown to return to their original home ground from distances up to about 30 kilometres.

Taxonomy. Forty years ago Schwarz (1930) in his introductory remarks to what has proved to be the last published general review of this genus expressed the opinion that its systematics were obscure. This is, to say the least, somewhat of an understatement. As it stands today *Genetta* is a confusion of forms, with the definitions of the classic species uncertain and the status of later creations—at times recognised as valid species, at others bandied about as mere races betwixt one reputed species and another—a tangled skein with no clear guiding threads giving hope of any generally acceptable unravelment Over the years no less than 44 discrete species have been described in Africa, apart from several forms rated from the start as racial. Most of these have now been either reduced in status or synonymised, and G. M. Allen in his Checklist of African Mammals (1939) recognised only 6 species and 27 subspecies. This is far from being the last word.

There is something inherently wrong in a situation wherein authors so frequently disagree over the status or validity of forms and their opinions regarding their essential diagnostic characters; or have changed their own minds in these matters; and in which museum labels so manifestly bear witness to uncertainty in determination. Two plain facts emerge: the original descriptions have, in the light of greater knowledge and more abundant material, often been pitifully inadequate; and the taxonomic significance of the characters chiefly relied upon for diagnosis has been greatly overvalued since most suffer the disability of considerable idiosyncratic variation. As long ago as 1910 Thomas & Wroughton, writing of *stuhlmanni* and *suahelica*, two of Matschie's creations, said: "... we have a series of over a dozen, the extreme individuals of which are easily separable; but these extremes are linked up by the intervening individuals in such a way that after most careful examination of both skins and skulls we have been obliged to acknowledge that we cannot find any constant character by which these forms may be separated ...".

It is possible to compile a long list of characters that have been used taxonomically, but they can be briefly categorised as the nature of the pelage, its colour in various situations on the body, and the colour, size, number and shape of the markings. These, and others, can build up into a very large number of combinations; and if, as has been the tendency, each of these is regarded as constituting a valid form there is considerable scope for taxonomic chaos. The difficulty is to decide which characters can, in fact, be relied upon, and to what degree. This can only be determined from long series of restricted provenance. One such, and the best for which published information exists, is the series of 46 specimens, 24 adults and 22 immature, collected by the American Museum expedition to the north-east Congo, and assigned to *G. pardina fieldiana.*

How careful the taxonomist must be, and how far more limited than was originally supposed are his morphological resources in *Genetta*, are indicated by J. A. Allen's (1924) analysis of this collection: "This species, like its congeners, presents, when adult, a wide range of purely individual variation, not only in size and coloration but in cranial characters and in the teeth, especially in the size and form of m^2 . . . In coloration the variation from the norm is toward, on the one hand, an extreme gray phase with blackish markings, on the other, a rufous phase with deep brownish buff instead of a gray ground color and dark brown markings (black strongly mixed with rufous). The dark tail-rings are black or blackish in both; the light tail-rings are much lighter in the gray extreme than in the rufous extreme, being white or whitish in the former and strongly suffused above with pale rufous in the latter. The light tail-rings are usually seven, but vary in number from six to eight, besides the terminal half ring, broken by the black of the upper side of the apical portion of the tail. The light rings are usually much broader on the sides and under surface of the tail than on the mid-dorsal line, where in some specimens they are nearly obsolete, especially beyond the fourth from the base. The light rings are occasionally as wide as the adjoining dark ones, but usually somewhat narrower, and frequently only about half the breadth of the dark ones. The black tail tip varies in extent (measured from the last full ring on the dorsal side) from 70 to 150 mm (in one specimen 220 mm) . . . It is unnecessary to describe in detail the irregularities in the size, number of rows and the arrangement of the spots on the sides of the body, since they are more or less different in each specimen, and often different on the two sides of the same specimen. Neither is it necessary to more than note that the relative width of the light and dark tail-rings is exceedingly unstable and hence has no taxonomic value. Yet such inconstant features were once made the basis of an elaborate synopsis of the species of the genus *Genetta*, noteworthy mainly for its puerility and pernicious results . . . " The synopsis referred to, in which over thirty different species are distinguished, was that of Matschie (1902). Apart from such idiosyncratic variation as demonstrated by this Congo, and other, series, the intrinsic mutability and untrustworthiness of external characters may be further judged from the experience of Schwarz (1930) who, in 20 years' study of the genet question, had observed animals in captivity to manifest, as the result of environmental change, such alteration of appearance as might rank of specific worth.

Matschie aside, since the majority of forms have been named purely from external characters and frequently from single specimens, not always adult, it will be appreciated that there has been considerable scope for confusion and misunderstanding. Moreover, there has been some tendency to assume that because a specimen derives from the locality broadly named as that from which the type was reputed to come it was in fact that species, and on this basis invest the species with characters not truly pertinent to it. And authors have not infrequently fallen into the trap of assuming that characters present in one or two specimens, such as black forelegs or an inner cusp on p^3, are diagnostically valid.

The findings of Schwarz in his 1930 review of the genus, have, to all intents and purposes, formed the basis of all subsequent accounts. Unfortunately his diagnostic characters do not always stand up to examination, being, in the light of more abundant material, sometimes misleading, sometimes frankly inaccurate. These matters are dealt with in the course of the species descriptions which follow. Meanwhile, it may be said that it seems almost impossible to build any lasting structure on the existing shaky foundations—shaky because of the ill-definition of many of the reputed forms including some at least of the early classic species. An attempt has been made in the present account to go back to first beginnings and to draw attention to some of the difficulties and misconceptions which have since arisen. In the consequent arrangement of West African forms use is made of species-groups, not from any great conviction but as a convenient way of indicating probable relationships at the upper levels whilst leaving the field clear at lower levels for the subsequent indication of colour and other variations which undoubtedly often exist in the groups here designated species and which may later be thought worthy of nominal distinction. Two subgenera, besides the nominate one, have recently been proposed, *Pseudogenetta* Dekeyser and *Paragenetta* Kuhn. The former has here been rejected; the latter retained, though no cranial material, on which its validity depends, has been examined. This leaves the provisional organization of the genus in West Africa as 8 discrete species divided between 4 species-groups in the typical subgenus, with a 9th, single, aberrant species in the second subgenus.

The following facts and opinions are here given for what they are worth in casting possible light on relationships in this genus. Sympatry, and hence presumed specific isolation, is, so far as can be assumed from non-existent or limited habitat data, demonstrated by British Museum specimens between *senegalensis*, *pardina* and *thierryi* in the Wukrum Hills (Nigeria); between *pardina* and *cristata* in the Mamfe district of Cameroun; and between *poensis* and *johnstoni* in eastern Liberia. However, crosses are known to be possible in the genus, though no investigation has been made into the fertility of the offspring. Zuckerman (1953), recording the known cases of deliberate hybridization in zoos, lists a cross, in 1858, between *genetta* and *senegalensis*; in 1859 between *genetta* and *tigrina*, 3 young being born; and in 1885 between *genetta* and *pardina*, resulting in the birth of a single kitten. Finally, Pocock (1915a), from study of the anatomy of the scent glands, came to the conclusion that two groups of related forms could be recognised: first *tigrina*, *pardina* and *rubiginosa*; and second *genetta*, *dongolana* (= *senegalensis*) and *felina*.

It may be as well to offer a word of warning. In view of the diversity of opinion held over the years amongst authors, zoo superintendents or museum taxonomists regarding the identity of different forms, the naming of some, if not all, of the above species should be regarded with a certain amount of caution. This applies to the literature in general.

KEY TO THE SPECIES OF *GENETTA*

(Previous key page 166)

1\. A medial dorsal stripe present, frequently longer-haired than the neighbouring pelage, mostly intense black and nearly always (except *poensis*) contrasting by reason of its continuity and/or colour with the, usually, browner and broken rows of spots. Condylobasal length of adult skulls over 80 mm. (Exceptional skins giving rise to doubt will not conform to the following alternative key characters) 2

Spinal stripe either obscure or, more generally, present but never black, very narrow but nevertheless nearly always more or less clearly split longitudinally into two by a streak of pale hairs; the whole, usually clear-cut, dorsal pattern of spots or lines individually very narrow (mostly under 10 mm wide), and generally ginger-brown on a buffish ground. Condylobasal length of adult skull under 80 mm . . . **thierryi** (*page* 214)

2\. The back of the neck with a small crest of erect hairs, or the hairs on its anterior part directed forwards and parted posteriorly from the backwardly directed remainder by a whorl. Tail soft and woolly, the bristle-hairs not much exceeding the underfur in length, clearly ringed, both above and below, from root to tip. Skull with no sagittal crest on the anterior part of the braincase; the postorbital constriction nearly always less than the interorbital breadth; an internal cusp mostly present on p^3 . . . 3

No nuchal crest or other abnormality of the fur of the neck 4

3\. Back of the neck with a short erect crest; background colour of the dorsal pelage mostly pale buffish. . . . . . . **cristata** (*page* 198)

Back of the neck without a crest but with the hairs directed forwards, and a whorl; background colour of the dorsal pelage a warm golden-brown **bini** (*page* 200)

4\. Tail densely woolly and soft, the abundant underfur dominating and being almost as long as the rather narrow, relatively inconspicuous bristle-hairs; ringed pretty clearly to the tip. Mandible rather flat, with the incisors and canines directed forwards; p^4 about 6·6 mm long, m^1 about 5·6 mm broad . . . . **johnstoni** (*page* 217)

If the tail is ringed clearly to the tip it is not soft and woolly. Mandible not flattish, teeth larger 5

5\. Tail ringed to the tip and clad with very long bristle-hairs which completely dominate and far exceed in length the relatively insignificant underfur, and is hence rather harsh. The postorbital constriction greater than the interorbital breadth; a complete sagittal crest mostly absent 6

The soft tail, in which the abundant underfur is not completely dominated by the bristle-hairs, has at least 75 mm, and generally far more, of the distal end entirely black or with only slight indications below of pale rings. Skull with the postorbital constriction almost invariably less than the interorbital breadth; a complete sagittal crest present at least in old males 7

6. Larger and greyer; head & body about 490 mm; condylobasal length about 93 mm; dorsal ground-colour rather cold whitish-grey; pale rings of the tail with relatively little sandy-brown adulterating the white; top of the hindfoot very pale grey, sharply demarcated from the intense black of the underside, which spreads round the back of the heel ***genetta*** (*page* 191)

Smaller and buffier; head & body about 440 mm; condylobasal length about 85 mm; dorsal ground-colour a warmer buff; pale rings of the tail almost entirely sandy-brown above, pure white below; hindfoot almost pure white above, black below but without the black spreading conspicuously round the back of the leg . . . ***senegalensis*** (*page* 193)

7. Size small, head & body estimated at about 450 mm; spots fairly large and separate, brownish on a pale whitish-buff ground-colour; tail clearly ringed white and black with only a relatively short all-black distal portion . . . . ***pardina*** (*page* 209)

Size larger, head & body about 500 mm; tail much more obscurely ringed, the pale annulations being often much adulterated with darker colour, even those near the base; a long, sometimes very long, distal portion wholly black or indistinctly marked below with partial pale rings. . 8

8. Spots large and few, wholly black or annulate, mostly separate, in about 4 rows, on a dull buffy-grey ground-colour . ***genettoides*** (*page* 210)

Spots small and numerous, in about 5 or 6 rows, wholly black, those adjacent to the spinal stripe coalescing into longitudinal bands; ground-colour much as in *genettoides*; tail predominantly black . . ***poensis*** (*page* 212)

A. ***gennetta*** Group

General. There are two members of this group occurring in West Africa: what appears to be *genetta* itself and *senegalensis*. The latter is undoubtedly closely related to the former, sharing with it a number of fundamental characters; but it is almost certainly wrong to regard it as nothing more than a race. Many years ago, Rüppell (1836) expressed the firm opinion that a single species ranged from southern Europe to the Cape, differences in the size, shape and colour of the spots being nothing else but climatic variations of one and the same animal, the skulls all being the same. While it is not possible to make the sweeping inclusions that Rüppell visualised there is nevertheless a basic truth in his assertion; and though they are of no immediate concern to West Africa it is perhaps worth recording the opinion that both the extra-limital *tigrina* and *felina*, in so far as they can be identified from their poor diagnoses, are more closely allied with the group now under consideration than with any other. At any rate, specimens from southern Africa in the British Museum which have in the past been ascribed to *felina* seem, with very little question, to be *genetta*.

Description. The characters which define this group, and which very readily differentiate its members at sight from the others are these. The dorsal pelage is very long, though in the tropical forms it is less so but nevertheless still appreciably longer than in the other groups; most typically it is 30 mm or more long; but if the forefinger

PLATE 3

Senegal Genet. Genetta [illegible] [illegible] Genet. Genetta [illegible] [illegible] Genet. [illegible]

is run up backwards through the pelage the latter is seen to be at least as long as, and usually considerably longer than the depth of this digit. From about the mid-back to the root of the tail is a continuous, yet-longer-haired, spinal stripe, almost invariably black but sometimes dark brown. This is erectile.

The tail is very long-haired, generally noticeably wider at the root than at the tip; it is almost always clearly annulated throughout its length, the margins of the rings not sharply defined owing to the partial overlap of the long bristle-hairs of the next proximal ring; there are 8 to 10 dark rings, and the tip in West African forms is white or with only a slight sprinkling of black. The dorsal aspect of the tail has the pale rings, either wholly or at least along a medial line, washed with red-brown; but below they are more or less pure white. The general appearance is of a rather rough, wiry structure due to the fact that the very long bristle-hairs far exceed in length the relatively insignificant underfur. In this the group differs abruptly from *pardina* and *servalina.*

Neither the colour nor the spots are diagnostic of the group. The ground-colour varies from a pale creamy white to a colder light grey; the spots may be light brown or almost black of uniform colour or, in the case of the darker ones, slightly dusted over with red-brown. They vary in size from very small (10 × 5 mm) to moderately large (40 × 30 mm), oblong or roundish, set in five rows on each side of the spine, the fifth, or lowest, row being frequently much less well defined or incomplete. The spots are for the most part clearly separate, but sometimes, especially over the rump and in the line or two adjacent to the spine, tend to run together longitudinally.

The forelegs are, in West Africa, pale above but sometimes darkened on their inner and lower surfaces. At least the foot and sometimes the whole hindleg is pale on the upper side and dark below.

Skull. In the skull, the intertemporal constriction is either about equal to or, more generally, greater than the interorbital breadth. There may or may not be a sagttal crest. p^3 generally has a large inner cusp, but this is sometimes lacking.

Taxonomy. Two forms are thought to exist in West Africa. Though most authors concur in thinking that the various forms of *genetta* are closely related there is some disagreement regarding the taxonomic level of naming. Schwarz (1930) dealt with them as conspecific but separable into (undefined) subspecific groups; thus *afra* and *senegalensis*, though assigned to different groups, become nomenclaturally *G. genetta afra* and *G. genetta senegalensis.* On the other hand Cabral (1966), while admitting that this may be the case, has suggested that the *G. genetta* group is in fact a superspecies comprising three independent species, the above forms becoming ascribed to *G. genetta* and *G. senegalensis*. Something of this latter view is adopted here, using the term species-groups rather than superspecies.

The two West African species may be separated by the key given on page 189. It should be noted that the characters there given are not necessarily of extralimital application.

GENETTA GENETTA (Linnaeus) European Genet

Viverra genetta Linnaeus, 1758, *Systema Naturae*, 10th ed. 1: 45. Spain.
Genetta afra F. Cuvier. 1825, in Geoffroy, E. & Cuvier, F. *Histoire Naturelle des Mammifères . . .*, pt. 52,

pl. 195 and pt. 51, text. Barbary. The specific name is Latin for African. Here taken as a valid race.

Genetta vulgaris Lesson, 1827, *Manuel de Mammalogie, ou histoire naturelle des Mammifères*: 173. A renaming of *V. genetta* Linnaeus. *Vulgaris* is the Latin for common.

Genetta barbara Hamilton Smith, 1842, in *Jardine's Naturalist's Library*: **35** (**13** of Mammalia): 171. Barbary, which the Latin specific name indicates. This is most probably synonymous with *afra*, a form of which Hamilton Smith was, apparently, ignorant.

There are other names of purely extralimital interest.

This genet, most typically from the Mediterranean region and originally described from south-western Europe is, in all likelihood, an introduction into the latter area from northern Africa. The species is of disputed range within the latter continent. Ellerman, Morrison-Scott & Hayman (1953), for example, following Schwarz (1930) regarded *felina* and other forms from the south as races of *genetta*, whereas Roberts (1951) excluded this species altogether from his account of South African mammals, according it no mention whatsoever.

However, the existence of *genetta* as a species in the southern half of the continent is of no immediate concern to this present study. Its range in northern Africa is. It is generally agreed that *genetta*, in the form *afra*, occurs throughout the Mediterranean fringe of Africa from Libya to Morocco; and it is known also that its range extends down the Atlantic coast to the south-west at least as far as Mogador (Cabrera, 1932). How much further it ranges down this coast does not seem to be recorded.

The assumption in this present work that it extends at least as far as Thiès in Senegal is based on a single British Museum specimen, No. 9.11.2.34. In view of the provenance of this specimen it was labelled *senegalensis*. In fact, it bears extremely little resemblance to Cuvier & Geoffroy's plate and description from which Fischer derived his diagnosis of this species; on the other hand it does correspond fairly well to their plate of *afra* and to other British Museum specimens of this deriving from northern Africa.

Genetta genetta afra F. Cuvier — North African Genet

The range of pattern and size of this animal in western Africa cannot, of course, be told from the single above mentioned specimen available. The pelage is long and rather harsh, its superficial ground-colour pale grey adulterated with very light brown and a little black, both derived, respectively, from the subterminal zones and the tips of the bristle-hairs. The markings superimposed on this background are deep blackish-brown with a slight over-wash of yellowish-brown hairs. There is a very deep brown, almost black, spinal crest of long hairs from just short of the shoulders to the root of the tail. On either side of this the spots are set in four clear longitudinal rows with a faint indication of an incomplete fifth. The spots of the row next to the spinal crest are rather irregular in shape, on the whole rather narrow, and tend to join; all the rest of the spots are to all intents and purposes independent. Those of the second row are the largest, the anterior four being 15 to 20 mm wide and the biggest some 40 mm long. The base of the fur is darkish grey; and there is a great abundance of very long, fine underfur (about 13 to 15 mm) amongst which the long (38 to 42 mm) bristles that form the outer contour of the coat stand fairly widely spaced at the base though they come together closely distally to form a continuous cover to the whole body.

The tail is rather shorter than the body, long and coarse haired, with eight dark rings, the basal two narrow and rather indistinct and a very small black tip. The bristles measure about 50 to 60 mm near the root; the underfur only 14 to 17 mm. The long hairs of one ring overlie the bases of the hairs of the next more distal ring for some considerable length so that the lines of demarcation between the rings are not at all sharp.

The forelegs are pale, only slightly spotted; the hindfeet are whitish above in very sharp contrast to the black of the outer aspect of the foot and the back of the ankle joint. The face has the usual genet markings: a white patch under the eyes separated by a blackish patch from the white area beside and below the rhinarium. The chin is white centrally but is bordered by blackish lower lips.

Skull. This in the single specimen available, a moderate-aged male, has a low, sharp sagittal crest extending the whole length of the cranium. The intertemporal constriction is a trifle wider than the interorbital breadth, the postorbital processes short, with sharp points. p^3 has a large, sharp, internal cusp; the antero-external cusp of p^4 is bifid; m_2 is fairly large, quadrate, with 4 clear cusps. The bulla is shown in fig. 28a.

The measurements are given in the table on page 219.

GENETTA SENEGALENSIS (J. B. Fischer) Senegal Genet

Viverra senegalensis J. B. Fischer, 1829, *Synopsis Mammalium*: 170. Senegal.
Viverra dongolana Hemprich & Ehrenberg, 1833 (*fide* Sherborn), *Symbolae Physicae seu Icones et Descriptiones Mammalium* . . . , dec. 2, folio k: 2. Dongola, Sudan.
Viverra leptura Reichenbach, 1836, *Regnum Animale*, 1: 23, f. 270.

This has been variously regarded as a discrete species or as merely a subspecies of *genetta*, a matter that has been discussed above. The exact, or even approximate, locality in Senegal from which this animal was first described is unknown.

Taxonomy. Fischer seems fairly obviously never to have seen this genet but to have framed his diagnosis from Cuvier's description and plate (in Geoffroy & Cuvier's *Histoire Naturelle des Mammifères* . . .) published in December 1821. It was called by them the Genette du Sénégal but not given a binomial Latin designation. The scientific name and description must therefore officially date from Fischer, 1829, though, as in the parallel case of *G. tigrina*, the diagnosis is not first-hand but extracted from an earlier work.

Since Fischer's diagnosis is nothing more than a Latin description of Geoffroy & Cuvier's plate the characters originally ascribed to *senegalensis* can best be gathered from this last and its accompanying notes. The species is shown as a considerably paler animal than *afra*, almost cream in colour, the black spots being in only 4 rows either side of the spinal stripe. Each of the innermost two rows consists of 4 spots only, long and very narrow and quite separate, the spots of the two outer rows being shorter and more rounded. The tail is shown as having 10 black rings and a white tip; the hindleg as having a sharply cut off black mark above and on the angle. The chin was said to be black; the coat not remarkably long; but the hairs of the tail were, making it look bigger than it really was. In Cuvier's original description of the Senegal genet (Livraison XXV) the tail was given as the same length as the body (i.e. about 500 mm); but later, in the second description of *afra* (Livraison LII) it was mentioned incidentally as being about 175 mm longer, the proportions in the two species being thus very different.

Although at one time and another a number of specimens in the British Museum have been ascribed to *senegalensis* there is none that at all convincingly corresponds to the very pale animal with widely separate, sharply defined, dead black, linear markings illustrated by Geoffroy & Cuvier. The nearest seems to be a *dongolana* specimen from Shendy (Sudan), No. 1939.1768, in which the spots are brown and roundish but slightly confluent, making them appear long and narrow The tail-rings are 10, not very clear-cut; the tip white, though mixed with a little blackish. The black mark on the hindleg is fairly abruptly defined. The pelage is not markedly long but there is a long shiny black crest from the mid-back.

Hemprich & Ehrenberg's description of *dongolana* is limited in scope, and a good deal of it is irrelevant in being a comparison with the purely Madagascan *Fossa*. However, they state that *dongolana* is a whitish, not a grey, form, with a blackish line from the middle of the back and black spots overlain with cinnamon, there being no mention of their shape, size or arrangement. The tail is described as differing very widely from *genetta* and "singularly short", the number of rings unstated.

The specimen, No. 1939.1768, mentioned above as most closely representing *senegalensis* corresponds pretty well to this sketchy description and there seems little doubt that the two forms are really one and the same.

Distribution. This being so, we have a range for *senegalensis* from Senegal to the Nile and beyond (Setzer, 1956) to the Red Sea, that is to say transcontinentally through the Sahel and Subdesert zones of vegetation. Actually, as will shortly be seen, it occurs also further south in the Sudan and Doka zones. Specimens exist in the British Museum from Aouderas (Aïr—Subdesert); Fort Lamy (Chad—Sahel woodland); Zuarangu (Ghana—Sudan woodland); Farniso and Kabwir (Nigeria—Sudan woodland); Zaria district and Wukrum Hills (Nigeria—Doka woodland). It is also probably this species which A. J. Hopson (private communication) observed to be frequent in creeper-hung trees in the Yobe Valley, near Yo, Lake Chad (Sahel).

Description. The Senegal genet, as represented by these specimens (Plate 3), is a distinctly pale animal with a background colour of whitish, cream or buffish, and spots that are mostly light or medium brown but more rarely blackish-brown. They vary in size but are never large, rarely having a maximum diameter of more than 20 mm and usually less. One unusual example from the Wukrum Hills has very small spots, bearing the same relationship of pattern to the other skins as the servaline does to the serval. They are also very variable in shape but could be described in general as irregularly round or oval, occasionally oblong; and though here and there, chiefly over the rump, joined together, they are in general sufficiently widely separated for there to be as much or more ground-colour as spots showing. In this last, as in

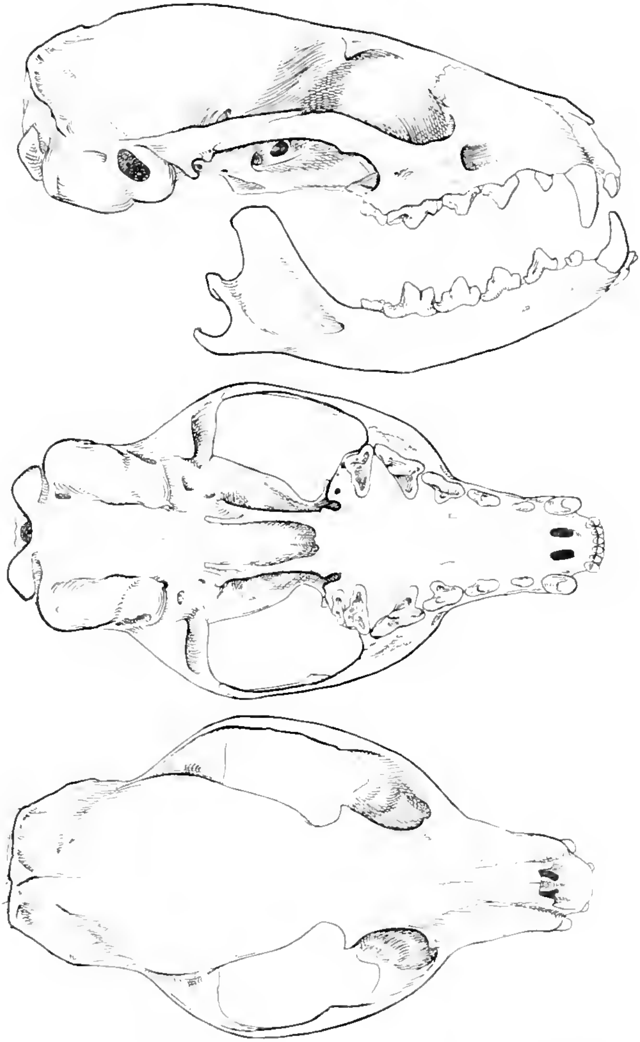


Fig. 29. *Genetta senegalensis*: skull, B.M. No. 1939.1766, ♂, × 1

other ways, they differ from the small-spotted *servalina* in which the spots dominate the ground-colour.

The pelage, although considerably shorter than in *genetta*, is nevertheless still long by comparison with other West African species, the bristles, in typical non-moulting specimens, measuring about 25 to 30 mm over the rump, the underfur about 12 to 14 mm. There is a long-bristled spinal crest from just posterior of the shoulders to the root of the tail. This is almost always black but in some cases merely deep brown.

The distinctive character of the tail unites all these skins and shows their affinity to *genetta*. It is long-haired, the coarse, terete bristles measure from 45 to 55 mm near the root, the underfur 13 to 15 mm. As in all this group, the annulation, though mostly quite clear, is not sharp-margined because of the overlap of the long bristles. For this reason the basal two or three rings are difficult to determine; and this, in some measure, accounts for differing opinions regarding the number of rings. The most usual number of dark rings is 10, though in some cases there seem to be only 9. The tip of the tail is white but often has a few black-tipped hairs mixed with it. The dark rings may be black or deep brown; the pale rings are always pure white below, but dorsally they generally have a good deal of light-brown mixed with them, especially medially, or are entirely golden-brown. The length of the tail seems to be irregular. Only 5 skins have field measurements; and in these, two tails measure slightly less than head & body, one appreciably less, and two appreciably more.

The forelegs are pale above and blackish below. The hindfeet are white above; the legs are blackish below and on the outside and back of the lower leg (tibia) but not usually entirely around the ankle as in *genetta afra*. The usual genet white facial markings are present—below the eye, around the rhinarium and between the eyes. The chin is always white medially, bordered by a broader or narrower black area running along the lower lips.

From the limited figures available and from the general appearance of the skins this genet would seem to be smaller than the animals living in northern Africa and Europe (*genetta*). The actual mean measurements of British Museum specimens will be found in the table on page 219.

Skull (fig. 29). Seven skulls, of which only five are mature, exist in London. Though the latter are pretty even in size they show, as throughout this genus, confusingly irregular characters, the various inconsistencies being distributed over all the specimens, irrespective of sex, and not confined to one or two exceptional examples. In two females and one male there is no trace of a sagittal crest other than a posterior portion adjoining the supraoccipital crest; in one other oldish male there is a clear, but very low, crest across the whole length of the cranium; and in the third, oldish, male such a rudimentary crest is partly present. In four of the specimens p^3 has a large internal cusp; but from the fifth, a medium-aged female, all trace of this is completely lacking. In this skull, also, m^2 is very much reduced in size. The development of the postorbital processes varies from long points to fairly short ones. One lower jaw has a large quadrangular, four-cusped m_2; but in the remainder this tooth is triangular and three-cusped.

B. *servalina* Group

The animals included here are usually regarded as a single species covering four described subspecies; but the two forms occurring in West Africa seem to be sufficiently distinct to constitute two discrete though, as in the case of *genetta*, very closely connected species. This will be dealt with more fully below in the taxonomic section.

Description. There is little room for doubt in the determination of the servaline genets. The characters, especially in comparison with *genetta* are very distinctive., The dorsal pelage is short compared with that of typical *genetta*, though not markedly shorter than in *senegalensis*; but it has none of the harshness of the *genetta* group, being instead rather silky. This is because of the quite different form of the bristle-hairs (20 to 25 mm long) which, in this group, are only expanded for the distal one-third of their length, tapering abruptly proximally to a long narrow pedicel not readily distinguishable by eye from the underfur, than which it is not a great deal wider. The distal portion is of oval section, not terete. The underfur is from 15 to 18 mm long. The ground colour in this group is, in general, redder than in *genetta* because the pale-grey-ended underfur that forms its basis is overlain by bristles that have wide subterminal bands of red-brown or even bright orange. This reddening always shows but varies in extent, being sometimes in young skins and at moult considerably reduced. The pattern is of very numerous, small-sized, dense black spots not always very clearly disposed in longitudinal lines; but where they can be counted they form at least seven such on each side of the body. The spots are generally well under 20 mm diameter; and they are mostly separate though occasionally they may coalesce near the spine. There may or may not be a spinal crest.

The tail is the other very characteristic feature of this group. It is subcylindrical, relatively short-haired and soft-furred, and very distinctly annulated from root to tip, the edges of the rings being fairly sharply cut. The bristle-hairs do not greatly exceed in length the abundant underfur. Whereas in *genetta* the tail broadly matches the body colour, in *servalina* it, as a rule, forms something of a contrast by reason of the fairly pure white of its light rings. The dark rings, which are generally black or very deep brown, are usually 10 to 12 in number, the tip being white, though as a rule not so purely white as the remainder of the light rings. The alternate rings are subequal in breadth or, more commonly, the white narrower than the black. The tail is shorter than the head & body. The legs may be black or pale; the usual genet pale facial markings below and between the eyes and around the rhinarium are present but mostly more obscure than in *genetta*.

Skull. There are not enough mature skulls to make comparisons with the *genetta* group particularly useful. The characters are variable. In the six skulls available the sagittal crest is restricted to the extreme posterior segment in four and, across the main body of the braincase, is incipient in two, a medium-aged male and a very old female. The internal cusp on p^3 is large in two examples; and in the others ranges from vestigial through a mere bulge to a low tubercle. Both m^2 and m_2 vary a good deal in size, and the latter may be quadrate with four cusps or triangular with three. The postorbital processes may be long fine points or blunt and deflected. From such variable material it is scarcely possible to derive any useful diagnostic characters. The most constant feature is that the intertemporal breadth is narrower than the interorbital; but in one case it is appreciably wider. In the *genetta* group examples it is always wider.

Taxonomy. The group is usually regarded as a clear-cut one. Today it is universally held to be monospecific although in the past three discrete species were named. In this present account it is suggested that there are three valid species, two of them occurring within the area dealt with in this work.

The group first became known when in 1855 Pucheran described *servalina* from Gaboon. His brief Latin diagnosis was not in itself very precise; but since it makes it clear that the spots are extremely numerous, the limbs almost completely black, and the tail long with broad black and narrower white rings the species is readily recognisable and has never been questioned. At the same time Pucheran named a second specimen from the same area *aubryana*, the description being vague, the only apparent difference from *servalina* lying in the ground-colour. As this last is always variable the two names have for long rightly been regarded as synonymous.

In 1902 Thomas described *bettoni* from Kenya as a discrete species on the score of smaller size and annulate spots. This, which has proved to be a very common form in eastern Africa, is now regarded as nothing more than a race of *servalina*. The annulation of the dorsal spots is not constant; but the markedly small size of the skull and the shortness of the rostrum and palate probably justify Thomas's original evaluation as a species. The same cannot be said of Lönnberg's *intensa* from the Congo, the author himself being doubtful of its validity as a race of *servalina*. Of more immediate concern to West Africa is the third named race of this species, *cristata* Hayman. Paler ground-colour and pale forelegs apart, there are certain features of this animal which appear to the present writer to entitle it to consideration as a discrete species. These are the possession not only of a black spinal crest, absent from true *servalina*, but of an erectile nuchal crest as well. The distribution, so far as we at present know, lies between the Cross River and the Sanaga; whereas *servalina* itself is found, in West Africa, only to the south of the latter river, that is to say entirely extralimitally.

The evidence that *servalina* occurs as far west as the River Niger, as stated in Schwarz (1930) and Rosevear (1953) is slender. No record has been traced to account for Schwarz's assertion; the green spot shown on map No. 181a in Rosevear relates to a rather poor skin collected by the present writer near Benin and of doubtful standing. Though from its general appearance, including the typical short-furred, wholly-annulated tail, it obviously belongs to this present group it is certainly neither *servalina* nor *cristata*. The ground-colour is a richer orange-brown than in these forms; the spots are appreciably larger and less numerous—so much so that it was originally thought to be a "*maculata*". This was later altered to *servalina* by R. W. Hayman. The forelegs are black, much as in *servalina*, but there is a very clear, black spinal crest on the lower back, not occurring in that form, though no nuchal crest as in *cristata* The tail has only nine black rings, the tip (the 9th) being black Whether this is a species or merely a race is open to question. It is here treated as a new species in its own right.

The two, consequent, West African forms can be readily told apart by means of the key on page 189.

GENETTA CRISTATA Hayman Crested Genet

Genetta servalina cristata Hayman, 1940, *Trans. zool. Soc. Lond.* **24**: 686–688. Okoiyong, Mamfe Division, Cameroun. Type in the British Museum, No. 39.323, ♂; skin in good condition, skull good except for the loss of four upper teeth. The subspecific name was given with reference to both the nuchal and spinal crests.

Distribution and general. This genet (Plate 3) is known in the British Museum from 5 adult and 9 young or juvenile specimens, all from the Cross River—Cameroun forests. Only 3 of the adult specimens are complete with both skin and skull. The majority of these come from various places in the Mamfe Division, collected by Sanderson (1940): Mamfe, Binjong, Bashauo, Olulu and Okoiyong; but there are others from the Rumpi Hills (Kumba Division, Cameroun) and Oban (south-eastern Nigeria). In addition to these, Eisentraut (1963) records 2 specimens from Mount Cameroun at Buea and Malende. The whole area of known distribution, therefore, lies between the Cross River basin and the Cameroun Mountain, a heavily forested and, until recently, secluded region, about 100 miles long by the same wide, well north of the Sanaga River, south of which the species is replaced by *servalina*.

Description. In the *servalina* group the ground-colour of the dorsal pelage is somewhat variable from specimen to specimen; but in so far as a generalisation can be made it is rather paler in *cristata* than in *servalina* itself. It is buffish-grey; the orange-brown subterminal rings of the individual hairs adulterate this colour to a greater or lesser extent in different examples, sometimes scarcely at all except round the anterior edges of the black spots. The latter vary a little in size and shape but most typically may be regarded as round, and 10 or 15 mm in diameter, though sometimes they tend to become rather longer than broad. They are, in general, independent but there is in some specimens a greater tendency to unite than in others; and almost always they form short lines near the spinal crest in the region of the hindquarters. The bristle-hairs of the lower back are about 20 to 22 mm long; the underfur some 10 to 13 mm. In *servalina* the belly is dark, almost blackish-brown; the chin and throat are lighter but nevertheless darkish grey and, especially in the latter, washed with golden-brown; *cristata*, on the other hand, is considerably paler below; medium buffy-brown on the belly but the chin and throat cold whitish-grey with little or no warm over-wash.

The black spinal crest becomes noticeably long from the mid-back to the root of the tail; but it is, in a shortened form, really continuous with the nuchal crest. This latter is much shorter than the main spinal crest being, indeed, little longer than the surrounding fur from which it stands out by reason of its erectness instead of being adpressed and directed backwards. Though it is most conveniently referred to as the nuchal crest it, in fact, has its origin, in a very low form, on the front of the face from about between the eyes, whence it continues over the crown to the neck where, the fur being longer, it becomes far more obvious. It is caused by the direction of the hairs, which converge towards the medial line. On the neck it involves the central black stripe and the brown-ringed contiguous hairs, and is thus of mixed colour, not wholly black like the spinal crest. It is of interest to note that rudimentary traces of the frontal crest are to be found in typical *servalina*.

The tail may have fewer black rings than *servalina*, the type having only 8 clear rings, though others, including all the juveniles, count up to 10; but the reckoning of the terminal rings is open to argument, there being a very obscure narrow darkening that could or could not be regarded as a ring. The tail-tip is really white, but because of this indecisive blackening becomes greyed. The forefeet are in their upper portion light-coloured and spotted similarly to the back, but become blackish towards the toes and on their outer and lower aspects. The hindlegs are somewhat similar but often carry a distinct pale, greyish, patch over the metatarsal region above.

Skull. There is no particular distinction between *cristata* and *servalina*. From the very few examples available for comparison it is just possible the inner cusp of p^3 is better developed in the former than in the latter, as in the three available specimens it is large in two and represented by a prominent swelling in the third. All skulls have a posterior sagittal flange; but a crest across the length of the braincase is rudimentary in two, and absent from two, an old male and a fairly old female. This old male is the only specimen in which the postorbital breadth is greater than the interorbital. The transverse breadths of m^2 and m_2 are rather greater than in *servalina*. The bulla is illustrated in fig. 28c.

Habits. Sanderson (1940) characterised the habitat as scrub, low tangled vegetation and bare ground below trees. He considered the species as definitely terrestrial, only one specimen having been seen in a low tree, and that returned to the ground to make its escape.

GENETTA BINI *spec. nov.* Benin Genet

The erection of this species from one very incomplete specimen seems to be justified by its apparent difference from other known forms, from its extreme western provenance, and the wide gap of 750 kilometres separating it from its nearest recorded neighbour, across the two faunal barriers of the lower Niger and Cross Rivers. It is, in fact, described below from a, in some respects, poorish skin devoid of any supporting skull.

Description. The type, B.M. No. 50.315, ♂ (Plate 4), was collected for the present writer in December 1938 by R. H. Hide, a forest officer, in the Ohosu Forest Reserve some 65 kilometres north-west of Benin City, western Nigeria, altitude 250 metres. Although appreciably different in detail, the overall resemblance of the pelage and tail patterns to *servalina* make it quite certain that it belongs to that group. The ground-colour of the dorsal pelage is of a much richer red-brown than in the two other more commonly known western species, or in the more golden-brown of *intensa* from eastern Congo. This is because the subterminal bands of the bristles are both broader and more deeply coloured than in the other species. The pelage length is much the same as in *cristata*.

This new proposed form (Plate 4) differs from *servalina* in the possession of a long black spinal crest from the mid-back to the tail; and from *cristata* by the absence of a nuchal crest. The fur on the back of the neck, however, is directed forward and meets the backwardly directed hair of the frontal region in a line across the crown between the ears. Where the differently orientated hairs of the neck and back meet there would appear to be something in the nature of a whorl; but the only skin is so poorly made that the position here is a little obscure.

The greatest difference between this new and the other species, however, lies in the size, shape and number of the spots. They are much more irregular, less round, in shape, and appreciably larger and fewer in number. Many of them are subquadrate or triangular, 20 mm or more across, those of the middle lines being larger than those near the spine or lower down. Between the shoulder and the hip there are not more than 7 or 8 in a row as compared with 10 to 12 in the hitherto known forms. A few merge over the rump and one or two are confluent with the spinal crest. Owing to the make-up of the skin and the virtual absence of the belly it is not possible to say precisely how many rows there are, but it is probably 6.

There are 9 dark rings on the tail including the black tip. The pale rings, which are only about half the width of the black ones, although white below, are dorsally distinctly more coloured than in the other species of this group, especially the proximal ones, being greyish with a fair mixture of reddish and black hairs. The bristles of the proximal black rings are rather longer than normal and overlap the light rings more than is usual. The chin and throat are medium grey, fairly well spotted. Although most of the legs are present there is only one foot, the left forefoot. The upper arms are deep grey and spotted on top but black beneath like the whole of the remainder of leg and foot. The lower parts of the hindlegs are blackish all round.

Nothing is recorded of this animal except that it lives in closed high forest, and the only specimen known smelt strongly of musk. The name Bini, pronounced bee-nee, is the name of the ethnic group inhabiting Benin and the surrounding district.

C. *pardina* Group

In all the confusion that exists in the genus *Genetta* the greatest, without question, concerns the three classic species, *tigrina* (1778), *felina* (1811) and *pardina* (1832). The last is of closest concern to West Africa; and though it has in some measure, through the attribution of the same forms to one or the other, become involved with the first an endeavour must be made initially to sort out the question of *pardina* alone.

With the *pardina* group we reach a remarkably mixed assortment of forms, far and away the most variable in visible characters. Whether the group embraces more than a single species is an open question. The animals lying at opposite ends of it are assuredly markedly different in appearance; yet there seems to be no clear-cut division between them. Great play has been made by taxonomists with spot size and colour; with the number of tail annulations and the relative widths of the light and dark rings; and with the colour of the feet. There is little doubt that these characters, and others less often taken into account, are subject to considerable variation, possibly to some slight degree local but for the most part individual; though from the largely disjoint study material in the British Museum—scarcely any two from the same locality, apart from questions of age and sex—it is hardly possible to do more than conjecture that this must be so. However, the 46 specimens collected by the American Museum Congo Expedition, by reason of their restricted provenance, cast a more certain light on the matter. J. A. Allen's detailed comments on variation of supposedly diagnostic characters as exhibited by this series have already been quoted on page 187.

Description. In the face of the wide inconstancy thus revealed it seems difficult, if not impossible, to find dependable characters that might serve to define *pardina*. In truth the matter boils down to a similarity of tail structure and markings throughout an otherwise capricious group, serving to differentiate the animals included here on the one hand clearly from *genetta* and on the other, less emphatically, from *servalina*. This tail is of the relatively short, backwardly-directed-haired, subcylindrical type characteric of *servalina*, differing manifestly from the very long-, coarse-haired type of the *genetta* group in its extremely soft and silky nature. It differs from that of *servalina* in being appreciably more melanistic, the pale rings being not only fewer in number but, as a rule, of far less width than the black ones. Further, the terminal portion of the tail, sometimes only about 75 mm, sometimes very much more, is almost wholly black, particularly above, there being, not uncommonly, faint traces of white partial-rings on its underside. It is, in this species, more convenient to count the pale rings than the dark; but often there are only half-rings, or less, visible on the underside but not the top. The count varies, therefore, on the two aspects, dorsal and ventral, of the tail. Taking the latter, there are usually 6 to 8 pale rings or partial rings, but in exceptional specimens there may be one less or more. Even in the basal portion the rings are often far more obscure above than below. Their lesser number, the (as a rule) narrowness and relative obscurity of the pale rings, and the long black end to the tail serve as a distinction between even the small-spotted forms of this species and the *servalina* group, in which the rings have a sharp clarity, are subequal in width, and continue, above and below, to the distal end.

Taxonomy. The mix-up over *pardina* stems partly from Matschie (1902) and partly from Schwarz (1930), both, in an obscure situation, having long been regarded as the ultimate authorities; and what they have said, surmised or hinted at has, often blindly, been followed. Added to this is, at least as far as the British Museum is concerned, a plethora of specimens from the rain-forest belt and a paucity from the drier inland areas. Now, Isidore Geoffroy, clearly as the result of specific enquiries, described *pardina* as emanating from the interior of Senegal, that is to say from one of the more arid types of woodland, Sudan or Sahel, certainly not from the closed forest. There is a temptation today, and both Matschie and Schwarz succumbed to it, to criticise early notions of West African geography and to amend reputed provenances to suit what seemed to them to be the facts. It cannot be denied that this is sometimes justified; but there is no reason whatsoever to suppose that Geoffroy was in this particular case misled. Senegal had for long been intimately connected with France and in Geoffroy's day was certainly closer, and a far more likely source of living animals, than any more heavily forested part of West Africa.

Matschie showed himself to be in two minds regarding the vegetation and distribution proper to the species. On page 1135 of his paper he connected *pardina* with the coastal belt of Togo; but on page 1142 he gave as the range first north Cameroun, secondly Togo; and implied possible synonymy with *poensis*, a forest form. Schwarz, too, who first identified *pardina* with *maculata* (a synonymy since necessarily reversed) was not very clear regarding the ecological background proper to the species. In a footnote on page 277 he said, in translation: "*Genetta maculata* is patently the same as

Genetta pardina I. Geoffroy, so that the second, more used, name must disappear as clearly a synonym. Matschie (1902) has already shown that *maculata* is no north African form as the original description says . . . (It) doubtless emanates from upper Guinea and, since it was imported live, can very well, like the type of *G. pardina*, stem from Senegal, which was at that time one of the most important export countries for African animals". In other words he agreed to its relatively dry-zone origin. Yet in his main text, near the top of the same page, Schwarz quite unequivocally rated *maculata* (as he called the species) an upper Guinea closed-forest ("Waldgebiet") animal, ranging from the Niger to the Gambia—thus vegetationally, and possibly distributionally, running counter to Geoffroy's "interior of Senegal". J. A. Allen had obviously adopted an entirely different view of the distribution of *pardina* in that he had ascribed the major part of his north-eastern Congo material to the species. Further, in another footnote, on the previous page, while allowing the species a certain degree of range in climate, Schwarz none the less still confined it to the high-forest: "While among the forms of the moist forest *G. maculata* produces a small-spotted type '*poensis*', the spots in the marginal areas of the forest are large and the ground-colour pale—'*maculata*' ('*pardina*'), '*genettoides*'; intermediate types '*dubia*', '*johnstoni*' ". Attractive and reasonable as this hypothesis may seem, it will be seen shortly that Schwarz was quite wrong in connecting spot size with humidity.

Relatively recently an extremely interesting set of 10 flat skins, in only very fair condition and unfortunately without skulls, has been received by the British Museum from Mr. J. D. Carter. They all emanate from a very restricted area some 30 kilometres long, in the Petico–Zo locality of the Wukrum Hills, 25 kilometres north-east to 25 kilometres north-west of Lau, which lies on the upper Benue River in Nigeria at about 11°30 East. This area is in the Sudan woodland zone. The interest of this series lies in the fact that it shows that no less than three quite distinct, though very similarly coloured, taxonomic forms, *senegalensis*, *pardina* and *thierryi*, live sympatrically; that eight of the skins which are *pardina* display a wide range of size, shape and colour of spots, some of them being close enough to Geoffroy's description and illustration to make it clear that the type specimen of *pardina* may well have come from the Sudan zone and that Schwarz's limitation of the species distribution to the closed forest was misleading. It must, in all fairness, be added that one exceptional skin, No. 39.132, from a small island in the mouth of the Volta River, near Ada, is not dissimilar from these Sudan zone specimens, though of a slightly colder tone, and quite distinct in its paler ground-colour from all southern Ghana forest material. But although so near the coast and thus expectedly in the wet-forest zone, this area is, in fact, one of remarkably low rainfall, not greatly exceeding that of the much more inland Sudan zone, and the vegetation of a dry littoral kind, together with some mangroves.

Because of the wide range of pattern and colouring in the *pardina* group the present writer is rather sceptical of the usefulness, or the feasibility without considerable further evidence, of drawing nomenclatural distinctions between the various forms. The extremes are very distinct and could support independent names; and it thus seems unjustifiable to apply precisely the same term to the pale, creamy-buff, large-spotted animal of the dry open country and to the relatively dark, greyish, small-spotted inhabitant of the dense rain-forest. But, though there are considerable lacunae in the study material, there is some reason to suppose that the forms are wholly clinal, and in the attempt to differentiate everything one could be faced with devising an almost endless string of names, the limit of whose application was anything but clear-cut.

In the face of this the question of what to do with *pardina* is a difficult one. The course adopted in this work is to regard it as a species-group, calling the pale open country forms *pardina*, the large-spotted forest form *genettoides*, and the small-spotted forest form *poensis*. This is more a matter of convenience than anything else and can at once be shown to be illogical since, while differentiating between the extreme forest forms, it fails to do the same for the dry-zone forms; and, as regards the forest forms themselves, whether a specimen is large-spotted or small-spotted must often remain purely a matter of personal opinion. But it has this merit: that it does not burden an obscure situation with a mass of new names that more abundant material and deeper continental-wide research would almost certainly show to be unnecessary and inept.

This decision having been made it is necessary to examine and discuss the standing of certain named forms in more detail in order to explain the difficulties which have arisen over some and the reasons for the rejection of others from the West African list. The earliest of these is *maculata* Gray, 1830, which since Schwarz (1930) has been generally accepted as synonymous with *pardina*. Owing to doubts and contradictions in Gray's diagnosis the position is, in fact, not absolutely straightforward. His English description is of a grey-brown animal with a brown erectile crest from the shoulders to the tail, and spots in 3 rows on each side, the 2 innermost square, those next to the spine largest and nearest together, the lowest series roundish; below these are scattered black-brown spots. There would thus appear to be 3 clearly defined rows of spots on each side with further spots, not disposed in lines, below them, a not unusual arrangement in the genets, giving rise to the common diagnosis "spots in 4 or 5 rows on each side". But Gray's Latin diagnosis gives the spots as in 6 rows with scattered round spots on the flanks. In view of the English description this could logically be taken as meaning a total derived from two sides of 3 each. The accompanying illustration, however, clearly shows 6 well-defined rows of independent spots on a single side; and since Gray must presumably have seen the drawing before publication it might be taken that this is what he, in fact, meant—though it scarcely accords with his verbal description of 3 series of spots with scattered spots on the sides of the belly. Neither does the illustration bear out the written description of the tail. This states that there are 7 black bands increasing in breadth towards the end. The picture, however, shows 8 together with a black tip making, in all, 9 black bands, which show no appreciable increase of width.

Schwarz, synonymising *maculata* and *pardina*, drew attention to the fact that Matschie had already expressed the view that the former was no North African animal, as Gray had stated, and had noticed, also, the discrepancies between Gray's diagnosis and his illustration. Schwarz, ignoring the confusion over the spots and confining himself to the tail, expressed the view that the written description "may be regarded as authoritative as it speaks of 7 dark tail-rings, which agrees with the upper Guinea genet. Apart from the inexactness of the drawing of the tail the picture shows a long-legged, long-faced genet that doubtless emanates from upper Guinea . . .". It will be seen that Schwarz accepted or rejected the illustration to suit his own theory and his own definitions. He further supported his view by a pure guess that the country of origin of Gray's specimen was really Senegal.

With doubt cast on the body pattern and on the tail there seems little enough in the type description that may be picked upon as usefully diagnostic apart from large, quadrangular, more or less separate spots. One thing is certainly lacking from both verbal and pictorial descriptions: any reference to the markedly melanistic tail with the extra-long black tip and pale half-rings which are the essential characteristic of all *pardina*. The illustration is, too, of a distinctly more tapering and finely-tipped tail than is general in that species. The true country of origin of Gray's specimen is, in fact, not without relevancy; for his figure is, apart from an extra line of spots on the flank, not a bad representation of *genetta afra*, which, if the animal came from North Africa as he said, it could well be.

The name *maculata* has been rejected as unavailable because of prior occupation. Were this not so it could justifiably be abandoned on the grounds of obscurity of definition. This latter also renders its correct position in synonymy uncertain, but in order to avoid introducing unnecessary confusion it has herein been retained in its customary place under *pardina* in the synonymic list which follows later on page 209.

It is perhaps of general interest, as a commentary on Gray's confused diagnosis, to quote here a view of his reliability written not from the purely zoological angle but as a pointer to his character: "He published a steady stream of brief zoological papers with such haste that in a number of instances he changed his mind and published a second paper correcting his first; indeed, in some cases he soon published a third paper amending his second". (Paden, 1964: 13).

The forms *poensis* and *genettoides* will be commented on in their own appropriate sections later. The status of a few other names must be examined here. The first calling for attention is *fieldiana* Du Chaillu, 1860, because from time to time West African specimens have been referred, directly or indirectly, to it or it has been stated to occur in that region—as, for example, in Rosevear (1953). Du Chaillu's description is not very helpful but makes it probable that his animal belonged, in fact, to the *pardina* group. This is fairly clear from the tail, which was said to have 7 dark rings, the first incomplete below, the last indistinct; the last 5 inches of the tail brownish-black. Other points in the description tend to confirm this. The size of the spots is not given; but, indirectly, by mentioning that the two lateral rows on each side of the spinal band are broken up into five or six smaller longitudinal spots he indicates that these must in fact be largish, as in *genettoides*.

J. A. Allen (1924) treated *fieldiana* as a race of *pardina*; but Schwarz (1930) regarded it as a subspecies of *tigrina*, being followed in this by G. M. Allen (1939). In view of the character of the tail this latter classification seems improbable. Not much is revealed by skulls in *Genetta*; but there is a Du Chaillu skull of an old animal in London (No. 1645a, sex?), without a skin, that conforms pretty closely to the general run of the *pardina* group except that it is on the whole rather below average size and has an unusually narrow intertemporal constriction. However, it is matched in this latter by one of the large-spotted *genettoides* from Ghana (No. 46.397). The standing of *fieldiana* is only incidental to West Africa but is regarded herein as pertaining to the *pardina* species-group, the name being probably synonymous with *genettoides*.

Matschie's *dubia*, the exact provenance of which in West Africa is unknown, is also almost certainly *genettoides*. No set description of *dubia* was given by Matschie and diagnosis of the form must be built up from his scattered key characters. The most significant of these are: spots large, in 5 rows; tail short-haired, the hairs not more than 25 mm long at the root; the tail itself very short, two-thirds of the head & body length (there is a misprint in the key), with only 6 pale rings, which are at most as wide as the dark. Tails are, in the *pardina* group, normally rather shorter than the head & body length (about 85 per cent); but it is doubtful whether such an extremely short-tailed animal exists except as a freak or the result of accident. The form *dubia*, therefore, is here regarded as, in fact, *genettoides*. Schwarz, also, put the two in synonymy.

Cabrera's *insularis*, described from Fernando Póo in 1921 because no trace of *poensis* itself had so far come to light on the island, must next be considered. Schwarz grouped this with *tigrina*; but Cabrera himself likened it in general to *pardina*, of which he considered it to be an island representative. He described it as having few spots, large and annulated for the first two rows, which are more irregular and imperfect than in *pardina*, many of them formed from two black spots enclosing an intermediate, ill-defined reddish space; the base of the pelage infused with cinnamon, the flanks and thighs very bright; the feet grey. No mention is made of the tail. There is no reason to suppose that Cabrera's estimate of taxonomic relationship was wrong and that Schwarz was more justified in allocating the form to *tigrina*. The form is, therefore, in this work synonymised with *genettoides*; but it is possible that with further collecting it may be found to merit some more independent status within the *pardina* group.

No form is attributed in this present work to *tigrina*; but since this species has so often been mentioned in previous paragraphs and has been held to occur in West Africa it is necessary to consider the question here. *G. tigrina* constituted one of Schwarz's six basic forms. Indeed, it was certainly one of the major species since he divided it into three groups embracing 11 subspecies besides 8 other named forms sunk into these as synonyms. According to him its range was the entire high-forest block except west of the Niger, and the neighbouring dry woodlands; the savannah north of the forest, including west of the Niger as far as Senegal; also Sudan and Ethiopia; and East Africa to the coast and to the Cape. It was thus in Schwarz's view extremely widespread, both geographically and vegetationally. In view of the importance attached to this name its standing and the difficulties connected with it must be examined in some detail.

The species must under the International Code be dated from Schreber, 1778, though this author clearly states that the animal was unknown to him and that his description was copied from that of Vosmaer and the accompanying plate. Schreber quoted as his source the French edition of Vosmaer (1771) though the description had originally been published in Dutch in the same year. But whether the French or the Dutch version be taken Schreber's re-writing of it in German was not always very accurate, as when he said there was a black stripe from head to tail whereas Vosmaer quite clearly described it as running from the middle of the back. It may be as well to add here that the plate accompanying Schreber's type diagnosis is, as far as outline is concerned, an exact copy of Vosmaer's or perhaps made from the same block; but the colouring, in the British Museum version at least, is of a very markedly darker brown than in any of four different copies of Vosmaer.

Very few characters of any taxonomic value are, in fact, given by either author. Schreber stated that there were many irregular brown spots; this he derived purely from the illustration, Vosmaer having made no reference to them. This picture, which carries the subscription that it was drawn from life, depicts them as extremely irregular in shape, that is to say neither roundish nor squarish but with far more jagged outlines than are found in any existing genet skin. This is explicable in that, if the drawing was truly made from a living animal, the fur may well have been in a rough, wind-blown state, not brushed smooth as in a prepared specimen. This would argue a long, loose pelage; but it is difficult to make the markings of any existing specimen of genet take on the size, appearance and positioning of the blotches depicted by Vosmaer's artist.

The tail was described as ringed with black and white and having a black or brownish-black tip; but the number of rings was not stated, nor does the illustration make this clear, the only two, very narrow, pale rings visible, near the distal end, run at a slope such as is found in no genet. The dark tip is relatively short, narrow and pointed. The overall impression given is that of a long-haired structure, matching the similar inference respecting the dorsal pelage made above. Other, more minor, points cannot be touched on here.

Clearly there is very little that is reliable in the way of characters to be squeezed out of the original diagnosis. When we come to consider what has been made of *tigrina* since by Matschie (1902), Thomas (1906, 1908), Schwarz (1930) and Roberts (1951) we get a pretty mixed picture, sometimes in direct conflict with the type description and/or its illustration. Each has attributed to the species characters of his own devising. Matschie, for example, definitely stated that the hairs at the tail root were at least 30 cm (*sic*) long; that, despite the obvious taper in the illustration, it was about as broad at the base as at the tip; that the last quarter of its length was black with only traces of narrow half-rings below; that the first two dark tail rings, neither visible in the illustration nor described, were at least as wide as the succeeding pale rings. This may be *tigrina* Matschie but it certainly is not *tigrina* as described by Schreber. Again, Thomas & Schwann (1906) stated, directly and indirectly in their key, that the whole undersurface and forelimbs were dark-brown or black—which from Schreber and Vosmaer was patently untrue; and, in fact, Thomas & Wroughton (1908) modified this to forefeet black—the original description ("feet with a lot of brown") and the illustration belying this misleading assertion. Schwarz endowed *tigrina* with a number of new characteristics: short legs, short face; pear-shaped bullae, strong post-orbital processes and a distinct sagittal crest—all very inconstant characters in *Genetta* skulls. He stated the pelage to be variable but never shaggy, with large, mostly brown-centred spots; and the tail to have 8 to 9 dark rings. Other uncertainties and contradictions in diagnosis concern the inner cusp on p^3.

The characters which most authors concur in for *tigrina* and which do not conflict with Schreber's and Vosmaer's descriptions, and which also accord with specimens from the reputed region of provenance, South Africa, are: that the pelage is longish, with large, mostly independent spots in about 4 longitudinal rows, and a dark, probably erectile stripe on the lower half of the back; the tail with about 8 dark rings and a dark tip; the legs and feet with a good deal of dark colour on them, especially the back of the hindleg contiguous to the heel, the hindfoot having at least some grey on its upper side. However, in view of the doubt and conflict of interpretation that *tigrina* has engendered a good case could be made for the abandonment of the name. But whatever attitude may be adopted towards this, it seems clear that, in so far as it is possible to gather, the animal intended by Vosmaer and Schreber is probably more akin to the long-haired *genetta* group than to the relatively short- and soft-furred *pardina*; and that as regards specimens from eastern Nigeria and Cameroun, as well as Allen's eastern Congo series, Schwarz's hypothesis about distribution is entirely at fault, these animals being certainly *pardina*.

The question of *rubiginosa* Pucheran, 1855, is often involved with that of *tigrina*, as to whether they are either one and the same, the former a race of the latter, or specifically discrete. Though of no first-hand concern to West Africa, the following, which emerged incidentally from the wide investigations necessarily made, may be added here as an appendix to the above. Pucheran's curt Latin diagnosis would appear to be too vague to be of any real use whatsoever: whitish-grey washed with tawny; the spots of the back almost totally rusty; the tail furnished at the base with four rusty rings then four black. That is all. It is too obscure, in the light of now known colour variability, to render *rubiginosa* certainly determinable. It seems almost pointless to continue trying to tie such ill defined names to specific forms. Schwarz looked on *rubiginosa* as a synonym of *tigrina*, though Thomas in his 1908 key had—with what justification is surely open to question—devised his own distinction between them: that in *tigrina* the spots were large and the forefeet black, whereas in *rubiginosa* they were of medium size and the forefeet pale.

Skull. The general form of this in the *pardina* group is very much as in other genets. Possible points of distinction, such as the existence of an inner cusp on p^3, or of a sagittal crest, are as variable as in other groups. One differential character alone is practically constant: in fully adult skulls the postorbital constriction is, with few exceptions, less, and sometimes markedly less, than the interorbital breadth, this difference being on the average greater than it is in the *servalina* group. No significant variation of external appearance can be detected in exceptional examples. On the average the excess of interorbital over postorbital breadth is of the order of 2 mm. At its greatest it may reach 5 or even 6 mm, the latter width dropping to as little as 8·0 mm, the cranial constriction becoming a very marked feature of the skull. One skull in which this occurs, No. 46.397, is a quite typical large-spotted *genettoides* from Oda (Ghana); the other, No. 1645a from Gaboon, has no skin.

Of the two adult skulls in which the intertemporal breadth is greater than the interorbital, one has an excess of only 0·1 mm. In the other, No. 27.8.12.1 (Ghana), the excess is 4·1 mm; and there are interesting differences in the teeth, p^1, m^1 and m^2

being smaller than normal, especially the last which is only half the usual size and lacking from one side. A similar state of affairs with regard to m^2 exists also in a Mamfe skull; but neither skin is in any way out of the usual run of *genettoides* save that the Ghana animal was in full moult.

Two other skulls have unusual features but both are without skins by which to check their standing. No. 61.42, from Musaia (Sierra Leone) is narrower across the upper carnassials than any other specimen and also has an appreciably smaller p^4 and m^1. And No. 68.493 has remarkably long, backwardly directed postorbital processes, measuring 27·1 mm across in contrast to a mean of 19·5 mm. These points are mentioned since they have at one time or another in single skulls been regarded as having some taxonomic significance. There is no clear reason to suppose that they have; the material available for study is quite inadequate to provide sound data; and they are connected with no readily detectable external differences. Other characters which have been used taxonomically yield, as regards British Museum specimens, the following data. An inner cusp on p^3 is of irregular occurrence and is independent of age or sex. In adult skulls of the *pardina* group it is present and large in 9 specimens, small in 3, and lacking from 4. As for a sagittal crest: it is present in 8 old skulls, 3 of them ♂, 5 of unknown sex; and it is absent from 4 medium-age skulls (2♂♂, 2??). There are no adult female skulls from which to derive data. Finally, the nature of the postorbital processes has been suggested as of possible taxonomic significance. However, they show no fixed form, in length, pointedness or direction, varying from short, blunt and deflected to sharp and long-pointed irrespective of other characters.

The three West African species included in this species-group may be separated by the key on page 189.

GENETTA PARDINA I. Geoffroy — Pardine Genet

Viverra maculata Gray, 1830, *Spicilegia Zoologica* . . ., **2**: 9, pl. 9. Type locality given as North Africa but in the opinions of Matschie (1902) and Schwarz (1930) this should really be West Africa. This was described from a living animal in the Tower of London and there does not appear to be any preserved type. The specific name is the Latin word for spotted. Preoccupied by *Viverra maculata* Kerr, 1792 (= *Dasyurops maculatus* Kerr). See p. 205 herein.

Genetta pardina I. Geoffroy, 1832, *Mag. de Zool.* 2nd year, class 1, pl. 8 and accompanying text. Interior of Senegal. The name is a diminutive of the Latin *pardus* lepoard.

Genetta pantherina Hamilton Smith, 1842, in *Jardine's Naturalist's Library*: **35** (13 of Mammalia): 171 No type locality given. This, from the Greek *panther* leopard, would appear to be nothing more than a renaming, or misnaming, of *pardina* I. Geoffroy resulting from the French name also given by Geoffroy at the head of his description, G.(enette) panthérine.

Distribution. As understood in this present work, and as defined above, *pardina* occurs in the drier open woodlands from Cameroun to Senegal. How far east it ranges in these belts has not been determined; but the present writer has little doubt that East African forms from as far afield as Tanzania, and usually nomenclaturally associated with *tigrina*, belong, in fact, to the *pardina* group, if not *pardina* itself. West African specimens of *pardina* exist in the British Museum from the Wukrum Hills (Northern Nigeria, Sudan woodland) and Fort Lamy (Chad, Sahel woodland).

Description. The series of 8 flat, partly incomplete skins from the Wukrum Hills has already been referred to. No two skins are precisely alike in their colouring and marking. Six have the ground-colour a sort of creamy- or sandy-buff; the seventh is rather greyer; and the eighth somewhat more whitish—though, nevertheless, still palely washed with sandy tips. There is an erectile spinal crest from the shoulders to the tail, black in most cases but rusty in two. On each side of this are four well defined lines of spots, ranging, in different skins, between almost entirely black to almost entirely red-brown, some being obscurely black-ringed with rusty centres. The sizes and shapes of these markings are highly variable. In some skins they are wholly independent, in some coalesced longitudinally into short lines; some are roughly quadrate, some more oval, some rounded; and in one skin they are almost linear, the width of the blotches being only some 7 or 8 mm, as contrasted with twice this or more in other skins. The dense soft underfur is about 17 mm long, the fine-shafted bristle-hairs about 24 mm.

The tails are relatively short-, soft-haired and exhibit dorsally 5 to 7 pale rings and a black end portion 75 to 150 mm long, this terminal part interrupted laterally and/or below by 2, occasionally 3, partial white rings. The legs and feet have been mutilated; but are pale rather than black, though the inside of the hindleg appears to be dark, at least in some cases.

The Fort Lamy skin differs in being of a more yellowish-brown colour and a less well-defined pattern of wholly brown spots. The fulvous colour, which extends also to the rings of the tail and to the undersurface of the skin itself, seems as if it might be due to drying over a smoky fire.

Skull. There are no skulls.

Habits. No special notes regarding habits accompany the skins. There is no reason to suppose that open-country genets differ materially in these from their closed-forest kindred except in so far as they probably more frequently make use of rock crevices for shelter and breeding than high-forest forms do; and ground birds, francolins and guinea-fowl, doubtless play a more prominent role in their dietary.

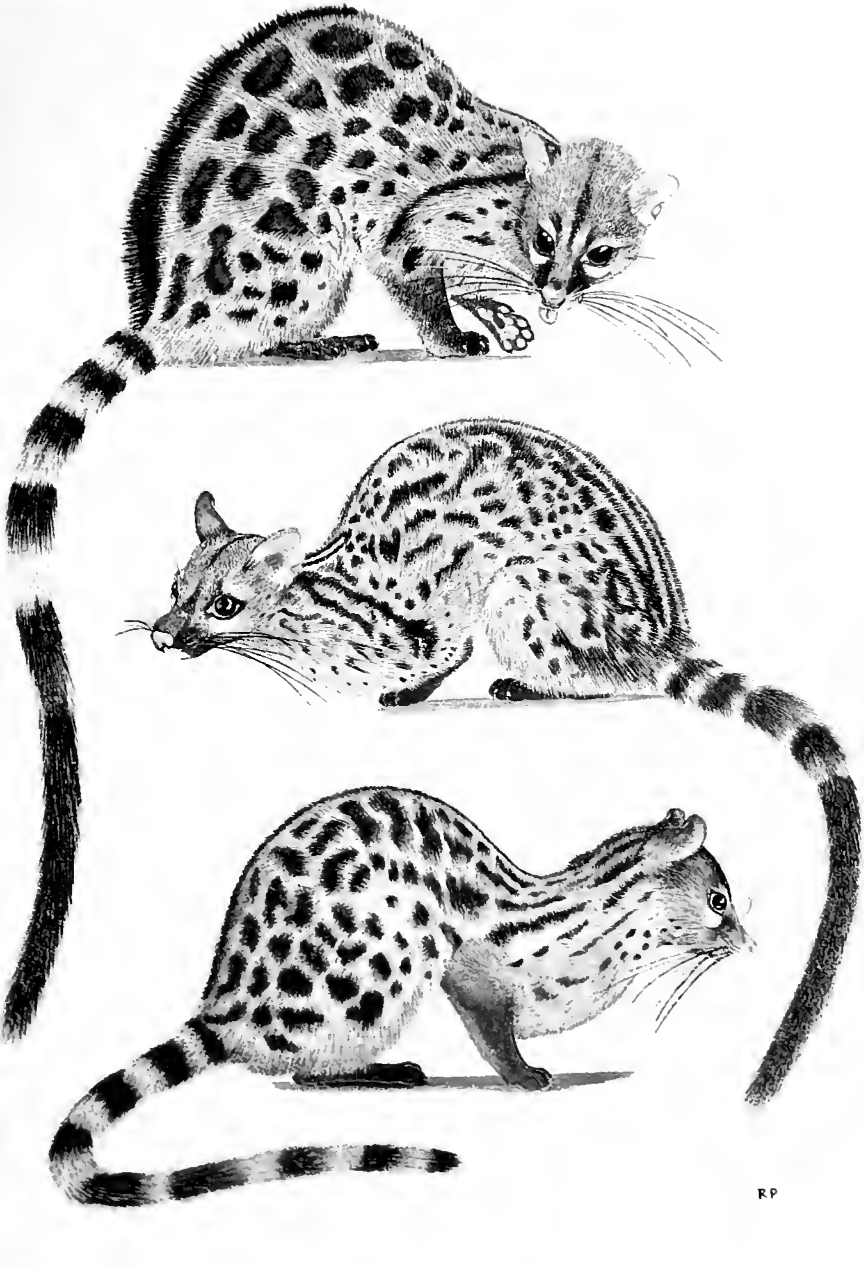
GENETTA GENETTOIDES Temminck Pel's Genet

Viverra genettoides Temminck, 1853, *Esquisses zoologiques sur la côte de Guiné:* 89. River Boutry and Elmina, Ghana. According to Jentink (1887 and 1892) there are four types in the Rijksmuseum van Natuurlijke Historie, Leyden: 2 mounted ♀♀ with skulls separate, from the River Boutry; and 2 mounted animals of unknown sexes from Elmina. Temminck coined this name from *Genetta* and the Greek termination *-o-eides* implying resemblance, from *eidos* form.

Genetta fieldiana Du Chaillu, 1860, *Proc. Boston Soc. nat. Hist.*, **7**: 302. Interior of Gaboon. This was named in honour of his "distinguished fellow citizen", Cyrus W. Field.

Genetta dubia Matschie, 1902, *Verh. des V internationalen Zoologen-Congresses zu Berlin, 1901*: 1141. West Africa, locality unknown. The Latin word *dubia* has several meanings, of which doubtful was that most likely in Matschie's mind in reference more to the species' uncertain standing (p. 1137) than to its indefinite provenance.

Genetta insularis Cabrera, 1921, *Bol. R. Soc. esp. Hist. nat.*, **21**: 261. Rebola, Island of Fernando Póo. The specific name is from the Latin *insula* island.



Pel's Genet (*Genetta* [illegible]) Small-spotted Genet (*Ge*[illegible]) Benin Genet (*Ge*[illegible])

Distribution. This form (Plate 4) inhabits the closed-forest and neighbouring Guinea woodland, plentifully from Gaboon to Sierra Leone and thence, less commonly, to Gambia. The localities from which specimens exist in the British Museum are too numerous to cite; but, closed forest apart, it may be worth mentioning that the most inland places which have yielded specimens are Katsina Ala (Northern Nigeria), Musaia (Sierra Leone) and Fouta Jallon (Guinea). These Guinea zone specimens may possibly come from high-forest remnants or extensions ("fringing forest") rather than from the more open woodland itself; but on this point there appears to be no positive information.

Description. As typically described this form comes from the Ghana coastal forests. One such skin in the British Museum, No. 57.9.16.3, is, in fact, from its history, almost certainly one of Pel's original specimens and therefore a paratype of Temminck's *genettoides*. Temminck wrote at some length of this genet, regarding it as very closely related to *genetta* itself. He gave no clear account of the dorsal markings, laying his greatest emphasis on the nature of the pelage. From this and from his description of the tail—not at all bushy, the hairs being half as long as in *genetta*, the annulation irregular, the black rings wider than the white, the terminal third black with brown half-rings below—it is abundantly clear that he was wrong in his estimation of relationship and that the form without doubt belongs to the *pardina* group.

It has already been explained that pattern and colour are very variable and that there seems to be no clear-cut division between this form and *poensis*. In the most typical *genettoides* the spots are fairly large, separate, oval or quadrate, either wholly black or with varying amounts of ginger-brown hairs at the centre, making them to a greater or less degree annulate. In size, those nearest the black spinal stripe are 30 to 40 mm long and 15 to 25 mm wide. They are in 4 rows, with, often, a small part of a fifth; and there are about 5 of these large blotches in the innermost row between the shoulder and the hip. The legs may be either pale or blackish; but neither this nor the colour and size of the spots is regarded as having any real taxonomic significance. The hindfeet are dark above with a more or less pronounced pale streak running along the inner edge from about the base of the 2nd digit.

Between this and *poensis* at the other end of the scale, with small-sized spots too numerous to count, there are all manner of intermediate stages of size, colour, shape and independence. Some are deep black and remarkably clear-cut; other brownish and confused. These variations show no connexion with localities. Two corresponding to the deep-black clear-cut category come, the one from Sapoba (Benin) west of the Niger, the other from Ikot Mbo (Calabar) well to the east; and from Ejura (Ghana) come fairly large-spotted and very small-spotted skins. The last, however, is pretty young, and it is possible that its markings would increase in size with age.

The pelage in *genettoides* is of medium length and fairly soft, and consists of abundant, very fine, rather sinuous underfur 12 to 14 mm long together with finely stalked, terminally broadened and flattened bristle-hairs measuring 19 to 21 mm. Ground-colour is usually of a mediumly-dark grey washed with pale brown; but one very-large-annulate-spotted skin from a small island in the mouth of the Volta River near Ada (Ghana, strand and mangrove vegetation, of very low rainfall) is a pale whitish-grey, not dissimilar in tone from open-country *pardina* itself but without this latter's warmer cream-buff tint.

All, of course, have the typical *pardina* group tail, short-haired, smooth, subcylindrical, and silky in texture. This last is because the bristle-hairs, which are only some 19 to 22 mm in length, are slender and taper to a very fine base. The abundant underfur is about 9 to 11 mm long and plays a prominent role in determining the texture and shape of the structure. All this, while vastly different from the extremely long, coarse bristles of *genetta*, is not unlike *servalina*; but in *genettoides*, as in others of the *pardina* group, black is the dominant colour since the pale rings (mostly whitish) are generally much narrower than the dark and only completely encircle the tail in the basal half. The black end portion is usually at least 75 mm in length and often much more, with 2 or 3 half-rings (or shorter) below, or sometimes with no trace whatsoever of white.

Skull. The bulla is shown in fig. 28b. Nothing appears to distinguish the larger-spotted *genettoides* from the smaller-spotted *poensis*. No comparison, either of form or of size, can be made with open-country *pardina* itself since no skulls of this last are available for study.

Taxonomy. Sufficient has already been said regarding this in the introductory remarks to the group.

Habits. There are no collectors' field notes furnishing any useful information peculiar to *genettoides*. One specimen was trapped in a farm, one shot at night; and the species is said to be fairly common in Sierra Leone. The first of these collectors' remarks runs counter to Sanderson (1940) who said that this species in Cameroun (under the name *G. tigrina fieldiana*) inhabited low trees in both high deciduous forest and rain forest, occasionally entering old secondary forest, but never recently cleared land, *i.e.* "cultivated land and tertiary growth". Common observation also casts doubt on what Sanderson wrote, since these genets are fairly reliably known to come into open cultivated compounds and farms for the purpose of stealing fowls.

GENETTA POENSIS Waterhouse Small-spotted Genet

Genetta poensis Waterhouse, 1838, *Proc. zool. Soc. Lond.*: 59. Island of Fernando Póo; but doubt was cast on this provenance by Pocock (1908b). Type in the British Museum, No. 55.12.24.412, sex ?; skin only, in fairly good condition, but legs incomplete.

Description. The doubtful validity of this species (Plate 4) but its descriptive usefulness have already been briefly discussed above. It remains to enter into this matter a little more fully.

The species *poensis* has suffered more ups and downs than possibly any other form of *Genetta*. Waterhouse himself thought that his newly proposed species was nearest to *pardina*; and Matschie (1930), possibly acting on this opinion and seemingly never having seen the skin or read the description with much care, synonymised the two. Pocock (1908b) was astonished at this as "it would be hard to find two more dissimilar species in the genus". This is very true, as reference to Geoffroy's plate and diagnosis abundantly shows, and if these alone are taken as the sole criteria of *pardina*.

The markings of *poensis* (Plate 4) are widely different from the large, squarish, independent blotches of fully typical *pardina*. They are very abundant, narrow, of much the same width as the spinal stripe or even less (*i.e.* rarely more than about 10 mm), the two rows on either side of this being largely united into similar almost black bands but in fact comprising some 8 or more spots between the shoulder and hip. Besides these partial stripes there are about four more longitudinal rows of roundish or oblong, more or less independent spots on each side.

Spots apart, one of the first striking differences between the type skin of *poensis* and other specimens of the *pardina* group is its golden-yellow ground-colour. Indeed, with this colour, the abundant narrow spots and the forelegs being black, the skin at first sight closely recalls *servalina*, but is at once distinguished by its typical *pardina* tail with its lengthy black distal portion and indistinct or partial pale rings. The authenticity of this colour, however, has been called into question. Pocock (1908b), acting on a hint from Oldfield Thomas, thought that the yellowish tone might well be due to drying over a smoky fire. It is now not possible to be sure. The only West African specimen in the British Museum at all resembling it in its warm colour is the animal herein named *bini*; But there is a marked difference in that the reddish colour of the latter is bright and lively whereas that of the *poensis* type is dull, pervasive and seems very likely to be adventitious. This is, in a way, confirmed by other specimens closely conforming to the *poensis* pattern, Nos. 1938.7.25.5 and 57.12.5.1, in which the ground-colour agrees well with that of the ordinary run of high-forest genets of the *pardina* group. The same may be said of No. 39.686 from west of the upper Cavally River in north-east Liberia. But this specimen, which was figured by Pocock (1908), has somewhat aberrant features. In it the rows of spots adjacent to the spine are more concurrent than usual and also in places join the crest itself so that the medial dorsal pattern is rather darker and more confused than in other examples. The fur of the back of the neck is not in good condition but it appears that the linear pattern is there not so clearly defined as in the type and Kumasi specimens. Added to this is the fact that the tail is almost completely melanistic, the pale annulations consisting solely of 5 rather obscure, basal half-rings. Moreover it is very short, recalling what Matschie must have meant for *dubia*; but it is by no means certain that it is all there.

Pocock's scepticism regarding the identity of *poensis* with *pardina*—or with *genettoides*, which he would at that time have regarded as *pardina*—is excusable. Yet, in the light of more abundant material than was available to Pocock, it seems to the present writer that the two may well be demonstrated in the future to be the same, *poensis* being at the small-spotted end of a pattern range. Nevertheless, until that time, and in the present state of doubt, it seems worth while retaining the name even if only for its succinct convenience in description. It must be noted, however, that were it to become established that transition from large to small spots was in fact of this nature, or that spot size was simply a matter of individual idiosyncrasy within a single species, then the name *poensis* would have to replace *genettoides*, which it antedates.

Pocock was also inclined to doubt the island provenance of *poensis*. In this, in view of the early date of its collection and the imprecise conception of West African geography at the time, he may well be justified. At any rate, nothing similar has come to light since from Fernando Póo. One of the skins referred to above as most closely conforming to the type came from Ghana, the other is, unfortunately, also an early one and labelled merely "West Africa". It will be seen from the clinal nature of the *pardina* forms that it must often be difficult to assign smaller-spotted specimens unhesitatingly to a specific form. Apart from the type and the other skins just mentioned, it would seem that a few specimens from the closed forests of Ghana, Western Nigeria, and possibly Cameroun, might be regarded as *poensis.*

Skull. There is no type skull; but that belonging to the skin which, apart from colour, very closely agrees with Waterhouse's diagnosis of *poensis*, No. 1938.7.25.5, collected at about 64 kilometres north of Kumasi (Ghana), is far larger than any other of the *pardina* group, being between 7 and 8 per cent larger in many measurements but with a toothrow rather more than 20 per cent longer than average. It is tempting to regard this as validly diagnostic and as confirming the specific distinctness of *poensis*; but it would be very ill-advised to jump to conclusions on the strength of this single specimen. This is the more so as the only other adult skin closely resembling *poensis* (No. 57.12.5.1) has a skull that differs quite appreciably in form and is of average size with an average toothrow.

Habits. Nothing whatsoever has been recorded of habits specially pertaining to *poensis.*

D. *thierryi* group

The relationship to other genets of the species included under this heading is obscure; but, for various reasons, it seems to merit separation from the species-groups so far dealt with. Since there is only one such species known it cannot logically be considered as part of a species group, and it is so dealt with here solely for the purpose of maintaining uniformity of treatment.

GENETTA THIERRYI Matschie Hausa Genet

Genetta thierryi Matschie, 1902, *Verh. des V internationalen Zoologen-Congresses zu Berlin, 1901*: 1142. Hinterland of Togo from latitude 9° N. onwards. Specimen No. 19015 in the Institut für Spezielle Zoologie und Zoologisches Museum der Humboldt-Universität zu Berlin is herein, below on page 215, designated as lectotype. There appears to be no record of exactly who Thierry was, in honour of whom this was named; but since he was an Oberleutnant it is probable that he was an army officer posted to Togo.

Pseudogenetta villiersi Dekeyser, 1949, *Bull. Mis. natn. Hist. nat. Paris*, (2) **21**: 421–424. Messirah, Senegal. Type in the Museum National d'Histoire Naturelle, Paris, No. C.G.1952, No. 4 (I.F.A.N. 48.5.32 (453)), stuffed skin and skull; 6 paratypes in the Institut Francais d'Afrique Noire, Dakar. Dr. Villiers after whom this was named is a well-known West African collector and zoologist.

Taxonomy. It is necessary to discuss this first before any pronouncement can be made respecting distribution and other matters. So far as published literature reveals there does not appear to have been any critical re-examination of Matschie's material since his erection of the species at the beginning of this century. There is therefore no first-hand description additional to the rather inadequate account which can be put together from his keys. The characters there given yield the following: the spots are small and very narrow, sometimes several united into a long stripe; colour is not mentioned, but there are 4 complete rows with at least 9 spots in the first row, and those of the third row further apart than their length. Both fore and hindfeet are pale. The tail is short-haired, the hairs not longer than 25 mm at the base; some upstanding hairs at the root; there are 10 pale rings, the last few visible only on the underside; the light rings at most as broad as the dark ones.

By the kindness of Dr. Renate Angermann of the Institut für Spezielle Zoologie und Zoologisches Museum der Humboldt-Universität zu Berlin it has now been possible to study some of Thierry's specimens used by Matschie. There is no type of *thierryi*, nor did Matschie ever label any of these skins with names. According to Dr. Angermann (*in litt.*) there is "a series of 10, all of them prepared in the same manner, all without skulls and without precise dates or locality ("Togo")". Of the 3 skins examined in London 2 belong, without question, to the *pardina* group; the third, No. 19015, agrees, as near as can be told, with Matschie's key characters for *thierryi* and also with several skins in the British Museum from the interior of Ghana—that is, from the area neighbouring that from which Matschie described this species. The present writer, and R. W. Hayman (1935) previously, had independently come to the conclusion that these British Museum specimens represented what Matschie intended by *thierryi*, an opinion which has been strengthened to virtual certainty by comparison with the Berlin material. Dr. Angermann has written that the majority of the series of 10, not sent for study, agree with specimen No. 19015, which is here designated as lectotype.

Before proceeding further with this question it must be said here that it does not appear to the present author that there is any good reason to believe that *villiersi* Dekeyser is materially different from *thierryi*, or that *Pseudogenetta* Dekeyser, of which genus *villiersi* was made the type species, merits separation from *Genetta* even as a subgenus. This latter opinion was held also by Kuhn (1960).

Distribution. On this basis, specimens of *thierryi* exist in the British Museum from Senegal (Bakel and an unspecified locality), Sierra Leone (Rokupr), Ghana (Ejura, and Mole Reserve) and Nigeria (Wukrum Hills, north of Lau on the Benue). These provide 11 skins and 7 adult or fairly adult skulls. The Berlin Thierry skins are labelled as coming from Borugu, Togo, which would appear, from an old German colonial map, to be the equivalent of Borgu, 10°46N, 0°34E, about 30 kilometres north of Sansanne Mangu, just in the Sudan woodland zone. It is not known on what grounds Matschie gave the distribution of the species as Dahomey and Togo westwards; these specimens show that it ranges through the open woodlands of the Guinea, Sudan and Sahel zones from at least the upper Senegal River to the western side of Northern Nigeria. Further, and of considerable taxonomic interest, the last British Museum specimen cited above demonstrates that three species, *senegalensis*, *pardina* and *thierryi*, are sympatric within a restricted area just north of the Benue. The Sierra Leone specimen is interesting in that Rokupr, though nominally in the closed-forest zone, is today in the Invasive Guinea woodland zone where very little forest now remains, and the species therefore is presumably a fairly recent immigrant. F. de Beaufort (1965) also records specimens (under the name *Pseudogenetta villiersi*) from Guinea, Ivory Coast, Dahomey and Cameroun.

Description. These specimens furnish the following description of *thierryi* (Plate 3). This is a distinctly smaller species than the others, as the measurements given in the table on page 219 show. The general impression is that of a pale, small-spotted genet. The actual tone and the spot colour vary not only from place to place—the Sahel woodland specimens are lighter than those from the Guinea belt—but also within a single locality. The Berlin specimen, No. 19015, has appreciably brighter red spots than the general run of British Museum material, though the rather obscure markings of the aberrant No. 19.7.7.3710 referred to below are almost the same bright colour. Speaking generally, then, the ground-colour is buffish, to a greater or lesser degree speckled with deep brown or black hair-tips. One of the most obvious differences from all the forms hitherto dealt with is the absence of a prominent black, and generally obviously erectile, spinal stripe. A medial stripe nevertheless exists; but it is of precisely the same brown colour as the rest of the dorsal markings and is very frequently itself narrowly split longitudinally down the middle by a line of paler hairs. It is narrow, at most 10 mm wide, and on either side of it are 4 rows of spots which are no wider, and often narrower, than this. Those in the rows adjacent to the medial stripe may be united into almost continuous lines, or they may be almost entirely separate. Those of the next row are sometimes partly coalesced; but in the two outer rows they are always quite independent and often slightly broader and rounder than in the inner series. Over the back of the neck these rows are continued as much narrower lines or series of spots, sometimes very clear, but sometimes eventually becoming confused anteriorly. They are not always easy to count but, in broad terms, there are something like 10 spots in the inner row between shoulder and hip. The colour of the markings, while uniform throughout a given example, may be deep brown or ginger in different specimens from a single locality. The pelage is fairly short, that is to say, the bristle-hairs about 15 to 20 mm long, the underfur about 12 mm. There are spots on the upper thigh but the rest of the hindleg and all the foreleg is pale buff, or even becoming whitish towards the feet.

The tail is something between *genetta* and *pardina*. It has the long blackish terminal section with pale half-rings of the latter: but, though it is a very much narrower structure, it has, particularly near its base, something of the longer-, backwardly-directed-haired appearance of the former, and with its less clear-cut boundaries to the rings as well. Its bristles are about 25 to 28 mm long, the underfur 15 to 17 mm. There are 8 or 9 pale rings and half-rings, and occasionally some very slight indication of a tenth. Though all tails conform to this general pattern they do vary considerably in the clarity or obscurity of their annulation, in the length of their hair, especially basally, and in the colour of the dark rings, which varies from blackish to orange-brown.

One of the two Bakel skins, No. 19.7.7.3710, while obviously *thierryi*, is exceptional. The medial pattern of spinal line and contiguous rows is rather confused; and the remainder of the spots are even smaller than normal. The basal portion of the tail is very long-haired, almost of a *genetta* character.

Skull. Apart from its markedly smaller size this corresponds closely to the general pattern of *Genetta*. There is no old male skull amongst the British Museum material and this may account for any but the most vestigial indication of a sagittal crest, except, of course, in the extreme posterior of the cranium where there is, as throughout the genus, a short, sharp flange forming a T with the pronounced supraoccipital crest. Without exception in the 6 skulls examined, the intertemporal constriction is some 2 mm or more broader than the interorbital breadth. There is a clear, and usually large, internal cusp on p^3. The molars, both upper and lower, are smaller than usual, m^2 being particularly reduced; and m_2 is for the most part subtriangular with only rarely more than 3 cusps.

Habits. Nothing particular is known of the habits of *thierryi*. However, since it is an inhabitant of the open woodlands where for the most part the trees are of low stature and their crowns do not afford a great deal of visual protection, it is possible that this species more commonly breeds in holes in the ground or amongst rocks than the closed-forest forms do.

Subgenus **PARAGENETTA** Kuhn, 1960

Kuhn's Genets

Some of the main characters which serve to distinguish the animal covered by this subgenus from those included in *Genetta sensu stricto* have been given briefly in the key on page 189; and as there is only a single species at present known in *Paragenetta* all further information relative to the subgenus can be gathered from the account of *G. johnstoni* which follows.

GENETTA JOHNSTONI Pocock Johnston's Genet

Genetta johnstoni Pocock, 1908, *Proc. zool. Soc. Lond.* for 1907: 1041, pl. 54, f. 1 & 2. About 25 to 30 kilometres west of the Putu Mountains, eastern Liberia. Type in the British Museum, No. 8.8.23.1, sex?; flat skin only, in good condition apart from lacking head and forepaws. This was named in honour of Sir Harry Johnston, a well-known explorer and collector, who wrote a detailed account of Liberia.

Genetta (*Paragenetta*) *lehmanni* Kuhn, 1960, *Säugetierk. Mitt.* 8: 154–160, f. 1–12. Kpeaple, Liberia. Type in the Museum Alexander Koenig, Bonn, No. 57.11, sex unknown; adult skull only. This was named after Dr. Ernst von Lehmann of the Museum Alexander Koenig.

General. This species has had an erratic history. It was first described from "flat, native-prepared headless skins", with no skulls, collected about 1907 by Mr. Leonard Leighton. There were originally five specimens (Pocock, 1908b: 1038) but only the type and one other exist in the British Museum. The former bears a Zoological Society of London label but was registered, in 1908, as having been presented to the Museum by the collector. The second did not come to the Museum until 1930, when it was registered as presented by the Zoological Society but bears a label in Pocock's handwriting as the paratype figured by him alongisde the type in his original description.

The new species was thought to have nothing special about it apart from its slightly different pattern of spots and tail. Pocock, indeed, thought that it might, with more complete data, prove to be nothing more than a subspecies of *pardina*. No further material, however, was forthcoming, and there the matter rested until over half a century later a genet skull from Liberia, without a skin, came to the notice of Kuhn. The cranial, and especially dental, characters of this were sufficiently different from the general run of genets to merit, in his opinion, not only the erection of a new species, *lehmanni*, but its assignment as well to a new subgenus of its own. No connexion with Pocock's *johnstoni* was suspected until, at last, a complete specimen of skin and skull, demonstrating the synonymy of the two, was collected by Kuhn near Tappita (Liberia) in the early 1960s. The British Museum still has no skull assignable to this species.

Distribution. *Genetta* (*Paragenetta*) *johnstoni* is now known by specimens from the following Liberian localities: west of the Putu Mountains, Kpeaple, Bo, Tappita, forest south of Freemantown (Kuhn, 1965). These are all in the western part of the country, well inland from the coast in dense forest; but it is not known whether the species is restricted to this locality or ranges further east and west. It does not occupy the area to the exclusion of other species since Pocock (1908b) records *poensis* as forming part of the collection obtained there by Leighton. There is no information as to the degree of commoness of *johnstoni*. The small number of specimens known might seem to argue rarity; but this region is relatively poorly explored zoologically, and the fact that the original collector obtained no less than five skins indicates that such a deduction might well be erroneous.

Description. The type and paratype are of slightly different appearance, the latter being a shade paler, its spots appreciably less concurrent. The following description is basically that of the type. The pelage is dense, soft and not very long (bristles 20 mm, underfur 15 mm). The ground-colour is yellowish-brown. There is a black, moderately long-haired and almost certainly erectile spinal crest, some 10 to 12 mm wide, from well short of the shoulders to the root of the tail. On either side of this are four fairly clear rows of spots of approximately the same width as the spinal stripe and short confused portions of a smaller-spotted fifth and sixth. These spots are blackish-brown more or less heavily speckled with red-brown, so that in the paratype the latter colour dominates, the contrast between the spots and spinal line being considerably more marked than in the type itself. In this latter the first two rows on either side of the black medial stripe are almost wholly coalesced into complete lines. Because of this it is not really possible to count the number of spots in the first row accurately; but there would appear to be basically something in the nature of 8 or 9 between the shoulder and hip. These series continue forward over the back of the neck in the usual genet fashion, either (paratype) as independent spots or (type) united into fine lines. The belly is whitish. The thighs are heavily spotted; but in the type the remainder of the hindlegs and feet are deep blackish-brown. The sides of the neck are also well spotted; and what remains of the forelegs shows them to be so too; but in the type the markings are obscured by a blackish suffusion similar to, but not so intense as, that of the hindlegs.

The tail resembles that of the *servalina* group more than any other. It is long, subcylindrical, of a soft and furry nature, that is to say densely haired, the hairs not markedly long, with the underfur playing as prominent a role as the not very much longer bristles—in this respect completely different from the *genetta* group. The annulation, also, recalls that of *servalina* in its relative clarity and its continuation, though less

Table 10: Numerical data for species of *Genetta*

	genetta (? *afra*)	*senegalensis*	*genettoides*	*cristata*	*thierryi*	*johnstoni* (from Kuhn)
Vegetation	Sahel?	Doka—Subdesert	Forest and Guinea	Forest	Guinea, Sudan, Sahel	Forest
Number in mean	1	5	9	4	6	2
Condylobasal length	92·9	84·8	93·4	93·4	75·1	93·0
Basilar length	(85·5)	79·0	85·9	86·0	69·5	—
Palatilar length	43·0	38·1	42·5	42·7	32·7	—
Zygomatic breadth	46·3	43·5	46·7	45·6	38·5	44·2
Upper cheekteeth breadth	27·8	26·4	28·0	27·8	24·0	24·4
Interorbital breadth	12·3	12·3	13·6	13·3	10·7	13·4
Postorbital constriction	13·6	13·5	11·5	12·6	12·8	13·0
Braincase breadth	29·3	28·8	30·8	30·9	28·5	—
Toothrow (c—m^2)	36·3	33·8	35·5	36·7	28·2	—
p^4 length	8·6	7·9	8·6	8·6	6·9	6·6
m^1 breadth	8·6	7·2	7·8	7·7	6·5	5·6
m^2 breadth	4·9	4·2	4·5	4·5	2·9	2·3
m_1 length	7·5	7·0	7·6	7·5	6·3	5·8
m_2 length	3·8	3·7	4·1	3·9	3·1	3·1
Head & body	(490)	438	503	540	390	—
Tail	(300?)	445	427	425	385	—
Hindfoot	—	78	80	90	73	—
Ear	—	44	40	46	38	—
RATIOS (per cent)						
Tail/head & body	(60?)	103	85	79	99	—
Zygom. br./condylob. l.	50	51	50	49	51	48
Braincase/condylob. l.	32	34	33	33	38	—
Braincase/zygom. br.	63	66	66	68	74	—
Palatilar l./condylob. l.	46	45	46	46	44	—
Interorb./postorb.	91	91	118	105	84	103
p^4/c—m^2	23·7	23·4	23·4	24·2	24·5	—
$m_1/m_2 + m_3$	197	189	185	192	203	187

clearly than in that group, practically to the tip. Though in the distal portion the last two or three pale rings are certainly more obscure than proximally, they are nevertheless clearly observable, above as well as below, as contrasted with the almost complete terminal dorsal blackening of the *pardina* group. In the two study specimens available it is difficult to know how much, if any, of the tail tip is missing. However, the tip would appear to be fundamentally one of the pale series; but in the type it is very heavily dusted with brown though still distinguishable from the penultimate, dark, ring. In the paratype, on the other hand, only a very small area of white is detectable, and the tip would be classified as black. There are 8 black rings, sometimes equal to, sometimes broader than the white.

Skull. In the absence of any skull from the British Museum the following is founded on Kuhn (1960). The species, and hence subgenus, differs from *Genetta* by the smallness of the teeth, only the incisors being of equivalent size. The upper incisors are somewhat tilted backwards, but the lower ones are more horizontal in the mandible than in *Genetta*, imparting the appearance of many Insectivores. Also the lower canines are more forwardly inclined in the jaw, though bent upwards in the middle. Because of this the chin is very flat. The upper canines show no sign of the fine longitudinal furrows generally present on the outer face in *Genetta*; they are more slender and more backwardly curved. The first premolar is just as high as in *Genetta*, only somewhat narrower. All the remaining premolars are much lower and narrower than in *Genetta*; the inner cusp on p^3 is only hinted at. The fourth upper premolar is altogether much smaller; m^2 is tiny.

The zygomatic arch is narrower than in *Genetta*; the supraorbital processes are strong; and a sagittal crest is absent except posteriorly.

Taxonomy. From the nature of the dorsal pattern one would be tempted, as Pocock was, to relate this species to the *pardina* group; from the tail the connexion would seem to be rather more with that of *servalina*. But the teeth clearly show it to stand apart from both of these and probably, also, justify the retention of the subgenus.

Habits. Nothing at all is recorded of these.

Table 10 shows mean measurements derived from such material as exists in the British Museum, or (*johnstoni*) from recently published figures.

Genus **POIANA** Gray, 1865

African Linsangs

Poiana Gray, 1865, Proc. zool. Soc. Lond. (for 1864): 520. Type species *Genetta richardsonii* Thomson. This name is generally thought to have been derived from the second half of the name of the type locality, Fernando Póo, often in English spelt Po; recently de Beaufort (1965) has suggested derivation from the vernacular name *oyan*; but Gray had coined the name 33 years before G. L. Bates's Benito River specimens first recording this name had come to notice.

General. The true linsangs are Asiatic, the name itself being a vernacular one for these animals used in parts of the East Indies. *Linsang* was also used (Müller, 1838) as the scientific name of these oriental forms but has now been replaced in part by the earlier *Prionodon* Horsfield, 1824, and in part by *Pardictis* Thomas, 1925. There is a degree of superficial resemblance, external and cranial between these last animals, from Nepal and Tonkin, and those from Africa; and despite the lack of any existing link it has often been thought that the relationship between these widely separated forms is close. This is examined in greater detail later; but it may be said here that there are certain clear differences which caused Simpson (1945) to place the Asiatic Linsangs in a separate tribe, the Prionodontini, the African forms remaining with *Genetta*, *Nandinia*, *Civettictis* and others of extralimital concern in the Viverrini. It can be argued from this and the fact that the name is strictly speaking East Indian that it is inappropriate to call the African animals linsangs; and, indeed, the French use the name poiane. But it would be difficult now to substitute this or any other specially coined English name for the generally accepted term African linsangs, which has the merit of indicating that other possibly related forms exist elsewhere.

Distribution. African linsangs occur only in tropical Africa within the forest belt, on the West Coast between Liberia and Gaboon, thence extending inland to the eastern half of the Congolese Republic from its extreme north-eastern corner (J. A. Allen, 1924) to about as far as 4° South (Schouteden, 1948). They are known also from the island of Fernando Póo. Whether the distribution is continuous throughout this range is quite another matter. To judge from museum material linsangs are very rare and probably extremely local in occurrence. This may not, of course, reflect the true position on the ground; chance or an especial cunning in the avoidance of traps or of exposure may account for the paucity of known specimens. Nevertheless, this seems unlikely and these animals can be pretty safely reckoned as some of the rarest in Africa. The recorded places of collection are listed below in the two specific accounts.

Description. African linsangs are in appearance very like small genets, to which, in fact, they are nearly related; but their long bodies, clothed with spotted pelage, are yet more slender and lithe than in *Genetta*, their legs even shorter, and their ringed tails relatively longer. The head is small and the face pointed, the prominent ears upstanding and oval and with a fairly large bursa, the posterior flap arising above behind the pinna. The two West African species differ in their coloration but the general impression is that of a paler or darker brownish animal liberally marked with black spots which are rounded or oval and always small or very small. These are not quite so clearly disposed in regular longitudinal lines as in the genets, but about 4 or 5 rows can be detected on each side of the body. There may or may not be a narrow spinal line. The back of the neck is marked with three, or sometimes four, black lines or linear series of spots, which posteriorly are continuous with the dorsal markings.

The dorsal pelage is soft and very short but dense, comprising abundant fine underfur into which are mixed not very much longer bristle-hairs, flattish and slightly expanded distally but with long slender stalks scarcely distinguishable, even under magnification, from the fine underfur. The underparts of the body are whitish or creamy, without any markings.

The short legs are spotted and terminate in 5-toed feet which are clad, and especially on the sides and below, with dense, very short hair giving them a velvety touch and appearance. The sharp claws are not quite completely retractile. The soles of the feet carry the usual naked pads, the subdigital ones very small and rounded: the central pad on the forefoot consists of four anterior and lateral pads together with a partially divided posterior pad, the space enclosed by these being entirely bare or only very slightly hairy. On the hindfoot the central pad is composed of four distinct pads; but this foot is chiefly remarkable for its medial, narrow, naked pad, divided anteriorly, and extending nearly to the heel. It is the presence of this pad that is one of the chief differences between the African linsangs and the wholly hairy metatarsus of the oriental ones.

The tail in *Poiana*, as in *Genetta*, is a very distinctive structure. It is narrow, more truly cylindrical from root to tip than that of any genet, and very long. It is, indeed, often stated, as a firmly diagnostic character, to be longer than the head & body; but this may not always be so. The measurements given by G. L. Bates, an experienced and extremely painstaking collector, show the tail to be the longer in only half of the

6 specimens of *richardsoni* collected by him and measured in the field, the mean length of all 6 specimens working out at 95 per cent of the mean head & body measurement. It is true that this does not accord with the figures given by J. A. Allen (1924) where in all of 4 specimens, 3 of them juveniles, the tail exceeds the head & body. The greatest excess of tail over body, 52 mm, in the Bates specimens occurs in his youngest animal, a subadult: it is also a subadult that exhibits the largest difference, 53 mm, in Allen's Congo series. The tail is clad with dense, more or less erect, underfur and only very slightly longer, soft, bristle-hairs. There are from 10 to 14 dark rings according to species, somewhat narrower than the intervening pale ones, which may sometimes by faintly divided by very narrow accessory dark rings.

There appears to be no published account of the definite existence or absence of scent glands; and no live or spirit material has ever existed in London from which this question could be determined. But Pocock, who, was intensely interested in this matter, said in a footnote (1933: 970) that he had found evidence on made-up skins of their existence in *Poiana*.

Skull (fig. 30). Since no skulls of *leightoni* exist in the British Museum the following description applies more especially to *richardsoni*. Apart from its considerably smaller size the *Poiana* skull differs most obviously from that of *Genetta* in its lesser development of the posterior region. Although an occipital crest does exist it is relatively inconspicuous, often little more than a ridge, and there is no very marked excavation of the posterior braincase to rise again, as in *Genetta*, to elevated occipital flanges. Nor is there any short posterior sagittal crest, as throughout that genus. It may be mentioned here that in these matters the oriental linsangs differ from the African, their skulls more closely agreeing with those of the genets. The braincase is smooth and ovoid: the postorbital processes may be sharply pointed, though never lengthy, or they maybe poorly developed and blunt; and in 4 of the 7 London skulls this region is fenestrated. The postorbital constriction is wider than the interorbital breadth, the difference averaging rather less than 2 mm. The rostrum is narrow and pointed. The zygomatic arch is strong and in most cases has a well-developed, pointed, jugal process; but this appears to be a question of age since this section of the circumorbital ring is more or less absent from the subadult skull. The bullae are fairly large, the posterior portion far exceeding the anterior part, the two being conspicuously divided by a waist; the meatus is large. The post-dental palate is relatively longer and narrower than in *Genetta*, and the notches that separate it from the main palate shallower and rather less obvious than in that genus.

The dentition normally differs from that of *Genetta* in having one less upper molar, $\frac{3\ 1\ 4\ 1}{3\ 1\ 4\ 2} = 38$: but m^2 may be occasionally present, though minute, as in B.M. No. 1.11.21.7, a medium-aged female; m^1 varies a good deal in the London specimens but is on the whole more reduced than in *Genetta*. In the mandible, which is relatively weak and flat, m_2 is minute and seems, like its upper counterpart, to be on the way out. The canines of both jaws have minute longitudinal furrows along their outer faces, a character they share with *Genetta* and *Nandinia*, and one so unusual that it must assuredly indicate phylogenetic affinity.

Habits. Exceedingly little is known of the linsangs in life. Their apparent rarity and purely local occurrence, their secretive and almost certainly nocturnal habits have prevented their way of life from being observed save by a limited number of African hunters who, in the way of things, have never recorded what they know. African linsangs, at least, seem never to have been kept in captivity, either in zoos or, more locally, as domestic pets. Further, it is possible that more specimens have not come to light because of some special value traditionally attached to the pelt. Over a century ago Allen & Thomson (1848) recorded: "This is a rather scarce animal at Fernando Po, and as the skin is considered one of the most sacred and valuable amulets or charms of the Edeeyahs, they are unwilling to part with it. The small specimen in the British Museum, presented by Dr. Thomson, was skinned from the mouth, and is a proof of the ingenuity of that singular people". The special significance of these rare skins noted by these authors in Fernando Póo seems to be reflected also in Liberia where, according to Dr. Hans-Jürg Kuhn in observations referred to below, the

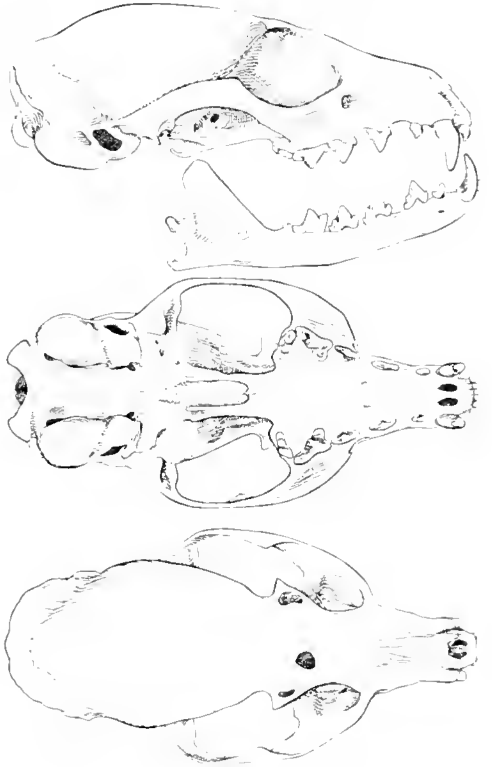


FIG. 30. *Poiana richardsoni*: skull, B.M. No. 98.3.19.11, ♂, × 1

pelts are used to make medicine bags, that is to say containers for materials regarded as possessing exceptional properties and worth. However, the mystical value of the *Poiana* skin doubtless varies with different individuals or may have suffered a decline, since Seimund, responsible for the greater part of British Museum collecting in Fernando Póo, recorded that a tail and fragments of a pelt were "got in exchange for rum".

Habit notes boil down at present to two collectors, Bates & Kuhn. The former (1905), who characterized *Poiana richardsoni* in Cameroun as a rather rare little beast, said that it was found only in the forest, sleeping in the daytime on thick tangled vines, and walking (? waking) only when disturbed. A female brought to him in October had milk in two teats; and he was told that these animals produce two young at a birth. More recently, Kuhn, in an unpublished communication quoted in Walker (1964), as a result of intensive mammal collection and study in Liberia, has given the most abundant information so far available. In this he states that the nests are round, at least 2 metres and usually more from the ground, and of green material, several animals sleeping there for a few days and then moving on to construct a fresh nest. Further, although these animals have been recorded as using abandoned squirrel dreys as shelters, he was informed by reliable African hunters that the reverse was the case, squirrels taking over abandoned linsang nests. Kuhn says that the diet includes cola-nuts, insects, young birds and plant material. Doubtless it also covers small rodents and possibly reptiles as in the genets. This is the sum total of our present knowledge.

Taxonomy. It has often been assumed that the African linsangs, *Poiana*, are closely related to the Asiatic linsangs of the genera *Prionodon* Horsfield and *Pardictis* Thomas in spite of being very widely geographically separated with no known connecting forms. Both groups are tropical rain-forest dwellers; and Misonne (1963 and 1965) has shown that the existence of any forest bridge between Africa and Asia later than the Oligocene is improbable. The likelihood of either group's being an offshoot of the other, or both the relatively recent descendants of some common linsang stock is remote; and the affinity between the African and Far Eastern genera is, in fact, considerably more distant than often supposed. *Poiana* is without doubt more closely akin to *Genetta* than to *Prionodon* and *Pardictis*. This is in some measure expressed in Simpson (1945) by the allocation of the two groups of linsangs to different tribes, the Viverrini and the Prionodontini.

Resemblances which on the surface appear striking are on closer examination seen to be not so exact, and are assuredly fortuitous, the result rather of convergence than of affinity. The position cannot be more than summarily glanced at here. Any correspondence between the skulls is no more than frequently occurs in this family; and, in fact, the supraoccipital region and the zygoma are of diverse forms in the two groups. Loss of the posterior molars, giving rise to similarity of dental formulae, is of common evolutionary occurrence and of no overriding significance. Against this numerical consonance, the forms of p^1 and of m_2 are distinctly different. In the Asiatic linsangs both of these teeth are somewhat more complex, p^1, when not too worn, being clearly tricuspidate; while m_2, in them, is far more laterally compressed and more sharply, unevenly and lineally cuspidate than the rather squat quadrate or triangular tooth of *Poiana*, bearing in side aspect a passable resemblance to a small premolar. Finally, and quite significantly in a rare though slight character, the canines of the oriental species show no trace of the fine furrows on their external faces so typical of *Poiana* and *Genetta*. These cranial and dental disconformities are supported by external ones of pattern, pelage and feet, that make it clear that close affinity between the African and Asiatic linsangs is more apparent than real. As Pocock (1908) indicated, a character that would go far towards clinching the question of relationship, but about which no information was available, would be the presence or absence of perineal scent glands in *Poiana* since it is known that they are lacking from the Asiatic linsangs. A quarter of a century after pointing this out Pocock (1933: 970 f.n.) had convinced himself, by the re-examination of the same dried skins as were previously available to him, that there was, in fact, evidence in them of the existence of such organs; and he therefore concluded that the affinities of *Poiana* quite definitely lay with *Genetta* and not with *Prionodon*.

Three forms of *Poiana* have been described: *richardsoni*, *ochracea* and *leightoni*, the two last as subspecies of the first. No study skulls of these two exist, at least in London; but from external characters it seems probable that whereas *ochracea* is merely a colour variant of *richardsoni*, *leightoni* merits specific status. Only two of the three forms occur in West Africa, *ochracea* Thomas & Wroughton, 1907, being described from the Aruwimi River, eastern Congo. The two relevant species may be differentiated in the following way.

KEY TO THE SPECIES OF *POIANA*

(previous key page 166)

Dorsal ground-colour dull reddish-brown; belly off-white; no continuous dark spinal stripe; rings of the tail parallel-sided . . . ***richardsoni*** (*page* 225)

Dorsal ground-colour bright buffy; belly pure white; a narrow, more or less continuous dark spinal line present; dark rings of the tail rather chevron-shaped. . . . . ***leightoni*** (*page* 227)

POIANA RICHARDSONI (Thomson) Richardson's Linsang

Genetta richardsonii Thomson, 1842, *Ann. Mag. nat. Hist.* (1) **10**: 204. Fernando Póo. Type in the British Museum, No. 42.10.18.1, sex unknown; unmounted young skin, in poor condition; no skull. This was named in honour of Dr. John Richardson, Inspector of the Naval Hospital at Haslar. Thomson, whose name was consistently misspelt Thompson by Gray in synonymies, was one of the medical officers to the 1841 expedition to explore the Niger and co-author of the published account. A note in Gray's handwriting in the British Museum Register for 1842 indicates that it was he who actually prepared the description "for Mr. Thompson".

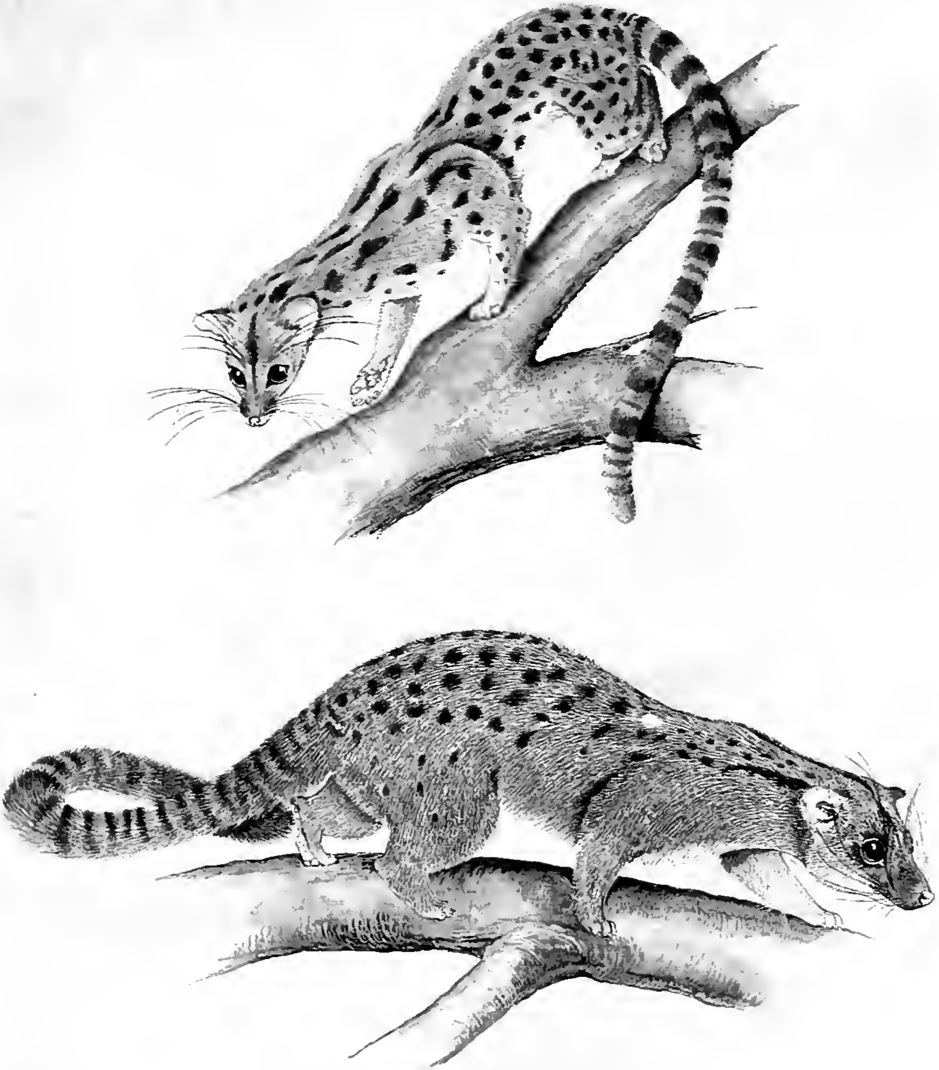
Distribution and general. This is the better recorded of the two African linsangs, the British Museum possessing 8 skins, one of which is juvenile, one fragmentary, and 7 skulls. These all come from the Bight of Biafra, that is to say more specifically, the island of Fernando Póo, Benito River in Spanish Guinea, and Bitye in lower Cameroun, G. L. Bates being responsible for all the 6 mainland, and only perfect adult, specimens. This area, of course lies wholly within the rain-forest belt. The skin referred to by Pocock (1908b) as being labelled from Sierra Leone has not been traced, nor any evidence found of its existence. However, one of the skulls, No. 1084a, was said to have come from Sierra Leone, the relevant note being in Gray's own handwriting on the page so numbered of his draft catalogue but under an 1854 Register number that does not, in fact, exist. But, though purchased from a third party, it was also stated to have been one of Fraser's collection—and, thus, with little doubt from Fernando Póo. It bears a label to this last effect; and Gray himself must have come to this decision since he quoted this skull in Gerrard (1862) and illustrated it, reversed left to right, (1865a and 1869), making no mention at all of Sierra Leone as one of *Poiana's* possible habitats. It does, indeed, seem highly unlikely that *richardsoni* does, or ever did, exist in Sierra Leone. Perret & Aellen (1956) obtained a specimen from Foulassi, Cameroun, which is not far distant from Bitye; and Auerbach (1913) recorded one from Yaounde, also Cameroun but somewhat further north.

Description. Richardson's linsang (Plate 5) appears to be the larger of the two West African species—though no measurements of *leightoni* seem ever to have been published; but it is still smaller than any known genet, to which animals it bears some considerable superficial resemblance. However, it has a yet more slender body; and it is very readily recognisable by the complete absence of any continuous spinal stripe, its small, round or oval, fully independent black spots, and its very long, absolutely cylindrical, annulated tail carrying 12 to 14 dark, parallel-sided rings.

The pelage of Richardson's linsang is short and soft, consisting of abundant, relatively straight underfur, 10 to 11 mm long, with which are mixed comparatively few, only slightly longer (13 to 15 mm) bristle-hairs. These are expanded subterminally into a narrow, flattish blade but taper proximally to a very long stalk almost as fine as the underfur. The base of all the pelage is medium grey, the visible pattern of the back being produced by either brown or black distal portions of the hairs. The ground-colour of this dorsal pattern is a sort of dull orangey-brown on which is superimposed a pattern of black spots. Down the spine is a discontinuous series of narrow, and hence rather linear, spots, on either side of which are about 4 rows of roundish or oval spots, well separated from each other. The back of the neck carries three, sometimes four, more or less parallel longitudinal black marks; the medial one (or two) narrow, sometimes a discontinuous series of spots, and on either side of this a far bolder, continuous band. The underparts are creamy or off-white, though the exact colour in life is difficult to determine from old and hence rather soiled specimens.

The head is small, the ears big and rounded, the upper lips pale. The proximal parts of both fore and hind limbs are spotted; the feet much the same colour as the back or a little more sepia. The outside edge of the hindfoot, in all but one specimen, is deep blackish-brown. The long tail is remarkable in its narrow, almost perfectly cylindrical nature and the regularity and clarity of its parallel-sided annulation from root to tip. The colour of the light rings above is precisely that of the ground-colour of the dorsum; but below is rather paler. The dark rings are deep-brown rather than black, that is to

PLATE 5



Richardson's Linsang *P* [illegible] [illegible]-spotted [illegible] (P[illegible] C[illegible])

say, noticeably paler than the dorsal maculation. In a number of specimens, but not all, a few, much narrower, relatively indistinct intermediate dark rings occur in a few of the pale annulations. The composition of the more or less upstanding tail fur is very similar to that of the back; abundant underfur 10 to 11 mm long, and bristle-hairs 13 to 14 mm long; but widely scattered guard-hairs about 20 mm long, also occur.

Skull (fig. 30). This has already been sufficiently described in the introduction to the genus.

Habits. There is nothing to add to what has been given above under the generic heading.

POIANA LEIGHTONI Pocock — Leighton's Linsang

Poiana richardsoni liberiensis Pocock, 1908, *Proc. zool. Soc. Lond.* (for 1907): 1043. This name is rejected as a *lapsus calami* in favour of that which next follows, *leightoni* Pocock, as explained thereunder.

Poiana richardsoni leightoni Pocock, 1908, *Proc. zool. Soc. Lond.* (for 1907): 1043–1045, pl. 54, f. 3. North-east Liberia, 24 to 32 kilometres west of the Putu Mountains, situated west of the Duboe and Cavally Rivers. Type in the British Museum, No. 8.8.23.2, sex?; a headless flat skin, lacking also the forefeet, but otherwise in fair condition; no skull. This name is accepted in spite of the apparent page priority of *liberiensis*, which was an obvious *lapsus calami*. It has generally been assumed that the *lapsus* must be in respect of the name *leightoni* used in the key two pages later than *liberiensis*. But that Pocock's real intention had been to give the animal the former of these names is clearly shown both by a printed amendment slip in the *Proc. zool. Soc.* and the fact that for his own private separates of his paper he had the name amended on page 1043 of the text to *leightoni* before the reprinting. Pocock's pen, therefore, obviously slipped in the inadvertent use of *liberiensis*, not *vice versa*. This name was given in compliment to Mr. Leonard Leighton of the Liberian Rubber Company whose small collection of mammals contained the type.

Distribution. Although Pocock named this as merely a local race of *richardsoni* it would seem, even from the very incomplete material in the British Museum that it is probably a discrete species, geographically widely separated from the Bight of Biafra animal. Pocock (1908b: 1038) mentions that Leighton obtained 6 skins; but only 2 ever came to the British Museum, the type in 1908, a second from the Zoological Society of London, *via* Pocock, in 1939. There are no skulls. Kuhn (1965) gives the following additional places in Liberia from which he personally has obtained specimens: Biple, Bongle, Deaple, Duotown, Igua, Siamonrovia, Tappita, on the road between Bia and Zwedru. All these are in north-eastern Liberia, rather further north than the type locality, and west of the upper River Cess. The vegetation is rain-forest. F. de Beaufort (1965) says the species also occurs in the Ivory Coast at Gagnoa. Like *richardsoni*, therefore, *leightoni* would appear to be a rare and very localized animal.

Description. Leighton's linsang is appreciably paler than Richardson's, the dorsal ground-colour being a sort of golden-buff. As in the latter species the maculation is black, though appreciably more intense; and the spots are of similarly small size but often of more angular outline. There is a definite, more or less continuous, narrow black spinal stripe. The dorsal pelage is very short, very soft and springy, the abundant underfur measuring about 10 mm, the bristle-hairs about 12 mm but exceptionally reaching 15 mm. The head and neck being missing from both British Museum specimens it is not possible to describe them; but what remains of the legs and feet seems to be quite similar to those of *richardsoni*. The belly and insides of the hindlegs are pure white, a clear distinction from the other species.

The tail is even softer than in *richardsoni*, clothed with very dense underfur about 7 to 9 mm long together with flat ended, long-stalked bristle-hairs 10 to 11 mm long. There are also scattered, terete guard-hairs up to 15 mm in length. The structure is readily distinguishable from that of *richardsoni* by its annulation. There are only from 10 to 12 dark rings, which are dense black or very deep brown; and these instead of being parallel-margined are more chevron-shaped, with a forwardly directed point. The tails of specimens so far known show no sign of intermediate dark rings. There are no measurements; but the skins as they stand are of a somewhat smaller animal than *richardsoni*, though they may possibly be only those of young adults.

Skull. No skulls exist in London, nor does there appear to be any published account.

Habits. Nothing whatsoever is known of these.

The following table gives the mean measurements of British Museum material of *Poiana richardsoni*; it is not possible to give comparative figures for *leightoni*.

Table 11: Numerical data for *Poiana richardsoni*

	richardsoni
Vegetation	Forest
Number in mean	7
Condylobasal length	67·6
Basilar length	61·9
Palatilar length	29·9
Zygomatic breadth	34·5
Upper cheekteeth breadth	19·4
Interorbital breadth	10·0
	Richardsoni
Postorbital constriction	11·6
Braincase breadth	24·1
Toothrow ($c—m^1$)	25·1
p^1 length	6·3
m^1 breadth	4·6
m_1 length	5·4
m_2 length	1·5
Head & body	384
Tail	365
Hindfoot	59
Ear	34
RATIOS (per cent)	
Tail/head & body	95
Zygom. br./condylob. l.	51
Braincase/condylob. l.	36
Braincase/zygom. br.	70
Palatilar l./condylob. l.	44
Interorb./postorb.	86
$p^1/c—m^1$	25·0
m_1/m_2 m_3	360

Subfamily **PARADOXURINAE** Gill, 1872

African and Asian Palm Civets, Binturong etc.

Taxonomy. Something has already been said, on page 163, of the disputed classification of the Paradoxurinae. Pocock (1929) considered that the African animal now to be dealt with merited separation into a full family of its own, the Nandiniidae, and thus be clearly more widely detached from the oriental palm civets with which it had customarily been associated, the latter remaining as the subfamily Paradoxurinae of the Viverridae. There is certainly a great deal to be said for Pocock's view of the taxonomic distinctness of the African and Asiatic groups. Resemblance between them, as in the parallel case of the linsangs, is with very little doubt largely fortuitous, being rather a matter of convergence than an indication of close phylogenetic affinity.

Such resemblance, in the present instance, concerns not so much an overall similarity of external appearance as the nature of the soles of the feet and a general correspondence of skull shape. The character of the feet was well investigated and analysed by Pocock (1915b); and the considerable differences that he found, together with those of other external features such as vibrissae, rhinaria, ear pinnae, and, more importantly, the form and siting of the perineal scent glands, led him with little hesitation to the conclusion of phylogenetic divergence now under discussion. He might have added that superficial resemblance of build in the skulls of the two groups is no more than runs through a wide area of these small carnivores; but that there are, in fact, important distinctions, notably in respect of the bullae and of dental form, that lend support to the conclusions he arrived at from external features alone.

With little doubt, then, the African and Asiatic palm civets are phylogenetically more separate than has been commonly accepted; but whether that division should be drawn at family level is another matter. Simpson, while indicating some degree of taxonomic distinction, rated it as no higher than tribal. This is probably insufficient; but Simpson's classification is nevertheless retained in this present work since, in the absence of a major revision, mere tinkering on a minor scale with currently accepted forms is liable to add more to confusion than it does to clarity.

The subfamily Paradoxurinae is divided by Simpson into three tribes: the Paradoxurini Simpson, 1945, and the Arctogalidiini Simpson, 1945, both Asiatic; and the purely African Nandiniini Simpson, 1945, with which alone we are here concerned.

General. In view of the probable disunion of the African and Asiatic animals at present covered by this subfamily, and the fact that there is only a single genus in Africa, nothing further is said here regarding the general attributes of the Paradoxurinae as a group since all matters relevant to this present work concerning distribution, form, skull, habits and so forth are contained in the following account. The name of the subfamily is formed from that of the Asiatic palm civets, musangs or toddy cats, *Paradoxurus* F. Cuvier, 1821, derived from the Greek words *paradoxus* strange, and *oura* tail—a name given mistakenly without any substantial justification for its etymology.

Genus **NANDINIA** Gray, 1843
African Palm Civets

Nandinia Gray, 1843, *List of the Specimens of Mammalia in the . . . British Museum*: 54; and 1865, *Proc zool. Soc. Lond.* for 1864: 529–530. Type species *Viverra binotata* Gray.

As this is a monospecific genus all relevant characteristics are to be found in the succeeding account of the Two-spotted Palm Civet.

NANDINIA BINOTATA (Gray) Two-spotted Palm Civet

Viverra binotata Gray, 1830, *Spicilegia Zoologica* . . . :9. Ashanti (Ghana). This was described from a specimen in the Netherlands Museum, Leyden; but the type no longer seems to exist since it is not listed by Jentink (1887 & 1892). The attribution of this name to Reinwardt, often given by authors (*e.g.* G. M. Allen, 1939), appears to be erroneous and stems from Gray (1843) where he himself accredited the name to that author. However, Reinwardt does not appear ever to have published it; and in later works Gray (1865 & 1869) indicated that Reinwardt had only suggested the name in manuscript. Incidentally, Gray more than once muddled his List of Specimens (1843) with his Catalogue (1869), the first of the two works cited in the previous sentence providing one such confusing example. The specific name is formed from the Latin *bi-* two, and *notata* marked, with reference to the conspicuous pale shoulder spots.

Paradoxurus hamiltonii Gray, 1832, *Proc. zool. Soc. Lond.*: 67; and 1835, *Illustrations of Indian Zoology*, **2**, pl. 10. In both cases the type locality is indicated, wrongly, as India; this was subsequently amended, in two old British Museum registers and in Gray (1843), to Fernando Póo. This revised provenance must also be regarded with considerable suspicion; it was in all likelihood due solely to Edward Cross of the Surrey Zoological Gardens, where the type animal had been displayed. It is well known that the knowledge of West African geography possessed by commercial importers in the early 19th century was extremely sketchy and most frequently conveniently crystallised itself into Fernando Póo, at which island nearly every ship called. Thomas (1904) rejected *Nandinia* from the island's fauna; Cabrera (1908) was doubtful; and no specimen seems to have authentically been forthcoming since the type. Type in the British Museum, No. 80a, ♂; skin in good condition except for an incomplete tail; skull with the back and floor of the braincase missing. The species was called after Dr. Hamilton.

General. The common name two-spotted palm civet for this animal is pretty firmly established in spite of several objections that can be lodged against its use. In the first place it could rather more sensibly be termed, as it sometimes is, the twin-spotted palm civet since the pelage has, in fact, a multitude of spots but only one matched pair of distinctively coloured ones, situated on the shoulders. It is also, less commonly, known as the tree civet; and this has possibly more to be said in its favour than the others as these animals spend a good deal of their lives in trees of all kinds, palms being probably relatively infrequent. It is interesting to see how the name palm civet came to be applied to *Nandinia*. It was not founded on any knowledge of the animal's habits, these being to this day largely unknown; but, as recorded in the introduction to this present subfamily, the African species now under discussion was considered to be very closely akin to certain Oriental viverrids, chiefly of the genus *Paradoxurus*. The best known species of this last Asiatic genus, *P. hermaphroditus* (Pallas), was called by Anglo-Indians the palm civet or toddy cat because it was reputed to climb the toddy palm (*Phoenix silvestris*) to steal the toddy ("wine") from the receptacles into which it was being tapped. Because of its supposed close affinity, *Nandinia* was regarded as the exact Ethiopian counterpart of the Indian animal, whose common name, with suitable qualification, consequently became transferred to it; though there is no evidence, so far as the present writer knows, either factual or in hearsay-folklore, that *Nandinia* climbs palms to get at the palm-wine.

Distribution. In general appearance the African palm civet (Plate 5), with its spotted body and long ringed tail resembles a heavily built dark brown-coloured genet. It would seem from its abundance in collections that it is probably the commonest of the African viverrids. It is widely distributed throughout the whole of the rain-forest block and some of the contiguous Guinea or Guinea-type woodland zone where there is fringing forest or forest remnants—for this is essentially an animal of fairly high trees and the shade of their dense crowns, not of exposure to sunshine in low-growing open-country species. The southern limit of its range is roughly a line drawn from 15° South on the west coast to 20° South on the eastern side of the continent; thence it spreads north to extreme south-western Sudan, taking in Uganda and south-west Kenya, on the one side and, on the other, Sierra Leone, and probably further west to Portuguese Guinea, though the specimen on which this last range is grounded was in fact a captive one (Monard, 1940). *Nandinia* is commonly stated to occur also in Fernando Póo. Something has been said on this subject above in the synonymy. The claim appears to be based on two specimens alone; the type, already dealt with, and another British Museum skin, No. 55.12.24.413. This latter formed part of a parcel of over a thousand specimens purchased in 1855 from the Zoological Society of London, and its reputed provenance is open to precisely the same doubt as given above in respect of the type of *hamiltonii*. The case for the occurrence of the palm civet on Fernando Póo is slender.

Description. The dorsal fur of *Nandinia* is dense, of moderate length, soft to the touch if quite clean, but slightly harsh if dirty. The overall colouring is variable in different specimens, some being appreciably darker than others; but it may be characterized in general terms as of a medium brown hue with blackish spots. The fur is deep sepia based throughout, the visible background colour and that of the dark maculation residing solely in the extreme distal portions of the hairs. The dominant component of the pelage is long, fine, dense, wavy underfur, measuring about 12 to 15 mm, though this varies somewhat with different skins and the state of moult. This has short golden-brown tips. Amongst this dense underfur are set, much more widely dispersed, rather longer bristle-hairs, some 20 to 23 mm, very slender throughout most of their length but, beyond the reach of the underfur, expanded into a stouter, terete or very slightly flat-sectioned terminal portion. The pointed tips of these are black; but the majority have a subterminal band of golden-brown, which often gives way proximally to a narrow creamy zone. This accounts for the rather nondescript slightly reddish-brown flecked with yellow of the back. The dark spots are the outcome of the lack of any subterminal zone, the entire distal half of the hair being black. In the two pale spots that normally occur, one on each shoulder, the reverse is the case, there being no black tips. There are also much longer black guard-hairs scattered throughout the dorsal pelage. The black, occasionally deep-brown, spots forming the dorsal pattern are of fairly small size and rather irregularly disposed, not more or less clearly arranged in longitudinal series as they are in most *Genetta*. Broadly speaking they are roughly subcircular, about 10 mm in diameter, or less, mostly independent of one another, though in a few cases tending to coalesce transversely. But in some specimens they are much smaller. There is no black spinal stripe or crest, although occasionally in some skins there is a combination of spots that gives some impression of a medial stripe.

The flanks are almost completely unspotted; the belly is yellowish and clearly, though not sharply, divided from the flanks. The two yellow or creamy spots on the shoulders are somewhat oval and at their maximum are about 25 mm long and very plain to see; but they vary and are often indistinct or sometimes virtually lacking. Forward of these lie the markings of the neck. These are considerably variable but basically consist of a medial black line reaching to the crown of the head between the ears. This is flanked on either side by another, more or less parallel, black line reaching to the base of the ear. There may be a row of dots, sometimes very faint, between the medial and outer band; or this last may itself by broken up into spots; or some or all of these elements may be entirely lacking. However, in most, though not all, West African specimens the three main black lines are clearly present. The face is greyish-brown, without distinct markings. The ears are very rounded, low in height but broad at the base; and a bursa is always present, its semicircular posterior flap arising, both top and bottom, behind the pinna.

The feet are 5-toed, each digit armed with a very sharp, well-curved claw like a cat's in shape and similarly retractile. They are slightly webbed between the basal parts of the toes. The soles are very characteristic, apart from the naked, well-developed pads almost completely densely but shortly hairy. In the forefoot the palmar and the carpal pads are united; a central depression bounded by the four main palmar and two carpal sections naked but of granular appearance. The 1st digit of this foot is joined to its section of the palmar pad by a naked strip; and there are four small triangular naked areas just anterior to the other sections. In the hindfoot the plantar and tarsal pads are similarly joined, but the latter unite into a single, large pad, very wrinkled or ridged posteriorly and reaching almost to the heel. There are similar small naked areas forward of the central pad and also joining it to the 1st digit.

The tail is somewhat longer than the head & body, bushy and woolly throughout its length but usually distinctly broader proximally than distally. It is darker above than below through the presence of long-black-tipped hairs, which in some specimens impart a wholly blackish appearance to the terminal four inches. Its covering consists, like that of the body, of abundant, long, dense underfur, about 30 mm in length; and of sparser bristle-hairs, normally measuring about 40 mm but which here and there attain almost 60 mm. The tail may be loosely described as ringed; but it is very irregularly so, nothing like the genets or linsang, the "rings" being unevenly spaced and mostly only half-rings across the dorsal side, or sometimes little more than broad patches. The scent glands have been fully described by Pocock (1915b); those of the male are situated anterior to the penis, those of the female in front of the vulva.

Skull (figs. 31 and 32). This is considerably larger than that of *Genetta* but otherwise superficially very similar. The braincase is long, ovoid, and bounded anteriorly by a marked intertemporal constriction which is narrower than the interorbital breadth. The supraorbital processes are long and sharp. In old males and very old females there is a pronounced sagittal crest, which posteriorly joins a broad, flange-like supraoccipital crest. The zygomatic arch is strong, almost semicircularly curved, the jugal process slight.

The most notable peculiarity of the *Nandinia* skull lies in the bulla, the posterior part of which is generally held to be entirely cartilaginous and is lacking from normally prepared specimens. A detailed description of this auditory region is given by Hough (1948), who finds it, despite the peculiarity now under discussion, otherwise quite typically viverrine. She accepts the generally held view that the entire posterior portion of the bulla (the entotympanic) is unossified; Van Valen (1963), however, disagrees with this, holding that "the dorsomedial side of the entotympanic is commonly, perhaps always, ossified in mature and nearly mature individuals, contrary to the usual statement, although normally there is a cartilaginous region between the tympanic and ossified entotympanic where they approach each other". Be this as it may, for practical purposes of recognition almost every prepared *Nandinia* skull has the main bulbous portion of the tympanic bulla, so conspicuous a feature of other carnivorous skulls, lacking. In this it is unique amongst the living (but not fossil) carnivora, and exceptional as regards the mammalia as a whole. The anterior, wholly ossified, portion around the meatus is often missing too, but for the entirely different reason that it has been swept away through lack of its normal mechanical support provided by the bony posterior region. The lack of a posterior portion of the bullae is accompanied by a second peculiarity of the *Nandinia* skull. In other Feloidea, in which the bullae are fully ossified, the paroccipital processes are closely applied to their posterior faces, over which they spread to a greater or less extent; in *Nandinia* there is no ossified bulbous portion to which they could become attached and they stand isolated as conspicuous components of the posterior part of the skull, long and pointed, and distinctly more canoid than feloid in appearance.

The dental formula is $\frac{3\cdot1\cdot4\cdot2}{3\cdot1\cdot4\cdot2} = 40$. The upper incisors are set in a straight or slightly curved, compact row, the outer ones being somewhat stouter than the inner ones. The upper canines are much straighter than usual, grooved on the outer face as in *Genetta* but more obviously so; and also on the inner face, a character that is obscure in, or lacking from, the genets. There is nothing remarkable about the rest of the cheek-teeth except that m^2 is very small, peg-like; and, in fact, considering the much greater size of the animal the whole series is small in comparison with *Genetta*.

The lower jaw is strongly built, with deep rami. The incisors are bifid; the canines are more curved than the upper ones and are similarly grooved on both outer and inner faces, the latter sometimes rather indistinctly. The posterior molar is relatively small, but nevertheless much better developed than the upper one.

Habits. In spite of its being both widespread and numerous not much is known of the life of the two-spotted palm civet. Something has already been said, in the opening paragraph dealing with this animal, of its conjectured affinity with the Asian *Paradoxurus*, in respect of habits as much as of phylogeny. Though *Nandinia* does climb palm trees, and has been shot in them, there is at present no significant evidence that, despite its common English name, its habits are in any exclusive or predominant way connected with them, and particularly in so far as thieving palm-wine is concerned. In an area such as West Africa where wine-tapping is so abundantly practised such a habit, if it existed would be a matter of common everyday knowledge. This is not so.

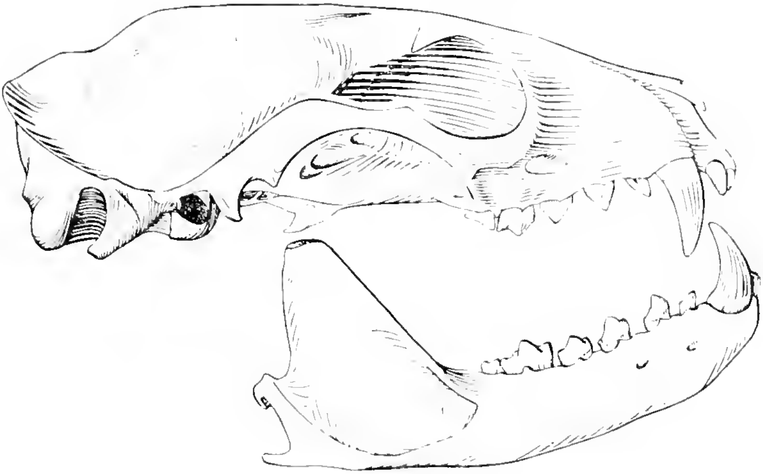


FIG. 31. *Nandinia binotata*: skull, B.M. No. 48.814, sex ?, × 1; lateral view

Further, ex-Anglo-Indians, relying on parallelism with Asiatic species, have in the past saddled *Nandinia* with the character of being "a noted fowl thief", certainly a more credible failing in a viverrid than wine-bibbing. In combination of these two reputed habits, the present writer was warned many years ago that it was foolhardy to preserve oil-palms standing in one's compound since there might always be a palm civet lurking therein, ready to descend at night to rob the fowl-house. Whether this danger is real is open to some doubt; for this small carnivore is, in truth, largely vegetarian. G. L. Bates (1905), who has recorded more of this animal in its natural surroundings than anyone else, wrote: "... there is no doubt that the usual food of the Nandine is vegetable. It never catches chickens, as do other *Viverridae*". And T. S. Jones has the impression that ripe palm fruits form a significant part of the diet. On the other hand, Thorneycroft (1958), writing in Malawi implied that the only time the palm civet was, as a rule, encountered, was "in connection with raids on the hen house". He also supposed a pair he saw in the bush to be interested in a flock of guinea-fowl. And R. W. Hayman has noted (*in litt.*) that 6 adult specimens taken by him in the Ituri forest in 1930 were all lured by baits of offal into traps set on the ground between the buttresses of giant trees.

The fruit-eating habit is well confirmed by those who have kept *Nandinia* in captivity. Ball (1955) for example, who reared a young specimen in Nigeria, found it to eat banana at an early age; and this remained its favourite fruit though it would eat, also, pawpaw and avocado. This animal was, in addition, given crickets and other insects, fat moths being very welcome; but as it was difficult to obtain a sufficiency of such items the young palm civet was eventually provided with a small lizard each day. Such food had to be quite fresh, for even if it was only a little stale it would be refused. This animal also accepted scraps from the table of a varied kind such as might come from ordinary human meals, including fish and pieces of meat; and it was very fond of sweetened condensed milk and of chocolate. It hardly ever drank water.

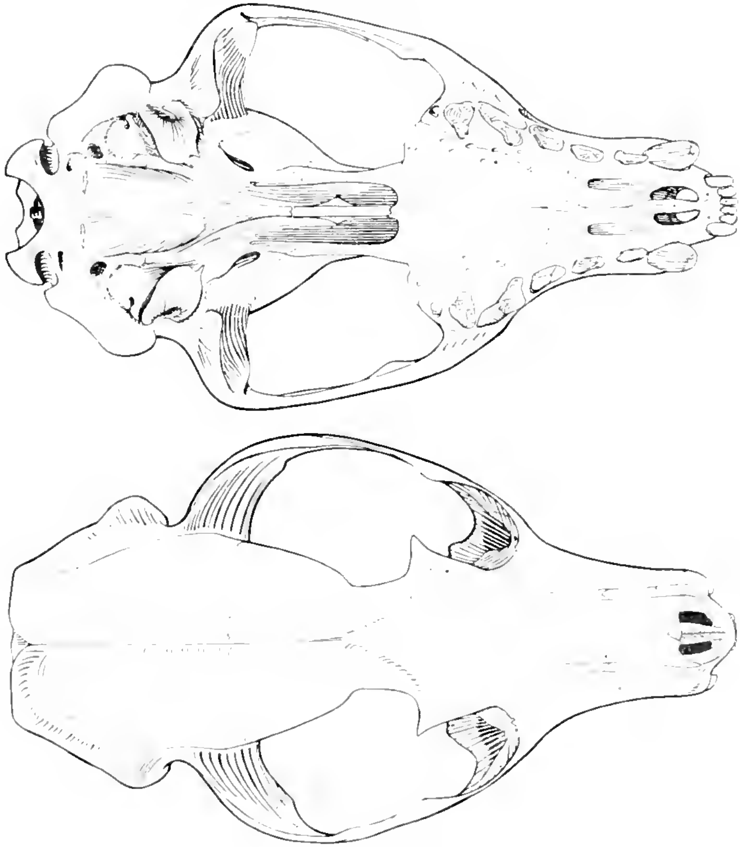


FIG. 32. *Nandinia binotata*: skull, B.M. No. 48.814, sex ?, × 1; palatal & dorsal views

All this is doubtless a fair indication of the sort of dietary in the wild: a good deal of fruit tempered with insects, small rodents, birds or anything of like kind offering itself easily. Bates, in fact, records raids by a two-spotted palm civet, repeated over a series of nights, on the shreds of flesh still attached to the skeleton of a chimpanzee hung up to dry. He also indicates that the fruits of the umbrella tree, *Musanga cecropioides* R. Br. and of the climbing, yellow-flowered cucurbit *Cogniauxia podolaena* Baill. are recognised to be such favourite foods of this animal that they are used by local hunters to bait traps set with the object of capturing *Nandinia*. Sanderson (1940) found the stomachs of his many Mamfe specimens "invariably" crammed with vegetable remains—that is to say plantains when caught near farmed land.

The two-spotted palm civet is nocturnal. Under natural conditions it wakes at about sunset and goes to bed soon after dawn, being, presumably, active during most of the night. It may therefore sometimes be seen in the half-light at either end of the day; or it may be picked up by the red glow of its eyes in a torch in the darkness of the forest at night. Since this animal is both arboreal and terrestrial such glimpses may be either on the ground or on the lower branches of trees. The sight of a pair of glowing eyes peering down through the blackness can be rather eerie. These nocturnal habits are basically retained in captivity but may be partially overcome in response to the offer of food. Climbing for this viverrid, with its extremely sharp cat-like claws, is a matter of considerable ease; indeed Bates, in connexion with the nightly visits to the chimpanzee skeleton mentioned above, makes it clear that the animal concerned in this must have walked some distance clinging upside-down to the underside of the ridge-pole of a hut. Its sure-footedness is also indicated by Ball (1955) who relates how his domesticated animal used to spring onto the curtains, scramble to the top and walk along a curtain-rod only 13 mm in diameter. In climbing vertically up the bole of a tree the claws may well receive assistance from the large, rough-surfaced pad under the hindfoot. It always climbs down head first, Taylor (1970) giving a series of pictures of the successive moves.

Probably the majority of its foraging, however, is carried out on the ground; and this is one reason why it is fairly readily trapped. When on the ground it either prowls in feline fashion or proceeds at a trot, though not very fast. Thorneycroft (1958) records an interesting incident concerning the palm civet's capacity for leaping. He observed one high up a tree, frightened by the barking of dogs at the foot, to sail gracefully—"almost float"—to the ground in an effort to escape, descending at "an angle greater than half a right angle", legs and tail fully stretched out. The landing on the bare ground was perfect, on all four feet, at a considerable distance from the tree. This performance was rapidly repeated from a neighbouring tree; but an attempt to reach a third tree was foiled by the dogs. Taylor (1970) rates *Nandinia* as the most efficient African viverrid at jumping.

During daylight hours the two-spotted palm civet curls up tightly and sleeps. Bates said that it did this in thick tangles of vines in the tree-tops. This is a little surprising in that climbers do not very commonly form tangles such as would naturally provide suitable beds for quite heavy animals; especially in the upper strata of trees, at which level lianes have generally achieved a good deal of independence. Tree-tops, also, would seem to imply a good deal of sunlight, whereas *Nandinia*, in common with most daytime sleepers, prefers deep shade. Tangles certainly exist; but at fairly low levels or in partially destroyed forest to which sunlight has been admitted. It would seem probable that for their daytime sleep these animals would more commonly seek the shelter of holes or well-shaded crooks where large branches join the bole. There seems to be no record at all of an actual breeding nest. This must almost certainly be a hole; but whether up a tree or in the ground it is impossible to say. According to Walker (1964) the period of gestation is about 64 days, the litter size being 2 or 3. Juvenile specimens exist in the British Museum captured in February, March, May, June and August, thus indicating that breeding may take place in either the wet or dry season.

Two-spotted palm civets, if obtained very young, have shown themselves to make charming, friendly and trusting pets, though suspicious of and aggressive towards strangers. Given the free range of a house they have been said to preserve it free of rats and snakes. Ball (1955) found his young animal to enjoy games, even fairly rough ones, with a dog, but not with a cat. This author also records that though his palm civet had the habit of marking out certain areas with its scent glands it never at any time had, itself, any offensive odour. Its fur, which was rather rough and bristly, always had a pleasant, warm, musty smell. Bates heard two palm civets calling to each other in the evening in the forest with a kind of faint kittenish mewing; Ball's pet when pleased uttered a sort of *cwuck-cwuck* sound mingled with a purr; but when annoyed gave a shrill, rattling warning note. This animal was also responsive to human utterances, recognising the sound of its master's voice, and answering to its name and coming to a whistle.

Taxonomy. Three races have been described from other parts of Africa. These are dependent on variations of colour or pattern. Some degree of variation is common; J. A. Allen (1924) writing of nearly 75 north-east Congo specimens said that there was amongst them "a wide range of individual variation in coloration"; and the British Museum West African material, of about 50 skins, displays appreciable variety of both colour and markings. It is therefore difficult to know how far races founded on these characters may be justified. At least one Sierra Leone skin has a more intense colour that recalls Cabrera & Luxton's *intensa* from the southern Congo; but it is not quite the same, and the pattern is certainly less marked. And though nuchal striation becomes obscure in certain other West African specimens there is none exhibiting the complete absence of any trace of dark markings in this area that is the main characteristic of Thomas's *gerrardi*. J. A. Allen found this to be the case also with his Congo series; and since, moreover, there are in London several skins from East Africa with this distinguishing feature it seems probable that *gerrardi* is something more than a mere individual extreme. Allen considered the third named race, *arborea* Heller, "to be surprisingly different". It would therefore seem that these races are justified; and, that being so, the West African two-spotted palm civet is correctly designated *Nandinia binotata binotata* (Gray). If colour alone is regarded as a valid subspecific distinction it is always difficult to know where to stop; but it is possible that the appreciably paler skins of the Cross River basin (south-eastern Nigeria and Cameroun) may merit a distinguishing name.

Table 12: Numerical data for *Nandinia binotata*

	West Africa general
Vegetation	Forest
Number in mean	17
Condylobasal length	96·2
Basilar length	91·0
Palatilar length	42·6
Zygomatic breadth	53·4
Upper cheekteeth breadth	29·8
Interorbital breadth	18·0
Postorbital constriction	14·0
Braincase breadth	32·2
Toothrow (c—m^2)	35·9
p^4 length	7·6
m^1 breadth	5·4
m^2 breadth	2·0
m_1 length	7·2
m_2 length	3·0
Head & body	484
Tail	554
Hindfoot	85
Ear	37
RATIOS (per cent)	
Tail/head & body	115
Zygom. br./condylob. l.	55
Braincase/condylob. l.	33
Braincase/zygom. br.	60
Palatilar l./condylob. l.	44
Interorb./postorb.	128
p^4/c—m^2	21·2
$m_1/m_2 + m_3$	240

Table 12 shows the average size of 17 fully adult West African specimens in the British Museum.

Subfamily **HERPESTINAE** Gill, 1872

Mongooses

Distribution. The last of the three West African subfamilies of the Viverridae, the Herpestinae, has, like the other two, an Asiatic as well as an African distribution; and, like the Viverrinae, just finds its way, as something of a rarity, into southern Europe. This is the largest of the three subfamilies, in respect of the number of different genera, of species, and almost certainly of individuals. It is in Africa that the group reaches its maximum development. As contrasted with 2 genera in Asia there are something in the nature of 16 in Africa, the majority, it is true, monospecific. Distribution is mostly south of the Sahara, much of it almost entirely tropical, though some species range to South Africa which, moreover, has a few genera peculiar to itself. In this present account West Africa is credited with 9 genera covering 10 species.

General character. Nevertheless, all members of the group, whatever their size or colour, have much more in common as regards both appearance and habits than is often the case with other subfamilies; something, neither exact of definition nor completely general, which nevertheless enables them all to be readily recognised as mongooses (Plates 6, 7, 8 and 9). This is, for the most part, a long subcylindrical body carried close to the ground on short legs and clad as a rule in a rather coarse, long and bristly pelage, nearly always to a greater or less degree speckled; a sharpish face with low rounded ears set well down on the sides of the head; and a tapering tail that is nearly always loosely haired, sometimes shaggy, and most often only a little shorter than head & body. The ears, which differ from those of other West African viverrines in never having a bursa, may be completely closed by tightly folding together.

Mongooses, certainly in West Africa, fall into two clearly distinct size classes: small, having a head & body length of under 400 mm and a weight usually well below 2 kg (*Mungos*, *Crossarchus*, *Galerella*); and large, with a head & body length of about 500 mm or much more, the adult body weight being from 3 to 5 kg (*Herpestes*, *Atilax*, *Ichneumia*, *Galeriscus*, *Xenogale*). *Liberiictis*, whose bodily characteristics are unknown, can nevertheless, from its skull size, be certainly reckoned as belonging to the latter class, though a little smaller than the others.

The pelage in the Herpestinae is composed almost invariably of longer or shorter, fine dense underfur and abundant, flattish-sectioned, much longer, annulated bristle-hairs; but *Mungos* is an exception in that the underfur is virtually lacking. The tail, which is of somewhat variable shape but usually distinctly tapering from root to tip, is clad in the same way but the bristle-hairs are often much longer and sometimes give the structure a shaggy appearance. Mostly it is uniformly coloured throughout its length, generally similarly to the dorsum; but *Ichneumia* and *Galeriscus* form notable exceptions to this, while in *Herpestes* and *Galerella* there is a sharply contrasting terminal tuft of jet-black or red. All the fur is erectile in anger or alarm.

The rather pointed face ends in a naked rhinarium which, in different genera, takes on somewhat different shapes, involving the naked area itself, the nostrils, and the infranarial depth and character of the upper lip. Pocock (1916c), who figured several genera and laid some taxonomic significance upon the differences he cited, used live or recently dead zoo animals as the basis of his observations; but the relevant points are not often clearly to be seen in preserved specimens.

The shortness of leg in the mongooses has already been mentioned; but there are several other noteworthy features attaching to the limbs in this subfamily. The majority of species are sub-digitigrade, but *Crossarchus* has by comparison a noticeably more clumsy, flat-footed stance and gait. The feet themselves are in most genera fairly powerful, but in *Galerella* are of slender build. Mostly there are 5 digits, but *Galeriscus* has only 4 on each foot, while in *Galerella* the pollex and hallux are much reduced and sometimes lacking. In all cases except that of the marsh mongoose (*Atilax*) digits II to V are joined by webs, never very pronounced and sometimes only basal. The claws are mostly strong, and on the forefoot long, in some cases (*e.g. Mungos, Crossarchus*) very noticeably so; but in *Galerella* they are quite different, short, slender, curved and relatively sharp; in fact, much more adapted to climbing than in most. Finally, the soles, particularly those of the hindfeet, are diverse in respect of the amount of furry covering they carry, being either entirely hairy (*Ichneumia, Galeriscus, Xenogale*), hairy in the posterior part only (*Crossarchus, Galerella*), or entirely naked (*Mungos, Herpestes*). *Atilax* is mostly naked but seems to be variable.

Like other viverrids the mongooses are provided with scent-glands probably for the purposes of recognition and territorial marking though possibly not defence; but little actually definite has so far been positively determined regarding such uses. There are, in the Herpestinae, always a pair situated either side of the rectum, the external orifices of their ducts appearing either diametrically lateral to the anus or slightly above. Both these orifices and the anus itself are surrounded by an upstanding, fairly thick, elliptical or subcircular wall forming a sac which is capable of closure, not by the contraction of a circular sphincter muscle but by the juxtaposition of the upper and lower sections of the rim in a lip-like action. The form of the glands, the siting of their openings, together with the shape and nature of the sac, though conforming to this broad general pattern are, so far as known from limited investigation, variable in detail from genus to genus. A somewhat malodorous liquid seeps from the external glandular orifices into the sac and accords to the animal a faint odour, normally not highly objectionable; but whether a more energetic and active expulsion of fluid, as in the polecat, is practised under stress by mongooses in general is not clear, though one such case is referred to on page 306.

All these matters are dealt with in some detail and with illustrations in Pocock's paper on the external characters of the mongooses (1916e), though by no means all West African species are covered.

Skulls and Dentition. As might be expected, mongoose skulls more closely resemble those of the nearly related genets (Viverrinae) than those of any other West African carnivores. There are, apart from size, certain clear differences, which can be seen by a comparison of fig. 29 with fig. 36. In dorsal aspect the rostrum in the Herpestinae, with the notable exception of *Liberiictis*, is broader; and the also very much broader frontal area combines with the complete or almost complete orbital ring to give the structure a quite different appearance in this region. In the ventral aspect the much longer post-dental palate of the mongooses is at once obvious; and the bullae instead of being long are for the most part much more highly and acutely domed. Mostly the anterior portion of the bulla is very much smaller than the inflated posterior chamber, with the single exception of *Galerella* in which the two are subequal.

The dentition in the Mungotinae is remarkable for its variety. There may be 36, 38 or 40 teeth due to diversity in the number of premolars, which may be $\frac{3}{3}$ in *Mungos* and *Crossarchus*; $\frac{4}{3}$ in *Galerella*; or $\frac{4}{4}$ in *Ichneumia*, *Galeriscus*, *Xenogale* and *Liberiictis*. Both *Herpestes* and *Atilax* are capricious in this respect, the former having either 3 or 4 lower premolars, the latter exhibiting the same variation both above and below. Occasionally skulls occur in these two genera with differing numbers of premolars on either side. The form of the cheekteeth is also widely variable in the different genera, being sometimes fairly typically carnivorous with sharp-edged flesh-cutting carnassials (*Xenogale*, *Atilax*), sometimes sharply-cusped insectivorous (*Mungos*, *Crossarchus*), and in one case, *Galeriscus*, frankly crushing. In some species the dentition is relatively reduced in size, and this is particularly so in *Liberiictis*.

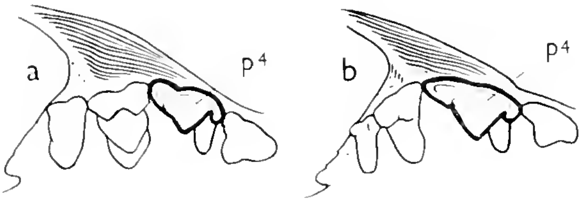


FIG. 33. Herpestinae: illustrating the two contrasting positions of the cheekteeth:
a. p^4 well anterior to the root of the zygoma (*Ichneumia albicauda*, B.M. No. 25.5.12.13);
b. posterior corner of p^4 about level with the zygoma (*Xenogale naso*, B.M. No. 10.6.1.14)

There are two distinct types of herpestine skulls in accordance with the positioning of the cheekteeth in relation to the zygoma (fig. 33 a & b). There are two reference points: firstly the extreme posterior corner of the upper carnassial; secondly the point, mostly fairly obvious though not exactly defined, at which the lower curve of the zygomatic arch arises from the main body of the maxilla, just above the toothrow. In one category of skulls (*Herpestes*, *Xenogale*, *Galerella*, *Atilax*), the posterior corner of p^4 is situated at this point and, in consequence, m^1 lies wholly posterior to it, its outer face forming a sharp angle with the outer face of the carnassial. In the other category (*Ichneumia*, *Galeriscus*, *Crossarchus*, *Mungos*, *Liberiictis*), the corner of p^4 and all or at least part of m^1 lie anterior to the reference point, mostly very clearly so, but in some *Mungos* skulls the root of the zygoma is rather obscure. In this group the outer faces of p^4 and m^1 form only a shallow angle with each other, or even a gentle curve.

Habits. Compared with other groups the habits of the mongooses have in some respects been relatively well recorded, though often more as regards their everyday behaviour as captive animals than as concerns the more secretive aspects of their lives in their natural environments. This is because, by reason of some of their activities and the exceptional readiness with which many of them take to domestication, they have excited man's sympathetic interest over many centuries. Of all wild African mammals there can be little doubt that mongooses make the most acceptable pets, presenting much less difficulty of control and management than monkeys and offering in return a certain indefinable charm together with unending interest, amusement, often surprise and sometimes apparent affection. The subject must, of course, be taken in hand while still very young; and, with this proviso, probably nearly all species can be turned into quite lovable, diverting, playful companions—and even useful additions to the household since there is no doubt that one of these creatures helps to keep the premises free of undesirable pests, be they rodents, reptiles or cockroaches. However, not all West African species have yet been tried out in this respect. Of those that have, probably the kusimanse (*Crossarchus*) would lead as favourite—from the point of view of size as well as ardency of spirit. Accounts of this and other species will be found below in the appropriate sections.

Of all the activities or reputed activities of mongooses that for which they are most widely famous is snake-killing. There is a good deal of misapprehension and misinformation about this. It is often sweepingly believed that all mongooses make a regular practice of deliberately seeking out and destroying snakes, the ancient Egyptians going so far as to say that *Herpestes* habitually entered into long preparation for the fray by encasing itself in layers of hardened mud as an impenetrable protection against the fangs of its opponent. The information relative to snake-killing is by no means so positive as generally supposed. Possibly several species will kill a snake if they should happen in the course of foraging to come across one and it was not too large; but it is extremely doubtful whether any would purposefully seek out snakes in general as a matter of sheer innate enmity, as popular renown would have it. Certainly as far as the mongooses dealt with in this present account are concerned *Herpestes ichneumon* has since ancient times had a reputation, though seemingly unconfirmed by modern observation, for an exceptional devotion to killing snakes; *Mungos mungo* and *Ichneumia albicauda* have both been reliably reported as doing so and eating their prey; but for the other species evidence is either lacking or merely hearsay. Indeed, Cansdale is quoted in Hinton & Dunn (1967) as observing that his tame kusimanse was afraid of even a dead snake; and recorded (1946) the same thing of a marsh mongoose.

There can be no doubt, however, that where a fight between a mongoose and a snake does take place the former is aided to victory by two things: its great speed and agility which enable it to spring upon its enemy, make an effective bite and leap clear before its opponent can strike; and the deceptive nature of its long-bristled coat in full erection, giving a false impression of size and misleading the reptile into striking at what proves to be nothing more solid than hair. It has been experimentally shown that some mongooses are markedly more resistant to the effects of snake venom than other animals are, though they nevertheless succumb to a sufficiently large dose.

A peculiar activity that is more certainly common to part, if not all, of the subfamily is the practice of smashing objects by throwing them against something hard—usually interpreted as being basically intended for cracking open eggs, but on good evidence applied to other things, some familiar as foods, some strange, and some frankly useless. This operation is carried out in two ways. The more spectacular is hurling the object, with the forepaws, horizontally backwards through the hindlegs against a rock or wall; the other is to stand upright, hold the object in the forepaws against the chest and then cast it with surprising force vertically down to the ground. Both methods are very effective; and if they do not immediately achieve the desired end are repeated until they do. West African species that have so far been observed to act in one or the other of these ways are *Ichneumia albicauda*, *Mungos mungo* and *Atilax paludinosus*.

As for more general habits, mongooses may be diurnal or nocturnal, solitary or gregarious. They are, by and large, pretty omnivorous, taking flesh when they can get it, killing and eating small mammals, birds and their eggs, snakes, lizards, probably frogs, crabs, sometimes fish, snails and, seemingly always as an essential mainstay, insects, particularly orthoptera, beetles and their grubs. Some, at least, greedily eat fruit; and in captivity more exotic foods. Not a great deal has been recorded of shelters and breeding nests; but it would seem that all species normally use convenient holes in the ground, in fallen logs, amongst tree roots or gaps between boulders. Some live communally in so-called warrens but consisting usually of a single chamber though with two or three entrances. It has sometimes been asserted that mongooses are generally fairly closely associated with water. While this is clearly so in the case of some, such as *Atilax* and possibly *Herpestes*, it is not so obvious with other genera; and without question these animals are sometimes encountered at some remove from the nearest river.

Little has been recorded of the various steps and behaviour patterns in raising a family. Courtship play and coupling have been seen, as noted later, in the case of *Mungos mungo*; and some rare and very interesting though brief observations on the period of gestation and frequency of pregnancy are given in the account of *Crossarchus*. Litter size can, to all intents and purposes, only be guessed at: 2 to 3 would seem to be the commonest, but some species have been credited with 4 or even 5.

One other peculiarity may be mentioned in this general sketch of the subfamily. All mongooses, as already described, are furnished with anal scent glands, one of the chief uses of which is for the demarcation of territory. This activity is carried out in two different ways: one is by squatting down and dragging the circumanal sac across the ground; the other by the much more unusual method of standing erect, upside down on the forepaws—called in gymnastics making a "handstand"—and in this position pressing the scent pouch against trees, rocks or other objects well above ground level. The purpose of this is not altogether clear since the warning patch is well above the nose level of any mongoose of similar species that should happen to trespass on the territory. The scent, of course, diffuses and would doubtless be picked up at a distance by a keenly attuned nose; but the advantage gained or the end served by deliberately making it less obvions is obscure.

Mongooses have little direct economic impact upon mankind. Their sometimes ornamental skins occasionally provide simple pouches, scabbards and so forth in village communities; and their flesh similarly helps to reduce animal protein deficiency in areas where the more conventional butchers' meat is scarce or irregular in supply.

Indirectly they may be regarded as in some measure beneficial in helping to keep in check a varied list of creatures many of which can be looked upon as undesirable; but, on the other hand, it must not be overlooked that they also take birds such as francolins and guinea-fowl that are themselves of human food value; and that in killing lizards and frogs they are disposing of potential insect destroyers. They themselves are preyed upon by the wild cats and dogs, hyaenas, pythons and hawks. Certainly they fill an important role in the complex network of nature; but the sum total of their effect on man himself, one way or another, is probably not very great. Mongooses of various kinds, mostly under very confused nomenclature, are credited (Stiles & Baker, 1935) with a long list of parasites, both external and internal.

Taxonomy. Düker's (1957) unorthodox belief, founded on observation of living animals rather than study material, that the Herpestinae are in fact more nearly related to the Mustelidae than to the Viverridae has been referred to earlier on page 163.

The nomenclatural position in the Herpestinae is exceedingly involved. Had anyone deliberately set out for malign reasons to devise a situation so complex as to be almost beyond comprehension he could scarcely have bettered the labyrinthine confusion that by chance came about in this group. The binominal system of Latinised nomenclature was devised to overcome the imprecision of vernacular names; but in the Herpestinae the absurd position arose wherein in using the name *Mungos mungo* it became advisable, or even necessary, to make clear, in the vernacular, whether reference was intended to the common mongoose of India or to the only distantly related banded mongoose of Africa. This is only one of several traps and obscurities. Fortunately J. A. Allen eventually went into the matter with extreme thoroughness (1919b and, more fully, 1924) and by reasoned argument brought order out of chaos. In consequence there is little need for more than brief mention of this past complexity here; and all systematists must for long be deeply grateful to Allen for his painstaking unravelment of so tangled a skein. Those to whom the matter is one of detailed interest must study his accounts, where they will find a score of pages crammed with the history and pitfalls of herpestine nomenclature.

Allen's findings have been pretty generally accepted; but though, thanks to his labours, the situation has been cleared up as far as modern writings are concerned the fact must always remain that the study of early literature is rendered highly misleading and difficult of comprehension without a good deal of knowledge of this complex history. So many scientific names, both generic and specific, and so many animals of no present interest to West Africa are involved in the muddle that no good purpose would be served by their mention here; but the general warning may be given to the West African student who attempts to derive information from natural histories or scientific literature published well into this century to be cautious in interpretation of *Mungos*, *Herpestes*, *Crossarchus*, *mungo*, *fasciatus* and *ichneumon*, in various combinations with each other or with other genera such as the previously all-embracing *Viverra*.

In this general note the main questions of present interest are those of the name and the status of the mongooses as a taxonomic unit. In Simpson's classification (1945) they stand as a subfamily, the Herpestinae, of the Viverridae; but some authors, notably Pocock, had previously regarded them as constituting a family in its own right.

Pocock (1916e and 1919), examining the question almost purely from the standpoint of external characters, felt strongly that this was their correct taxonomic rank; and since at the time he believed *Herpestes* to be preoccupied and *Mungos* consequently the valid name for "the typical mongooses" he called the family the Mungotidae. J. A. Allen (1919b) showed this to be an error and the family, or subfamily, name to be more logically and correctly derived from *Herpestes*. More important than mere nomenclature is the question of the taxonomic rank to be assigned to the group. There is a good deal in favour of a reassessment of the Viverridae and its component subfamilies. The mongooses exhibit morphological differences, external, cranial and dental, that in sum present a strong case for independent family recognition. But this is a matter essentially beyond the limited scope of this present work. It involves questions far wider than the mongooses, indeed the whole present conception of the Fissipeda. To deal with such fundamental matters piecemeal in a regional work is probably to lead more to confusion than clarity, and the major lines of Simpson's classification are therefore adhered to for the purposes of the present account.

As regards the full generic use herein of *Galerella* and *Xenogale*, the arguments will be dealt with later under their appropriate heads; but it may be said in this general account that, despite a broad overall resemblance of the skulls of these two genera and that of *Herpestes*, the present writer fully supports Allen's opinion that there is a sufficient degree of difference, external and cranial, to warrant regarding these three as generically distinct. It must be added that this view is not shared by G. Petter (1969) from the consideration of tooth structure alone. Similarly, Oldfield Thomas's conclusion that *Galeriscus* is generically separable from *Bdeogale* seems, on several counts detailed later, to be quite justified. His reservation of *Galerella* for *ochracea* alone, with the consequent erection of *Myonax* to cover the remaining species in this complex is, however, not accepted, the arguments in favour of such action being at present not fully convincing.

Thus, in this work these 9 genera are considered to be valid for West Africa: *Mungos*, *Herpestes*, *Crossarchus*, *Atilax*, *Ichneumia*, *Galerella*, *Galeriscus*, *Xenogale*, *Liberiictis*. These may be separated by the following keys:

KEYS TO THE GENERA OF HERPESTINAE

(previous key page 163)

A. Cranial characters

1. Condylobasal length of the mature skull about 92–96 mm; the rostrum long and narrow (length of skull anterior to the postorbital processes very nearly equal to that posterior); all the cheekteeth very small for the size of skull (e.g. breadth of p^4 is less than 6 mm) . . . ***Liberiictis*** (*page* 336)

Mature skull usually either appreciably longer or markedly shorter than the above; rostrum short, blunt and mostly broad (length anterior to the postorbital processes nearly always appreciably less than that posterior); cheekteeth relatively much larger 2

2\. The posterior outer corner of p^4 lies very close to the point where the outer posterior margin of the maxillary root of the zygomatic arch arises, and all or nearly all of m^1 conseqently lies posterior to this point; the outer face of m^1 forms a sharp angle with that of p^4 (fig. 33b) 3

The posterior outer corner of p^4 lies well anterior to the point defined above, and all, or a great part, of m^1 is consequently also forward of it; the outer face of m^1 forms a very obtuse angle with that of p^4 (fig. 33a) . . 6

3\. Condylobasal length of the mature skull about 100 mm or more; the anterior chamber of the bulla flattish and much smaller than the inflated posterior portion 4

Condylobasal length of the mature skull under 70 mm; the anterior chamber of the bulla inflated and more comparable in size with the posterior portion . . . . ***Galerella*** (*page* 307)

4\. Postdental palate about as broad as long; the interorbital breadth over 19 mm *and* the cheekteeth light in build, the occlusal outline of the narrow upper carnassial being scalene, its anterior breadth appreciably less than the external length . . . . ***Xenogale*** (*page* 329)

Postdental palate longer than broad; if the interorbital breadth is as much as 19 mm then the cheekteeth are strongly built, the occlusal outline of the stout upper carnassial being more nearly equilateral, the anterior breadth usually well over 80 per cent of the external length 5

5\. Width of the rostrum at the canine alveoli nearly always less than 20 mm, never much more; greatest breadth across the outsides of the cheekteeth less than 33 mm; breadth of p^4 less than 7 mm; length of m_2 less than 5·5 mm . . . . ***Herpestes*** (*page* 266)

Width of the rostrum at the canines 22 mm or more; breadth across the cheekteeth over 33 mm; breadth of p^4 over 7 mm; length of m_2 over 5·5 mm . . . . ***Atilax*** (*page* 291)

6\. Condylobasal length of mature skull well over 100 mm; premolars $\frac{4}{4}$ . . 7

Condylobasal length of mature skull well under 100 mm; premolars $\frac{3}{3}$. . 8

7\. Posterior upper cheekteeth about as broad as long, subquadrate in outline; upper canines straight, tall, above average size, laterally compressed and with peculiar, sharp, knife-like anterior and posterior edges; postdental palate broad (about 14 mm); interorbital breadth considerably greater than the postorbital constriction . . . . ***Galeriscus*** (*page* 321)

Posterior upper cheekteeth generally markedly wider than long; upper canines curved and of normal subconical form; postdental palate narrow (mostly well under 14 mm); interorbital breadth usually rather narrower than the postorbital constriction, occasionally a little wider ***Ichneumia*** (*page* 300)

8\. Occlusal surface of upper molars subtriangular in outline, the lingual portion clearly converging proximally to a sharp apex; skull narrow, the zygomatic and mastoid breadths under 50 per cent and 40 per cent respectively of the condylobasal length . . . . ***Crossarchus*** (*page* 279)

Lingual portion of the upper molars elongate and more or less parallel-sided, the proximal margin rounded; skull broader, with zygomatic and mastoid breadths over 50 per cent and 40 per cent respectively of the condylobasal length . . . . **Mungos** (*page* 248)

B. External characters

The external features of *Liberiictis* are at present quite unknown.

1. Both fore and hindfeet with only 4 digits and soles completely hairy up to the main pad; a very large mongoose with black legs contrasting with the paler, usually grey, dorsum . . . . . **Galeriscus** (*page* 321)
   Feet with 5 digits (occasionally *Galerella*, small mongooses, have the 1st digit much reduced or lacking). 2
2. Digits II to V entirely unwebbed; hind soles usually quite naked, but sometimes partially hairy; a large, most often entirely blackish-brown mongoose . . . . **Atilax** (*page* 291)
   Digits II to V with small webs connecting at least the basal joints. . . 3
3. Pelage dark blackish-brown, slightly grizzled on the head and neck; size large (head & body about 520 mm); the long nose projecting well beyond the lips; hind-sole completely hairy . . . **Xenogale** (*page* 329)
   Pelage of a lighter colour 4
4. Entire forelegs and hindfeet almost black, contrasting strongly with the rest of the long, loose pelage; the long-haired tail mostly unicolorous, white or black, but sometimes coarsely parti-coloured; hind-sole almost completely hairy . . . . **Ichneumia** (*page* 300)
   Not like this. 5
5. Size large, head & body 500 mm or more; tail broad at the base, much narrower distally with a conspicuous, contrasting, long black tuft; soles naked . . . . **Herpestes** (*page* 266)
   Size considerably smaller 6
6. Pelage short, close-lying, of fine texture and finely speckled; tail terminating with a conspicuous black or reddish tuft; head & body of small size (about 350 mm) and very slender; claws very short; sole of the hindfoot naked for about three-quarters of its length. . **Galerella** (*page* 307)
   Pelage longer, coarse; animals of small size but stocky build; claws of the forefeet very long 7
7. Pelage with abundant long underfur; one or two whorls on the back of the neck; nose very long; sole of the hindfoot hairy on the proximal quarter **Crossarchus** (*page* 279)
   Pelage virtually without underfur; no nuchal whorl; nose of normal length; sole of the hindfoot naked to the heel . . . **Mungos** (*page* 248)

Genus **MUNGOS** E. Geoffroy & G. Cuvier, 1795
African Mungos

Mungos E. Geoffroy & G. Cuvier, 1795, *Magasin Encyclopédique*, 2: 184, 187. Type species *Viverra mungo* Gmelin. This is a formalisation of an Indian vernacular (Marathi) name, *mangūs*.

Ariela Gray, 1864, *Proc. zool. Soc. Lond.*: 565. Type species *Herpestes taenianotus* A. Smith. Derivation of this name is not certain but is most probably from Shakespeare's light and airy spirit Ariel, given with reference to the swift and lively movement exhibited on occasion by small mongooses.

Mungos Gray, 1864, *Proc. zool. Soc. Lond.*: 575. Type species, by virtual tautonymy, *Herpestes mungo* Desmarest (= *Mungos fasciatus* Gray).

Taxonomy. The fact that a vernacular name from India is officially, and properly, applied to a wholly African genus is but one slight indication of the muddle that has existed in the nomenclature of the mongooses. However, this point of etymology is of minor importance compared with the chaos in scientific naming due to misunderstandings regarding the proper application of the names *Mungos* and *Herpestes*. It is not necessary to recount the full details here; those interested should consult J. A. Allen (1919b or 1924). Nevertheless, the following brief summary is given as a caution to those who might otherwise be misled by the study of bygone papers or books.

For a reason which today is not altogether clear Thomas, for whom the name in its specific form had been "so utterly barbarous" that it could be ignored in favour of a later one (1882: 90 f.n.), suddenly (1907) substituted the use of *Mungos* for *Herpestes* which he had up to a short time previously (1906) employed in connexion with the identical species, *gracilis*. This use of *Mungos* for species previously known as *Herpestes* was continued by Wroughton (1907). At this time the specific name *mungo*, under the genus *Herpestes*, was that widely accepted as pertaining to the common Indian mongoose (e.g. Blanford, 1888); and Wroughton, expressly stating that this was the oldest specific name for this species, and without comment replacing *Herpestes* by *Mungos*, thus introduced the combination *Mungos mungo* for this Indian animal. Four years later J. A. Allen (1919b) showed that *Mungos* was "untenable as a genus name for any Indian mongoose" and should, in fact, be applied to the banded mongoose of Africa, to which, further, the specific name *mungo* was correctly applicable. There was therefore a sudden and sweeping change of meaning of the term *Mungos mungo* from the common Indian mongoose to the banded mongoose of Africa. This latter application is accepted today without question; but without a knowledge of this history some references in literature are liable to misinterpretation. It is, for example, used in the now outdated sense of the common Indian mongoose in Pocock's important papers and keys (1916e and 1919).

Only one other question of taxonomy arises in connexion with this genus: that of whether it properly embraces *Crossarchus* as well, either completely synonymously or as a subgenus. In this present work the two are regarded as quite distinct, a matter that is more fully dealt with under *Crossarchus*.

Distribution and general. The genus *Mungos* is wholly African and, as at present understood, comprises two species, *mungo* and *gambianus*, the latter purely West African, the former widely distributed, in many somewhat different local forms, throughout the continent south of the Sahara. Neither species enters the closed forest as such though they may occur within the nominal forest belt marked on maps where the original vegetation has been greatly destroyed or is mere open coastal scrub. The genus is well represented in museum collections and may be reckoned as moderately common in the field, *gambianus* in West Africa, *mungo* elsewhere in the continent. The latter species, however, seems from the paucity of specimens collected, to be rare in the territory covered by this present work, its centre of distribution lying, apparently, far to the south-east.

Description. The two species differ markedly from each other in superficial appearance, the one being conspicuously cross-banded, the other an irregular mixture of colours. Apart from this, they are very similar in general form, being both of smallish size and stout, with short legs and a short tapering tail. The contour dorsal pelage consists of annulated bristle-hairs; in *mungos* the various corresponding colour zones fall together thus giving rise to a marked and very regular transverse pattern of alternating light and dark bands; whereas in *gambianus* they are randomly dispersed and consequently result in a diffuse speckling. Both species in form, and one (*gambianus*) in general colouration as well, closely recall *Crossarchus*, and it is for this reason that the latter has by many authors been identified with *Mungos*. But, the marked pattern of *mungo* aside, there are clear differences. Externally, the most readily observed of these are, in *Mungos*, an almost complete lack of underfur; absence of an extra-long, overshot snout; and a hindfoot whose sole is naked to the heel. Further, more detailed, external description will be found under the two separate species.

Skull (fig. 34). This belongs to the category of small-sized skulls having a condylobasal length of less than 75 mm. Two other West African genera fall in this category, *Galerella* and *Crossarchus*. From the former, *Mungos* can be immediately distinguished by the more forward positioning in its jaw of the upper carnassial; in *Mungos* the posterior outer corner of this tooth, p^4, is situated anterior to the posterior root of the maxillary process, with all or a great part of m^1 also lying in front of this point. Differentiation from *Crossarchus* is a more difficult matter; there is little that is absolute to go on, it being almost entirely a question of comparative lengths or proportions. The difficulty is added to by an almost complete lack of West African *mungo* skulls in the British Museum, data in respect of this species consequently having to be taken largely from extralimital material, which amongst itself is pretty variable. The slight differences can best be appreciated by a comparison of fig. 34 with fig. 37. The *Mungos* skull is mostly somewhat broader; of 11 adult specimens measured only one had a zygomatic breadth slightly under 53 per cent of the condylobasal length; whereas *Crossarchus* rarely exceeds 52 per cent and is almost always less. But the most obvious difference in the dorsal view is the long narrow rostrum of *Crossarchus* in contrast to the noticeably shorter, broader and blunter structure of *Mungos*. This discrepancy of length is, in skulls from which the suture has not been obliterated, almost always reflected in the mid-line length of the nasals: 16 mm or more in *Crossarchus*, 14 mm or less in *Mungos*—but there are some extralimital exceptions to the latter. Also clear is that the postdental palate, where it becomes parallel-sided, is in *M. gambianus* and the

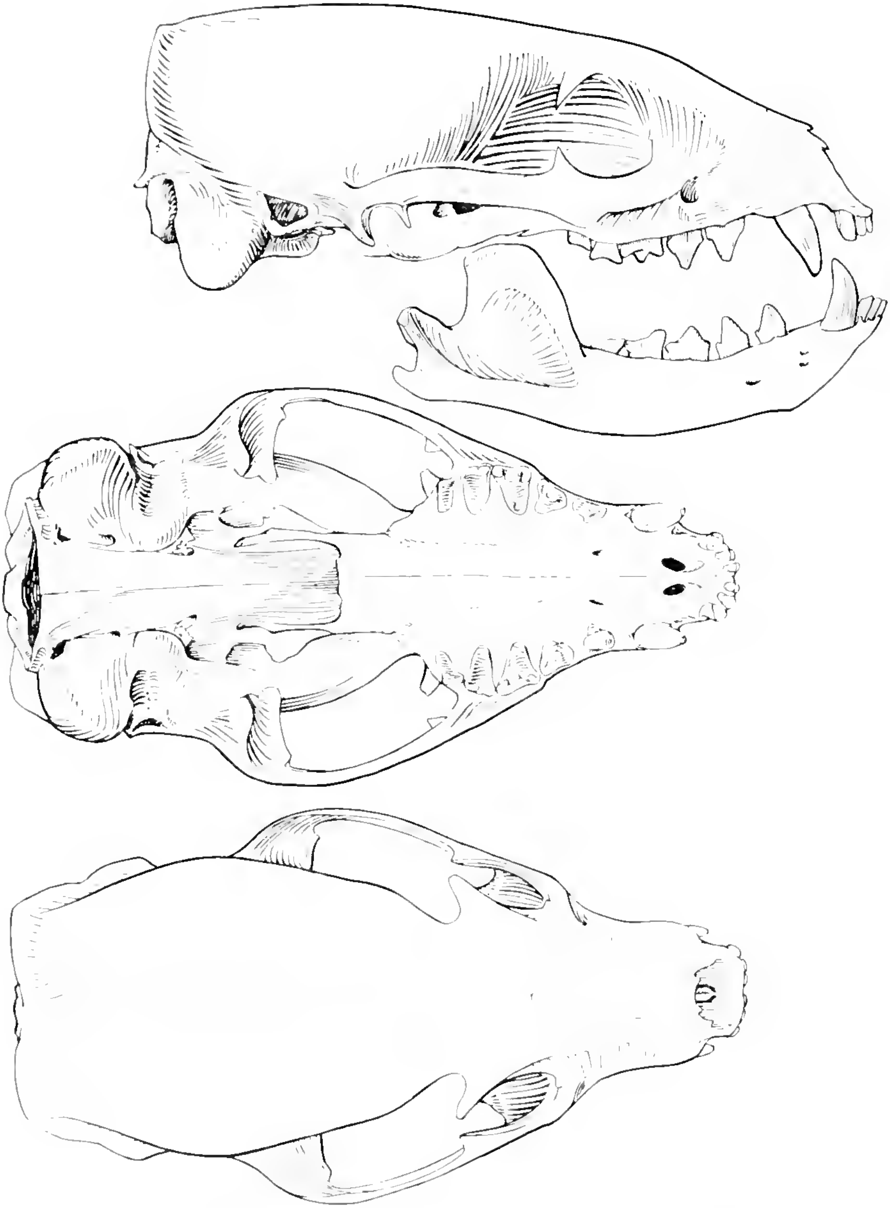


FIG. 34 *Mungos gambianus*: skull, B.M. No. 36.10.30.12, ♂, × $\frac{3}{2}$

type of *M. caurinus* always conspicuously shorter than broad, though in other *M. mungo* there are exceptions; in *Crossarchus* the two measurements are about equal.

The general appearance of the *Mungos* skull varies slightly. The postorbital constriction may be equal to or markedly more or less than the interorbital breadth. The postorbital processes are mostly short and sharp, never, even in the oldest skulls, joining up with the jugal processes to form complete orbital rings. A sagittal crest may be well-developed but in most available West African specimens it is either poorly represented or completely lacking, including well mature or oldish skulls. A supraoccipital crest is clearly present even in very young skulls and becomes broad and flange-like in fully adult animals. The depth of the bones forming the zygoma is, for mongooses, relatively shallow. The anterior portion of the bulla is smaller than the well-inflated posterior chamber and carries on its ventral aspect a marked transverse depression and fissure covering the greater part of its breadth; and this makes the auditory meatus a flat oval.

In *Mungos* there are, apparently with complete constancy, only 3 premolars on each side, above and below. The outer cusps of the upper carnassial are low and without any marked cutting function; its inner heel, as with those of the two molars, terminates in an almost equally high sharp cusp, and the whole cheek dentition appears adapted more to an insect diet than to anything else. m^1 is a fairly big tooth, generally somewhat wider transversely than the carnassial; m^2 is commonly wider across than the lingual section of m^1 but in exceptional cases is much reduced or may be lacking from one or both sides. In the lower jaw the carnassial is a tooth of little or no more importance than any of the others; in young animals it carries three small, subequal cusps, the two lingual ones closely juxtaposed. These cusps soon become obliterated with wear, as do those of m_2 also. In both jaws the canines are, for the Carnivora, relatively short.

Habits. What is known of these will be found below under the two separate species. No general generic account can be given; for while there exists a number of observations relating to the continentally-spread *mungo* next to nothing is recorded of the purely West African *gambianus*.

MUNGOS MUNGO (Gmelin) Banded Mongoose

Viverra mungo Gmelin, 1788, in Linnaeus' *Systema Naturae*, 13th edition, **1**: 84. Type locality given as Asia, but fixed by Ogilby (1835), *Proc. zool. Soc. Lond.*: 101, as Gambia; though Thomas (1882) believed it to be more probably the eastern part of the Cape Province of South Africa, and Roberts (1929) wrote that "By common consent the type locality is taken to be Natal . . .". The name is derived from the Marathi vernacular *mangūs*, being simply another form of the generic name.

Herpestes fasciatus Desmarest, 1823, *Dictionnaire des Sciences naturelles . . .*, **29**: 58. Type locality given as India, but as this was merely a renaming of *mungo*, above, the same considerations apply. The specific name is a Latin word meaning enveloped with bands, given in reference to the pelage pattern.

Herpestes gothneh Heuglin & Fitzinger, 1866, *Sber. Akad. Wiss. Wien*, **54** sect. 1: 560. Type locality Kordofan. The specific name is the Arabic term for this animal. Possibly usable subspecifically for certain West African specimens.

Crossarchus talboti Thomas & Wroughton, 1907, *Ann. Mag. nat. Hist.* (7) **19**: 374. Type locality Bornu, north-east Nigeria. This was named after its collector P. Amaury Talbot, at that time a member of Boyd Alexander's "Niger to the Nile" expedition. Available subspecifically.

Crossarchus fasciatus mandjarum Schwarz, 1915, *Jb. nassau. Ver. Naturk.* **68**: 63–64. Type locality Bate, near the Uham River, Cameroun. This race was called after the Mandjia tribe dwelling around the headwaters of the Shari River. Available subspecifically.

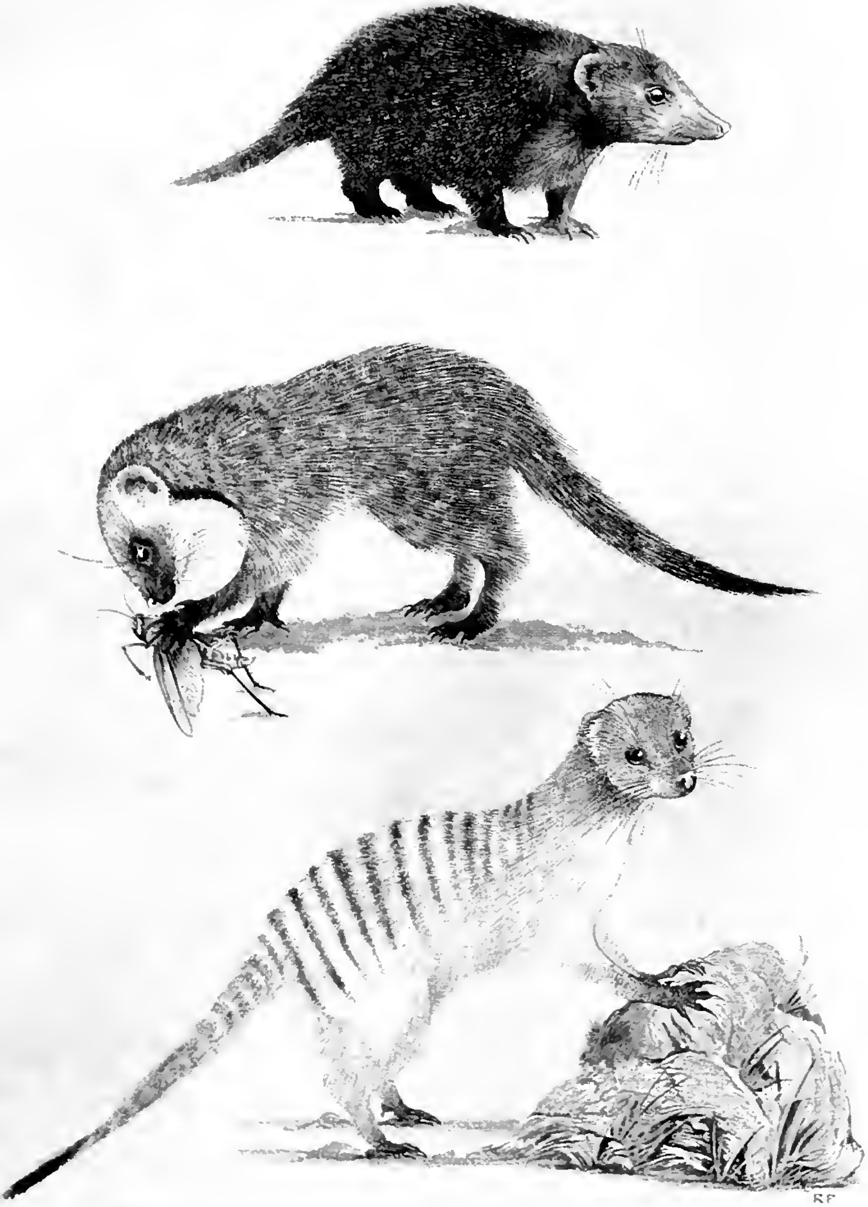
Mungos caurinus Thomas, 1926, *Ann. Mag. nat. Hist.* (9) **17**: 182–183. Type locality Gunnal, Portuguese Guinea. The name is from the Latin *caurus*, the north-west wind, because of the situation of the specimen's source relative to the main distribution of the genus. Available subspecifically.

Distribution. Like several other mongooses—of the genera *Herpestes, Atilax, Ichneumia* and *Galerella*—*Mungos mungo* has a wide distribution over the continent south of the Sahara ranging from Senegal to almost 30°S. It is an inhabitant of the open grass-woodlands, never of the closed forest, and seems to be centred more on south-eastern Africa than anywhere else. At any rate, although fairly common in that region it is apparently rare in West Africa, whence only 4 skins exist in the British Museum. These are from Gunnal in Portuguese Guinea (2), Bornu in north-eastern Nigeria, and Fort Lamy (Chad). But the species is reputed to have a wider distribution in West Africa than this would imply, for specimens were brought to England from Gambia in 1835, which caused Ogilby to regard that as the real type locality; and Schwarz (1915) described the race *mandjarum* from Bate near the Uham River in the Central African Republic (about 6°41N, 17°02E). These extremes embrace a wide variety of open-woodland vegetation: Guinea, Doka, Sudan and Sahel.

Description. With its prominently and uniquely cross-banded pelage this mongoose cannot be mistaken for any other in West Africa (Plate 6). This is one of the smaller mongooses, the head & body length being of the order of 380 mm, the tail about 230 mm, and the weight 1 to 1·5 kg. It is therefore just slightly more bulky than *Crossarchus*. The pelage is fairly long and slightly rough in appearance in life though possibly not quite so much so as in the kusimanse. In prepared skins it generally lies very flat, and this is because it lacks the usual cushioning support of dense underfur, this category of hair being almost totally absent. The bristle-hairs are of flat section, about 24 to 31 mm long, and are markedly ringed light and dark. There are, almost without exception, four regions of annulation. The long basal section may be either pure white or this colour interrupted by one or two indefinite blackish areas. The three distal zones are always the same: a deep, blackish-brown ring, an off-white or yellowish ring, and a black tip, usually longish. But there is no common length for each of these zones, and especially the basal one, even in a single specimen; for since the hairs arise at different points of the skin such irregularity is necessary for the corresponding zones to fall coincidentally from dispersed points of origin and so produce a total pelage effect of alternating light and dark transverse bands.

This cross-banded pattern applies only to the top of the back posterior to the shoulders; it fades out on the flanks; and the shoulders, nape and head are an ordinary random "pepper and salt" mixture. The hairs of the underparts are plain or very inconspicuously annulated, and may be very sparse, leaving much of the belly almost naked. The hairs of the throat are directed forwards and outwards; those of the chin are directed backwards, so there is a pronounced line where the two meet; as there is, also, along the side of the neck, backwards from the lowest point of the ear, where the outwardly directed hairs of the throat oppose the downwardly pointing neck pelage.

PLATE 6



Kusimanse [illegible] Gambian Mongoose [illegible] [illegible]'s Banded Mongoose
[illegible]

The head is broad and the muzzle fairly blunt. The largish, rounded ears are positioned well to the side of the head. The tail, which is in broad terms about three-quarters of the head & body length, is long-haired but not bushy, of a nondescript speckled colouring like the anterior portion of the body pelage, but always with a blackish terminal zone. It is evenly tapered from base to tip, very much in the manner of *Crossarchus*. The legs are speckled; but the backs of the forefeet and the digital area of the hindfeet are generally, but not always, dark, even blackish. The digits are webbed between the proximal joints; the claws are very long, particularly those of the forefeet, deep basally and fairly well curved; and the sole of the hindfoot is naked to the heel.

The scent glands have been described in some detail by both Chatin (1874) and Pocock (1916e), the former dealing with the male, the latter the female. The sac surrounding the anus and the orifices of the glands is subcircular in shape and very large compared with most species. The glandular system itself is more complex both in external appearance and in structure than in other mongooses; for, besides the usual simple pair of organs with single orifices either side of the anus, there are subsidiary glands and ducts. The floor of the deep-walled sac is not a plain surface but is complexly wrinkled in the male, and in the female comprises integumental folds or depressions. Summarising Pocock's description of these latter, there are two pairs of depressions, an upper and a lower, above the anus, and a lateral pair situated one each side of the rectal orifice and more distant from it. Each of these six depressions contains a small glandular pit with several secreting pores, none of which, however, represents the true anal glands found in other species. The orifices of these, the normal glands, are to be found on each side of the sac close to the inner margins of the two lateral folds. These true anal glands are a pair of large muscular sacs containing a dark-coloured, strongly smelling, oily fluid which escapes into the sac. The smaller, subsidiary glands are very different, of a more rudimentary nature in the female; but in the male, according to Chatin's description, appear to have become more highly developed and to approximate to the true anal glands both in their structure and in the nature and amount of their secretion.

Skull. A general description of the *Mungos* skull has already been given above; here is not a great deal to add to this in respect of the species. There is, in fact, in the British Museum only one adult West African skull of *mungo* from which to derive data for comparison with five adult *gambianus*. Recourse is therefore necessary to extralimital material of the former, and of this there is an abundance. Hayman (1936) first drew attention to significant differences between the skulls of the two species. The most unusual of these concerns the carotid foramen, which in the species now under discussion is a largish round opening in the basisphenoid, but which in *gambianus* is obscured, as described under that species.

The *mungo* skull appears to be slightly broader than that of *gambianus* its zygomatic breadth averaging about 56 per cent of the condylobasal length as compared with only some 53 or 54 per cent in the other species. The posterior projection of the pterygoid process is narrow and club-shaped, terminating in a small knob. In the great majority of extralimital *mungo* skulls measured the interorbital breadth is greater than the postorbital constriction, whereas in the available *gambianus* material it is almost always less. The most obvious distinction between the two species lies in the teeth, which in *gambianus* are strikingly smaller. This is in some measure brought out in the table of measurements on page 265.

Habits. Because it is not uncommon and occurs in large and noisy parties in relatively open country the banded mongoose has possibly more frequently attracted attention to itself and been observed than any other African species. Moreover, it has often been kept as a pet or zoo specimen. There are consequently a good many notes on certain aspects of its life and behaviour—though not a single one emanating from West Africa. The most complete and up-to-date field accounts are those given by C. D. Simpson (1964 and 1966) and Neal (1970). These relate to the animal in the wild in the southern and eastern part of the continent and to captive or semi-captive individuals but can with little doubt be taken as applying equally well to the forms occurring in the territory covered by this present work. The notes which follow herein are indebted in large measure to the patient work of both these observers.

The banded mongoose is probably wholly diurnal in its activities. Like the kusimanse it hunts in companies which as a rule number between half-a-dozen and a score. Occasional packs of 30 or 35 have been reliably reported; but now and again claims to have seen very much larger congregations, even up to 100, have been made. If these estimates were accurate they concerned very exceptional gatherings. It is, in any case, generally no easy matter, except at the nocturnal shelter itself, to count even a moderate-sized band or merely to estimate their numbers with close accuracy since at any given moment a large proportion of the party is on the move and often in and out of the undergrowth. The members of the unit keep fairly close together but not in tightly packed formation unless they are travelling purposefully from one given point to another, say a new nest or fresh feeding grounds; or if danger threatens, when they bunch together or fall into line, head to tail. The younger members of the group may from time to time lag behind the rest, delayed by play and a lack of that fervent application to the business of food-finding commonly exhibited by their elders. Realising their separation they hasten forward and often actually run ahead of the main body. Whether, in point of fact, a single individual ultimately determines the general direction taken by the party is unknown; but since it appears that some sort of dominance is recognised between different members of the community it seems at least probable that there is a tacitly admitted leader whose movements are instinctively followed.

Throughout these foraging expeditions a fairly continuous twittering is kept up, partly the outcome of the excitement of the hunt, and partly as a means of keeping together by the creation of a communal spirit. Pocock (1916e) thought that it was one of the functions of the anal glands in the gregarious mongooses to assist in holding a group together by scent. This may be true in the more static sense of recognising and clinging to known friends rather than risking the society of strangers; but while on the move it seems certain that sight and hearing, both highly developed senses in this species, play the greatest part in maintaining close contact between all members of the company. This, at any rate, was the opinion of Simpson. Nevertheless, should a few get cut off from the main body for any length of time, by being frightened into taking cover, Neal observed them to rejoin the main party by pursuing exactly the same intricate route as that taken by it, a procedure that could only be accomplished by scent. The combined voices of a party of banded mongooses on the forage do, in fact, carry a considerable distance. When it is necessary to sound an alarm or to demand the full concentration of the pack the twittering takes on a shriller, more urgent note.

Foraging for food in the banded mongoose is no leisurely, part-time affair as it has the appearance of being in so many carnivores. It is a highly active, continuous performance, every fully adult member of the unit displaying not only an astonishing voracity but a dedicated eagerness and keen inquisitiveness as well. The party fans out slightly and every root, grass tuft, fallen log, rock, hole or crevice within the ambience of each individual is determinedly explored, surface litter raked apart and such stones as are readily movable turned over in the search for insects, their larvae, spiders, worms, snails, lizards, mice, eggs, fledglings and other small creatures that may help to satisfy seemingly insatiable appetites. Travel is therefore slow. An acute sense of smell enables insect grubs, caterpillars and chrysalids to be sniffed out though well hidden below the soil or in tussocks. These are then rapidly dug out with the long claws of the forefeet. Droppings of large animals are of particular interest and eagerly broken apart since they are often the source of a plentiful supply of insects, especially dung-beetles and sometimes masses of dipterous larvae. Because of their richness Neal found dung trails to be an important factor in determining the direction of the hunt; and it is possible that the paucity of such animals as elephants, buffalos and other large game in West Africa accounts in some measure for the relative scarcity there of the banded mongoose. Mostly, each individual hunts purely on its own behalf, quickly gobbling down what it discovers before predatory interference from others can take place. But occasionally larger prey is the object of communal attack; Simpson records having once witnessed a pack of about 10 of these mongooses kill a large sand snake—*Psammophis sibilans*, a species that occurs also in West Africa. In such an attack the mongooses fluff out their fur, dash in for a quick bite at the snake's body and leap clear before it can strike.

Simpson's statement that prey such as mice are killed by shaking, dog fashion, is interesting as running contrary to the habit of the in many respects similar kusimanse, in which Ewer (1968) observed that shaking was not carried out. Larger prey that cannot be demolished at a gulp by one individual is pounced upon by the pack in general, each member that can get at it ripping off as big a chunk as it can and carrying it off to consume at leisure apart from its companions. There seems no doubt, however, that insects are the basic food, and vast numbers must be eaten in the course of a day. In captivity a wide range of human foods is accepted; but in sharp contrast with the kusimanse, fruit was found to be not very acceptable to captive specimens of *mungo* though it is said that, as in a number of other small carnivores, fallen fruits form part of the natural diet. If water is available these animals drink, by lapping, once or twice a day; but though the species has often been held to favour the vicinity of water, companies have been observed in pretty arid territory where bodily water requirements must be satisfied by extraction from food. It is possible that in such localities wild fruits play a more important role.

No one has yet succeeded in following a pack continuously throughout the day, though both Simpson and Neal have observed them for long periods, the latter with binoculars from vantage points. It is not certainly known, therefore, whether or not hunting is, in fact, unremitting throughout the entire daylight hours. For any animal to be persistently and so vigorously active as banded mongooses from dawn to dusk would be a severe tax of energy, and it seems at least possible that they, like so many other animals, large and small, nocturnal as well as diurnal, suspend their pursuit of food for a period, or periods, of rest. Be this as it may, at the end of the day, at least, the entire company seeks the shelter of a common warren. This communal resting place may occasionally, in suitable territory, be more or less on the surface amongst boulders, tree roots or other convenient cover; but more often it is subterranean, having as its basis a burrow originally dug out by some larger fossorial animal such as an aardvark, or, more commonly, a hole beneath a deserted termite mound. This last certainly seems to be the favoured site, particularly if it is on a slope affording a clear view round, has partial shrubby cover and a not too distant water supply. Entrances of convenient size are dug or enlarged with the long-clawed front paws which cast the excavated earth backwards between the hindlegs much in the common herpestine manner of "egg-throwing".

Once the general appearance of these warrens has been grasped it becomes, according to Neal, fairly easy to pick them out. If one has been in occupation for any length of time it can be readily identified by the piles of droppings on its summit and scattered for some distance around. There are generally two or three separate entrances and several feet of internal tunnels leading to a central chamber. In the deserted warren excavated by Neal this chamber measured some 1·0 by 1·5 metres and had a mid-height of 0·5 metre. There were also two side tunnels leading to small chambers; and it is likely that this special accommodation is for the use of breeding mothers.

It would appear that more than one community may occupy a single warren; for Shortridge (1934) mentions "an unusually large colony of at least thirty individuals" that daily divided into several troops which hunted independently. A warren may, by and large, be occupied for a long period of months; though not necessarily continuously, for the pack may, possibly when food runs short in the immediate vicinity, temporarily desert it for other warrens within its hunting territory. Simpson observed one pack to use three different warrens located within an area of more than a square mile. Besides these more or less permanent nocturnal shelters there may be within a territory other temporary "bolt holes" to which a foraging company can retreat in the face of danger; and it is at least possible that such established refuges, above or below ground, may be used for a recuperative phase of inactivity during the heat of the day. Two general points concerning warrens may be mentioned here. The first is that a good deal of noisy activity, clearly audible from above, takes place below ground; and the second, that Simpson found the entrances to abound in fleas.

The extent of a hunting range has not been closely investigated and there is nothing to indicate the sort of area covered beyond Simpson's incidental observation just quoted. Nor is there much information concerning scent-marking of boundaries. Neal makes no reference to this at all; but Simpson recorded that there is little activity of this kind during food foraging but that it was common at drinking sites. The methods of registering scent signals follow the usual pattern: pressing the anal pouch against convenient trees, logs or rocks, sometimes at ground level, sometimes by raising the hindquarters well into the air; and, besides this dabbing, marking by dragging the anal region across the ground.

According to Simpson (1966) the birth and nursing of the young takes place "in a grass-lined chamber deep in the warren". Whether this statement is derived from actual excavation of the site or is deduced from the fact that a tame female offered several alternative possibilities for a natal chamber always chose a dark box accessible through a tunnel in a mound of soil is not clear. Sexual maturity occurs certainly in females at the age of 9 or 10 months, possibly a little later in males. In heat, a good deal of the more active, deliberate courtship seems to be carried out by the female, lying on her back and wrestling with the male, or flattening herself against his back and rubbing her vulva through the fur. Both sexes, however, become playful, jumping around, pouncing on each other, or nudging with the head; and during this the male also "scents" the female, though seemingly less designedly than in her case. His anal glands become enlarged and exude quantities of a white secretion with which the female unavoidably becomes covered during this precoitional romping. Finally, the two animals generally chase each other round and round in ever narrowing circles, or the male may circle the female, his tail held high. Neal observed mounting to be repeated three or four times, with a short chase between each; and on one occasion a second male, which had been watching throughout, mounted soon after the first male had separated.

The period of gestation is in the nature of 2 months, its precise length being as yet undetermined. It is not possible to derive information regarding a preferred breeding season in West Africa from the limited material available; but it seems probable (C. D. Simpson, 1966) that, like the kusimanse, these mongooses are capable of breeding more or less continuously. From 3 to 5 young seems to be the general number at a birth; but a litter of 6 has been recorded. They are born blind, with a dark skin and a fine transparent pelage which, however, faintly reveals black cross-banding on shoulders and rump. The eyes open about the 10th day. At between 2 and 3 weeks the pelage begins to become more apparent; and it starts to assume adult appearance after 6 weeks, though it does not attain its mature coloration until the age of 3 months. The young appear to be held in common; for in one community Neal observed that when the pack left on the daily forage one female remained behind to suckle and look after the eight young. And on return of the party to the warren in the evening all the females nursed any of the young without distinction.

The weight at birth is about 20 g but this increases very rapidly, though the figures published by Simpson (1964) exhibit an extremely wide variation between different individuals. One young male achieved what may be regarded as a fully adult weight of 1·75 kg as early as about 5 months; an adult male, on the other hand, is given as only 1·55 kg; but, an adult female reached the exceptionally high weight of 2·25 kg. As regards longevity, one banded mongoose is known to have lived in captivity to the age of 11 years; and another of 8½ years.

Several miscellaneous matters of behaviour must be briefly glanced at. In connexion with feeding it is interesting to note that the backward egg-hurling procedure common to several members of the subfamily is well confirmed in *mungo*. It has been observed and illustrated by C. D. Simpson (1964 and 1966), Davis (1966) and Kinloch (1964). The force with which this is carried out is surprisingly powerful; nevertheless, an egg does not always crack sufficiently at the first attempt, in which case the action is determinedly repeated until success is achieved. This procedure is, however, not reserved solely for eggs but is employed with other desirable but encased foodstuffs, some of them necessarily strange to the mongoose; and, moreover, as Kinloch has shown, is applied to a variety of quite unprofitable articles, including even a bunch of keys. One observation involving this behaviour, made by Davis in the Bronx Zoo, is of especial interest in as much as it concerns large millipedes so commonly occurring in Africa. A banded mongoose, discovering after repeated attempts that its teeth were unable to pierce a coiled up specimen of one of these, finally hurled it through its hindlegs against the wall twice, thereby cracking the hard chitinous coat sufficiently for its teeth to effect penetration. This achieved, the millipede was then readily consumed. Neal, in fact, found these myriapods to constitute a very important item in the dietary in Uganda, *mungo* droppings invariably showing clear and abundant remains of the chitinous shell.

Like others of its kind this mongoose is almost wholly terrestrial and probably normally has little urge to climb for any distance up vertical tree trunks. Its long, almost straight claws are scarcely adapted to this; and more especially to getting down again. Kinloch describes a few rather inept attempts at tree climbing made by his pet *mungo*, in which, it is true, the upper branches of acacias were attained but descent thence found too nerve-racking to be undertaken. Simpson, too, in his opening paragraph (1964) makes some mention of tree climbing; but this may refer to a pack of banded mongooses that, escaping from hunting dogs, scrambled to the top branches of a tree that had been pushed over by elephants. The sloping trunk and interlacing branches of this would, of course, considerably lessen the difficulty, both of getting up and of getting down. Where there are positive footholds such as offered by the wire netting of a cage it is known that *mungo* can reach a good height from the ground. Apart from an ability to scramble over low obstructions it can leap onto them provided they are not more than 500 mm or so high. Though banded mongooses often live near water Simpson says that they never seem to take to it of their own accord and are, in any case, poor swimmers; on the other hand, Dalton (1961a) records how a pet of this species leapt into a flooded river in order to rejoin her on the other bank and successfully swam across.

Play is an important factor in the lives of all young carnivores, and this fact is constantly illustrated by juvenile and subadult banded mongooses, both in the vicinity of the burrow and while actually on the move during forays. Play follows the common pattern of mock-fighting, chest to chest wrestling, tail-chasing and scampering after each other. Simpson found, however, that play does not occupy much of the adults' time. These, basking in the early morning sun or resting around the warren after the day's hunt, go in for a good deal of grooming of their own or other adults' fur. At these times, too, but especially in the morning after rising, they like to stretch their limbs out quite straight fore and aft, lying with their bellies pressed to the soil. Play and other intercourse within the group, however, whatever it may appear on the surface is not necessarily on a socially equal basis; for domination of one animal over another is established, in the observation of Simpson, by putting the foreleg across the shoulders of the inferior animal and seizing this latter by the back of the head lightly in the jaws. Such ascendency by no means always belongs to the male. Simpson noted female dominance in two different groups, in one of which a female established her position over two males of the same litter at the age of about three months.

All who have studied banded mongooses in the wild or had dealings with them at closer quarters have been impressed by the obvious acuteness of the senses of sight, hearing and smell. These animals, though recklessly courageous in the face of close danger, are at all other times highly suspicious of possible attack and timorous to the point of fleeing for cover at the least imagined threat. This caution and an obsessive curiosity that is often vital to the discovery of food hidden in soil or vegetation lead to a constant exercise of these highly developed senses. Both at the warren and frequently during the course of the daily excursion one, or sometimes nearly all, of the group will sit upright on the haunches, or if necessary stretch up fully erect on the hindfeet, and peer round, intently watching and listening. High sounds seem to make more impression than low; and there has been no suggestion that crackling is a terrifying noise as it is to the kusimanse. Simpson noted that pet animals could pick him out visually at some distance, and that lizards climbing trees or insects flying away were followed by sight. Neal found that this constant vigilance and acuteness of perception rendered close observation of a pack a matter of difficulty since a stationary Land Rover or other strange object at about 40 metres aroused nervous suspicion, and the slightest movement was detected at 20 to 25 metres, at which distance, also, the click of a camera attracted attention.

A display of wariness can be seen on the occasion of leaving or return to the home. The banded mongoose is not so early a riser as other diurnal animals, mostly making its first appearance an hour or so after sunrise rather than in the grey light of dawn. Before actual emergence from the warren the immediate vicinity is carefully scrutinised from the mouth of an entrance hole, and if all looks clear one or two adults come out and, if it is an old termitarium, mount to the top of the nest and stand or sit erect scanning the surrounding territory. Then, if no danger threatens, there is a general exit followed, as a rule, by a period of play, sun-basking, yawning, stretching, grooming and defaecation before moving off on the day's forage. The return home is commonly effected a little before night closes in; though should the afternoon be heavily overcast the pack, possibly deceived by the poor light, may arrive at the home territory considerably earlier. The returning party never enters the warren direct but pauses to rest and relax at a little distance from it. Thence, approach to and actual entry into the nest is carried out in gradual and cautious stages, puncuated by the usual play and grooming activities, until the final bolt down an entrance tunnel as night falls.

Banded mongooses have a range of different calls and notes. That most commonly heard is the rather bird-like twittering of the whole pack when on the hunt. This may change when danger is suspected to a strident note of alarm; but if a single individual is scared or threatened it spits rather like a cat and growls, and if this proves ineffective it alters to a staccato chatter of rage—or, rather, of blind fury, for at these moments one of these mongooses will hurl itself without reserve in attack at whatsoever has aroused its anger. At the other end of the scale, in moments of pleasure the note uttered is something of a low whine or even a kind of soft purr.

The species appears to have few natural enemies apart from birds of prey, which it quite obviously holds in considerable fear; for a hawk may swoop swiftly from the sky, seize an individual and be safely away without the possibility of counter-attack; whereas the combined tooth-power and lightning agility of 20 or 30 enraged mongooses must be a considerable deterrent to almost any ground predator. Nevertheless it is said that the larger carnivores such as lions and leopards will pursue and attack a *mungo* hunting party. As some sort of defence against assault from the sky, of which their keen eyes give them early warning, these mongooses instinctively bunch together in tight formation; and this may possibly have the beneficial effect of deceiving hawks and eagles, making them more hesitant of attacking an apparently large body than they would be of attempting the comparatively simple task of picking up isolated individuals.

The majority of mongooses, obtained sufficiently young, make excellent and fascinating pets, and *Mungos mungo* is no exception. These animals, however, cannot be kept confined to small cages but must be given more or less free range. This being the case it should be fully realised before taking on the responsibility for such a pet that, while the effort is usually very rewarding, a great deal of time and trouble are unavoidably involved in feeding, play and general watchfulness, together with good-humoured patience in the face of inevitable accidents to possessions due to an insatiable curiosity, and restraint sometimes in response to slight personal injury, the outcome of an incalculable uncertainty of animal temper. The banded mongoose is at heart a very friendly creature, with its own kind, with humans, and often with dogs; in domestication it becomes trusting and, at least apparently, affectionate. It is by nature a cleanly animal, easily house-trained; and its bodily smell is, as a general rule, slight and inoffensive. Its feeding is a matter of simplicity since it avidly accepts a very wide range of foods. All this has been vividly brought out by Kinloch (1964).

Taxonomy. A species such as *mungo* with a pelage composed predominantly of light and dark ringed hairs must inevitably display a range of colour variation, within a single population as well as, in the wider aspect, in response to differing ecological conditions. No less than 16 subspecies are, indeed, listed in G. M. Allen's African Checklist (1939); and although, in the type descriptions of these, general body and tooth sizes receive occasional reference and rarer emphasis, the great majority of the forms are, in fact, described almost purely on the basis of colour, and in almost every case from one or two specimens only.

Without question, clear differences of colouring exist between specimens; but even now, after many years of collecting, the amount of material available for study is for the most part quite insufficient to judge reliably the constancy of colour in any given locality, and hence the real validity of presumed races. Thomas, erecting *caurinus* on the basis of two differing specimens, himself thought that "probably it will be found to grade hereafter into others of the banded forms . . .". Certainly as far as West Africa is concerned it is futile to pretend to the accuracy of determination implied by a third name. Four specimens alone exist in the British Museum from the region. Two of these, from a single locality and both ascribed by Thomas to *caurinus*, one being the type, differ very distinctly from each other in coloration. The other two, from well separated localities but both ascribed to *talboti*, one the type, also differ from one another, possibly due to age, possibly not. Until a great deal more material has been gathered together for study it seems pointless to go into finer division than the species and imply a degree of understanding that does not exist.

Moreover, for practical purposes in a work such as this present it is not possible to go any further. The plain fact is that with only a couple of sharply different forms to differentiate or with comparative specimens actually in the hand such expressions as "paler" or "darker", "pinker" or "buffer" may well be full of meaning; but with a range of several delicate nuances it is an almost impossible task to convey absolute colour to a student possessed of a single skin. Very few users of this present work have access to standard colour charts; and even with these at hand the task is still fraught with difficulty since the selection of colours in them is too limited to find an exact match for the slight nauances involved. In any case the colours themselves vary quite appreciably in different parts of the pelage.

However, since certain names have been connected with West Africa the following notes are given for what they are worth. At the outset it must be pointed out that there is uncertainty regarding the precise appearance of even the nominate race since three different African localities have been assumed to be the type locality. If Ogilby was right in thinking this to be Gambia—and there is no positive reason for supposing his guess to be less accurate than those of Thomas or Roberts—then *caurinus* might fall into the category of a synonym.

Mungos mungo gothneh (Heuglin & Fitzinger) Kordofan Banded Mongoose

This was described from Kordofan (Sudan) in the Sahel zone of vegetation but has sometimes, with possible justification, been assumed to range westwards through this same belt at least to the eastern side of Lake Chad. If it does this there is no reason why it should not range yet further. The only clue to its appearance given in the type description, and that almost useless, is that the white colour of the underside is less well developed than in *zebra*, an Ethiopian species. Measurements of a few Sudanese specimens assumed, from their locality of origin, to be *gothneh* are given in the table on page 265.

Mungos mungo talboti (Thomas & Wroughton) Talbot's Banded Mongoose

The brief distinguishing features of this race (Plate 6) from Bornu (north-east Nigeria) were given as medium size and very pale coloration—though Schwarz later wrote that it was not always so pale as Thomas & Wroughton had said. What specimens Schwarz had as a foundation for this statement, and on what grounds those specimens, differing as they must have done from the type, could be held to be *talboti* is not clear. A second specimen in the British Museum from Fort Lamy, and determined two years later as this race, is, in truth, somewhat darker; but it is a juvenile and not strictly comparable. Further, the two may, though not certainly, have come from different vegetation zones; Fort Lamy lies in the Sahel, *Acacia raddiana*, type of vegetation, but Bornu is a district covering a large area which includes both Sudan and Sahel woodland. Comparison was made in the type description with *somalicus*, the general appearance being characterised as even paler than in that race; and *talboti* was said also to have a black tip to its tail, a feature that certainly does not show very clearly today in the type, the end of the tail being missing.

Mungos mungo mandjarum (Schwarz) Schwarz's Banded Mongoose

Bate, whence the type specimen of this race came, is in the Central African Republic (6°41N, 17°02E) and in a much moister vegetation zone, Doka woodland, than is usual for this species. Possibly for this reason its coloration is duller: Schwarz described the form as very like *talboti* but at once distinguishable by its darker, more yellow or brownish ground colour, especially on the head and neck, and feet that are quite black. He also ascribed to this race two other specimens from 180 km further south, from the source of the Pama River, which flows into the Ubangi and is hence just extralimital to this work and in the Guinea woodland zone.

Mungos mungo caurinus Thomas North-west Banded Mongoose

Thomas described this race as "rather small"; the skull of the type, an old animal, in fact exhibits little difference of measurement from Sudan specimens presumed to be *gothneh*. The general colour was said by him to be "nearly as dark as in typical *M. mungo*, quite unlike that of the pale *M. talboti* of Bornu". In the type the colour is certainly relatively dark; but Thomas omitted to say that the specimen was in moult and that in consequence the bands are obscure or entirely lacking from the posterior half of the back. A second specimen, young, taken at the same place (Gunnal, Portuguese Guinea) six weeks earlier is very different; and if it is compared with the type of *talboti* it will be seen that though the flanks of *talboti* are paler the backs match exactly. The material available is quite inadequate to form the basis of any expression of opinion on the validity of this proposed race, the type locality of which lies in the Guinea woodland.

MUNGOS GAMBIANUS (Ogilby) Gambian Mongoose

Herpestes gambianus Ogilby, 1835, *Proc. zool. Soc. Lond.*: 102. Gambia. Type in the British Museum No. 55.12.24.226, ♀; skin in fair condition but probably much faded since it was once mounted and on exhibition, and with half the tail missing; skull much damaged.

Distribution and general. Although there has been some confusion regarding the genus of this mongoose, it having for a long time been held to be *Crossarchus*—and, indeed, so classified in G. M. Allen's Checklist (1939)—there seems never to have been the slightest question respecting the species. Quite different in general appearance from its strikingly cross-banded near relative *mungo*, it does, in fact, bear considerable external resemblance to the more distant *Crossarchus obscurus*, with which it has in consequence quite often been confused both in the field and in the museum (Plate 6). The essential distinctions between the two are brought out in the section devoted to this latter species and need not be further entered into here.

This is a small-sized mongoose apparently entirely of West Africa, its known range being from Gambia to western Nigeria. It occurs almost exclusively in the Guinea woodland zone just inland of the high forest but may penetrate into the rather similar Doka belt. However, it has also been obtained from Bonthe island on the coast of Sierra Leone, the vegetation of which, apart from fringes of mangroves, consists of sand ridges and sparse grass. How the species got there is an interesting speculation; but its presence there implies that it may also be discovered in other stretches of coastal scrub such as the Accra plains, Ghana. G. S. Child (private communication) records that packs are not infrequently to be seen in the dry-season throughout the Borgu Game Reserve area in western Nigeria.

The actual places from which the 11 British Museum specimens came are: Gambia, unspecified (2); Sierra Leone, Bonthe and Dumbaia; Ghana, Ejura (4) and Bole; Togo, Kete Krachi; Nigeria, near Shepeteri, Ogun Forest Reserve. Only 6 of these are adult.

Description. The overall colour of *gambianus* varies somewhat with the area from which the specimen comes; but the broad general appearance is that of a smallish, dark brown, heavily speckled mongoose, with a head & body length of some 350 mm and a tapering tail measuring about three-fifths of this. The face, though not exactly blunt, lacks the conspicuously long protruding snout so characterstic of the rather similar-looking kusimanse.

The pelage is fairly long and fairly harsh. On inspection it will be found, like the other species of this genus, *mungo*, to lack any obvious sign of underfur below the contour coat of bristle-hairs. These latter are flattish, but not quite so much as in other genera. They vary considerably in length as regards extreme examples, from 30 to 52 mm; but the more representative range is from about 35 to 45 mm. The annulation of these bristles is distinctive and serves as one of the points of difference between this mongoose and the kusimanse, as explained in the description of that species. In the proximal half there may be four zones of coloration, but these are not always all present. Exceptionally there is a basal white portion measuring 3 to 5 mm; the next distal zone, present in most specimens, is black and averages 5 to 7 mm; nearly every specimen exhibits the next zone, which is white and averages 5 mm; and this is very often, but not always, followed by about 1 mm of deep yellow, dividing the proximal region from the three terminal, and constant, rings. First of these is a black zone the length of which varies between different specimens, in a Ghana example averaging 11 mm, in a Nigerian one 18 mm; there is then a golden-yellow subterminal zone averaging from 5 to 7 mm; followed by a fine black tip which averages 5 mm, is rarely less than 4 mm, and may reach 10 mm. Because of the much longer subterminal yellow zone the overall pelage colour in *gambianus* is almost always rather lighter than in *C. obscurus*, the ticking having a considerably coarser appearance than the fine puctulation of the coat in this latter. Unlike the nearly related *mungo* there is not the least suggestion of the corresponding colour zones falling together in the pelage and therefore no hint of any regular transverse pattern.

The fur on the belly is very scanty and, for the most part. unicolorous red. On the throat it is unicolorous white, or yellowish, and directed outwards and upwards from a longitudinal medial parting. Where its direction comes into opposition with the shorter, posteriorly directed hair of the neck it curves backwards and forms a more or less distinct white line. The short fur with which it comes into contact is blackish; so a characteristic *gambianus* pattern is formed along the side of the neck, from the ear to the foreleg, of two longitudinal black and white lines, but much clearer in some specimens than in others. The rounded ears, set well down on the sides of the head, are clad with short, speckled hair, both inside and on their backs. Since the nose is not elongated the depth of the upper lip from the rhinarium to the mouth opening is short, quite different from the kusimanse. The arms and legs are ticked with yellow in the manner of the back, but the backs of the forefeet and at least the digital area of the hindfeet are black. The toes are slightly webbed; the sole of the hindfoot naked to the heel. The evenly tapering tail is mostly speckled but has a longer or shorter black terminal region. No one appears to have investigated the form of the anal scent glands and pouch.

FIG. 35. *Mungos gambianus*: bulla, 2

Skull (fig. 34). This follows the general *Mungos* pattern as described above under the generic head. There are, however, certain points of difference from *mungo*. The most interesting of these, to which Hayman (1936) first drew attention, is the existence in *gambianus* of a projection of bone from the antero-internal angle of the bulla which at least partially covers and obscures the relatively small carotid foramen in the basisphenoid, with which bone it eventually becomes fused around the latero-anterior rim of the foramen (fig. 35). This structure appeared to Hayman to be unique in the carnivores; but a similar bony projection is, in fact, to be found from time to time in other mongoose skulls, especially in *Herpestes ichneumon*, as for example in B.M. No. 95.9.4.6 and B.M. No. 33.3.3.5. It can be seen also, though less well developed, in the type of *Crossarchus ansorgei*, B.M. No. 10.4.8.7. Judging from the slender material at present available, five adult specimens, this is a somewhat narrower skull than that of *mungo*, the zygomatic breadth averaging about 53 or 54 per cent of the condylobasal length. The interorbital breadth is less than the postorbital constriction in four of the five adult skulls, in the fifth the two measurements being equal. Whereas in *mungo* the postdental palate is generally slightly broader than long, in *gambianus* the difference is more marked, the length being only about half the breadth. The posterior part of the pterygoid process is broad and flat, quite different from the narrow, club-ended projection found in *mungo*.

The most obvious difference between the two species, however, lies in the teeth. These in *gambianus* are remarkably small, very considerably less in bulk for an almost similar-sized skull. The visual sharpness of this distinction is only partially conveyed by the measurements given in the Table below.

Habits. To all intents and purposes nothing is known of these, not a single field note being provided by any collector and no independent observation having been recorded apart from the fact that one of T. S. Jones's specimens from Bonthe was young near the end of June. In a personal communication he states that he collected another young specimen at the end of September; and young or very young ones have been collected in Ghana during January and February. It is therefore not even known whether this species shares in any way the communal habit of *mungo* and the

Table 13: Numerical data for species of *Mungos*

	mungo *?gothneh* (ex Sudan)	*mungo* *caurinus* (Type)	*gambianus*
Vegetation	Sahel	Guinea	Guinea and Coastal scrub
Number in mean	4	1	5
Condylobasal length	67·0	66·2	69·9
Basilar length	62·3	61·2	65·0
Palatilar length	33·7	32·6	35·1
Zygomatic breadth	37·3	39·5	37·4
Upper cheekteeth breadth	23·1	22·8	21·7
Nasals, length	18·3	—	18·8
Interorbital breadth	14·0	14·0	13·4
Postorbital constriction	12·1	13·8	14·2
Braincase breadth	26·9	27·4	28·3
Toothrow (c—m^2)	22·8	23·1	22·9
p^4 length	5·3	4·4	4·3
m^1 breadth	6·5	5·6	5·2
m^2 breadth	4·5	—	4·0
m_1 length	4·7	4·1	4·2
m_2 length	4·4	—	3·6
Head & body	—	385	350
Tail	—	235	210
Hindfoot	—	72	69
Ear	—	26	23
RATIOS (per cent)			
Tail/head & body	—	61	60
Zygom. br./condylob. l.	56	60	54
Braincase/condylob. l.	40	41	40
Braincase/zygom. br.	72	69	76
Palatilar l./condylob. l.	50	49	50
Interorb./postorb.	116	101	94
p^4/c—m^2	23·2	19·1	18·8

similar kusimanse. It can only be assumed from the small size of the teeth that the food is weak and soft, probably almost entirely insects.

Taxonomy. There is no doubt, as Hayman (1936) pointed out, that *gambianus* is a fully independent species and not merely a West African race of *mungo*. No subspecific division of it has yet been suggested; and though it is true that minor differences of coloration can be found amongst the available material these are certainly too insignificant to justify any such distinction.

Genus **HERPESTES** Illiger, 1811

Typical Mongooses

Ichneumon Lacépède, 1799, *Tableau des divisions, sous-divisions, ordres et genres des Mammifères* . . .: 7. Not of Linnaeus, 1758. This name is Greek and means the tracker, from *ichneuo* to hunt, with reference to the reputed habit of hunting out and consuming crocodiles' eggs.

Herpertes Illiger, 1811, *Prodromus systematis Mammalium et Avium* . . .: 135; this misprinted spelling was corrected to *Herpestes* in a list of Errata on the final page (302, but actually unnumbered). Type species *Viverra ichneumon* Linnaeus, as designated by J. Anderson, 1878, *Anatomical and zoological researches . . . of the two expeditions to Western Yunnan* . . ., 1: 171. The name, as stated by Illiger, means creeper, from the Greek *herpein*, and was presumably given with reference to the animal's stealthy habit.

There are several other, extralimital, synonyms.

Taxonomy. *Herpestes* is a genus of very disputed scope. Illiger, in first naming the genus, gave no country of origin nor any type species—though he did cite the name ichneumon, which, as *Viverra ichneumon* Linnaeus from Africa, in fact, very much later (1878) became the type species by designation. Meanwhile, it was not long (1823) before the name became generically attached to a species from India, quickly followed by others from the far east. Thus the position soon became established in which the genus was widely regarded as satisfactorily covering all the Asiatic as well as several African species, a situation that holds today—though at one time or another attempts have been made by different authors to assign the eastern species to other genera (*e.g.* *Mangusta* Horsfield, 1822; *Urva* Hodgson, 1837; *Calogale* Gray, 1865; *Calictis* Gray, 1865). Palaeontologically, *Herpestes* is, indeed, regarded as having originated outside Africa and to have spread from its source over much of the oriental region and throughout a great part of Africa, dividing itself mensurally in the course of evolution into large species and small species.

The question of the generic identity of the Asiatic species is necessarily of relatively minor interest to the area now being covered; there are much more urgent problems concerning the genus in Africa. In that continent, apart from the type species *Herpestes ichneumon*, basically from Egypt but, including its southern representative *caffer*, spread from the Mediterranean to the Cape, there have been ascribed to the genus one other large species, named by de Winton *H. naso*, and a host of smaller animals belonging to a multitude of forms, of which *sanguineus*, *gracilis* and *ochraceus* may be mentioned as of prime importance to the present study.

To deal with these small mongooses first: all were assigned generically by their original authors to *Herpestes* as, at least outwardly, nearly resembling *ichneumon* though on a smaller scale. Gray (1865a), however, split up the large assemblage of species, both African and Asiatic, by that time ascribed to *Herpestes* into a number of smaller genera erected by him for this purpose. *H. sanguineus* and *H. gracilis* were placed in *Calogale*, and *H. ochraceus* in *Galerella*. The former genus comprised Indian as well as African species; but eventually, largely through the work of Thomas (1882), it became restricted to oriental mongooses. Gray's genera did not, in fact, find much favour; the African species continued to be associated with *Herpestes* (or *Mungos*, which as part of the general nomenclatural mix-up, was then the more commonly accepted name for this group) until J. A. Allen (1924) made out a good case for reviving *Galerella* generically to cover all the small African forms. But this name, though widely recognised and understood by African mammalogists, has been little used in literature. The reasons are several. Four years after Allen's paper Thomas (1928) drew attention to it, only to express the opinion that *Galerella* was, in fact, applicable solely to the north-east African *ochracea*, which had been named type species. He consequently erected *Myonax* to accommodate the numerous remaining pan-African forms to which Allen had shown the name *Herpestes* to be inappropriate. *Myonax* then became the fashionable name for the majority of these small African mongooses until a few years later Schwarz (1935) expressed the opinion that there was no justification for it since there were no generically valid morphological distinctions between *ochracea* and the others, thus restoring *Galerella* to the scope that J. A. Allen (1924) had accorded it. However, G. M. Allen (1939) in his Checklist did not accept this view and *Myonax* consequently, though somewhat latently, remained current during the period of relative nomenclatural inactivity brought about by the second world war. Simpson's Classification (1945) published at the close of this period, at once to become the universally accepted criterion of nomenclature, sank both *Galerella* and *Myonax* in *Herpestes*; and this widespread and numerous group of small mongooses thus underwent its fifth change of generic name, *Mungos—Herpestes—Galerella—Myonax—Herpestes*, in 20 years. The current practice is, following Simpson, to use, at choice, *Galerella* or *Myonax* subgenerically.

The argument for not generically separating the Asiatic and African mongooses under consideration here, as briefly expressed in Ellerman, Morrison-Scott & Hayman (1953: 119 f.n.), is that "it should be borne in mind that although the small African mongooses appear very distinct from *H. ichneumon* (the type of the genus) there are many more small species of *Herpestes* in tropical Asia". However, the present author accepts J. A. Allen's contention that the small mongooses under discussion merit full generic separation as *Galerella* from the large Egyptian mongoose, *Herpestes*. The characters taken into consideration in this and in the rejection of *Myonax* will be detailed later in the account of the first of these genera. It is now necessary to glance at the other large species named by de Winton *Herpestes naso*.

In his preliminary notes on the carnivora collected in the north-eastern Congo J. A. Allen (1919b) found it necessary to erect a new genus, *Xenogale*, to cover what he thought to be a hitherto undescribed forest mongoose, which he named *microdon*. Hayman (in Sanderson, 1940) satisfactorily showed that this species was identical with de Winton's long-established *Herpestes naso*; the question remains simply one of genus—is *Xenogale* validly separable from *Herpestes* at generic level? In erecting his new genus Allen adduced a number of differential characters, both external and cranial, that he regarded as sufficient to separate *Xenogale* from *Herpestes*, *Ichneumia* and *Atilax*, to each of which the new mongoose bore some measure of resemblance. These characters will be entered into later in the appropriate place; meanwhile, here it must be said that Hayman, in the work just cited, rejected Allen's arguments on the grounds that though *Xenogale* did exhibit well-marked differences from the African *Herpestes ichneumon* these were, in fact, no greater than the divergence of this last from certain Asiatic species commonly allocated to *Herpestes*. This, of course, raises the basic question of whether these oriental mongooses are properly included in *Herpestes* or whether, like *Xenogale*, they would be better split off as Gray and others long ago contended should be the case. It is true that a decision on this point of taxonomy must affect West African nomenclature; but the matter is too wide to be decisively probed in connexion with this regional investigation. It can only be said here that the present writer considers Allen's proposal to be correct, and that it is justifiable as well as convenient to regard *Xenogale* as generically independent.

In this work, therefore, instead of *Herpestes* being taken as covering *ichneumon*, *naso* and the *sanguineus-gracilis-ochraceus-pulverulentus-ratlamuchi-etc.* complex, either integrally or divided into the subgenera *Galerella* and *Xenogale*, it is regarded as applicable solely to the Egyptian mongoose, *H. ichneumon*.

In view of this reduction in scope, questions of general generic description, habits and so forth are reserved for the account of the single species which follows.

HERPESTES ICHNEUMON (Linnaeus) Ichneumon or Egyptian Mongoose

Viverra ichneumon Linnaeus, 1758, *Systema Naturae*, 10th ed., **1**: 43. Egypt, on the banks of the Nile. The specific name is Greek and means tracker, given because this mongoose was since ancient days reputed to hunt out crocodiles' nests to rob them of eggs.

Ichneumon pharaon Lacépède, 1799, *Tableau des divisions, sous-divisions, odres et genres des Mammifères* . . .: 7. This name associates the animal with the Pharaohs of Egypt.

Ichneumon aegypti Tiedemann, 1808, Zoologie . . ., **1**: 364.

Ichneumon major E. Geoffroy, 1812, *Description des Mammifères qui se trouvent en Egypte*, **2**: 139 (footnote). Egypt. The specific name is the Latin for larger and was given because the mongoose described (based on La Grande Mangouste) was thought to be bigger than others in the group dealt with by Geoffroy under the general heading of ichneumons.

Herpestes ichneumon occidentalis Monard, 1940, *Archos Mus. Bocage*, **11**: 193–194. Mansoa and Cacheu, Portuguese Guinea. The name *occidentalis* is Latin for western. Valid as a race.

Herpestes ichneumon aithos subsp. nov. Described on page 276 of this present work. Type locality Newton, Sierra Leone. Type specimen in the British Museum No. 53.130, ♂ of medium age; skin complete and in good condition, skull with cranium badly damaged and partly missing. One meaning of *aithos* (Greek) is red-brown.

Herpestes ichneumon mesos subsp. nov. Described on page 278 of this present work. Type locality Anara Forest Reserve, near Kaduna, northern Nigeria. Type specimen in the British Museum, No. 50.320, ♂ of medium age; skin fair, hindfeet and part of the tail missing; skull structurally complete but with 15 teeth missing. One sense of the Greek word *mesos* is in the middle of two extremes.

Distribution and general. This is almost certainly the oldest-known mongoose to western civilization. It figures in ancient Greek and Latin literature; but long before that it was depicted on Egyptian tombs and temples nearly 3000 years B.C. It was certainly revered in Egypt and was commonly mummified. The so-called Egyptian mongoose is, in fact, distributed over the length and breadth of Africa from the Mediterranean to the Cape, though it is not found everywhere. Basically it is an open-country animal but forms are also known, though less frequently, in the dense forest. It is, moreover, the only mongoose in the European fauna, occurring in Spain and Portugal. It is also found in Palestine but, curiously enough, does not seem to have received mention in ancient Jewish writings as it did in those of other neighbouring pre-christian civilizations.

One of the names it was known by in early days was Pharaoh's rat; but so far from being a nuisance it was widely revered in Egypt, most probably primarily because of its pest-destroying value, being kept in temples and the houses of the rich largely for its snake-killing propensity, and being honoured in priestly circles for its reputed enmity to the crocodile. Throughout the long and doctrinally varied history of Egypt this mongoose was, in fact, at different times or places credited with a number of mysterious or momentous attributes which cannot be entered into here. Doubtless having its origin in Egyptian practice, the ichneumon seems also to have been kept in some well-to-do Roman households; but this was without religious significance and was most likely little more than a matter of possessing a rather unusual domestic pet, though some idea of pest discouragement may have played its part too.

Description. The ichneumon (Plate 7) is one of the larger mongooses, having an adult weight of 3 to 4 kg, a long, relatively slender head & body of some 550 to 600 mm together with a notable tail measuring roughly nine-tenths as much. This is a very short-legged animal considering the size of the body, standing only some 150 to 200 mm at the shoulder. In fact the long pelage, especially that of the hindquarters, often reaches to near the ground, hiding much of the legs. As in most mongooses, the face is long and pointed, the muzzle terminating in a naked black rhinarium; the rounded ears are short but wide and are set on the sides of the head. The highly speckled pelage is coarse, consisting of long wiry bristle-hairs, annulated with several rings of alternating light and dark colours, and fairly long, abundant, fine, richly coloured underfur. The bristle-hairs are long throughout all the pelage right up to the nape but are especially so over the rump, where they sometimes attain a length of 65–75 mm. The underfur measures 15 to 22 mm. The fur of the head, face, chin and neck is similarly coloured and speckled but very much shorter and close-lying. The area around the eye is bare. Two widely distinct colour forms of pelage occur in West Africa, together with a third intermediate form, all described in detail later.

The tail is of characteristic appearance. It is very broad basally being there clad with very long hair which obscures its junction with the similarly long-furred body. From this stout root it tapers to about its mid-length whence it continues to almost the end as narrowly subcylindrical and terminates in an intensely black, long-bristled tuft. The short legs and the feet are fairly powerful, the latter all with five long digits, webbed in their basal half and armed with long, slightly curved claws. The soles of both fore and hindfeet are naked. There are anal scent glands, opening not within the rectum but into an external oval sac which surrounds and encloses their orifices and that of the anus itself. These have been described and figured by Chatin (1874).

FIG. [illegible] *Herpestes ichneumon*: skull, B.M. No. 9.11.2.10, sex ?, 1

Skull (fig. 36). The skull is long and rather narrow, terminating anteriorly in a very short, blunt but narrow rostrum. The ovoid braincase carries, with few exceptions, a well-developed sagittal crest in males and females alike, posteriorly joining the broad, flange-like supraoccipital crest in a T. The frontal region is fairly broad and, for the most part, inflated to a slightly higher level than the cranium, quite smooth and falling away in an even curve to the rostrum, and also laterally to the orbits. The ratio of the interorbital breadth to the postorbital constriction is pretty widely variable being sometimes 10 per cent less, sometimes 10 per cent more. The postorbital processes nearly always meet and fuse with the jugal processes to form complete circumorbital rings. The nasal sutures also fuse and disappear fairly early. The zygomata are strong and broadened through most of their length. The postdental palate is clearly longer than it is wide; the anterior part of the bulla small, the posterior chamber very inflated, high.

The incisors, top and bottom, are in a compact straight row, the outer ones larger than the inner. The upper canines are slightly curved, the lower ones rather more so. There are always 4 upper premolars on each side; and there are mostly 4 in the lower jaw; but of 11 skulls examined 3 mandibles have only 3 premolars on each side, and one has 4 and 3. The anterior premolar is always very much smaller than the rest, a simple peg. The posterior outer corner of the upper carnassial lies near the outer posterior root of the maxillary process. m^1 is of moderate size, short but wide, its bulk about that of the buccal section of p^4, its outer face forming a sharp angle with that of this latter tooth. The outer and anterior cusps of the lower carnassial (m_1) are markedly larger than the inner posterior one. m^2 is small, its transverse width about that of the lingual portion of m^1, its bulk clearly less.

Habits. In spite of the fact that the alleged habits of this animal have been written of, spoken of, and handed down almost as folklore for many hundreds of years the truth is that very little that is up-to-date and reliably factual has ever been recorded. The ichneumon has a long-established and almost unassailable reputation as the prime enemy of both crocodiles and poisonous snakes, having, besides courage, such dedication to the destruction of the latter that it was reputed in ancient times habitually and deliberately to prepare itself for the fray by covering itself in successive layers of mud, drying out each in turn, until it was enclosed in a thick fang-proof armour of hardened clay. With this protection it was able to seize its opponent in its jaws; when, instead of biting it to death, it flung it into the Nile to drown. As for its other foe, not only did it, according to the ancients, destroy crocodile eggs but it also regularly and courageously leapt down the open throats of these animals, which commonly sleep with their mouths agape, and ate its way through the internal organs, making an exit through a hole gnawed in the belly wall. The crocodile was presumably supposed to remain placidly on dry land until this intestinal tunnelling had been brought to a conclusion and a safe emergence achieved. Even modern accounts of this mongoose are invested with some air of fantasy, as when Brehm (1880) describes a family on the hunt, the male in the lead, closely followed by his mate, and she again by the young ones all in line close behind one another "as though the whole chain of animals were only a single being, somewhat resembling a remarkable long snake".

One may suppose that such ancient and persistent stories, together with the Greek name "tracker", must have some foundation in fact however slender. Also that there should be some significant basis to religious veneration, although this last would seem to be discounted by the sacred ibis, which has little to it beyond its rather striking coloration yet was embalmed in countless numbers. The crocodile story may well be a simple enhancement of egg destruction as an important factor in the control of these greatly feared reptiles. Nevertheless, it has been suggested that even this last reputed practice may be pure invention since nest-robbing would be difficult if not impossible with the female crocodile constantly on the watch in nearby undergrowth. But that Nile monitors (*Varanus niloticus*) acting in consort can rapidly create havoc in a cache of crocodile's eggs is well-established, and the marsh mongoose has been said to be a great destroyer of these too (page 297); so there seems no good reason why *Herpestes* should not behave similarly. However, no record has been traced of such depredation having been reliably observed.

In regard to snake-killing one must distinguish between habit and ability. While ichneumons may kill and consume snakes met with in the ordinary course of foraging, it is very unlikely that plain inborn enmity would lead them purposefully and regularly to seek out these reptiles. The ancient Egyptians knew, and doubtless honoured, the ichneumon's capacity to attack and overcome so dangerous and feared an opponent as the asp or cobra; and possibly the spectacle of such combats was from time to time staged in or around temples, where these mongooses were habitally kept as sacred animals. Yet there seems to be no record of anyone ever having witnessed a fight between ichneumon and snake in the wild; or, for that matter, any recent account of a staged one. Hinton & Dunn (1967) in writing a general work on mongooses and all that was known of them obviously combed the literature pretty closely; but they make no reference to any fight, even a put-up one, between a snake and an Egyptian mongoose. Even such verbal accounts from travellers as may from time to time come one's way may be open to some question since there has in the past been a good deal of traffic between India and Egypt; those who claim to have seen such set fights are rarely competent to tell one kind of mongoose from another, and the Indian mongooses are not unlike the ichneumon in appearance. Flower (1932), indeed, recorded that itinerant conjurers were often to be seen in Egypt with the small Indian mongooses as part of their stock in trade.

It is, in fact, Flower who gives the most positive, though very brief, account of the habits of *Herpestes*, at least in so far as Egypt is concerned. He says that it is diurnal and crepuscular, never to be seen in the early morning but on the move equally in brilliant noon-day sun and in the dusk of evening. It must be noted that other observers state it to be positively nocturnal or possibly nocturnal as well as diurnal; and T. S. Jones (personal communication) says that in Sierra Leone it appears to be largely nocturnal. Flower characterises it as hunting around in leisurely fashion; and it seems to be little disturbed by the presence of people or vehicular traffic since it has been known to cross Cairo streets, force motor-cars to slow down, and to have been run over by a tram. It is as though the ages have passed it by and it still expects the protection and respect that were its heritage in ancient Egypt.

Herpestes is, indeed, very unsuspicious and easily trapped. It takes readily to water and swims well, being sometimes caught by accident in fish-traps when it is attempting to rob them (Pitman, 1954). It is, in fact, commonly, but not exclusively, riparian, dwelling and hunting amongst reeds and other dense undergrowth; at the same time it is by no means averse to woodlands, open country at a distance from water, and even to montane grassland (Ansell, 1965). When living on river banks it is said to feed on fish and possibly crabs and frogs; but away from such a locality it takes small mammals, birds, insects and reptiles. It has a doubtful reputation as a fowl thief. T. S. Jones states that in Sierra Leone it will certainly attack chickens when it gets any chance; and it has been said to play havoc in a fowl house and to be detested for this reason throughout modern Egypt. Flower (1932), on the other hand definitely states that the peasants assured him that the ichneumon never steals chickens—though a fairly well authenticated record of the destruction of seven geese was once sent to him by a medical officer. Flower's assertion is the more interesting in running directly counter to views expressed by Zeuner (1963) that *Herpestes* had declined from the position of a sacred and much respected animal in ancient Egypt to that of a widely hated pest in later times due to the introduction of the domestic fowl from India and its eventual spread amongst all classes, with consequent bitter resentment of depredations amongst both birds and eggs which had come to occupy a highly important place in the Egyptian domestic economy.

Little, then, that is reliable or not controversial has been recorded of the daily and yearly life of the Egyptian mongoose, and it is to be regretted that no systematic field study of it has so far been undertaken, as it has for some of the larger carnivores. The fact is that, while such predators as lions, cheetahs, hyaenas, jackals or hunting-dogs are fairly readily observable and capable of being followed, the ichneumon, though widespread over the continent and not uncommon, besides being of less immediate economic moment presents considerably more difficulty. It spends much of its time in rather concealed conditions of dense ground vegetation and can, as a rule, be caught sight of only for brief moments as it hurries from one cover to another. Hoogstraal (1964), however, states that sometimes these mongooses sit, play or move slowly in easy sight of humans. The gait is normally a quick, purposeful trot.

For the rest, it is known that *Herpestes* shelters, and doubtless breeds, in burrows, which may be of its own making or taken over from some other excavator; but gaps in rocks, holes under tree roots and similar convenient cavities are also made use of. So far as limited observations indicate there seems to be no fixed breeding season; there are no West African juveniles in the British Museum from which deductions might be drawn, but one Sierra Leone specimen taken on 2nd November contained two foetuses. Beyond this, definite figures for the number of young in a litter are almost non-existent; but though these animals probably lead much of their lives in solitary fashion they have been said when raising young to go about in family parties of about half-a-dozen. Like other viverrids, the ichneumon can emit an offensive odour when alarmed or otherwise excited; and like so many other mongooses, when caught young, it takes readily and kindly to domestication and makes an admirable pet. In view of the fact that it has been known in this capacity for five thousand years it is remarkable that more has not been recorded of its behaviour, its nature, likes, dislikes, eating and sleeping habits, postures, breeding, period of gestation, litter size, parental care, voice and so forth. However, there is one detailed account (Dücker, 1960) of mating-play, copulation and parturition as exhibited by a young pair, of a single litter born in captivity. Play of sexual significance started between these two when they were only about 15 months old; but real sexual readiness, evinced by a swelling and redness of the vulva, did not come about for another 6 months. Considerable wooing play took place thenceforward together with repeatedly unsuccessful attempts at coition. The male frequently uttered an *oo-oo-oo* sound, which was answered by the female. At moments of great agitation this cry became something like *he-he-he-he*, rising in speed and intensity to a pitch of excitement. When copulation was actually achieved the act took some 4 to 5 minutes, during which the male repeatedly nudged the female in the region of the throat with wide open muzzle. Two young were eventually born at a half-hour interval; but owing to the long-drawn-out nature of the mating period it was not possible to tell the actual period of gestation. From the dates indicated it might lie anywhere between, say, 7 and 11 weeks.

After the birth the parents were both very excited, running and climbing about the cage; but it was some time before they took any notice of the cries of their young. At length, after about a couple of hours, the mother carried the babies, separately and held by the middle of the body, into the sleeping box, where they simply lay on the floor while the parents sat snuggled up closely against one another taking no interest in their offspring. The only occasion on which they seemed to be aware of a parental duty was when the cage was approached and they growled and erected their fur. Next morning there was no sign of the babies, which must have been eaten by their parents—a common event in nature, and more so under the unnatural stresses of captivity. Ten days after parturition the female was again in season and the pair strongly sexually interested in one another. This would seem to confirm that breeding is not merely an annual event related to a particular time of the year. Also, it might be inferred that two is a common litter size—there is the London record of two foetuses, these two parents were themselves twins, and they had two offspring. No further records were possible with this pair since the female suddenly died. It may here be noted that a specimen has been known to have lived in captivity to the age of about 12¾ years (*Int. Zoo Yr. Bk.*, **2**).

Taxonomy. The broadest question is whether there is, in fact, more than one species in the genus; that is whether the separation of the southern African animals at this level, as *caffer*, from the northern ones, once the practice, is valid. It seems fairly unanimously held today that the species *ichneumon* satisfactorily and correctly covers all mongooses of this genus from Spain to the Cape; and this view is held in this present work.

With so wide a distribution it is obvious that local races must almost certainly exist; but the problem here is not so easy of solution. With a pelage of the composition of *Herpestes*, consisting of a top coat of long annulated bristle-hairs in which black and white play a dominant role there is, as in other similar genera, particular scope for an almost infinite variety of effect due to slight differences of ring width or nuances in the tone of the two main colours or the transitional zones between them. Some of these may be simply idiosyncratic; others may, in truth, be peculiar to all the inhabitants of a locality or set of conditions, though the plain fact is, as so commonly the case, that existing study material is often too meagre to establish on a firm basis whether such divergencies are sufficiently constant over a given area to justify nomenclatural recognition.

Ten or eleven races of *ichneumon* are, in fact, currently recognised, only one of them, *occidentalis* Monard from Portuguese Guinea, definitely West African, though it has been suggested that *parvidens* Lönnberg from the lower Congo possibly reaches Lake Chad. One incontrovertible fact exists, however: there are in West Africa two very distinct colour extremes, the one pale grey, the other dark red-brown. The former is not very dissimilar from specimens from the type area, Egypt—which, not unusually, differ somewhat amongst themselves. But in the West African examples the hairs of the dorsal pelage have rather wider and whiter rings; the underfur is orange, whereas in Eygptian material it may sometimes be redder, sometimes drabber; and the belly is better clothed, with longer, paler ("off-white") hairs. Monard's description of *occidentalis*, though in respect of individual components detailed, fails to convey the overall appearance of the coat. His type has not been seen; but by the courtesy of Dr. Villy Aellen and Dr. J. L. Perret of Geneva it has been possible to make a direct comparison of a small but adequate sample of the type pelage. From this and Monard's characterisation of the underfur as orange it seems sufficiently clear that the three pale West African *Herpestes* in the British Museum are indeed *occidentalis.* These are all from the Guinea or Doka woodland.

The five dark form specimens, of very marked contrast to those just dealt with, are, with one possible exception gone into later, animals of the closed forest zone between western Nigeria and Sierra Leone. There is nothing in the large London collection like these dark reddish-brown skins except an aberrant one from Spain, and they would thus certainly seem to merit a descriptive name of their own. It might be deduced from this that *Herpestes ichneumon* is pale grey in arid country becoming deeper and redder as the atmospheric humidity increases; but there is an intermediate form which comes not from an intermediate ecological zone but, so far as can be told from the very limited material available of each of these forms, from somewhat further inland than the pale form, that is the drier Doka and Sudan zones. These skins partake rather more of the reddish forest colour than they do of the grey; but the pale rings are broader and whiter. Since they do not fit into either category they, too, though less obviously, seem to justify a distinctive name.

The subspeciation described below hinges entirely upon coat colour; there are two other specimens of West African *ichneumon* in the British Museum, one from Gambia (no locality) the other from Oda (Ghana), which since they consist of skulls only cannot be particularised. No satisfactory evidence for the existence of Lönnberg's *parvidens* in West Africa has been found in this present investigation.

Herpestes ichneumon occidentalis Monard — Western Ichneumon

Distribution. Monard had two specimens before him when he named this race, an adult female from Mansoa and a male from Cacheu, both in Portuguese Guinea and both, according to the author, in dense tropical forest. The following are the particulars and description of the three London specimens believed to represent this race. They come from Thiès (Senegal), Cape St. Mary (Gambia), and Kita Sudan (Upper Guinea)—which seems most likely to be Kita in the former French Sudan, now Mali. The first two places are situated in Guinea woodland, the last in Doka.

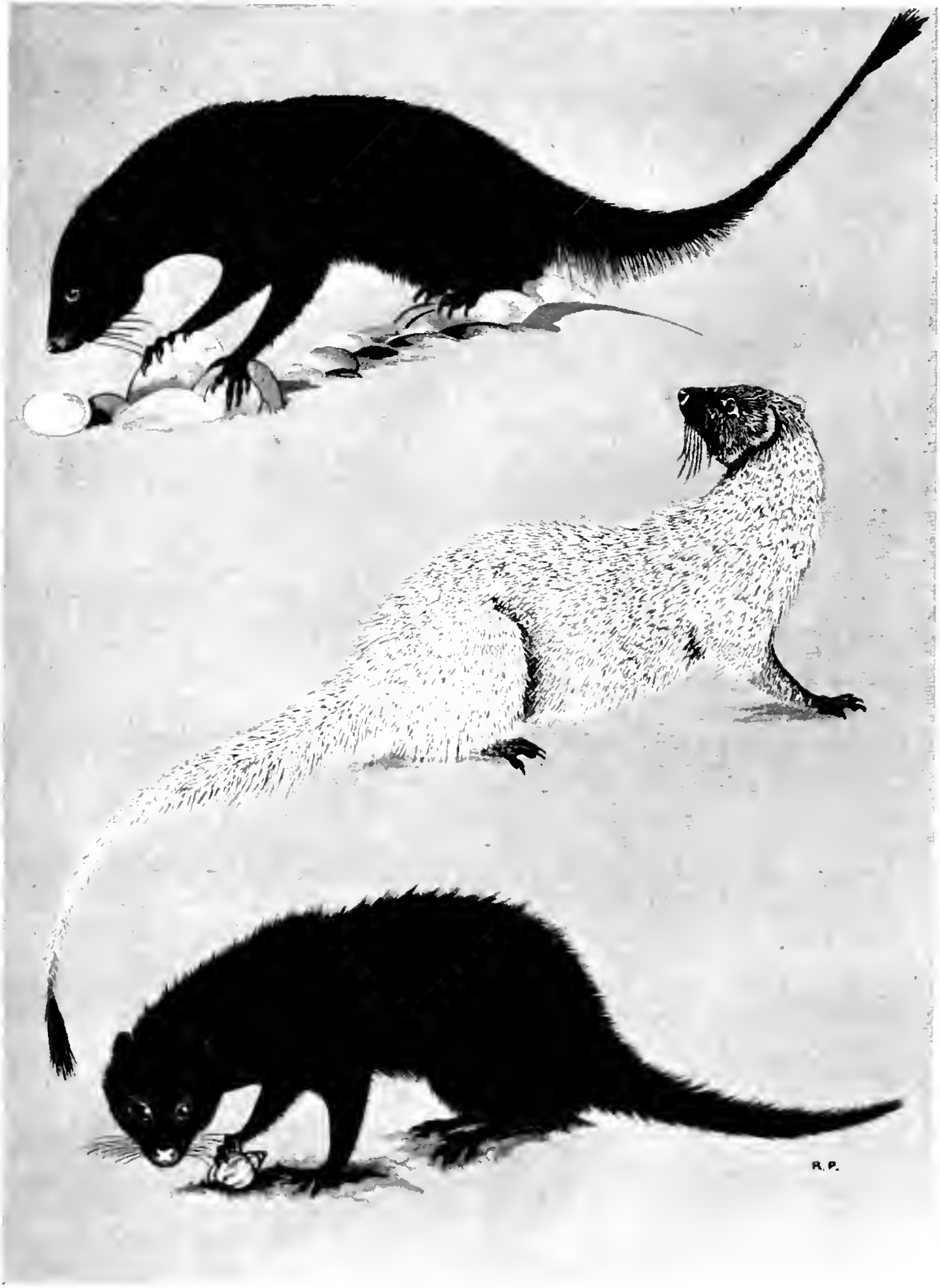
Description. The overall impression of the dorsal pelage of these is pale grey flecked with chocolate (Plate 7). The fairly dense, fine, not very long underfur, on the average about 15 mm though individual hairs may be longer, is, as Monard described, a beautiful orange colour. This is almost completely concealed, in repose, by the very long (at the lower back 60 to 65 mm) bristle-hairs. These are ringed black and white, the basal and two other zones white, separated by two major dark zones and ending with a rather short black tip; that is to say 6 alternating rings. The "black" is seen on close examination to be really a very intense red-brown; and there are some rings in which this true nature of the pigment is more apparent than in others; and there is always a brief transitional zone to the white where it becomes progressively less dense and hence pale red. The coat, therefore, always displays a fair amount of reddish colour, mostly deep, which, as the corresponding zones of the hairs come to lie somewhat together, tend to form short, very irregular, transverse lines or chevrons.

On the belly the underfur becomes very pale buff, and the still very long bristles cream, with one, or sometimes two, rather pale, inconspicuous dark rings. The hairs of the head and face have the same sort of colouring as the back but are quite short, with correspondingly short annulation. The same can be said of the legs, where, however, the dark element is more prominent; so that, while the dorsal pelage may be said to be grey speckled with dark, the legs are dark stippled with white. The tail is similar to the back in the broad basal half, beyond which it becomes much more yellowish-brown up to the long pure black terminal tuft.

Skull (fig. 36). It is not possible to draw useful conclusions from the single skull available for study. There are in this only two marked differences from the remaining West African material, and these may well prove merely idiosyncratic: the zygomatic breadth is appreciably greater than in the others, amounting to 55 per cent of the condylobasal length as compared with rather less than 50 per cent; and the breadth of m^2 is less than in any other specimen.

Herpestes ichneumon aithos *subsp. nov.* Forest Ichneumon

Distribution and general. The contrast between this and the last is very marked (Plate 7). Five specimens exist in the British Museum; these come from Newton (Sierra Leone); Wulade, Kissi country (northern Liberia), 2 specimens; Idumiye Ono, 4 miles north of Iseluku, west of Asaba on the River Niger, Benin Province, Nigeria (these are spelt Idumuje Uno and Issale Uku on modern maps); and Senegal, no specified locality. The first four of these lie within the closed high-forest belt, though Newton has become degraded by fire and cultivation into grass with patches of secondary bush near water. The last would seem to be possibly an exception, though, in the absence of



Forest Ichneumon *Her* [illegible] *ardi* Western Ichneumon *H* [illegible]
Marsh Mongoose *Atilax paludinosus*

an exact locality and the fact that in 1863, when the specimen was registered, the limits implied by "Senegal" were not precise, one cannot be at all sure of the vegetation. There is another ground for not blindly accepting at its face value this accrediting of an apparently high forest mongoose to predominantly dry open woodland country in the vicinage of the Senegal River. The collector was the late 19th century controversial author Winwood Reade. It is a fact that on this visit to the then very little known and not very well comprehended western side of Africa he went to Gaboon, Angola, Casamance, Gambia and Senegal, in that order. He might easily have said, speaking generally, when visiting the British Museum that he had just returned from Senegal and had brought some specimens for identification, thus conveying a wrong impression; whereas the specimens may quite well have been obtained at various points of his tour; this one, for example, in the forests of Gaboon, whither he had gone deliberately to follow the footsteps of the then famous collector Du Chaillu.

The Newton (Sierra Leone) specimen, collector T. S. Jones, B.M. No. 53.130, a mediumly-aged ♀, gravid with 2 foetuses, is nominated as type of this new race because, although the skull is badly broken, the skin is complete; whereas the only perfect skull in the material available has the skin incomplete.

Description. The overall impression of the dorsal pelage is a deep reddish-brown abundantly ticked with yellow. The underfur is of an appreciably deeper rufous shade than the orange of *occidentalis*; it is about 15 to 18 mm long, and though in a large measure hidden by the bristle-hairs it does to some extent show through and help to account for the reddish impression of the pelage. The bristle-hairs are not much more than 50 mm long, and their annulation is quite distinct from that of *occidentalis*; for whereas in this latter race there are, including the black tip, about 6 alternating rings in which the light and dark are not very different in length, in this newly proposed form there are about 9 or 10 rings, the dark ones very much predominant, the pale ones being mostly reduced to widths of 3 or 4 mm. The dark annulations are to all intents and purposes black; but the two narrow distal pale ones, the only ones which show beyond the underfur and constitute the ticking element in the pelage, are yellow or off-white. Because of the vastly different widths of the annulation in the two races the actual physical appearance of the pale ticking irrespective of questions of colour, is very distinct in *occidentalis* and *aithos*, being in the former long and longitudinally almost continuous, but in the latter very short, very much interrupted and numerically very abundant. There is a fuller note on annulation at the end of this generic section.

The belly fur, though in all rather paler, is very similar to that of the back, being annulated yellow and blackish-brown. It is paler because the pale rings are far wider than they are dorsally. The neck and top of the head are fairly similar to the back but ticked more finely; but whereas in *occidentalis* the ticking continues forward almost to the rhinarium, in this new race it stops short about the level of the eyes, the upper part of the nose being clad with plain, dark blackish-brown bristle-hairs. The ticking on the chin, throat and underside of the neck is whiter than that of the back. The upper parts of the legs are ticked like the back but the feet are deep red-brown. The tail resembles the back throughout nearly all its length but is for a short distance before the black tuft very slightly redder.

Skull. The measurements given in the table on page 279 show that the zygomatic breadth is less than in *occidentalis*, amounting to 49 per cent of the condylobasal length. The interorbital breadth is less than the postorbital constriction. In the type skull there are only 3 premolars on each side of the lower jaw; in one other skull there are 4 on one side, 3 on the other; the third skull has the normal 4 on each side.

Paratypes. Other specimens examined are No. 7.12.17.1 (skull broken), and No. 7.12.17.2, both Liberia; No. 63.5.9.7 (no skull), Senegal; and No. 13.11.6.1 (skull perfect), western Nigeria. Although in these the shade of yellow in the ticking, and the width of the pale annulations do not absolutely correspond with those given above for the type, the differences are too slight to be of any account.

Herpestes ichneumon mesos *subsp. nov.* Nigerian Ichneumon

Distribution and general. Three specimens in the British Museum collection are assignable to this: from Anara Forest Reserve, near Kaduna, northern Nigeria; from Kode area, 24 kilometres north-east of Lau (on the Benue), northern Nigeria; and from the Northern Territories, Ghana. The first of these places lies in the Doka zone, the second in the Sudan zone; the third specimen, having no clue to the precise locality, might have come from any of the Guinea, Doka or Sudan zones.

The Anara specimen, collector D. R. Rosevear, B.M. No. 50.320, a medium-aged to old ♂, is taken as the type of this new race. The skin is poorly stuffed, the hindfeet and part of the tail missing; the skull in itself is complete but has several teeth missing.

Description. There is no doubt of the intermediate nature of this proposed new race; in overall appearance it is appreciably redder than *occidentalis* but a markedly lighter-coloured animal than *aithos*. Like other features, the underfur in this proposed race is intermediate between the bright orange of *occidentalis* and the rich red of *aithos*. It is about 13 mm long. As in *occidentalis*, the bristle-hairs have about 6 annulations. Their overall length is somewhat shorter, about 50 to 60 mm: the pale rings, besides being shorter, are buff and the dark ones are a less intense red-brown. A comparison of this annulation with that of the other races is made below at the end of the account of this genus.

The underfur on the belly has lost most of the red of the upper side, becoming pale brown; the long bristles are buff and their dark rings relatively pale. The colouring of the head and face is very much that of the back but the hairs and their annulations very short; the speckling continues forward dorsally very nearly to the rhinarium, there being only a few millimetres of unspeckled hairs in this region, markedly less than in *aithos*. The forelegs are speckled, of a slightly darker tone than the back, the feet being a deep brown; the upper part of the hindlegs in the type is pale buffy-brown with very little obvious annulation; the proximal part of the feet is darkish with short speckled hairs similar to the head; their end part is missing from the type, but in another specimen is plain dark brown. The very long-haired tail is similar in appearance to the back; its terminal portion is lacking from the type and one other specimen (No. 56.250); but in the third specimen (No. 22.12.2.1) it becomes very rufous in the narrow part; and the terminal tuft is not the intense black of the other races but a little reddish throughout and more particularly so distally.

The two paratypes exhibit minor, but not significant, differences from the type as described above.

Skull. This has no very distinctive features discernible in the two sets of measurements available. It is of average width, the zygomatic breadth amounts to precisely 50 per cent of the condylobasal length. The braincase is a little narrower than in the other two races; the interorbital breadth is in one case (the type) larger, in the other

Table 14: Hair annulation in *Herpestes ichneumon* subspecies

	Basal region			Middle region				Terminal region			
	Dark	Pale	Dark	Pale	Dark	Pale	Dark	Pale	Red	Black	
occidentalis (7)	–	–	–	17	11	7	13	7	–	5	= 60 mm
mesos (12)	–	–	–	13	10	5	14	5	–	10	= 57 mm
aithos (5)	2	3	6	5	10	3	14	3	2	5	= 53 mm

Table 15: Numerical data for *Herpestes ichneumon*

	occidentalis	*mesos*, Type	*mesos*, means	*aithos*, Type	*aithos*, means
Vegetation	Guinea and Doka	Doka	Doka and Sudan	Forest	Forest
Number in mean	1	1	2	1	3
Condylobasal length	99·4	96·4	98·4	100·4	101·3
Basilar length	92·6	88·7	95·4	—	94·1
Palatilar length	56·0	52·5	54·2	—	55·2
Zygomatic breadth	54·8	48·1	49·2	50·6	49·8
Upper cheekteeth breadth	32·6	29·2	29·7	31·1	31·4
Nasals, length	—	—	24·2	—	23·5
Interorbital constriction	18·4	17·0	17·4	(18·2)	18·1
Postorbital breadth	17·9	16·1	17·3	20·5	20·0
Braincase breadth	36·1	32·8	32·9	35·0	35·3
Toothrow (c—m^2)	36·3	34·6	35·4	35·2	36·7
p^4 length	9·7	9·5	9·5	9·5	9·5
m^1 breadth	9·3	8·6	8·6	8·8	9·1
m^2 breadth	4·4	—	5·3	4·7	5·3
m_1 length	8·7	8·4	8·5	8·1	8·6
m_2 length	5·0	4·3	4·2	4·6	4·7
Head & body	—	600	600	545	545
Tail	—	300	300	492	492
Hindfoot	—	—	—	95	95
Ear	—	26	26	36	36
RATIOS (per cent)					
Tail/head & body	—	50	50	90	90
Zygom. br./condylob. l.	55	50	50	49	49
Braincase/condylob. l.	36	33	33	34	35
Braincase/zygom. br.	66	68	67	69	71
Palatilar l./condylob. l.	56	55	55	—	55
Interorb./postorb.	103	105	100	89	90
p^4/c—m^2	26·7	37·4	26·9	27·0	25·9

less than the postorbital constriction. The type specimen has 4, the other skull 3, premolars on each side of the lower jaw. The breadth of m^1 and the length of m_2 both seem to be less than in the other subspecies.

General comments. It must be repeated that no direct comparison of the specimen (No. 9.11.2.10) here assumed to be Monard's *occidentalis* with his type has been possible: if it should be shown to differ materially it would require a new subspecific name.

The table given on p. 279 shows a comparison of the lengths of the various annulations of the bristle-hairs in the three races, as illustrated by the mean values derived from a number of different hairs from each of a number of different specimens. The ring-margins are never clear-cut, the dark zone fading throughout a longer or shorter distance (mostly of the order of 0·5 to 1 mm) into the light zone, this transitional region exhibiting a pale red-brown colour. Precise measurement is therefore never possible; but, with this proviso and the fact that there are always occasional exceptions, the ring-widths are pretty constant in all the specimens examined and for the most part do not vary from the mean lengths shown below by more than 2 mm, usually less.

Three groups of zones may be recognised. There is a terminal region measuring 10 to 15 mm consisting usually of two zones, the finely tapering black tip and a proximal pale ring; but in *aithos* the transitional area between these two is of sufficient width and importance to merit separate recognition. Proximal to this terminal region is a second group of 4 annulations of the utmost importance in determining the appearance of the coat; for whereas it will be seen, in the table, that the width of the dark rings remains almost constant throughout all three races that of the pale rings diminishes very greatly, until in *aithos* it is a half, or even a third, of what it measures in *occidentalis*. It will be appreciated that, ignoring colour, this results in a marked difference of appearance. In addition to the two sets of rings just detailed, *aithos* has a further, long basal region of 3 (and in one hair specimen 4) alternating dark and pale bands. The length of this extra region is more than compensated for by the extreme shortening of the pale zones of the adjacent region, to which attention has just been directed, so that the overall length of the hair is, in fact, less than those with only 6 alternating light and dark bands.

Genus **CROSSARCHUS** F. Cuvier, 1825

Lesser Long-nosed Mongooses

Mungos E. Geoffroy & G. Cuvier, 1795, *Magasin Encyclopédique*, **2**: 184, 187. Type species *Viverra mungo* Gmelin; in part.

Crossarchus F. Cuvier, 1825, in F. Geoffroy & F. Cuvier, *Histoire Naturelle des Mammifères* . . ., **3**, pt. 47, Le Mangue: 3. Type species *Crossarchus obscurus* F. Cuvier, West Africa. This name was coined from the Greek words *crossotos* fringed, and *archos* anus, with reference to the appearance of the circumanal glandular sac, the wrinkled folds of which bear a fancied resemblance to the old-fashioned pleated collar known as a ruff.

Distribution. The genus *Crossarchus*, as at present constituted, embraces three species inhabiting mainly the closed forest block but sometimes reaching into the adjacent woodland zones by means of forest remnants or riverain extensions. Only one of these species, *obscurus*, is found in West Africa, where it is known from Sierra Leone to lower Cameroun at about 3°N. The other two species are *alexandri* from the Central African Republic and northern Congo; and *ansorgei* from north-western Angola. Where these mongooses occur they may be reckoned as moderately common animals since they mostly associate together in fairly large companies.

General description. The range of size of the three species is wide, from the small *ansorgei* with a head & body length of 320 mm and a skull of 58 mm to the relatively large *alexandri* which measures 450 mm and 81 mm; but even this latter is, of course, small in comparison with the really large mongooses such as *Herpestes*, *Xenogale* and *Galeriscus*. In between the two extremes of size in *Crossarchus* stands the very common West African *obscurus*. All forms are, most typically, darkish-brown animals ticked to a greater or less extent with golden-yellow, pale yellow, or even white; but *ansorgei* and an occasional *obscurus* specimen exhibit considerably less ticking than normal. The rather harsh pelage is composed of long underfur and considerably longer bristle-hairs; and there is, almost without exception, a whorl or whorls on the back of the neck. The snout is exceptionally long. The tail is shorter than head & body and tapers evenly from root to tip; and though it is clad with long bristle-hairs it is not, when in repose, in any way bushy. The legs are short; the 5-toed feet armed with very long claws and webbed between the proximal joints. The soles of the hindfeet are mostly naked except for the last quarter near the heel. The rectum is flanked by a pair of scent glands, their external orifices either side of the anus, all being surrounded by a thick-walled circumanal sac. While both *obscurus* and *alexandri* conform well to this general description, *ansorgei* is in several respects somewhat exceptional.

Skull. This is long and narrow especially as regards the rostrum, though this last is less marked in *ansorgei* than in the others. *Crossarchus* belongs to the category of mongooses in which the upper carnassial is set well forward of the root of the maxillary process, the cheekteeth being sharply cuspidate but not particularly sectorial. There are three premolars on each side, above and below. These are the essential generic points; the remainder of the skull characters may be gathered from the description of those of *obscurus* below.

Taxonomy. The type species *obscurus* was from the start assigned to *Crossarchus*, which F. Cuvier simultaneously especially erected to accommodate it; but though this genus has to a large extent managed to maintain its independence there has been some tendency to identify it with *Mungos*. Thomas, in his 1882 review of the mongooses considered *obscurus* to be congeneric with *fasciatus*, *zebra* and *gambianus*. These are now regarded as belonging to *Mungos* Geoffroy & Cuvier; nevertheless he ascribed them all to *Crossarchus* supposing this name to antedate *Mungos*, which he wrongly attributed to Gray, 1865. The complex muddle over the names *Mungos* and *Herpestes* has been referred to earlier in this work; it has been very fully dealt with and clarified by J. A. Allen (1924) and need not be gone into here. But since it has sometimes recently become the practice to treat the *Crossarchus* species as very closely allied to the banded mongoose, *Mungos mungo*, and to deal with *Crossarchus* either as completely synonymous with *Mungos* Geoffroy & Cuvier (Hill & Carter, 1941) or as merely a subgenus of it (Ellerman, Morrison-Scott & Hayman, 1953) it may be profitable to quote here Allen's opinion, which at the same time succinctly incorporates the views of others on this matter: "The restoration of *Mungos* to its proper place in nomenclature need not in the least disturb the stability of *Crossarchus* F. Cuvier (1825), which has, by monotypy, *Crossarchus obscurus* F. Cuvier as its genotype, for which and later described allied forms it should be retained. As thus restricted *Crossarchus* forms a group very different from the banded mongooses for which *Mungos* is available and to which it should be restricted. Gray showed good judgment in separating the two groups generically. Attention has recently been called to the generic distinctness of these groups by Pocock, he adopting for the banded mongooses Gray's unavailable name *Ariela*. He also calls attention to the fact that the inclusion of the two groups under *Crossarchus* was due to erroneous information concerning the structure of the anal glands. Before meeting with Pocock's paper I had become strongly impressed with their incongruity and their evident generic distinctness".

The two genera, especially as exemplified by *C. obscurus* and *M. gambianus*, share something of a common size and appearance; and it is difficult, as a glance at the keys given herein on pp. 245 and 247 will show, to separate them, either externally or cranially, on commonly accepted morphological characters. But this is not the whole story; and, like Allen and Pocock, the present author has little hesitation in regarding them sufficiently different animals as to justify separate generic assignment. They are therefore so dealt with in this work.

As far as internal division of *Crossarchus* is concerned, only the three species mentioned in the opening paragraph have so far been described. *C. alexandri* closely resembles *obscurus*, differing from it chiefly by its markedly greater size, and it is possible that the two may be conspecific. However, the present author regards the size distinction as more than racial and the two are accepted herein as specifically distinct. *C. ansorgei*, on the other hand, besides being considerably smaller, is aberrant in several respects, notably the shortness of the rostrum; and it seems at least possible that it is, in fact, not a true *Crossarchus*.

CROSSARCHUS OBSCURUS F. Cuvier — Kusimanse

Crossarchus obscurus F. Cuvier, 1825, in E. Geoffroy & F. Cuvier, *Histoire Naturelle des Mammifères . . .*, 3, pt. 47, Le Mangue: 3. Type species *Crossarchus obscurus* F. Cuvier, West Africa. The specific name is the Latin adjective meaning dark or dusky, given with reference to the pelage colour.

Distribution and general. The name kusimanse, pronounced in three syllables and sometimes spelt cusimanse, is of obscure origin. It is said to be a vernacular name but even its approximate source appears to be unrecorded; and it does not seem possible to trace its use back beyond Wood's Natural History published in 1861. It has also been used by German writers; but never by the French, who originally coined the term mangue, now confined to the genus *Mungos* and replaced, for the animal at present under discussion, by a simplified form of the scientific name, crossarche. The kusimanse has sometimes been referred to also as the Long-nosed mongoose; but if such an expression is used for *Crossarchus* it should be qualified as the lesser long-nosed mongoose since the very much larger *Xenogale naso* is similarly characterised by the unusual length of its snout.

The kusimanse is wholly a West African animal, ranging from Sierra Leone to lower Cameroun. The list of places from which it has been recorded is too lengthy to quote, and the fact is that it may be expected almost anywhere in the forest away from populous or much disturbed areas. It has been taken at an altitude of about 600 metres on the Cameroun Mountain and about 1000 metres on Mount Bintamane (Sierra Leone). It is found solely in the high forest, chiefly in the main block but occasionally in extensions of this vegetation into the contiguous grass-woodland zone; but it appears never to stray from these outliers into the grassland itself. Because it is diurnal it is rather more frequently encountered than most of the other mongooses; and when it is seen it is in some numbers since this species associates and hunts in companies. It is to be recognised in the field partly by this habit and partly by its small size, plump low-set body and dark faintly speckled coat, its noticeably long pink nose and its short tapering tail. It might from its size and superficial appearance be confused with the Gambian mongoose (*Mungos gambianus*); but this latter, apart from having a shorter muzzle, is a species of the Guinea grass-woodland and the two are therefore unlikely to be found in the same sort of place. Puchased skins, however, are another matter and recourse must be had to a close examination of the pelage.

Description. The kusimanse (Plate 6) is nearly the smallest of West African mongooses and has a head & body length of about 340 mm, a tail of about 170 mm and an adult body weight of from 1 to 1·5 kg. Before proceeding to the following detailed description it may be well to draw attention to the fact that some of the chief distinctions between *Crossarchus* and *Mungos* rest in the character, composition and annulation pattern of the pelage; and this applies to all known species of each genus, extralimital as much as West African. It is therefore as well to get a clear grasp of the points involved. As a matter of interest, it is not difficult to distinguish between the two genera by a single bristle-hair.

The fur of *Crossarchus* has mostly a rough, slightly bristly appearance, or very much so when erected, as it commonly is, in excitement. The most usual overall general impression is dark brown ticked to a very varying degree with yellowish. However, the basic colour ranges, less commonly, between something almost black, in specimens in which the ticking is reduced to a minimum, to a heavily speckled lighter brown in young animals, or even a very red-brown in juveniles. The pelage is composed of densely abundant, fairly long, slightly wavy, very fine underfur, and plentiful though much more widely scattered and very much lengthier bristle-hairs. The existence of dense underfur is, with a specimen in the hand, the most ready, and completely certain, distinction between *Crossarchus* and *Mungos*. It is some 17 to 19 mm long and carries alternating bands of dark and light colour, the basal one, occupying nearly half the length is dark, ranging in different specimens from chocolate to nearly black. Distally of this, and the visually most obvious zone when the fur is turned back is a grey, white or yellowish ring, 4 or 5 mm wide; and this is succeeded by a narrow black ring of about 3 mm and a golden tip of 2 mm, often obscure. The bristle-hairs are commonly

FIG. 37. *Crossarchus obscurus*: skull, B.M. No. 48.841, sex ?, × 2

some 37 or 38 mm long, though in specimens from some areas they may reach only 28 to 30 mm. They have a pale base followed by a long black zone, some 25 to 30 mm and thus occupying the greater part of the hair; distally of this is a narrow subterminal gold ring of 2 to 3 mm and a short black tip of about 2 mm. It is the lengths of these three terminal zones that, almost without exception, enable *Crossarchus* to be differentiated from *Mungos*, in which the median black is much shorter and the distal gold ring and slender black tip both appreciably longer. Juveniles are chiefly clad in dense underfur; bristle-hairs may be present but are relatively inconspicuous and do not, at first, exceed the underfur in length.

The underside is similar to the back but mostly somewhat more sparsely and shorter haired. One of the most characteristic features of the *Crossarchus* pelage is the presence of a pair of large whorls on the back of the neck a little posterior of the ears and crown; but though these are for the most part very conspicuous they are not always so and may, exceptionally, apparently be wholly lacking. The hair on the throat is directed forwards and there is therefore another whorl below, parting this from the chest. The low, rounded ears are situated very much on the side of the head, widely separated medially. The head and face are covered with very short, very finely speckled, medium-brown hair but there is a barish patch anterior to the eye. This latter organ is bright and keen. But the most noticeable feature of the head is the lengthy, fleshy nose with its pink rhinarium, a long way overshooting the lower jaw.

The tail is short, being as a rule not much more than half the length of head & body. It is markedly tapering from a fairly broad base, clothed with long bristles and underfur in a similar manner to the back, but not bushy except when the hairs are deliberately erected in anger. It often, at least in museum specimens, seems to be broken; when it is complete the extreme tip is dull reddish, there never being a black terminal zone as in *Mungos*. The legs and feet are dark-brown or blackish, the soles of the hindfeet partly hairy near the heels; the toes are webbed between their proximal joints; the claws, especially of the forefeet, are very long, differing from those of *Mungos* in being rather more slenderly built, that is to say laterally more compressed and basally not so deep. In stance and run the animal is very flat-footed and this makes the already short legs seem even shorter in contrast to other mongooses which are clearly digitigrade. There are two scent glands situated one on each side of the rectum; their orifices and the anus are surrounded by a sac remarkable for the parallel ridges of skin connecting its upper margin to the anus (Pocock, 1916c). It was the appearance of these that gave rise to the generic name as explained above in the synonymy.

Skull (fig. 37). All known West African skulls have a condylobasal length of well under 75 mm. This is a narrower skull than that of *Mungos*, the zygomatic breadth being almost always (11 out of 13) less than 53 per cent of the condylobasal length. The braincase is in every way much narrower and less voluminous than that of *Mungos*, much more so visually than the measurements in the tables on pages 265 and 290 would suggest (compare figs. 34 and 37). In 11 out of 17 specimens the mastoid breadth is under 41 per cent of the condylobasal length, the remaining 6 being slightly over; whereas all *Mungos* skulls measured are over 41 per cent, mostly, except in *gambianus*, appreciably so. Two features which influence the overall appearance of the skull are curiously variable: firstly, in 9 specimens the interorbital breadth is greater than the postorbital constriction, and in 8 it is less, the range being from 85 to 159 per cent. Secondly, a sagittal crest is absent from 9 skulls, rudimentary or very poorly developed in 7, and prominent in 4. This, providing the sexing has been correctly done in the field, appears to have little to do with age or sex: only adult skulls are included, the best developed is in an oldish female, and one old male is devoid of any sign. A well developed supraoccipital crest is present in all adult skulls. The postorbital processes, although quite well developed, are, in comparison with those of other mongooses, nearly always relatively short and for the most part pretty widely separated from the short jugal processes. The zygoma is, for this family, a rather weak structure. The anterior portion of the bulla is always smaller than the posterior chamber; but its degree of development and the amount of inflation of the latter are both variable, so that their size relationship is pretty inconstant. However, the anterior chamber is rarely so deeply transversely depressed as it is in *Mungos*. The postdental palate where it becomes parallel-sided is, for the most part, about as long as it is broad, but may in a few cases be either slightly longer or slightly shorter.

Crossarchus belongs to that section of mongooses in which the posterior outer corner of the upper carnassial together with the whole of m^1 are situated anterior to the posterior root of the maxillary process. The upper incisors are compact; the four inner ones form an almost straight transverse row but the two outer, rather larger ones are set back and are more lateral than frontal in their positioning. The canines of both jaws are, for carnivora, relatively short. The premolars are, without exception in 20 skulls, $\frac{3}{3}$. All the cheekteeth are sharply and fairly evenly cusped, including the inner heels of p^3 to m^2. That on p^3 is nearly always conspicuous and sharp; and although a similar cusp often exists in *Mungos* it is usually not quite so clearly developed. m^2 is a well-developed tooth, appreciably bigger than the lingual portion of m^1. In the lower jaw the forward half of m^1 carries three cusps, one buccal, slightly the largest, and two lingual, not quite so closely juxtaposed as in *Mungos*; m_2 is also abundantly and sharply cusped. To judge from British Museum material both these molars retain their cuspidation to an advanced age. The dentition as a whole has little sectorial capacity but is well adapted to an insect diet.

Habits. *Crossarchus* is one of those animals the behaviour of which has been moderately well observed in the status of a pet but of whose life in nature little has been recorded. Accounts of the species have been published by Haig (1931, under the pseudonym "Bushman"), Naundorff (1936) and Ewer (1968); these mostly concern captive specimens, the first two each relating to one specific animal kept about the house, the last regarding items of observed kusimanse behaviour in deeper perspective as elements of a general study of mammalian ethology. To these can be added a few disconnected notes made by various field naturalists.

Crossarchus inhabits the rain-forest, ranging at a jog-trot through the fairly dense herbaceous undergrowth. It has been said to prefer the banks of streams; but though it is known to occur in such conditions and to consume water-loving animals there is at present little factual evidence to indicate any particular preference for such sites. Opinion is almost unanimous that the kusimanse is in nature a purely diurnal mongoose. T. S. Jones (personal communication), for one, observed it to be so in the forest on Bintamane Mountain, Sierra Leone; and Haig (1931) found his tame specimen to sleep more or less peacefully from dusk to dawn. Yet Sanderson (1940) states positively that "at night the animals often visit cleared land and farms in search of food". Whether this contradictory observation was the outcome of night-trapping of a fair porportion of his 9 specimens is not clear. On the other hand, Durrell (1958), who worked in much the same area (upper Cameroun), writes of *Crossarchus* as not uncommonly seen by day. But this latter author also records watching a solitary animal fishing for crabs whereas the kusimanse is renowned for its custom of hunting in companies of a dozen or twenty or sometimes many more. This latter is without doubt the general habit of the species. It is presumed that these parties, comprising old and young specimens of both sexes, consist of one, two or three family units, probably, to judge from the breeding note given later, made up of parents and the surviving members of two or three litters still holding together. Whether these assemblages are fortuitous and temporary or have some greater or less degree of permanence is quite unknown. That the kusimanse is a highly sociable and apparently affectionate animal is testified to by all who have experienced these charming pets; and this sociability is not confined, in captivity, to the limited circle of those who regularly supply food and shelter but embraces a wide sphere of strangers, dogs, cats and other animals. It may, nevertheless, in excitement or greed but without deliberate malice, occasionally bite the hand that feeds it, without, however, effecting a great deal of damage.

In nature, a large part of the food intake probably consists of insects. The teeth are well adapted to such a diet. Those who have had the task of feeding these mongooses and at the same time keeping them in good health know that they avidly, and apparently necessarily, consume quantities of grasshoppers and crickets. T. S. Jones (personal communication) has observed that they are particularly fond of the grubs of mason-wasps, breaking open the mud nests with a great deal of excitement. But, of course, other things are taken. Naundorff mentions worms and snails; and it is also known that small river crabs are commonly eaten. Sanderson (1940), in fact, found the stomachs which he examined to contain nothing else but crabs and insects. Durrell (1958) observed a kusimanse to secure crabs by flinging them with the forepaws from shallow water to the bank; and he also recounts attempts to capture frogs in a similar manner—unsuccessful because immediately on landing they leapt away. As a domestic pet *Crossarchus* willingly accepts prepared foods such as cooked meat or chicken; and Haig found fruit salad, comprising largely orange and banana, to be greedily taken. Sweet biscuit, so distant from any food likely to occur in nature, was also readily eaten; and cooked egg was a titbit. In this last connexion it is interesting to note that Naundorff's kusimanse exhibited the widely used mongoose shell-breaking technique, using a ball, flinging it backwards towards a wall with its forepaws, at the same time bouncing its hindlegs off the ground to clear them out of the ball's line of flight. This appears to be the only record of this not uncommon mongoose procedure in *Crossarchus*.

Besides crabs, insects and other small creatures already mentioned it would seem that in nature the kusimanse must, at least from time to time, take more typical carnivore foods. Ewer records one stalking a small bird, using a cat-like crouching, slinking attitude of approach. In the same work *Crossarchus* is described as killing a mouse by a simple neck-bite without the addition of any dog-like shaking of the prey. It may be noted here that these animals drink readily in captivity.

Generally, a meal is not eaten straight from a dish in the manner of a dog or cat but individual pieces are flicked out with the paws onto the floor and taken from there. The forefeet, indeed, appear to be very sensitive and much-used structures as in some other mongooses (*cf. Atilax*, page 298). Naundorff found her kusimanse to use them much as hands. This animal ceaselessly handled everything in its path, turning objects over if they were at all moveable, including all manner of things in the house. This was doubtless part of the hunt for insects, spiders and similar creatures commonly hiding beneath stones or rotting wood. An intense curiosity is, indeed, one of the characteristics of this species which, during its periods of activity, endlessly explores cracks, crevices and holes of all kinds. Ewer (1968) says that they dig with their long claws and use the snout to assist in moving the soil aside; and also that they are good climbers. Others, too, have asserted that they can climb trees when alarmed; but it appears to the present writer that such statements may well give a wrong impression. *Crossarchus* can, and readily will, run up sloping objects whether they be tree trunks or human legs; but to scale a vertical bole like a cat with its claws is not within its capability. Nevertheless, if R. W. Hayman's experience with the very similar eastern Congo species *alexandri* is a guide these mongooses, given favourable circumstances, may be able to achieve considerable heights in trees, using epiphytic figs and closely clinging lianes as aids to climbing. This observer saw three specimens of *alexandri*, in north-east Congo, bolt up a big tree entwined by a *Ficus* up the stems of which the mongooses climbed. Two eventually got away but one attained about 12 metres before it was shot trying to hide by squeezing itself between the stout stem of the epiphyte and the tree trunk—a situation in which it in fact got lodged (personal communication). In the ordinary way, to climb any but low upright obstructions offering no positive footholds or other means of support seems a matter of difficulty; and this, too, was Haig's experience.

The senses of both sight and smell are excellent. Haig's kusimanse could spot a hawk in the sky, no matter how distant. Naundorff, too, found acuity of vision to be remarkable even at long distances; and there was no difficulty in distinguishing between persons, though possibly smell played a part in this latter. Without doubt, information conveyed by the nose plays a big role in the life of the kusimanse; and Naundorff observed that the correct friendly smell was important in producing assured relaxation. Nevertheless, if her pet animal lagged behind when out walking it found its way to her more by the sound of her voice than by her scent. Hearing, too, is well developed. Captive animals answer readily to their names, not only figuratively by coming when called but sometimes literally, also, by means of a grunt. Naundorff indicates that other words, or perhaps tones, were distinguished and elicited response.

As for their own voices, kusimanses utter a good deal of bird-like twittering when exploring for food, and a party of them on the hunt in the forest can produce quite a volume of sound. In anger they growl. At the same time they double their size by erecting the whole of the pelage until they take on the appearance of a very angry fluffy ball. They are for the most part very courageous and will attack strange dogs without hesitation if they deem it necessary, despite the vast discrepancy of size. Normally, however, they are very friendly little creatures and delight in play, either with human beings or such other animals as will tolerate them. They often invite friendly scratching of the head, legs, armpits or belly. There is a curious exception to their normal fearlessness; they become extremely alarmed at any loud rustling or crackling sound and at once retreat to cover. Both Ewer and Haig refer to this. The latter when travelling with his mongoose in relevant zones found it to be connected with the sound and smell of grassland bushfires; and one might reasonably suppose this to be a logical general explanation but for the fact that *Crossarchus* is, in nature, a rain-forest dweller where no such fires occur. Haig also observed his kusimanse to react in alarm to any overhead shadow which caused it to think that a hawk was hovering in the sky.

This mongoose is a clean animal, according to Haig readily house-trained. Naundorff never observed hers to take any steps to clean its fur yet it was always free of vermin. From time to time it suffered from an inconvenient smell owing to exudation from the anal glands. In nature these glands are used for the demarcation of territory, *Crossarchus* being one of several mongooses that for some unknown reason scent-mark objects well above normal nose level by standing on their hands and pressing the anal pouch against objects thus brought within reach. Ewer also mentions a simple dragging of the anus, in the female, across the floor.

There appear to be no published records relating to breeding in this species. The following information supplied by T. S. Jones is therefore of considerable interest. A very young pair was taken into captivity in June 1959; 10 months later, on 11th April 1960, the female gave birth to 4 young; 73 days after this, on 23rd June 1960, she again produced 4 young; and she was once more pregnant, and estimated at about 3 weeks from term, when 48 days later, on 10th August 1960, she was accidentally killed. This shows that in the kusimanse breeding can start at a pretty early age; that the period of gestation may be about 10 weeks; that litters follow in rapid succession, at least 3 a year being possible; and that 4 young at a birth seems a likely average. Of the state at birth nothing is known; but the very young are clothed with underfur alone, and their faces are not particularly long. It is only at the age of about 6 weeks (Haig, 1931) that the nose starts to assume its final remarkable length and that the bristle-hairs lengthen and begin to dominate the pelage. If breeding in the wild is as continuous as it would seem to be in captivity there can be little choice of season. Certainly, British Museum specimens give no clear indication of a preferred time of the year: juveniles have been taken in West Africa during April and August, and quite young specimens in December and January. As regards length of life, a single published record relates to a kusimanse known to have lived in the London Zoo for about 4½ years.

No one has ever described the natural nocturnal shelter or the breeding home of *Crossarchus*. In captivity the species always likes, when resting, to be covered with a cloth or to hide itself in straw; and as it has shown itself to be intensely interested in

Table 16: Numerical data for *Crossarchus obscurus*

	obscurus, means	*obscurus*, range
Vegetation	Forest	
Number in mean	19	
Condylobasal length	70·1	64·5–74·0
Basilar length	64·1	58·1–68·0
Palatilar length	37·7	34·3–39·4
Zygomatic breadth	36·0	33·9–38·8
Upper cheekteeth breadth	22·0	20·0–23·3
Nasals, length	19·8	17·6–22·0
Interorbital breadth	14·2	13·1–15·9
Postorbital constriction	13·3	11·5–15·8
Braincase breadth	27·3	25·8–28·7
Toothrow (c—m^2)	24·1	22·9–25·6
p^4 length	4·9	4·4–5·5
m^1 breadth	5·7	5·1–6·2
m^2 breadth	4·5	3·7–5·2
m_1 length	5·0	4·6–5·3
m_2 length	4·3	3·5–4·9
Head & body	337	316–369
Tail	166	150–190
Hindfoot	64	60–67
Ear	23	21–26
RATIOS (per cent)		
Tail/head and body	49	
Zygom. br./condylob. l.	51	
Braincase/condylob. l.	38	
Braincase/zygom. br.	76	
Palatilar l./condylob. l.	53	
Interorb./postorb.	107	
p^4/c—m^2	20·3	

holes of all kinds it must be assumed that parturition and family raising, at least, take place in a hole in the ground. The communal life of the kusimanse does, indeed, offer several interesting problems for field study in West Africa. What is the composition of, and what degree of stability attaches to the hunting parties? Are they single family units; or colonies comprising an aggregation of such units; and if the latter, do they meet fortuitously and spasmodically or is there a deliberate daily reunion? Do the companies range the forest at random, finishing at dusk far from where they set out at dawn; or are they centred on a permanent home, covering only a circumscribed territory and returning to it nightly? It might be considered most probable that with individual females producing one litter after another and with an association of females, therefore, almost continuously in labour or raising young, there must be some permanent focal point where they can safely remain. If this is so, it at once raises the question whether such a rendezvous is a single communal nest or a series of neighbouring, or even juxtaposed, homes in the style of a warren. No such common home or community has, however, been recorded, as it has in the case of *Mungos* and *Lycaon* (pages 256 and 88), though such a congregation must surely by now have attracted attention to itself. Alternatively, a gravid female, when her time arrives, might be left by a nomadic pack to fend for herself and, if successful, form the nucleus of a new party by the interbreeding of her young or the crossing of the mother again by one of her offspring. Such a system might well lead more often to failure than to success; but in a fast and frequently breeding society the wastage must necessarily, in point of fact, be high. Durrell's lone crab-fisher, mentioned earlier, may well have been such a mother whose litter had fallen victims to predators.

Taxonomy. There are very clear differences of colour and of the degree of speckling between specimens; but such distinctions do not, from present material, seem to be in any settled way connected with localities or other factors; and, in fact, very considerable variation exists within a single region as may be seen amongst skins from Cameroun. The drawing of racial distinction is therefore considered neither possible nor desirable upon present evidence.

ATILAX F. Cuvier

Marsh Mongooses

Atilax F. Cuvier, 1826, in E. Geoffroy & F. Cuvier, *Histoire Naturelle des Mammifères . . .*, part 54, text on the "Vansire": 2. Type species the "Vansire" of F. Cuvier *Herpestes paludinosus* G. Cuvier. The position is complex and is referred to below in the taxonomic section. The name is derived from the Greek *thylax* a pouch, with the prefix *a* denoting without, given in the mistaken supposition that this mongoose lacked the usual anal pocket enclosing scent glands.

Athylax Blainville, 1837, *Annls Sci. nat.* **8**: 272. Correction of the spelling of the above in accordance with its etymology.

Distribution and general. In spite of early confusion and doubt regarding its correct naming and identity, dealt with below in the taxonomic section, *Atilax* is today one of the few mongooses about whose generic independence and identity there is no dispute. The marsh mongoose, frequently also called the water mongoose is, as these names imply, possibly more closely associated with water than is any other species. Taylor (1970), indeed, states it to be the only viverrid known to be a good swimmer, and this is so for the region covered by this present work: but there are, of course, elsewhere in Africa the aquatic civet (*Osbornictis*), and in Asia the otter-civet (*Cynogale*). Yet it belies all expectation that might logically arise from this fact in being the only one of its kind to lack any sign of webbing between the toes—a character which, thus, constitutes an infallible external means of recognition. *Atilax* is widely spread in Africa south of the Sahara, from Senegal or Portuguese Guinea in the west, and Ethiopia in the east, southwards to the Cape. It is, of course, not of equal distribution throughout this extensive range, but it is almost certainly to be found where there is adequate permanent water and vegetation of sufficient density to afford secure cover; and in localities in which these conditions are well met it may even be regarded as common.

Different species have from time to time been named, but today the genus is universally held to be monospecific. This being the case, generic description, either of morphology or habits, is uncalled for, all matters relevant to these being contained in the account of *paludinosus* which follows.

Taxonomy. Reference has already been made above to the fact that the early history of the name *Atilax* and the precise animal to which it was intended to refer was subject to some doubt. Fortunately, J. A. Allen (1924) cleared the matter up and there is no point in going over the whole ground again and making more than a passing reference to it here. The question was of sufficient complexity to take Allen three or four pages of closely packed fact and reasoned argument. It was part and parcel of the vexed question of the identity of an animal known in early literature as the "Vansire" and variously described and referred to a complex mixture of different technical names by a number of early naturalists, including Buffon, Daubenton, Schreber, Erxleben, Flacourt, the two Cuviers, the two Geoffroys and others. The animal was alternatively held to inhabit Madagascar or various parts of the African continent; the names involved were *Viverra*, *Mustela*, *Galidictis*, *Galidia*, *Hemigalidia*, *Salanoia*, *Mangusta*, *Herpestes*, *Atilax*, *galera*, *paludinosus*, *elegans*, *vansire*, *voang-shire*, *urinatrix* and possibly more. Allen boiled all this down to the virtual certainty that the Vansire of Buffon & Daubenton (1765) was not that of F. Cuvier (1826), and that in the process of describing that animal the last author proposed the genus *Atilax* which, though in point of fact ineptly named from a supposed character that had no validity, was sufficiently described in another, the uniquely unwebbed toes, as to render its identity quite unmistakable. Allen's conclusions can be thankfully accepted and there seems no virtue in ever raking over this troubled soil again. It would be a fortunate thing for mammalian taxonomy if all early classic genera and species could be so satisfactorily and conclusively pin-pointed.

In the matter of species no serious challenge has been made, or long sustained, to the monospecific nature of the genus though Gray (1865a) proposed *robustus* from the White Nile and was followed in this by J. A. Allen (1924) who at the same time described *macrodon* from the eastern Congo. These, being extralimital, are of no particular concern to this work; but they are today usually regarded as nothing more than two of the ten local races so far described.

ATILAX PALUDINOSUS (G. Cuvier) Marsh Mongoose

Mustela galera Schreber, 1776, *Die Saugethiere in Abbildungen nach der Natur* . . ., pl. 135; 1778, text **3**: 493. Madagascar. Regarded as unidentifiable (J. A. Allen, 1924). The name *galera* is Latin for helmet, probably given with reference to the skull.

Mustela voang-shire Zimmermann, 1777, *Specimen zoologiae geographicae, etc.*: 487. Zimmermann, 1777, has been ruled an unavailable work (*Bull. zool. Nom.*, 1950, **4**: 547). This specific name is a transliteration of the reputed vernacular name.

Herpestes paludinosus G. Cuvier, 1829, *Le Regne Animal* . . . ed. 2, **1**: 158. Cape of Good Hope. The specific name is derived from the Latin *palus, paludis* a marsh, and refers to the habitat.

Mangusta urinatrix A. Smith, 1829, *Zool. J. Lond.* **4**: 437. South Africa. This specific name is the feminine form of the Latin *urinator* a diver, in reference to the animal's habit while foraging in the water.

Herpestes atilax Wagner, 1841, in Schreber, *Die Säugethiere* . . . Supplement, **2**: 305. South Africa. Derivation of this name is given under the genus.

Atilax vansire F. Cuvier, 1842, in E. Geoffroy & F. Cuvier, *Histoire Naturelle des Mammifères, etc.* Table générale, 3. This is the reputed vernacular name of the animal whose exact identity gave rise to so much confusion as explained above.

Athylax paludosus Gray, 1865, *Proc. zool. Soc. Lond.* for 1864: 557. The Latin adjective *paludosus* means marshy and refers to the animal's habitat. Cape of Good Hope.

Herpestes pluto Temminck, 1853, *Esquisses zoologiques sur la côte de Guiné*: 95–96. Dabocrom and River Boutry, both Ghana. Pluto was the Greek god of the underworld; the name was thus intended to indicate the entirely sombre, blackish appearance of the animal.

Atilax paludinosus guineensis Monard, 1940, *Archos Mus. Bocage*, **11**: 198–201. Catio, Portuguese Guinea

Distribution. There are more West African specimens of this mongoose in the British Museum than of almost any other species, and from a wider range of localities. This is probably a good measure of its relative abundance on the ground not only in West Africa but as regards the continent as a whole. The Marsh Mongoose is, in fact, a well-known species from a wide variety of localities from 12 or 14 degrees north southwards to the Cape.

In so far as the territory covered by this book is concerned there is an early specimen (1863) labelled as coming from Senegal, without any specified place, and this may possibly be correct or it may be nothing more than a loose generalization, not uncommon at that period, for somewhere on the western coast of Africa. However, the species is definitely recorded from as far west as Portuguese Guinea. Thence it is known from every West African country to Cameroun, and there seems little point in recording all the names of the many places at which it has been taken. All in the British Museum are from the closed-forest belt or the contiguous Guinea woodland; but this is not to say that this mongoose does not occur in the drier zones of vegetation, for extralimitally the species commonly inhabits *Acacia* country. The basic criterion for the habitat would seem to be the existence of adequate permanent water suitable for diving, swimming and fishing, bordered by sufficiently dense vegetation to afford safe cover. It does not matter whether that vegetation is of the forest, shrub and herb, type or close grass and reeds with no backing but fairly open country behind it. The most commonly used English name, marsh mongoose, must not be taken too literally but only as implying the sort of waterside habitat that may or may not be subject to some degree of inundation. The requisite conditions are undoubtedly of most frequent occurrence, in West Africa, in the rain-forest and Guinea woodland, in which forest river fringes commonly exist. There are in the former zone also extensive areas of freshwater swamp and of mangrove swamp, in the latter of which, despite the unpromising brackish nature of the water, the marsh mongoose is known to be common. There seems basically little reason why this animal should not be encountered over a much wider range of country than that from which it is at present recorded since rivers or lakes with bordering vegetation are common features of all but the most arid zones—and even here sometimes there are dense marshes. However, A. J. Hopson, an interested observer, states (in a private communication) that in 7 years on Lake Chad he neither saw it nor heard of any record of its occurrence there. There is, however, one important factor that has had a great influence on the actual present day distribution of this mongoose. Riverine vegetation is, for one reason or another, peculiarly prone to destruction, and especially for the purpose of cultivation. The enormous increase in human population and the concomitant agriculture that has taken place in the past three-quarters of a century has resulted, in West Africa, in the complete disappearance of vast areas of potential shelter for *Atilax*, and it can be said with considerable certainty that the occurrence of this genus in the drier woodland zones is today very much more restricted than it was fifty years ago.

Description. *Atilax* (Plate 7) is one of the group of larger mongooses, ranking with *Herpestes*, *Ichneumia*, *Xenogale* and *Galeriscus*, though, at least in West Africa, a little less in size than any of them, especially the last. It is usually described as a wholly "black" mongoose, that is to say of a very intense brown; but though this is its most common appearance there is, in fact, a considerable degree of colour variation and the pelage sometimes assumes a rich reddish-brown; or it may be a medium-brown and heavily speckled. In its normal dark form the animal can very easily be confused with *Xenogale naso*, a difficulty dealt with under that species.

The pelage of *Atilax* is long, glossy and fairly harsh. It is composed of dense, sinuous, fine, moderately long (about 15 mm) underfur and bristle-hairs, 32 to 40 mm long, tapering to a narrow base and of flat oval section. These, though abundant, do not always conceal the underfur. They have a longish pale-brown basal region, but any banding on them is irregular in situation and often obscure. In some specimens the bristle-hairs may be wholly dark, almost black, while in others there are indistinct white rings, narrow and inconspicuous. Some, on the other hand, are by contrast notable for a series of three very clear, pale, widely separated rings, which impart a "ticked" effect to the whole dorsal pelage. These are all narrow, that is not more than about 2 mm broad, the two lower ones whitish-yellow, the subterminal one orange. It will be seen, then, that it is not practicable to give any general description that might not be misleading of a coat that shows so many degrees of variation, except to say that the impression is mostly of a very dark animal. The underfur is similar in colouring to the back but a shade paler; the hairs on the throat are directed forwards.

The head of *Atilax* is wide, the muzzle not very long, the rhinarium broad and black with a furrow down its front face that is continued below as a naked strip parting the upper lips. The crown and cheeks are usually finely speckled; and there is mostly a relatively bare area around the eye. The ears are of the usual low, broad, rounded mongoose form, set well on the side of the head below the crown and rather obscured by a thick growth of hair in front of them. The tail, which is roughly two-thirds of the head & body length, tapers evenly from a broad base, not clearly differentiated from the body, to a narrow tip; and it is long-haired throughout but there is no terminal tuft. The short legs and feet are of much the same tone as the back or a little darker; the feet themselves all 5-toed, with strong but not exceptionally long claws, and notable as being, alone of all mongooses, completely unwebbed. The soles are wholly naked around the pads, and in the hindfoot this nakedness is continued posteriorly to the heel. As explained previously, the name *Atilax* was given in the belief that this genus was unfurnished with any glandular anal sac; but this is not so, the folds of skin surrounding and enclosing the scent glands and anus being, in point of fact, well developed. The glands are situated one on each side of the rectal orifice.

Skull (fig. 38). This is amongst the broadest of West African mongooses, the zygomatic breadth amounting on the average to some 58 per cent of the condylobasal length. The braincase is narrow ovoid with a well-developed, flange-like supraoccipital crest. There is always a short posterior section of sagittal crest joining this in a T; but development of the former over the main body of the cranium is variable. It is mostly better in the males than females: in existing British Museum material it is pronounced in 3 and low in 6 males, slight or very slight in 5 females and rudimentary in 4. In only one case out of 21 measurements is the interorbital breadth very slightly less than the postorbital constriction; it is mostly markedly greater, varying in extent from about 5 to 50 per cent more. The postorbital processes are long and sharp, and not infrequently nearly, and occasionally completely, meet the jugal processes to form an orbital ring. The frontal region is broad and slightly inflated; the rostrum short, blunt and broad; and in fully mature skulls the nasal sutures almost entirely disappear by fusion. The zygomata are strong, sometimes broadened in the middle section, sometimes not. The postdental palate is obviously longer than it is broad mostly from about 30 to 50 per cent but occasionally rather less. The anterior chamber of the bulla is small and flat; the posterior chamber very much larger, well inflated, rather pear-shaped.

Both upper and lower incisors are set in compact, practically straight transverse rows, the outer ones, especially in the upper series, being appreciably larger than the inner. All the upper ones, in unworn teeth, are clearly, though minutely, cusped on their posterior faces. The upper canines are rather compressed from side to side and are furnished anteriorly and posteriorly with sharp knife edges; but they are neither so large nor so straight as those of *Galeriscus*. The posterior outer corner of p^4 is situated very close to the point where the posterior outer corner of the maxillary root of the zygoma arises; and in consequence the whole of m^1 lies behind this point.

One of the standard characters generally given for *Atilax* is that the premolars are $\frac{3}{3}$; and this is so in nearly all southern and eastern African specimens. But in 26 British Museum West African, mostly fully adult, skulls it is true in only 9 cases; in 6 other skulls these teeth are $\frac{4}{4}$; in 5 they are $\frac{4}{3}$; in one other $\frac{3}{2}$; and in a juvenile $\frac{2}{2}$. The remaining 4 cases are more complex, the lower jaw having a differing number of premolars on either side: they are $\frac{4}{4/3}$, $\frac{4}{3/2}$, $\frac{4}{2/1}$ and $\frac{3}{3/2}$. It is true that the "extra" premolars are always very small; but they are little or no smaller than the corresponding teeth in genera characterised as habitually possessing 4. While it is clear that the anterior premolars in *Atilax* are on the way out it is obviously misleading in West Africa to state that the cheekteeth are $\frac{3\ 2}{3\ 2}$, the exceptions being, seemingly, appreciably commoner than the rule. m^1 is a large tooth, nearly as large as p^4; m^2 is small but not very small; that is, it is transversely somewhat wider than the lingual section of m^1 and is subequal to this in bulk. There is, however, a very occasional exception to this, the tooth being of reduced size. In the mandible the canines are much more curved than in the upper jaw; m_1 has, in its anterior half, three pyramidal cusps, equilaterally set and all very nearly the same height, not with the external one clearly the highest as in several other genera.

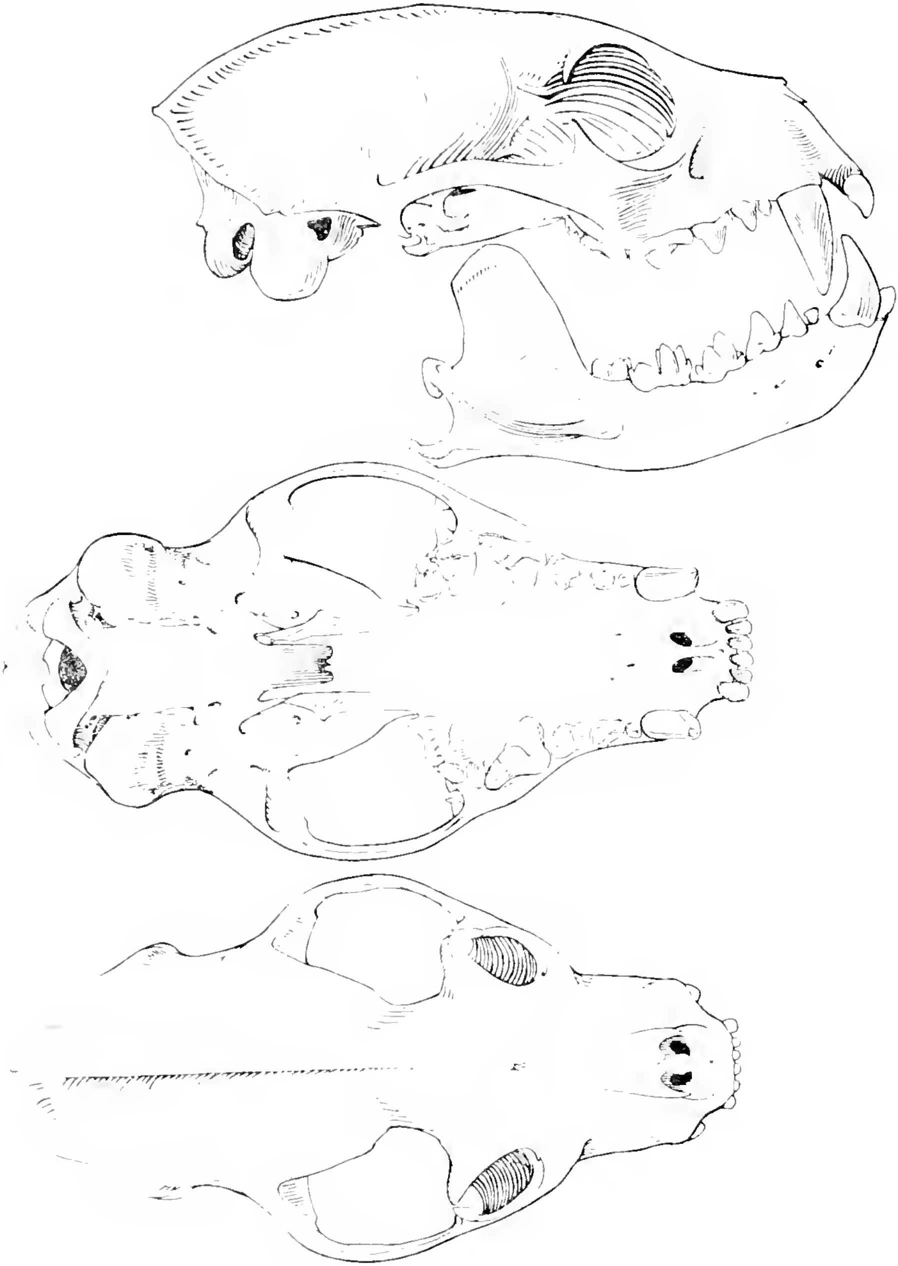


FIG. 38. *Atilax paludinosus*: skull, B.M. No. 13.4.1.1, ♂, × 1

Habits. Something has already been said of the water-haunting habits of this mongoose: it dives and swims almost as well as an otter and will travel below the surface for some distance. Indeed, it is said that when alarmed it will remain for a long period completely submerged except for its nostrils. Certainly when disturbed on land it makes off towards the nearest water and, if still pursued, plunges in. Taylor (1970) describes it as swimming by lateral undulations of the body with the back partly exposed. He observed a specimen to remain submerged for 15 seconds, and states that the fur becomes completely wet. Yet, in spite of all this, observers have from time to time reported *Atilax* from dry country at some distance from the nearest river. Little or nothing that is definite is known of the breeding habits of this mongoose; some say that it makes a nest amongst the reeds, others that it raises a family in a burrow in the banks of a stream. There are said to be two in a litter; but hunters in the Cross River forests insisted to Gerald Durrell that it consisted of only a single baby (personal communication). There is nothing from which any particular breeding season can be inferred in West Africa.

Except when actually bringing up a family the marsh mongoose lives singly or sometimes in pairs. Because of the hidden life it leads amongst dense waterside vegetation little is known of its daily habits, and because it is so little seen it has the reputation of being entirely nocturnal. In actual fact, although it may be active on bright moonlit nights, it is for the most part, as Lombard (1958) has pointed out, crepuscular rather than nocturnal and almost certainly carries out the majority of its foraging and feeding in the early morning and late evening. It is sometimes to be seen trotting along a path or a motor road at midday.

The food consists of frogs (these have been taken from the stomach of a Nigerian specimen), reptiles such as lizards, small rodents, a large number of insects of various kinds, fresh-water mussels and fish—though Lombard doubts whether it has the ability to capture large specimens of these last and thinks it probably confines its attention to smaller fry in shallow water. Crabs, too, are always cited as one of the staple articles of diet; but whether *Atilax* can satisfactorily deal with any but the smaller, softer-shelled varieties does not appear to have been adequately shown. To all this can be added an at least occasional diet of small birds and eggs; the nests of reed-haunting species such as rails and others must almost certainly be raided as opportunity offers. Stevenson-Hamilton (1947) rates this mongoose with the monitor lizard as the deadliest enemies of the crocodile, digging out and avidly consuming its eggs.

Several kinds of mongoose have been observed to crack eggs or similar shelled objects by hurtling them with the forefeet forcibly backwards between the arched hindlegs against a rock or other resistent body. Whether *Atilax* is one of these does not seem to have been recorded; but that it takes objects in its forepaws, stretches up and then flings them to the ground with great force is well authenticated. Steinbacher (1939 and 1951) describes how two separate captive specimens dealt with food problems in this way, the one with nuts, the other with snails that had withdrawn into their shells. Snails that were fully exposed were bitten into directly. It is of interest to note that nuts meant nothing to this second mongoose which made no attempt to open them as the other specimen had. Lombard (1958) observed *Atilax* to break mussels open using the same method. He also recorded that if an egg could not be bitten by the teeth it would be cracked on the ground, and a one-inch hole opened up through which the liquid egg could be licked.

The same author, who gives the most complete account of the habits of the marsh mongoose that has so far been published, describes how it uses its highly sensitive forepaws to feel about in the mud for river mussels; and also, on land, continually pokes them under rocks or into holes and crevices in the hope of finding insects. He says, too, that its very keen sense of smell enables it to locate articles of food, even subterraneous worms. Finally, he provides a rare record of a pet marsh mongoose having of its own free will on two separate occasions attacked and killed snakes. It did not eat them.

One other thing must be mentioned in connexion with feeding. *Atilax* is one of the many viverrines with a reputation as a fowl thief, and for this reason, as well as for its own value as protein food, it is much hunted. It may take eggs if they are readily available, as they so often are in Africa, but the fowl stealing, in a water-haunting animal which lives mostly on small prey, is probably exaggerated. However, it is the subject of a widely spread fable that must be mentioned here, though at present there seems to be no record of it in West Africa. In the vicinity of a fowl *Atilax* is said to stand still with its hindquarters towards the bird and to open the sac that surrounds and normally conceals the anus and the two laterally sited scent glands. The fowl, seeing the bright colours thus exposed, becomes curious and, thinking them to be those of some ripe and attractive fruit, advances to peck at the spot—whereupon the mongoose turns and springs upon its foolish prey. Pitman (1931 and 1954) in commenting on this belief is inclined to think that a tale so widespread in Africa might have some foundation in fact. The story is the more intriguing in the light of the literal implication of the generic name *Atilax* and offers an amusing comparison between the powers of observation of African field naturalists and European study mammalogists.

Like several others of its kind the marsh mongoose responds well to captivity and becomes very friendly—some specimens, at least, trusting enough to invite head scratching from complete strangers. When pleased it makes a purring sound, something after the style of a cat; when alarmed or displeased it growls. Having scent glands it has, at least occasionally, a musky odour; but it opens up the circumanal pouch and actively emits a malodorous fluid only as a last resort in danger. Normally these glands are used for recognition purposes, imparting a characteristic smell to the droppings, and being used more deliberately for demarcation purposes by being pressed against key boundary marks. Hediger (1949), Fiedler (1957) and Hinton & Dunn (1967) all say that *Atilax* carries out this delimitation of territory, if necessary, on high objects by performing a "handstand", thus bringing the anal pouch into a position well above the normal body level; but the taxonomic determination of the East African mongoose forming the basis of this observation is in some doubt.

In a cage, *Atilax* has shown itself capable of climbing several feet vertically up wire netting. Such a surface, of course, affords positive footholds difficult to equal in nature; nevertheless, it seems certain that low mud walls or trees with sloping trunks could be successfully tackled if necessary. The normal gait on land of the marsh mongoose is a steady trot with the tail stretched out behind, sometimes a little curled upwards. One of these animals is recorded (*Int. Zoo Yr. Bk.* **2**) as having lived 11½ years in captivity.

Taxonomy. A number of local races has been named. This is to be expected in an animal which exhibits such variation of external appearance as *Atilax* does; but whether such variations can be constantly related to localities or to definable ecological backgrounds is very much open to question. Two races have been set up for West Africa, *pluto* Temminck and *guineensis* Monard. Temminck's name was given to a blackish form from Ghana; and such animals certainly occur at various places in West Africa; but there are as many lighter, browner specimens current in the same areas. Monard described *guineensis* from Portuguese Guinea as being smaller than the typical form, with a less massive skull and with 4 premolars above and below. Measurements of West African material in the British Museum, including specimens from Portuguese Guinea, are not very different from those given for typical South African *paludinosus*

Table 17: Numerical data for *Atilax paludinosus*

	paludinosus, means	*paludinosus*, range
Vegetation	Mostly Forest and Guinea	
Number in mean	20	
Condylobasal length	100·6	96·0–106·5
Basilar length	91·3	87·4–98·8
Palatilar length	55·2	51·2–60·7
Zygomatic breadth	58·0	52·5–68·6
Upper cheekteeth breadth	35·5	33·3–38·3
Nasals, length	25·2	21·9–27·8
Interorbital breadth	19·9	17·3–24·0
Postorbital constriction	16·8	13·0–19·2
Braincase breadth	37·7	35·2–40·3
Toothrow (c—m^2)	36·2	31·8–40·1
p^4 length	9·8	8·3–11·2
m^1 breadth	10·5	9·2–11·8
m^2 breadth	6·5	5·0–7·6
m_1 length	9·5	8·4–10·8
m_2 length	6·3	5·2–7·2
Head & body	501	442–553
Tail	322	250–355
Hindfoot	96	84–102
Ear	33	28–40
RATIOS (per cent)		
Tail/head & body	62	57–71
Zygom. br./condylob. l.	58	
Braincase/condylob. l.	37	
Braincase/zygom. br.	65	
Palatilar l./condylob. l.	55	
Interorb./postorb.	118	
p^4/c—m^2	27·1	

by Roberts (1951); and the presence of p^1 and p_1, though commoner in West Africa than elsewhere, as shown above and in Hayman (1935), is of irregular occurrence. Before naming this race Monard submitted his data to Professor Bourdelle of Paris who, on Monard's own admission, seemed very dubious of the existence of any valid distinction between the Portuguese Guinea animals and typical material.

The present writer is very doubtful that local races can be usefully named and distinguished; and certainly not before considerably more abundant data than at present available have been gathered.

Genus **ICHNEUMIA** I. Geoffroy, 1837

White-tailed Mongooses

Lasiopus I. Geoffroy, 1835, in Gervais' *Resumé des Leçons de Mammalogie . . . professées au Museum de Paris* **1**: 37. Not *Lasiopus* Dejean, 1833, Coleoptera. Type species *Herpestes albicaudus* G. Cuvier. This name is derived from the Greek *lasios* hairy and *pous* foot, from the furry nature of the soles.

Ichneumia I. Geoffroy, 1837, *Annls Sci. nat., Zool.* (2) **8**: 251. A new name to replace *Lasiopus*, preoccupied. Type species *Herpestes albicaudus* G. Cuvier. The name, from the Greek, *ichneuo* to hunt or track, refers to the animal's habits.

Distribution. This is one of the commonest of African mongooses, ranging through the grass-woodlands, but not the forest, south of the Sahara, from Portuguese Guinea in the west and Sudan and Somaliland in the east to parts of the Cape Province in South Africa. It also occurs across the Red Sea in southern Arabia. The white-tailed mongoose is one of the largest and, when it lives up to its English name, certainly one of the most striking in appearance; but this unfortunately it does not always do, in many West African specimens the tail being black. The combination of size, white tail and black legs could lead to confusion with the Black-footed Mongoose (*Galeriscus*); but, apart from the fact of the ranges of the two species being quite different, the animal now about to be dealt with in this section has a far bushier tail and long, loose fur (see Plate 8).

Taxonomy. *Ichneumia* is one of the few African mongooses about whose identity, naming and taxonomy there has been a minimum of argument. Its striking appearance and clear-cut characters have from the start virtually prevented confusion with others, though in common with most mongooses it was at one period regarded as a species of the all-embracing genus *Herpestes*—which, as explained elsewhere (page 248), itself for a time became confused with *Mungos*. Thomas in his 1882 arrangement of the African mongooses set *Ichneumia* at the level of a subgenus of *Herpestes*; but Pocock (1916e) recognised it as a full genus, a status that has since remained unquestioned. Since *Herpestes* belongs to the group of mongooses with cheekteeth of a predominantly sectorial character set well back in the jaw, and *Ichneumia* to that with teeth of an obviously more crushing type set much further forward, it is doubtful whether the two genera are, in fact, particularly closely related.

As for the composition of the genus, it is universally regarded today as monospecific though a number of independent species have from time to time been erected. These mostly date from early days; but as recently as 1924 J. A. Allen, dealing with eastern Congo mongooses, referred them to *leucura* rather than the now generally accepted *albicauda* as it did not appear to him probable, on geographic as well as other grounds, that the two could be specifically identical. In this present work only *albicauda* is regarded as valid.

ICHNEUMIA ALBICAUDA (G. Cuvier) White-tailed Mongoose

Herpestes albicaudus G. Cuvier, 1829, *Le Règne Animal*, ed. 2, **1**: 158. Senegal. The specific name is from the Latin *alba* white, and *cauda* tail.

Herpestes leucurus Hemprich & Ehrenberg, 1833 (*fide* a MS note of Sherborn's), *Symbolae Physicae, seu Icones et Descriptiones Mammalium* . . . decas 2, folios *h*, *i*, *k*, Pl. 12. Dongola, Sudan. This name was derived from the Greek *leucos* white and *oura* tail.

Herpestes loempo Temminck, 1853, *Esquisses zoologiques sur la côte de Guiné*. "All the coast of Guinea"—almost certainly Ghana. The name was said to be a vernacular one meaning man-eater because this mongoose was held to rob graves and devour the corpses.

Ichneumia nigricauda Pucheran, 1855, *Revue Mag. Zool.* (2) **7**: 394. Senegal. The name is compounded from the Latin *nigra* black and *cauda* tail.

Distribution. This large mongoose (Plate 8) of striking appearance and a weight of about 5 kg is spread over a good deal of Africa south of the Sahara but avoids the high forest and the zones of intense aridity. It may, however, occasionally be found at places which are nominally in the forest belt but which have, in fact, been persistently cleared and are now open farmlands or invaded by Guinea woodland vegetation.

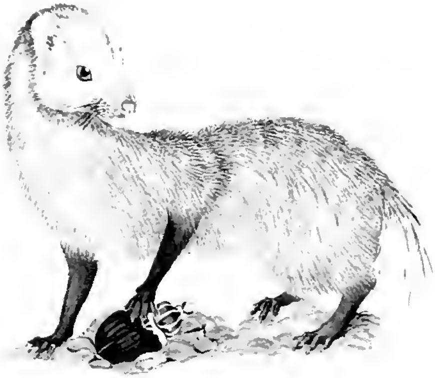
Dekeyser (1955) gives the range as extending as far west as Senegal; and Monard (1940) records specimens from four places in Portuguese Guinea. Thence, eastwards, it may almost certainly be expected anywhere in the Guinea, Doka and Sudan woodlands. The most inland specimen in the British Museum is from Maiduguri (north-eastern Nigeria); but a reliable observer stated a few years since that this animal was very commonly caught and brought in by dogs in Sokoto station (north-western Nigeria, 14°N.); and A. J. Hopson (*in litt.*) found it to be common amongst salt bushes (*Salvadora persica*) near the shores of Lake Chad and the adjacent dunes; and it was often seen at night on the outskirts of lakeside villages; but was never observed at any great remove from the lake itself. Angus Buchanan obtained three specimens at Farniso (Kano, Sudan woodland) but no others occur in his comprehensive collections from further inland in the more arid Sahel and Subdesert zones. Altogether, 21 skins and 15 skulls exist in the British Museum from Sierra Leone, Ghana and Nigeria. The white-tailed mongoose may therefore be regarded as being, in the right localities, fairly plentiful.

Description. *Ichneumia* ranks approximately in size with *Herpestes*, *Xenogale*, *Atilax* and *Galeriscus*, that is to say it has a head & body length of at least 500 mm and a weight of some 4 to 5 kg; but it is not likely to be confused in the field with any of these, *Herpestes* having a very sharply tapering tail with a contrasting black tuft, *Xenogale* and *Atilax* being mostly very dark animals, and *Galericus*, despite its superficially very similar black legs and white tail, is confined to the dense forests of the Cross River. *Ichneumia* is, in fact, a very easily recognisable mongoose, with a loose-furred buff or greyish-buff coat more or less heavily splashed with black, wholly black legs, and an abundantly long-haired tail which in its most typical form is brilliantly white (Plate 8). However, in West Africa it is at least as commonly black, there being in the British Museum collection 7 white to 12 black tails, and 2 half and half; but whichever it is, it and the black legs and feet both contrast sharply with the basically buff body.

The lengthy dorsal pelage is, in texture, loose, fairly soft and springy. It is composed chiefly of dense, relatively long, slightly wavy, fine underfur and extremely long, oval-sectioned bristle-hairs. The underfur measures 20 to 25 mm and is buffish, pale-brown or grey-brown and plays a considerable part in determining the overall colour impression. The bristle-hairs are always very long, reaching their maximum on the lower back; the actual length varies a good deal from specimen to specimen, in some measuring about 50 mm or even a little less, in others attaining as much as 65 mm. They also vary considerably in their colouring. There is usually a white base, which may be from 3 to 9 mm long, and then the remainder of the hair may be either all black or may comprise one or two white zones alternating with pale or very pale brown. The white is never very conspicuous as such in the general impression of the coat; but the pale areas of the bristle-hairs, together with the underfur, make up the basic pelage colour, the length and number of dark terminal zones determining the degree of superimposed black. These two elements, while producing coats that are recognisably similar, account for pale animals or dark animals. On the underside the fur is sparser and paler with many fewer bristle-hairs and, generally, much less black. The fur of the throat is directed forwards and meets that of the chin at the angle of the jaw in a transverse wave. In the very young the coat is always pale and contains very few black-ended bristle-hairs, which increase in number with maturity.

The head is of moderate breadth, the muzzle fairly pointed; both crown and face are paler than the rest of the upper pelage, speckled; and there is a bare area round the eye. The ears are low in height, rounded and very wide; the outer portion situated very much on the side of the head but the inner margins reaching much further up the crown than in most other African mongooses. Their forward aspect is rather obscured by a screen of long hairs rising in front of them. The median groove of the rhinarium is continued downwards as a narrow bare band parting the upper lip.

The hindfeet and all of the forelegs and feet are practically black, but differ from the similar ones of *Galeriscus* in having 5 toes in place of 4. These are webbed to the subdigital pads. The hindfeet are appreciably longer than those of other mongooses of similar size and *Ichneumia* tends to stand higher off the ground; the soles are completely, or almost completely, hairy up to the pads. The very long-haired, tapering and very shaggy tail is somewhat shorter than the head & body; but different collectors' figures give widely differing degrees of this, varying from 69 to 99 per cent. This is probably partly due to some measurements having been taken to the last joint, some to the tip of the fur. But irrespective of this there does seem to be a fairly wide variation of ratio from specimen to specimen; and this has something to do with the degree of



White-tailed Mongoose. Black-footed Mongoose.

maturity; Dalton (1961) recording that tail length increased enormously with advancing age. The tail, as already noted above, may be either white or black or half-and-half, black predominating in West Africa, though relatively rare elsewhere. MacInnes (1952) records being informed that both black and white tails may occur in a single litter; but no positive evidence is given. There is the usual herpestine anal sac surrounding and, when closed, concealing the anus and the two laterally sited orifices of the scent glands.

Skull (fig. 39). The West African material in the British Museum is very inadequate. Although there are 15 skulls only 8 are reasonably mature, and of these 2 are broken. If the skulls of the other large mongooses, *Herpestes*, *Xenogale*, *Atilax* and *Galeriscus* are compared with that of *Ichneumia* it is seen that, although the distance from the glenoid fossa to the condyles is much the same in every case, the length of skull anterior to this is, with the exception of *Galeriscus*, appreciably greater in *Ichneumia*. The postorbital constriction, too, is markedly broader in this than in other genera and the braincase consequently rather less ovoid. There is no great difference in measurement between the interorbital breadth and the postorbital constriction though the former is in the majority of cases, but not invariably, slightly the smaller. The whole frontal region appears broad and inflated. The supraoccipital crest is as in other genera a pronounced flange; the sagittal crest is mostly not very highly developed, but old females as well as old males occasionally produce a deep knife-edge. In fully mature skulls, but not young adults, the orbital ring is complete. The palate, though not wholly vaulted as in *Galeriscus*, is in most cases not entirely flat as in *Herpestes*, *Xenogale* and *Atilax* but has a broad, very shallow, medial, longitudinal depression, reaching approximately from p^2 to m^1. In these three genera also, there is very little extension of the palate immediately posterior to m^2; but in *Ichneumia* there is a shelf of bone sufficiently large to accommodate a further molar of fair size. The central postdental palate is somewhat longer than broad. The anterior chamber of the bulla is small, the posterior one highly inflated.

The toothrow is relatively somewhat longer than in other genera. The posterior outer corner of p^4 is situated well anterior to the posterior root of the maxillary process, m^1 correspondingly lying wholly anterior to that point (fig. 33a). There are always 4 premolars each side in both upper and lower jaws; and the anterior ones, although always small, are somewhat bigger than in other genera in which they are present. m^1 is a large tooth, equal in bulk to the upper carnassial; and m^2 is also large. The cusps are low, even in young teeth, and the occlusal surfaces of the posterior cheekteeth are adapted more to crushing than to cutting. The upper canines are subconical and slightly curved. The upper incisors are in a compact, very slightly curved row; all, unless well worn, are cusped on the posterior face, i^1 and i^2 minutely so, i^3, which is larger than the others, more pronouncedly so. The lower canines are short, strong and fairly abruptly curved. m_2 is only slightly smaller than m_1, and on both of these teeth the cusps are low and soon obscured; but when unworn those of the anterior portion of m_1 are subequal in size, the posterior lingual one being very slightly the smallest.

Habits. Although this is such a common and widespread mongoose very little that

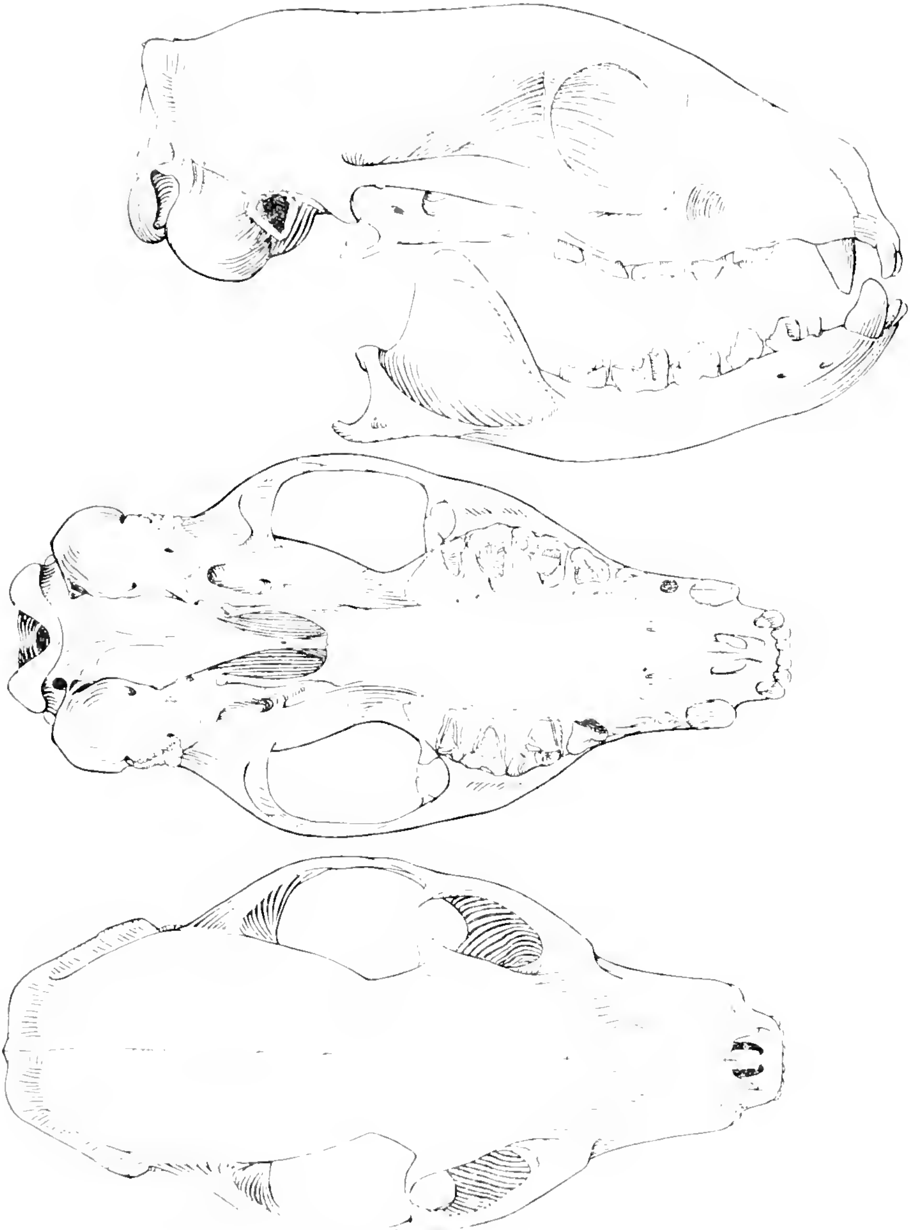


FIG. 39. *Ichneumia albicauda*, skull, B.M. No. 12.4.3.3, ♂, × 1

is precise has been recorded of its habits in the wild. It is always said to be shyer than most and reserved even in captivity—though this last is not always true, as will be seen later. *Ichneumia* is a large and conspicuous animal and one might suppose it, in consequence, to be well observed. It is certainly common enough in museum collections, but these specimens must be largely the outcome of trapping since no one seems to have recorded encounters with it in the field, apart from occasional views in the headlamps of cars. The fact is that, besides being solitary, it is pretty strictly nocturnal, spending the daylight hours hidden deep in holes or in dense undergrowth, the holes being those excavated or constructed by others—aardvarks, porcupines, termites and so forth. There are, nevertheless, exceptions to this: T. S. Jones (personal communication) has noted that one regularly crossed a garden in Makeni, Sierra Leone, every evening at about 5.0 p.m., being eventually killed by a gardener. Some writers connect *Ichneumia* with the vicinity of water; but it certainly occurs at more distant sites; and even when it does live in the neighbourhood of water it is not so aquatic as *Atilax*, though Taylor (1970) says that it does sometimes swim. However, Dalton (1961b), writing of a tame specimen taken to a stream, said that it made its feet wet but made no attempt to enter the water further.

There is no account of the breeding of this species, the period of gestation or the number of young; it can only be assumed that parturition and initial care of the offspring take place in a hole in the ground; and there are slight indications that two is probably a common litter size. The only two juveniles with relevant data in the British Museum suggest the dry-season as the favoured breeding period in West Africa, one having been taken on the 5th January, the other in February.

The white-tailed mongoose has the reputation not only of being shy but also of being unfriendly. However, if captured very young it can become a very charming pet. Dalton (1961b), who gives what appears to be the only full account of this animal in the home, describes it as of sweet and gentle disposition, never biting or scratching either in temper or in play. It romped round joyfully, with dogs or played with human beings, even with strangers. This animal was persistently nocturnal, retiring to rest in the morning, sleeping soundly throughout the day despite disturbance or unfavourable conditions, emerging in the evening to feed. It seemed equally satisfied with any kind of table food; it killed and ate rats, and consumed enormous quantities of moths and other insects that flocked to lamps at night. When allowed free range it would also claw out beetles; and at intervals it would stand up on its hindlegs, peering round for danger and chattering excitedly. Like many other nocturnal animals this one was not continuously active throughout the night but returned at intervals from its foraging to take a short rest. One of the most interesting observations made by Dalton is that the white-tailed mongoose, or this specimen at any rate, employs the common mungotine trick of breaking eggs by hurtling them backwards through the hindlegs—in this case against the leg of a table. The eggs were not proffered as food but discovered and stolen. This animal came to an early end through being found in someone's fowl-run, whither it had followed some wild specimens of its kind; but a white-tailed mongoose is known to have lived in captivity for nearly 12½ years (*Int. Zoo Yr. Bk.*, **2**).

In spite of the reputation of *Ichneumia* for shyness it would seem that it is not much afraid of human proximity; it has already been mentioned above that this mongoose used to be commonly caught by dogs in Sokoto station (Nigeria); and Pitman (1954) records that in Uganda it frequents towns in large numbers. This observer further (1931) gives a remarkable account of having watched a white-tailed mongoose, every hair on its head, body and tail erect, perform a dance in the bright moonlight in front of a fowl-run with the purpose of arousing the curiosity of the birds. Any which, in order to get a better view of this strange sight, thrust its head through the wire netting had it at once bitten off. This performance went on for several nights until the raider was trapped. Pitman's own curiosity had originally been roused by the discovery of mangled corpses inside the run without any sign of an intruder.

Roosevelt (1910) tells another peculiar story of this species, namely that it commonly climbs trees, steals honey from the hives set therein, and kills hyraxes "following them everywhere among the treetops". It would seem improbable that a mongoose with ill-adapted feet and claws, let alone one of the size of *Ichneumia*, would be able to climb tree stems with any facility or be much at ease chasing hyraxes along branches; and it would thus appear likely that this account of its habits must be a case of mistaken identity. Roosevelt also recounts another astonishing story of a white-tailed mongoose starting to eat a small puff-adder at the middle of its back before even attempting to kill it. The snake consequently turned and buried its fangs twice in the mongoose, which nevertheless took no notice, ate it all up, and showed no signs of having received any damage. That *Ichneumia* does, in fact, eat snakes is confirmed by an observation in Shortridge (1934) that a small cobra, rodents, large beetles and termites have all been taken from stomachs.

Finally, it may be added that in self-defence this mongoose can eject a very foul-smelling liquid which, *fide* Pitman, it is impossible to wash off, the odour persisting for a very long time; and T. S. Jones (private communication) was told by hunters in Sierra Leone that the recent passage of one of these mongooses can always be detected by the powerful smell.

Taxonomy. It has already been stated that only one species is today recognised as existing throughout Africa. It remains to examine the matter of races. Two are named for West Africa: *loempo* Temminck and *nigricauda* Pucheran; and G. M. Allen (1939) lists five others from elsewhere. These have all been described on colour or the size and character of the teeth. Whereas there is some slight evidence that drier zones are inhabited by averagely somewhat paler animals, and *vice versa*, the degrees of difference are slight and the practicability of drawing defined lines between forms non-existent. It has yet to be convincingly shown that described differences of size, corporal and cranial, or of dental cuspidation are constant to an area and do not fall within the range of variation normal to the nominate form.

The present writer holds the view that no sufficiently convincing case has been made out for the validity of any of the proposed subspecies. There is a wide degree of variation of colour in any area (see, for example, Monard, 1940); and factors such as moult and age also enter into the question. The data at present available are quite inadequate to constitute the basis of any practically useful subspecific naming. As regards the West African races in particular, Temminck's description of *loempo* fails to draw any clear distinction between it and *albicauda* itself; while Pucheran's *nigricauda* rests on the black tail which is known to be a commonly occurring variant.

Table 18: Numerical data for *Ichneumia albicauda*

Vegetation	*albicauda*, means Guinea—Sudan	*albicauda*, range
Number in mean	10	
Condylobasal length	107·2	98·6–115·7
Basilar length	99·7	91·2–107·3
Palatilar length	62·3	56·5–66·8
Zygomatic breadth	54·6	50·3–58·4
Upper cheekteeth breadth	33·9	31·3–36·6
Nasals, length	26·5	21·9–29·3
Interorbital breadth	21·2	18·6–23·7
Postorbital constriction	22·1	20·3–24·0
Braincase breadth	35·3	31·7–37·3
Toothrow (c—m^2)	40·2	38·4–44·0
p^4 length	8·1	7·7–8·9
m^1 breadth	9·0	8·1–10·0
m^2 breadth	7·6	6·5–8·2
m_1 length	8·4	7·7–9·0
m_2 length	7·4	6·5–8·2
Head & body	482	423–545
Tail	361	330–395
Hindfoot	107	99–121
Ear	40	33–50
RATIOS (per cent)		
Tail/head & body	75	
Zygom. br./condylob. l.	51	
Braincase/condylob. l.	33	
Braincase/zygom. br.	65	
Palatilar l./condylob. l.	58	
Interorb./postorb.	96	
p^4/c—m^2	20·1	

Genus **GALERELLA** Gray, 1865

Slender Mongooses

Galerella Gray, 1865, *Proc. zool. Soc. Lond.* for 1864: 564. Type species *Herpestes ochraceus* Gray from Ethiopia. This name was obviously intended as a diminutive of the Greek *gale* weasel, a basic component of a variety of combinations applied to a number of viverrids and mustelids, and in this present case especially apt for the small, slender, weasel-like mongoose for which Gray devised this particular variant.

Myonax Thomas, 1928, *Ann. Mag. nat. Hist.* (10) **2**: 408. Type species *Herpestes gracilis* Rüppell from Eritrea. The name is a combination of the Greek words *mys, myos* mouse, and *anax* king, implying, in Thomas's own explanation, "the King or Tyrant of the Rats and Mice", referring to the reputed ability of this mongoose as a domestic pet to rid a house of rats and other vermin.

Taxonomy. Something has already been said (pages 245 and 266) of the question of whether *Galerella* is synonymous with *Herpestes* or merits independent status; but the matter must now be entered into rather more fully, before proceeding further, in order to make the position adopted clear and to effect definition of the genus as understood in this present work.

Galerella was erected by Gray for an Ethiopian species, *ochracea*, which he had named some years earlier and at that time assigned to *Herpestes*. The proposed genus, however, never came into use during the next 60 years until it was revived by J. A. Allen (1924); and no new form has ever been directly ascribed to it as a genus except when in 1935 Schwarz, following Allen's lead, used it in connexion with two subspecies of *sanguinea*. There had, indeed, come into existence only one new species that might have been assigned to it, Heuglin's *ruficauda*, 1877, between its creation by Gray and its virtual killing by Thomas in his 1882 review of the mongooses. In this youthful paper Thomas made a sweeping condemnation of Gray's proposals in which, he wrote, "such a large number of untenable genera are formed, and so many bad species are made . . .". He retransferred all of Gray's 1865 genera back to *Herpestes* and set a nomenclatural pattern that lasted through several decades. In his more mature years, however, he came (1929), as a result of J. A. Allen's 1924 paper, to see that, so far as the animals here at present under discussion were concerned, he had made a mistake and that Allen was "unquestionably right in maintaining that the small African Mongooses should be considered as generically distinct from the larger Egyptian species, the type of the genus *Herpestes* . . .".

There was, indeed, no tinge of doubt or ambiguity about Allen's views through the use of minced words: "In general features *Herpestes* and *Galerella* are about as diverse as two genera can well be and be referable to the same subfamily . . .". He supported this exceptionally uncompromising opinion by contrasting the two genera in respect of overall size and form, of the tail, the pelage, limbs, digits, claws and soles, as well of cranial characters and dental formula. To sweep this aside by such a comment as ". . . it should be borne in mind that although the small African mongooses appear very distinct from *H. ichneumon* (the type of the genus) there are many more small species of *Herpestes* in Tropical Asia" (Ellerman, Morrison-Scott & Hayman, 1953: 119 f.n.) seems unfairly to diminish Allen's argument, in which size was only one, the least important, character adduced.

Apart from the vast disparity of size and the altogether more slender structure of *Galerella* the points cited by Allen as divorcing this genus from *Herpestes* are that it has a pelage of a very different character; a narrow distichous tail; short limbs with relatively small and weak feet in which the pollex and hallux are reduced; and soles furred for much of the proximal half. In the skull, *Galerella* differs in its uniquely inflated anterior chamber to the bulla; in the shape and siting of the postorbital constriction; and in the constant possession of only 3 lower premolars on each side, whereas *Herpestes* most commonly has 4. The present author finds that these differential characters are valid and in sum lift the matter beyond the compromise course now often adopted (*e.g.* Simpson, 1945; Ellerman, Morrison-Scott & Hayman, 1953) of making *Galerella* a subgenus of *Herpestes*.

In spite of Thomas's eventual broad agreement with Allen regarding the generic independence from *Herpestes* of the small African mongooses, however, he at once introduced into the controversy a second, cross argument in that he held that *Galerella* was applicable only to its type species, *ochracea*. This last, he maintained, differed in its skull and in the nature of its feet from the remaining numerous forms, for which he erected a new genus, *Myonax*. The skull in *ochracea* was said to be relatively shortened, and its bullae enlarged. The first is to some extent true; the second not so obvious. But Thomas placed most reliance on the feet, which in *Galerella*, in his restricted sense, he found "quite peculiar, very slender, narrowed throughout, with the naked area extended backwards in a prominent line to the heel, the corresponding region in the ordinary mongooses being hairy . . .". In addition, the hallux is very much reduced or entirely absent. Schwarz (1935) disagreed that anything more than a specific difference was involved; and Ellerman, Morrison-Scott & Hayman (1953) adopted the same attitude. Nevertheless, Thomas did, in fact, have something more of a case than these contrary views might indicate. The skull differences he cited exist, though sometimes in no very marked form; and close examination shows that without doubt the hallux is either entirely lacking in *ochracea* or at least far more reduced than in the other species; and the nakedness of the sole does extend, in most cases, further towards the heel. He could also have drawn attention to a difference in pelage character. But whether these points add up to a generic or even subgeneric distinction is open to doubt; and in this present work *Myonax* has been rejected as requiring more conclusive data than at present available.

Turning now from generic to specific level, one of the basic problems as far so West Africa is concerned is to determine whether the red-tail-tufted, pale-pelaged *sanguinea* and the black-tail-tufted *gracilis* are conspecific or not. This is but part of the far wider problem embracing the whole vast range of described forms from other areas of the continent, the whole matter boiling down to whether all these small-sized speckled mongooses belong to a single species complex spread over the whole of tropical and southern Africa or whether valid specific differences exist within a superficially similar group.

In so far as this present work is concerned two apparently distinct groups exist differentiated most obviously by the colour of the terminal pencil of the tail. These are either identical with or related to *sanguinea* and *gracilis*, two species described by Rüppell, the former with a red tail from Kordofan, the latter black-tufted from Eritrea. Wroughton (1907: 115–116) examined the question of specific distinction between these two and came to the conclusion that there was none; and since that time it has been customary to sink the latter in the former, which had page priority in Rüppell's work. Thomas (1917) was inclined to disagree; and in 1929 quite definitely did so when he deliberately named *gracilis*, not *sanguinea*, as the type species of his new genus *Myonax*. Wroughton had based much of his conclusion on a specimen, B.M. No. 6.10.2.9 from Erkowit near Suakin, which he regarded as intermediate between *gracilis* and *sanguinea*, the tail tuft being "half chocolate-brown and half black". The colour contrast is by no means so crystal clear as this description might lead one to visualise, and the tuft, in fact, has little or nothing of the intense jet-black that characterises the "*gracilis*" forms. Thomas thought it to be nothing more than "merely one of the ordinary *gracilis* type with a more or less bleached tail-tip". Wroughton formed his opinion on the basis, to all intents and purposes, of a single presumed aberrant, intermediate specimen. Thomas had never seen "examples of the true Kordofan *sanguineus*", that is to say topotypical material; or indeed, from the known history of the collections, any red-tufted specimen other than the one he then had before him and was in the process of naming *phoenicurus*. The opinions expressed by either author regarding the validity or otherwise of the two species can therefore scarcely be taken as carrying any greater weight than tentative guesses.

The truth is that the material available is still inadequate to form the basis of a really sound conclusion. There are no topotypical examples of *gracilis* from Massawa; but there are three skins, with only two skulls, from near Suakin, some 400 km to the north and, *fide* Keay *et al.* (1959), in precisely the same vegetational belt, Coastal Subdesert. It is of interest to note that these differ quite appreciably from each other in their general pelage coloration, both above and below; and this is not merely a matter of tone but of redness or greyness, demonstrating the degree of variation that may occur even within a restricted locality. None more than approximately resembles Rüppell's type illustration. One is that already referred to as possessing a parti-coloured tail; the other two are also of interest in this connexion. Although by the standards of early 19th century mammalogical description all three tail tips could well be classed as "black" none is, in fact, of quite the same pure jet-black that characterises so many of this genus. All have in some degree something of an exceedingly dark chestnut-red, in one case so intense as to pass for black except in critical comparison with the real thing. The skulls have almost precisely the same mean measurements as *sanguinea* from Darfur and are otherwise indistinguishable except for a rather narrower post-dental palate.

The present study material is far too meagre to support any firm decision regarding the taxonomic significance of red tails and black tails; but since there is no morphological distinction between specimens possessing the one or the other Wroughton's view that *gracilis* is synonymous with *sanguinea* is adopted in this work. To what degree the vegetational background plays a part is not clear. Red tail tips are unknown from moister forest habitats and in West Africa occur from the Subdesert to the Doka zone. On the other hand, in West Africa the black-tipped forms are found in the forest belt except for *cana* which came from Cape Verde (Guinea woodland). Extralimitally, black tailed *Galerella* are commonly inhabitants of drier vegetational types.

The position of *Galerella*, therefore, adopted in this present work is:

Galerella	*sanguinea*	*sanguinea* (Rüppell), 1835.	Extralimital.
,,	,,	*melanura* (Martin), 1836.	Forest.
,,	,,	*cana* (Wroughton), 1907.	Guinea woodland.
,,	,,	*phoenicurus* (Thomas), 1912.	Doka woodland.
,,	,,	*saharae* (Thomas), 1925.	Subdesert.

There is no present evidence that *G. s. mustela* Schwarz, 1935, from lower Cameroun occurs within the limits chosen for this work; but it might eventually turn up from the Cross River area.

Distribution and general. The genus is spread over nearly the whole of Africa south of the Sahara except for the extreme south-west. In the territory dealt with in this present work specimens are known from the extreme west at Cape Verde, Sierra Leone, Liberia, Ivory Coast, Ghana, western and northern Nigeria, and Aïr. There does not appear to be any preserved specimen or published record of the species from eastern Nigeria and that portion of Cameroun that lies north of the Sanaga River; but, in so far as the latter is concerned, Gerald Durrell (personal communication) obtained specimens at Bafut and Wum, roughly 20 and 50 km north of Bamenda. Over much of its range the genus can be said to be common; and this is true of the West African high forest form, *melanura*, but not, apparently, of the other races within the region. These are all distinctive little creatures that could scarcely be confused with any other mongoose or small mammal occurring in West Africa, except possibly, at a distance, a ground-squirrel.

Description. The *Galerella* mongooses (Plate 9) are all small, very slenderly built animals, weighing from 0·5 to 0·75 kg, with finely speckled pelage, sharp faces and longish tails. Head & body length is of the order of 300 mm, more or less. Field measurements are notoriously undependable, and in one relevant case, the type of *saharae*, those for the head & body and the tail appear from the dried skin to have been reversed by a usually extremely reliable collector (Buchanan). Considerable discrepancy arises in long-haired genera from whether the tail measurement has been made to the last joint or to the tips of the hairs; but so far as can be gathered from label data the tail in *Galerella* is for the most part somewhat shorter than the head & body, reaching some 85 to 95 per cent; though in a few cases it seems to be genuinely longer.

The pelage consists of long, very fine, dense or fairly dense underfur and abundant annulated, flat-sectioned bristle-hairs that do not so markedly exceed this in length as they do in many other species. The whole texture of the coat is fine, silky and sleek; and in this it may be said to differ from all other West Africa mongooses. The underfur is of variable length in all specimens, being composed of longer and shorter hairs ranging from about 6 to 12 mm. It is curiously variable in colour from specimen to specimen of the same race. The annulation of the bristle-hairs at first seems confusingly different in the different forms; but on analysis a fairly consistent generic pattern emerges. There are specific differences of ring-width and colour, and in a few cases a complication is introduced by the division of the two pale zones by a subsidiary darkish band; nevertheless, fundamentally the bristle-hair pattern is made up in the following way. There is a pale basal region whose range of mean lengths is from 8 to 11½ mm; distally of this lies a narrow blackish ring mostly 2 to 5 mm wide; and this is followed by a pale (white, yellow, orange) zone of very variable width ranging from about 1½ to 9½ mm; finally there is a brown or black tip of at least 2 mm but when unbroken or unworn reaching 5 mm, and very finely drawn out. Very occasionally this tip engulfs the subterminal pale zone, joining the next dark ring to form a long, wholly blackish distal half to the hair. The total bristle-hair length averages from 17 to 24 mm. The overall effect is of a finely speckled coat. In some specimens the different colour bands lie randomly; in others they fall to some extent in groups, giving rise to a somewhat irregular, rather narrow cross-banding, in no way comparable to the bold pattern of *Mungos mungo*. This is by no means an invariable feature of every specimen of the same form; where it occurs, the speckling takes on a rather coarser appearance than the fine punctulation produced by colour bands that are randomly disposed.

In many forms the underside is unicolorous and fairly sharply divided from the flanks; but this is not always so, especially as regards the common West African race *melanura*. Near each axilla there is a whorl of hair, and from here over the anterior part of the chest the hair is directed forwards; but on the throat, though the lie of the hair is abnormal in not being evenly directed rearwards, exact detail of arrangement appears to vary from form to form or specimen to specimen. Generally, here, the fur is directed outwards from a longitudinal medial parting, but further detail in this region is rather confused, there being sometimes a distinct gular whorl, and sometimes part of the hair is directed forwards and meets the opposing fur of the chin in a transverse ridge.

The head in *Galerella* is small, the face pointed, and the upper lip beneath the naked rhinarium very narrow. The rounded ears are very broad but low and set well on the sides of the head. The legs are short and speckled in the manner of the back; the narrow feet either similar or pale and more or less unicolorous. Both pollex and hallux are very much reduced, the remaining digits slightly webbed basally, the claws short and curved. The sole of the hindfoot is hairy in the posterior portion near the heel. The tail though clad with long bristle-hairs is not bushy but the hairs are arranged somewhat distichously, though this is less evident in some specimens, or forms, than others. In general it can be characterised as narrow, tapering from a moderate base to a fine tip, the terminal two or three inches being unicolorous, either jet-black or rufous. The main portion of the tail is of the same colour and speckling as the back on top but sometimes more or less unicolorous, paler, below or with a rufous medial longitudinal stripe. There is the usual herpestine subcircular pouch surrounding the anus and external orifices of the scent glands; but no one appears to have studied these latter in detail. The females carry two abdominal pairs of mammae.

Skull (fig. 40). *Galerella* skulls are the smallest of the mongooses occurring in West Africa the condylobasal length being always well under 70 mm. The long ovoid braincase terminates posteriorly in a broad flange-like supraoccipital crest; but in the vast majority of cases there is nothing more than a rudimentary or very slight sagittal crest. In only one of some fifty skulls examined, a mediumly-aged male, could this crest be characterised as well-developed into an erect flange of appreciable depth. The small extreme posterior section adjacent to the supraoccipital crest is nearly always present except in very young specimens. The relationship of the measurements of the interorbital breadth and the postorbital constriction is variable; the former is roughly constant at about 11 mm, more or less; but the latter ranges from less than 10 mm to nearly 14 mm even in the same group of approximately comparable ages, and the ratio of the former to the latter from 77 to 120 per cent. But whatever its

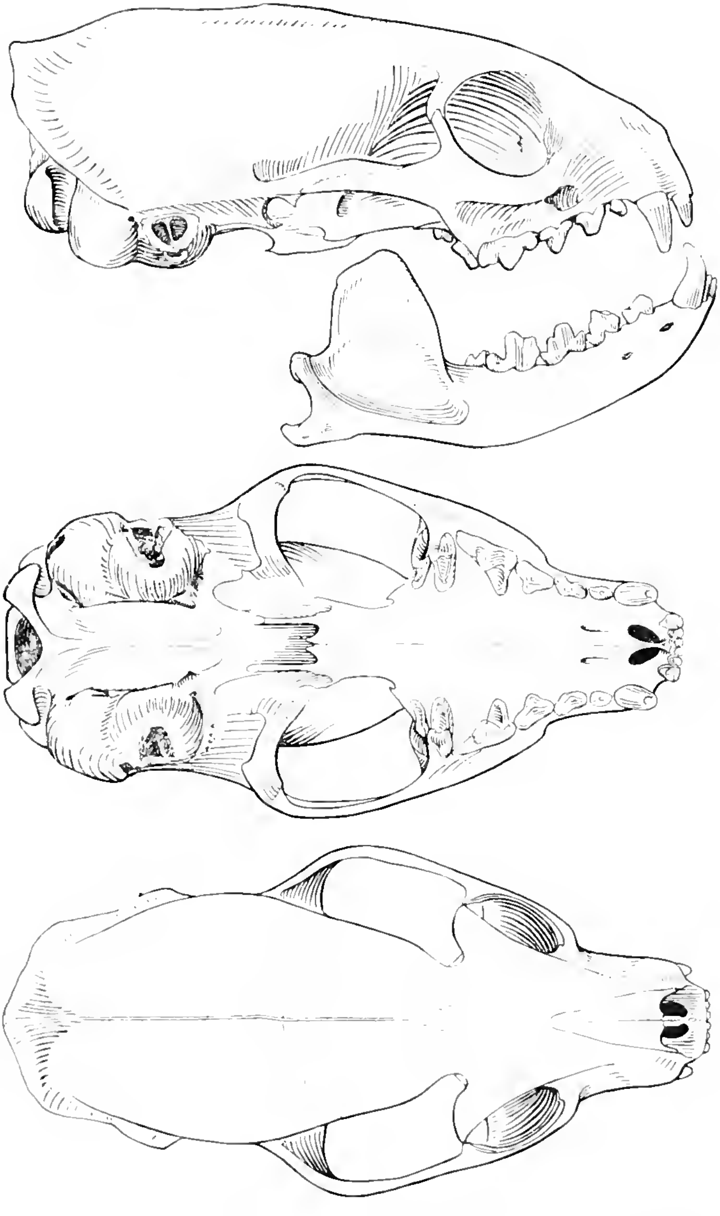


Fig. 40. *Galerella sanguinea melanura*: skull, B.M. No. 35.1.30.53, ♂, × $\frac{3}{2}$

relative size one of the chief features of the *Galerella* skull distinguishing it from *Herpestes* and *Xenogale* is the fact that this postorbital constriction lies immediately behind or even a little forward of, the back margin of the circumorbital ring, not several millimetres posterior to it as in the others (figs. 40, 36 and 44). In nearly every adult skull the postorbital processes unite, or almost unite, with the jugal processes to form ossified complete circumorbital rings. The frontal region is broad and rounded; the rostrum short and blunt. Fusion and complete disappearance of the nasal sutures takes place early. The zygomata are fairly strong, the zygomatic breadth about average, that is to say roughly half the condylobasal length. The postdental palate is rather narrower than it is long, sometimes more so than others, and occasionally markedly waisted. The bullae in this genus are unique amongst West African mongooses in that the anterior chamber is much more inflated than in the other genera and begins to be comparable in size to the posterior one, though less globular in shape (fig. 41).

FIG. 41. *Galerella sanguinea melanura*: bulla, × 2

The premolars are very constantly $\frac{4}{3}$. Only three skulls of many examined had the upper cheekteeth with the first premolar lacking from one side alone. The anterior upper premolar is always an extremely small tooth; all the remaining cheekteeth are, when unworn, very sharply cusped, the dentition having the appearance of being largely insectivorous. Nevertheless, the carnassials are relatively amongst the largest in the subfamily, the upper ones occupying 27 per cent of the length of the toothrow, and the lower one having a large sharp outer blade, the posterior outer cusp being the largest and the inner posterior the smallest of the three on the anterior portion of the tooth. m^1 is a fairly large tooth, but m^2 is much reduced and of less bulk than the lingual portion of m^1. The tightly packed incisors are in an almost straight transverse row; the canines are of moderate size.

Habits. Although mongooses of this genus are widespread and pretty common over a good deal of the continent south of the Sahara not much has been written of the details of their way of life. There may be some variation of habit between different forms; but because of the confusion which has long existed in respect of subgeneric classification and nomenclature this is a matter which must necessarily for the present remain obscure. The only course is to assemble on a generic basis the little that has been recorded, irrespective of the specific or racial names with which the observations were originally connected. As usual, there is almost nothing in the way of field notes from West Africa itself. Most recent accounts, in fact, all stem from a single source, the notes assembled by Shortridge (1934) concerning the genus in southern Africa; but Taylor (1970) has included the genus in his observations on locomotion made in East Africa. Except for a few odd scraps of information no other accounts of habits have been traced.

The shortage is due in part to the fact that few people appear to have kept *Galerella* as a pet; and seemingly no one who has done so has felt the urge to describe in writing the animal's nature and habits as revealed under these conditions. Opinions, indeed, differ regarding the possibility or desirability of keeping the slender mongoose as a house companion. Some have held that like others of its kind it is readily tamed (Astley Maberly) and makes a splendid pet keeping the home free of vermin and cockroaches; others have found it to take much less readily to captivity than most and to be largely untameable. Cansdale (1946), indeed, writing of the West African form *melanura*, could not understand why anyone should ever wish to keep it about the house since it was foul-smelling and in point of fact so objectionable that it was one of the few animals of the forest that nobody would eat. Illustrating the saying that one man's meat is another man's poison there is a note in Hinton & Dunn (1967: 10), under the name "Dwarf Mongoose", that according to Dr. S. Toye the hunters of Northern Nigeria eat it despite its unpleasant odour.

Galerella is almost entirely diurnal, hunting singly or in pairs at almost any hour of the day, though possibly more in the early morning than during the heat of the afternoon. It has been said to come out sometimes on moonlight nights. As it runs, not trots, (Taylor, 1970) along in search of prey it holds its tail out behind with the terminal half curved upwards; and since its size and sometimes its coloration are not dissimilar it may, especially when scurrying across a road, be mistaken for a ground squirrel, the nature and carriage of the tail, however, helping to distinguish it. It is widely agreed that this mongoose differs sharply from others in the relative facility with which it can climb trees, and even descend head-foremost, though it lacks the expert ability of the cats and squirrels. Its short, curved claws and light weight help it in this activity. Taylor (1970), however, while finding that this species was an able climber in as much as it would rush at wire or other rough surfaces and clamber up, considered that it was not really a controlled climber in that it generally fell down. There seems little doubt that the slender mongoose climbs not only to escape pursuit but also to seek part of its food in the shape of nesting birds and arboreal mammals. Taylor also observed that this mongoose frequently rose to its hindfeet; and from this erect standing position could, if it wished to reach something above it, jump vertically as much as 50 cm.

Like other mongooses it consumes a large number of insects. Ansell (1965) records taking a specimen near a grass fire where it was busily eating fleeing grasshoppers; but when the stomach contents were examined they were found to contain, besides insects, the remains of a squirrel. Apart from this one example the question of food materials has not been very carefully investigated; mongooses of this genus are credited with the usual range of prey—insects and their larvae, birds, eggs, rodents, lizards and snakes. As regards the last, Astley-Maberly (1959) wrote of a southern African representative of the genus that it will kill even large cobras, and Gerald Durrell (personal communication) found that they would readily eat snakes so long as these were not too large. Slender mongooses are also said to be poultry thieves if they get the chance; and Cansdale (1946) relates, in relation to the forest form *melanura*, an interesting Ghana version of the folk legend usually associated in other parts of Africa with *Atilax*. This is that *Galerella* lies on the ground displaying its open anal scent gland pouch, thus arousing the curiosity of some nearby fowl, which, supposing this pinkish structure to be something edible, pecks at it, chokes and gets caught and killed. As with other carnivores, wild fruits are said to constitute part of the dietary; and *Galerella* has been accused of digging up groundnuts in farms.

There is little information relating to breeding habits. The shelter, for raising the young as much as for regular nightly use, is said to be made in hollow trees, in holes in logs or in the ground amongst tree roots, or in crevices between boulders in rocky country. The number born in a litter has been recorded as 2 or 3, occasionally 4. Regarding development of the young or parental care there is nothing on record. One specimen of *Galerella* is known to have lived in a zoo to the age of nearly 6 years (*Int. Zoo Yr. Bk.*, **2**).

GALERELLA SANGUINEA (Rüppell) Slender Mongoose

Herpestes sanguineus Rüppell, 1836, *Neue Wirbelthiere zu der Fauna von Abyssinien gehorig, etc.*, pt 7, Säugethiere: 27, pl. 8 fig. 1, pl. 10 fig. 3. Type locality Kordofan, Sudan. The Latin adjective used as the specific name means bloody and was given in respect of the reddish tail tuft.

Herpestes gracilis Rüppell, 1836, *Neue Wirbelthiere zu der Fauna von Abyssinien gehorig, etc.*, pt. 7, Säugethiere: 29, pl. 8 fig. 2, pl. 10 fig. 2. Type locality the valleys west of Massawa, Eritrea. The specific name is the Latin word for slender, given with reference to the build of the body.

Cynictis melanurus Martin, 1836, *Proc. zool. Soc. Lond.*: 56. Type locality Sierra Leone. Type in the British Museum, No. 55.12.24.229, sex unknown; skin poor and with half of the tail missing; skull merely the anterior fragment of each jaw. This name is composed of the Greek words *melas, melanos* black, and *oura* tail, referring to the colour of the tip. Valid as a race.

Mungos melanurus canus Wroughton, 1907, *Ann. Mag. nat. Hist.* (7) **20**: 114–115. Type locality Cape Verde, Senegal. Type in the British Museum, No. 72.12.12.5, ♀; skin in poorish condition, skull with the right side and back of the braincase missing. The Latin word *canus* means grey or hoary, and refers to the overall pelage colour. Valid as a race.

Mungos phoenicurus Thomas, 1912, *Ann. Mag. nat. Hist.* (8) **10**: 280–281. Type locality Panyam, Bauchi, Northern Nigeria. Type in the British Museum, No. 12.7.9.2, ♂; skin and skull both in good condition except for the loss of both inner upper incisors. The specific name was coined from the Greek words *phoinix* purplish-red, and *oura* tail, and refers to the tail tip. Valid as a race.

Herpestes phoenicurus saharae Thomas, 1925, *Ann. Mag. nat. Hist.* (9) **16**: 189. Type locality Aouderas, Asben, Niger, 835 metres. Type in the British Museum, No. 25.5.12.12, ♂; skin in good condition but a little of the end of the tail missing, skull good except for one inner upper incisor missing.

Distribution. In view of the continued argument regarding the validity or otherwise of reputed species it is impossible to give any clear indication of the full distribution of *sanguinea*. As the species is understood in this present work, and explained in the taxonomic section on page 309, it is known in West Africa from Cape Verde to Nigeria, and is said to occur also in at least the Bamenda area of upper Cameroun; but, as regards this last, in the absence of specimens it is impossible to say which form is concerned. Racial identification is impossible also in respect of sightings in the Borgu Game Reserve of western Nigeria reported by G. S. Child (private communication). Extralimitally, *sanguinea* must, by definition, range to the Red Sea; and Schwarz's *mustela* from lower Cameroun is certainly part of the same complex; but how far south in the continent the species reaches is, at the moment, entirely a matter of opinion.

Description. The species conforms in all essentials to the broad general description already given for the genus; but the races into which it is subdivided are, within this framework, so diverse that any more detailed description must be reserved for each of these.

Habits. The habits so far as known have been dealt with above, and there is nothing that can be specifically added for *sanguinea*.

Skull (fig. 40). There are no differences from the general generic characters given above.

Taxonomy. In the broad review of the taxonomy of the genus the question of species was necessarily gone into and there is not much on this account that can be usefully added here. Whether there are different species in South and West Africa or whether they are all merely local forms of one species it is at present quite impossible to determine with any approach to finality; and it would seem that not only must more material be forthcoming but that, also, cytological and serological studies must be made before any fully satisfactory solution to the problem can be achieved. For South Africa, for example, Roberts in 1951 recognised 7 independent species, none of which was *sanguinea*; while in 1953 Ellerman, Morrison-Scott & Hayman cast the same 7 forms into 2 species, classing 4 of them as races of *sanguinea*.

Really, much the same confusion exists subspecifically. Something like 45 names are recognised as possibly having some validity in various parts of the continent—or, at least, in the absence of a general revision have not so far been seriously questioned. The fact is that with a speckled pelage and the wide diversity of ecological and climatological conditions existing in Africa an almost infinite variety of colour forms can exist. How many of these it is possible and useful to distinguish with a definite name is another matter. In West Africa, as elsewhere, two distinct colour forms stand out, those with a black tail tip and those in which it is rufous; but whether this has specific significance or is merely local or phasal nobody knows. Running alongside these two main types are pelage colour variations. Several of these have been accorded subspecific names and are separately described below; but their precise taxonomic value is an open question.

The West African races listed earlier can be differentiated by the following key.

KEY TO THE WEST AFRICAN RACES OF *G. SANGUINEA*

(previous key page 245)

1. Tail tip red 2

Tail tip black 3
2. Underside pale yellowish-brown . . . . ***phoenicura***
Underside white . . . . ***saharae***
3. Dorsal pelage basically deep rich red, speckled with black . . ***melanura***
Dorsal pelage basically buffish . . . . ***cana***

Galerella sanguinea phoenicura (Thomas) Western Red-tailed Mongoose

The two West African red-tail-tipped *Galerella* are, as exemplified by the types, both distinctly darker and redder than the majority of Sudanese *sanguinea*, in respect of the tail tip as well as of the dorsal pelage. The nominate, Sudanese, race is basically buff above; the tail tip pale orange-ochre rather than red; in *phoenicura* (Plate 9) the dorsal pelage has a considerable amount of red in it, particularly in the mid-lower back; and the tail tip is rich rusty-red. The belly is buffy. In this form the bristle-hairs average about 22 mm in length; their basal zone is buff, about 8 mm; there is next a deep brown zone of about 5 mm; the subterminal band is yellow-gold, also about 5 mm; and the deep-brown tip is about 4 mm.

Further collecting may well show that there is intergrading. The type of *phoenicura* was collected at Panyam in the Doka woodland at about 1250 metres on the Bauchi Plateau, north Nigeria; a second, younger, specimen taken at Kabwir about 50 km further east, on the edge of the plateau at about 760 metres and vegetation more of a Sudan woodland type, and assigned also, by Thomas, to *phoenicura*, is not so red, though it is considerably darker than typical lowland Sudanese examples of *sanguinea*. But it is closely matched by specimens from the Jebel Marra mountains of Sudan, taken at 2000–2500 metres, though the tail of the West African animal is of a slightly deeper red and the belly rather more yellowish.

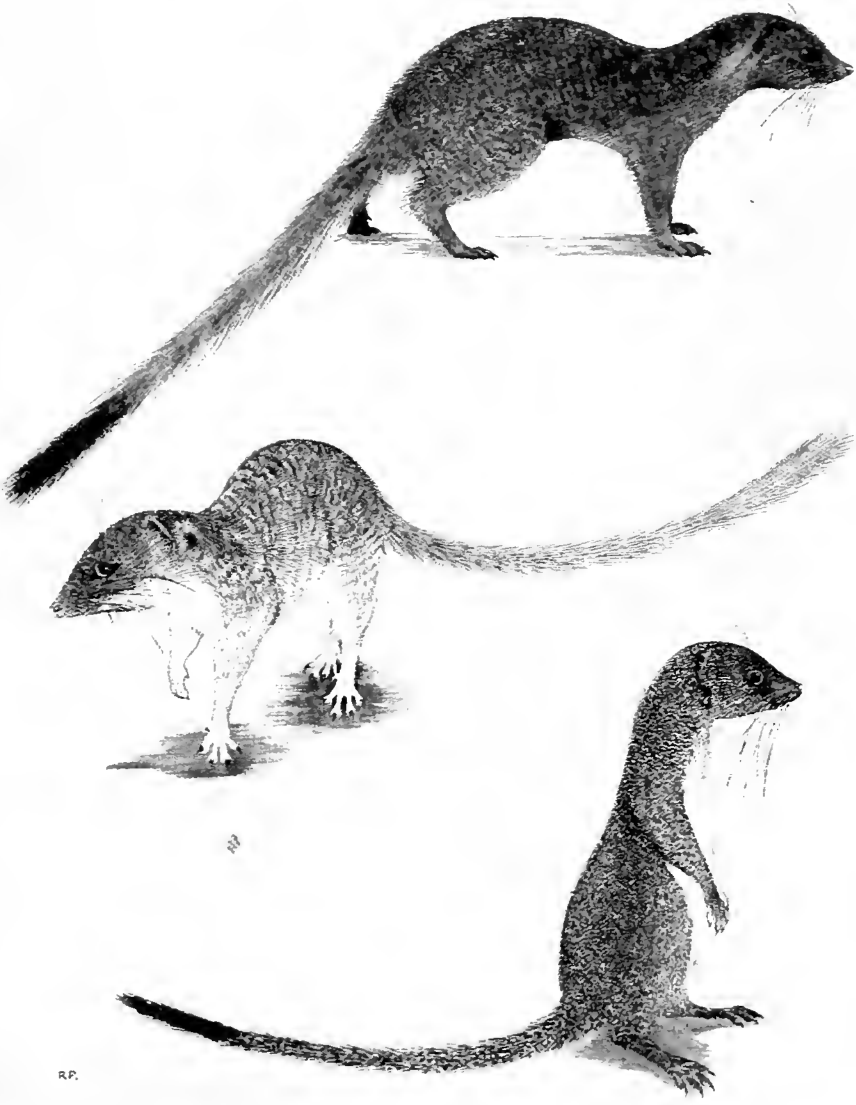
Galerella sanguinea saharae (Thomas) Aïr Red-tailed Mongoose

This differs very little from the above. The dorsal pelage is a more orangey-red; the tail tip deep chestnut through the admixture of a number of black hairs; and the underside is pure white. This last is the only clear difference between it and *phoenicura*, though the few available measurements indicate it as a somewhat smaller animal. The annulation of the bristle-hairs in this form appears to be very irregular; but their mean length is about 18 m .

Only two specimens are known, both from Aïr on the southern edge of the Sahara: one from Aouderas, the other from Tchsiderak, both in the Sub-desert zone, at an altitude of 750–850 metres.

Galerella sanguinea melanura (Martin) Forest Slender Mongoose

This is without doubt the commonest race of West Africa. Specimens exist in the British Museum from Daru, Njala and unnamed localities in Sierra Leone; Mount Barclay in Liberia; Beoumi in the Ivory Coast; Bibianaha, Kumasi, Mampong, Juaso, Tarkwa and a number of unspecified places in Ghana; a total of 20 specimens



Forest Slender Mongoose Ga[illegible] Western Red-tailed Mongoose Ga[illegible] Guinea Slender Mongoose Galerella [illegible]

as compared with a maximum of 2 of any other form. Kuhn (1965) also records this race from a large number of places in Liberia. All known collecting localities are in the high forest.

This race (Plate 9) differs from all others in its dark, rich orange-red dorsal colouring. Most specimens, but not all, exhibit a faint pattern of narrow black transverse banding. The bristle-hairs average about 19 mm in length. Their annulation pattern is more complex than in the other races by reason of the fact that the normally pale basal and subterminal zones are each divided by a dark intrusion so that each instead of being a single unit becomes three zones. Thus, the basal zone, totalling on the average 8 mm is divided up, yellow, brown, yellow, 4½ mm, 1½ mm, 2 mm. Distally of this lies the normal dark ring (deep brown), in this case exceptionally narrow, measuring about 2 mm. The succeeding pale zone becomes threefold, orange, deep brown, orange, 1½ mm, 2½ mm, 2 mm; succeeded finally by the tip which in this case is pale brown, about 3 mm. It will therefore be seen that instead of the normal four zones there are in *melanura* eight; and the deep, warm coloration is brought about by the amount of brown, orange and yellow in place of the white, buff or gold of the paler forms.

The underside is a little variable, sometimes orangey but mostly rather like the back but of a paler tone; the hinder part of the belly is more sparsely haired. The upper side of the distichous tail is like the back, but the lower side has a medial longitudinal unspeckled stripe of reddish-orange; the tip, for some 50 to 80 mm, is jet-black. The legs and feet have much the same coloration as the back. The size is relatively large as in *phoenicura*. The skull is shown in fig. 40.

Galerella sanguinea cana (Wroughton) Guinea Slender Mongoose

The type of this, which came from Cape Verde a hundred years ago, has an exceptionally finely speckled dorsal pelage with much less red in it than any of the other West African forms, and a jet-black tail tip (Plate 9). In broad terms it can be characterised as buff ticked with black rather than reddish ticked with black. The bristle-hairs have an average length of about 17 mm. The pale basal region is in this race divided into three by an intrusive pale brown band, there thus being a total of six instead of the usual four zones. The effect of fine speckling is due to the fact that all of these are narrow; from the base outwards they run as follows, with their mean lengths: white 3½ mm, pale brown 3½ mm, white 2 mm, black 4 mm, white 1½ mm, tip, black, 3 mm.

So far as can be told from the poor skin the underside is buffish, lightly speckled except over the hinder part of the belly; but the chest, throat and chin are greyish due to the pure white subterminal and basal bands and grey underfur. The type locality lies within the Guinea zone.

There are other specimens which, while not matching exactly, nevertheless fall into this category; that is to say with a black tail tip and predominantly buffish rather than predominantly reddish dorsal pelage. It would be possible, picking on slight colour differences both above and below, to give these separate distinguishing names; but it will almost certainly be found that they all intergrade. In this connexion it may be repeated here that there are two skins, both collected at Erkowit near Suakin on the Red Sea coast of Sudan, the one cold grey, the other warm buff; and these seem to demonstrate that there may be marked colour variation within a single locality let alone differences that may be expected within a wide-ranging cline. While all of the specimens mentioned in this section may be clearly recognised as pertaining to the "*gracilis*" category, not one of them corresponds more than approximately to the colour plate accompanying Rüppell's type description of that form. It can be argued that if all these animals do constitute part of a transcontinental cline then *cana* is synonymous with *gracilis*; but it is retained here for the time being as a convenient distinguishing label in West Africa.

The other two West African specimens in the British Museum that can be assigned to this race are No. 50.1571 from Lawra (Ghana, Doka woodland); and No. 7.7.8.72 from the River Fafa (Central African Republic, Doka woodland, c. 6°30N 18°20E). In the former the speckling is coarser than in the type and the dorsal colour is not

Table 19: Numerical data for *Galerella sanguinea*

	phoenicura	*saharae*	*melanura*	*cana*
Vegetation	Doka—Sudan	Subdesert	Forest	Guinea—Doka
Number in mean	1	2	8	1
Condylobasal length	66·8	60·4	64·9	—
Basilar length	61·3	55·6	60·2	—
Palatilar length	33·5	28·8	33·3	29·4
Zygomatic breadth	32·7	30·6	33·3	28·5
Upper cheekteeth breadth	20·7	19·2	21·0	18·7
Nasals, length	—	—	14·0	13·6
Interorbital breadth	12·2	10·8	11·8	10·1
Postorbital constriction	9·7	10·2	11·4	11·9
Braincase breadth	25·0	24·2	25·2	—
Toothrow (c—m^2)	24·4	22·2	23·1	21·3
p^4 length	6·6	6·1	6·5	5·7
m^1 breadth	6·0	5·5	5·9	5·1
m^2 breadth	3·0	2·9	3·4	2·9
m_1 length	5·6	5·4	5·8	5·3
m_2 length	3·1	2·7	3·2	2·4
Head & body	330	325	324	—
Tail	289	277	264	—
Hindfoot	61	56	59	?c. 48
Ear	28	23	27	—
RATIOS (per cent)				
Tail/head & body	88	85	81	—
Zygom. br./condylob. l.	49	51	51	—
Braincase/condylob. l.	37	40	39	—
Braincase/zygom. br.	76	79	76	—
Palatilar l./condylob. l.	50	48	51	—
Interorb./postorb.	126	106	103	85
p^4/c—m^2	27·0	27·5	28·1	26·8

far from the Kabwir specimen of *phoenicura*; but it differs from this latter by its black tail tip and dull orange belly. The latter is closer to the type dorsally; but the underside is dull orange as far forward as the throat.

There is no record of Schwarz's extralimital *mustela* (Efulen, lower Cameroun) having been captured within the boundaries taken for this present work. Dorsally this form is close to *cana*; but below it is appreciably darker, a drab brown; and the tail lacks any of the bright orange which marks its lower aspect in *cana*.

Genus **GALERISCUS** Thomas, 1894

Four-toed Mongooses

Bdeogale Peters, 1850, *Spenersche Z.*, 25th June 1850 (in which were published the *Sber. Ges. naturf. Freunde Berl.* for the meeting of 18th June 1850; subsequently made more readily available in the volume of reprinted reports, 1839–1859, issued by the Gesellchaft Naturforschender Freunde zu Berlin in 1912); and 1852, *Mber. K. preuss. Akad. Wiss.*, 81. Type species *Bdeogale crassicauda* Peters, as designated by Thomas, 1882: 81, Mozambique. In part, of recent authors. This generic name was derived from the Greek words *bdeo* to stink, and *gale* weasel.

Galeriscus Thomas, 1894, *Ann. Mag. nat. Hist.* (6) **13**: 522. Type species *Galeriscus jacksoni* Thomas, from Kenya. The name is a diminutive of *Galera*, Thomas having likened the external appearance of the species on which the genus was founded to the grison of Brazil, then known as *Galictis* (*Galera*) *allamandi.*

This genus covers two known species of mongoose, *jacksoni* from East Africa and *nigripes* from West Africa, the one from montane vegetation at 2500 metres, the other from the closed forest block.

Taxonomy. *Galeriscus* was erected by Thomas in 1894 to accommodate a new small carnivore from Kenya, to which he at the same time gave the specific name *jacksoni*. Later, Pocock (1916a) published a note pointing out that this genus "falls as a synonym of *Bdeogale*"; but while confirming that in his opinion this was correct he did not, in fact, claim this idea to have originated with himself but attributed it to a change of view (unpublished) on the part of Thomas himself. Thomas, on the other hand, would not seem to have concurred; for he subsequently (1928) asserted that the notion of synonymy, which extended beyond the mere genus, actually came from Matschie and from Pocock who considered *Galeriscus jacksoni* to be the same as the mongoose then currently known as *Bdeogale nigripes*. The paper in which Thomas (1928) dealt with this subject was, indeed, one of the last he ever wrote, and in it he, without reservation, expressed his mature taxonomic opinion that *Galeriscus*, type species *jacksoni*, was clearly generically distinct from *Bdeogale*, type species *crassicauda*. This view seems to have gone unquestioned up to at least 1941, for G. M. Allen (1939) listed the two genera separately in his Checklist, and Hill & Carter (1941) also used *Galeriscus* as a fully independent genus. Simpson (1945), however, included *Galeriscus* in *Bdeogale*; and Ellerman, Morrison-Scott & Hayman (1953) listed it, incidentally, as nothing more than a valid subgenus. Since then it has become customary to sink, or partially sink, *Galeriscus*—*e.g.* Grassé (1955), Dekeyser (1955), Walker (1964).

In point of fact no one appears ever to have published any reasoned argument for equating *Galeriscus* with *Bdeogale*. Thomas, originally led astray, to use his own words, by a poor and incomplete specimen, believed his newly named *Galeriscus jacksoni* to be related to the grison, belonging to an entirely different section of the carnivores, the Mustelidae; and it was not until he acquired better material that he came to see that it was really a viverrid. Matschie's correction was a bald assertion in a list of errata (1895: 147). When Pocock (1916a) published his brief statement of synonymy he cited as confirming Thomas's alleged view the single character of the structure of the ear, which was "like that of *Mungos* rather than of *Grison*". In effect, all this scrap of evidence amounted to was not the synonymy of *Galeriscus* with *Bdeogale* but that the former was, in fact, a viverrid not a mustelid, a very different matter.

Thomas based his view of the validity of *Galeriscus* on both external and cranial characters. Regarding the first, he considered that between "the two groups, *nigripes* and *jacksoni* on the one hand and *crassicauda* and its allies on the other, there is a difference of general appearance and coloration so conspicuous that if such a comparison had ever before been made a suspicion of the generic distinction of the two must have arisen". He went on to cite build, tail-shape, and colour; but the differences of form are not, in fact, so striking as one might be led to suppose, except possibly in the tails. Colour, of course, is of little moment in generic differentiation. The pelage of some old West African *nigripes* is, in its extreme shortness, sharply distinct from *Bdeogale*; but in younger examples as well as in East African *nigripes* and in *jacksoni* this distinction disappears; and the apparent difference may be nothing more than a matter of age, as discussed below.

The main case for the separate recognition of *Galeriscus* must rest on cranial and dental characters. Thomas drew attention to a few important differences; but there are more than he cited. The cranial distinctions are those of proportion. In *Bdeogale* the posterior part of the skull is very much longer; in fact, if the glenoid fossa of a *Bdeogale* skull is held level with that of *Galeriscus* it will be seen that the occipital condyles are almost level too, in spite of the very much shorter overall skull length. On the other hand the rostrum is relatively shorter. Expressing this in terms of percentages of the condylobasal length: the distance from the glenoid fossa to the condyle is under 30 per cent in *Galeriscus* and about 33 per cent in *Bdeogale*. The length of skull lying anterior to the front margin of the orbit is 31 to 34 per cent in *Galeriscus* and 28 or 29 per cent in *Bdeogale*; and the nasals are 24 per cent and 18 per cent. Other cranial differences are to be seen in the postorbital constriction, which in *Galeriscus* is situated appreciably more posterior to the processes than in *Bdeogale*; and in the shape of the postdental palate, which is roughly square in the former but somewhat longer than broad in the latter.

What is possibly the most significant distinction between the two genera lies in the posterior cheekteeth, which in *Galeriscus* are of a much heavier build and squarer shape, having none of the transverse narrowing of *Bdeogale*; m^2 is a much more important, larger, tooth.

Taking all these various differences into account and especially the clearly distinct characters of the teeth, the present author feels that, despite the apparently intermediate role sometimes played by *jacksoni* (though certainly not in the teeth and cranial proportions detailed above), Thomas was justified in regarding *Galeriscus* as validly separable from *Bdeogale* at generic level.

Distribution. As thus defined, *Galeriscus* has two species and a known distribution from the Cross River basin (eastern Nigeria) to the Congo and, possibly (Hill & Carter, 1941) northern Angola; and in the east as far as the highlands of Kenya. The one species, *nigripes*, is essentially a high forest, the other, *jacksoni*, a mountain species.

Description. These are moderate-sized to very big mongooses; *nigripes*, as it occurs in West Africa, is, in fact the largest of all. The pelage is mostly short to very short, dependent to some extent upon age, and is characterized by very dense underfur amongst which stand fairly long, annulated bristle-hairs which, when the coat is in repose, more or less conceal the underfur. The general overall dorsal colour is variable, usually a medium to palish grey but it may be deep brown or even red. The legs and feet are always deep blackish-brown, contrasting, except in the unusual dark forms, very markedly with the back. This striking feature is shared, in West Africa, with *Ichneumia*; but *Galeriscus* has only 4 digits on each foot.

Skull. A detailed description of the skull as it occurs in West Africa is given below in connexion with the species *nigripes*; here a few of the main generic characters are briefly given; some have already been discussed in the taxonomic section above. There is always a well-developed sagittal crest in both sexes; the interorbital breadth is always much greater than the postorbital constriction; and the circumorbital ring seems never to be complete.

GALERISCUS NIGRIPES (Pucheran) Black-footed Mongoose

Bdeogale nigripes Pucheran, 1855, *Revue Mag. Zool.* (2) 7: 111. Gaboon. The specific name is compounded from the Latin words *nigro* to be black, and *pes* foot.

Distribution. This, the largest of West African mongooses, is found only in one small corner of the region in the dense forests in the bend of the Cross River and around its headwaters. Eleven West African specimens exist in the British Museum, collected at Oban, Okuni, Ikom, Mamfe, Ossing and Bashauo, all these places being either on or at a short distance from the Cross River. Gerald Durrell (personal communication), who, besides more normal material, obtained the specimen mentioned in the following section at Bakebe, about 35 km south-east of Mamfe, was informed by experienced Africans that *Galeriscus* was a rare animal. In spite of excellent local hunters he was never brought a specimen in Kumba. Extralimitally, specimens are known from Bitye (lower Cameroun) and Como River (Gaboon); thence *Galeriscus* ranges across the central forest block to north-east Congo. Hill & Carter (1941) give it as reputedly occurring in northern Angola; but there appears to be no certain evidence of distribution south of the River Congo. While by no means common, it does not, in the localities where it occurs, seem to be particularly rare.

Description. This large mongoose (Plate 8) has, when full-grown in West Africa, a head & body length of 600 mm or more, and a tail measuring not quite two-thirds as long. The adult animal stands some 150 to 175 mm at the shoulder. Hayman (in Sanderson, 1940) expressed the opinion that, despite appearances to the contrary, eastern Congo specimens are not habitually smaller, the two series in the British Museum not being properly comparable in respect of age. The present writer, on the other hand, inclines to the view that some general difference of size validly exists.

The body is long and solidly built, the legs short and relatively slender, the neck long, the head narrow, the muzzle blunt. As a rule the general appearance is that of a light or medium grey animal, with markedly contrasting black legs and a whitish tail; but there is one eastern Congo specimen which has a dark brown body and a pale brown tail. Nothing as dark as this has so far been collected in the west, the dorsal colour there running from an almost pure unspeckled cream to a dark blackish-brown so abundantly ticked with white that the total effect is a medium buffish-grey. However, a remarkable specimen of this animal was obtained at Bakebe (Cameroun) by Gerald Durrell (personal communication). This, except for the black legs and white tail, was bright foxy red. Unfortunately when the animal died the skin of this hitherto unrecorded colour phase was not preserved; but there can be no doubt, from the general shape and appearance of the animal, critically assessed by an experienced field naturalist well acquainted with the species, that it was indeed *Galeriscus*.

The composition of the pelage is one of dense, fine, medium-brown underfur, 10 to 12 mm long; and relatively scattered, though in sum abundant, banded bristle-hairs, which form the contour coat and, except in young animals, very largely conceal the underfur. The texture of the coat presents some difficulty. Most of the West African specimens have very short fur, very close-lying; but some, and especially eastern Congo skins, have it longer and looser. Hayman indicated that this was probably simply a question of age; and there is good evidence that this is at least a contributory cause. In the pelage of old individuals the bristle-hairs are rather less than 20 mm long and are, with slight variation, annulated thus: white base 6 mm, brown ring 6 mm, white ring 3 to 5 mm, dark tip 2 mm; in a very young animal, by contrast, the bristle-hairs measure about 30 mm, there being only three zones: white 7 mm, brown 8 mm, and white 15 mm, with no dark tip. It will, thus, be appreciated that not only is the fur half as long again but is also far whiter in appearance. But general length of hair is not the only factor in coat texture. Old West African animals are remarkable for the closely adpressed and stiff nature of the fur. This is probably an outcome of moult, the coat on examination displaying a fair proportion of short, apparently only half-emerged bristle-hairs. In all likelihood there are several moults, the top (bristle-hair) coat progressively changing at each of these from a relatively long loose white-ended pelage to an appreciably shorter, more heavily pigmented and dark-tipped fur in which the individual hairs are themselves also somewhat stiffer.

The colour of the underside exhibits considerable individual variation from dark chocolate to off-white. This, too, may be to some degree connected with age. The top of the head is, as a rule, fairly similar in coloration to the back, though being much shorter haired is much more finely speckled. The face is of a paler tone from the eyes to the very large rhinarium, the anterior median groove of which is continued downwards as a narrow naked strip parting the upper lip. The ears are very wide but shallow, and abundantly hairy on both faces, the upper margin being whitish. The "black" legs and feet are really deep chocolate from just below the shoulders and the hips. There are only 4, shallowly webbed, digits, the hallux and pollex being suppressed. The sole of the hindfoot is hairy up to the pads; that of the forefoot is almost so except for a short naked V. The tail is long and loose-haired but not so bushy as in *Ichneumia*. It is predominantly whitish or very pale yellowish, but in some specimens is adulterated with dark hairs for a short distance from the root. Its shape is midly tapering.

Skull (figs. 42 and 43). The mature *Galeriscus* skull is conspicuously the largest of all West African mongooses. It is a long, relatively narrow structure, the zygomatic breadth being almost exactly half the condylobasal length. The braincase is ovoid and in fully adult animals of both sexes carries a sharp, sometimes strongly built, sagittal crest. The occipital crest is broad and flange-like. The postorbital constriction is very markedly less than the interorbital breadth, averaging only about 70 per cent of the latter, which in itself is unusually wide, being almost equal to the rostrum. The frontal region as a whole is slightly elevated and smoothly rounded; the postorbital processes neither very long nor very strong, their points a good deal separated from those of the jugal processes.

The zygomata are strong and fairly broad except posteriorly. The palate is distinctly broader and much more vaulted than the flattish palates of other West African genera, reaching its greatest depth of curvature roughly between the two third premolars. The postdental palate is square or only very slightly longer than broad and terminates in a broad U, almost always without sign of a median notch or cusp commonly occurring in other genera. The front section of the bulla is small, the posterior chamber well inflated. The whole posterior part of the skull is remarkably short, the distance from the glenoid fossa to the exoccipital condyles being considerably under half of what lies anterior to this; whereas in other large mongooses of roughly comparable size it is either more than half or not a great deal less.

The teeth in *Galeriscus* are quite different from those occurring in any other West African mongoose. In the first place, the posterior outer corner of the upper carnassial is situated far forward of the posterior root of the maxillary process, m^1 also lying wholly anterior to this point. Similar siting of the cheekteeth is found only in *Ichneumia*, *Mungos* and *Crossarchus*, of which only the first is at all comparable in size to *Galeriscus*. But in addition to this the *Galeriscus* cheekteeth have a shape and form of their own, being almost exactly as broad as long and hence of somewhat squarish appearance. Furthermore, they are low-cusped, the tall, powerful points and sharp cutting edges so characteristic of most fissipedes being very much reduced so that the teeth partake more of a crushing than sectorial nature. The lower molars match these, m_1 in adult skulls lacking any sign of a sectorial function, the only remnants of a cusp, or two small cusps, remaining at the antero-internal corner—though in juvenile teeth both m_1 and m_2 have five or six well-formed but low cusps each. m_2 is unusual in being, instead of clearly smaller, precisely as long as m_1 and almost equal to it in bulk. Every skull examined possessed 4 premolars above and below on each side. The upper canines are dagger-shaped, that is to say almost straight, flattened from side to side and, when unworn, with sharp knife-like anterior and posterior edges. The lower canines are short and much more curved.

The shape of the mandible is unusual in that, instead of the rami and the toothrows they support being straight, they curve away from the symphysis forming the shape of the wishbone (furculum) of a fowl.

Habits. Not very much is recorded of the habits of this little known mongoose. Although the jaws and dentition are powerful it may be supposed from the structure of the teeth that *Galeriscus* feeds mainly upon food that demands crushing, requiring little or no severing of flesh and bones connected with typical carnivores. Such a diet might be expected to include the larger insects and their larvae, myriapods, molluscs and possibly frogs. A label note on a Nigerian specimen does, in fact, state that this animal eats snails and corn (i.e. maize). Gerald Durrell (personal communication) found that captive specimens fed on frogs, freshwater crabs, beetle larvae and tortoises with great avidity; but they would not under any circumstances tackle a snake. H. Lang (in Wheeler, 1922: 328) records an interesting fact concerning 9 specimens collected in north-east Congo which revealed that this very large mongoose, besides a more regular carnivorous diet, fed on ants and termites. One stomach contained the latter, while driver ants (*Dorylus*) were found in three others, two of which were, indeed, crammed full with them alone. The insects were only partly chewed or even quite uninjured. Since almost every mammal, apart from the specially adapted pangolins and aardvark, carefully avoids contact with these unpleasant and potentially lethal ants it is puzzling to understand how unspecialized mongooses could make such a risky meal. Lang suggests that the ants may, in fact, have been dead ones "since they are often killed in masses when their droves are unexpectedly exposed to the deadly effect

FIG. 42. *Galeriscus nigripes*: skull, B.M. No. 20.10.26.2, ♂, × 1; lateral view

of the direct rays of the sun, as it may happen after a shower, when they are still on the march or feeding in great numbers on carrion". Such a phenomenon may from time to time occur; but, in West Africa, within the present writer's experience, could hardly be regarded as sufficiently common to constitute anything more than a very occasional source of supply. In contrast to the observations concerning less typical carnivore foods Hayman noted of ten specimens collected by him, also in north-east Congo, that most were trapped at offal baits, buffalo bones or monkey flesh. Lang made no direct comment on the contents of the remaining 6 stomachs in the Congo collection though he implied, at the opening of his note, that *Galeriscus* also has a more normal carnivorous diet. Indeed, unless the capture of something larger than insects and snails is undertaken it is difficult to understand the purpose of the

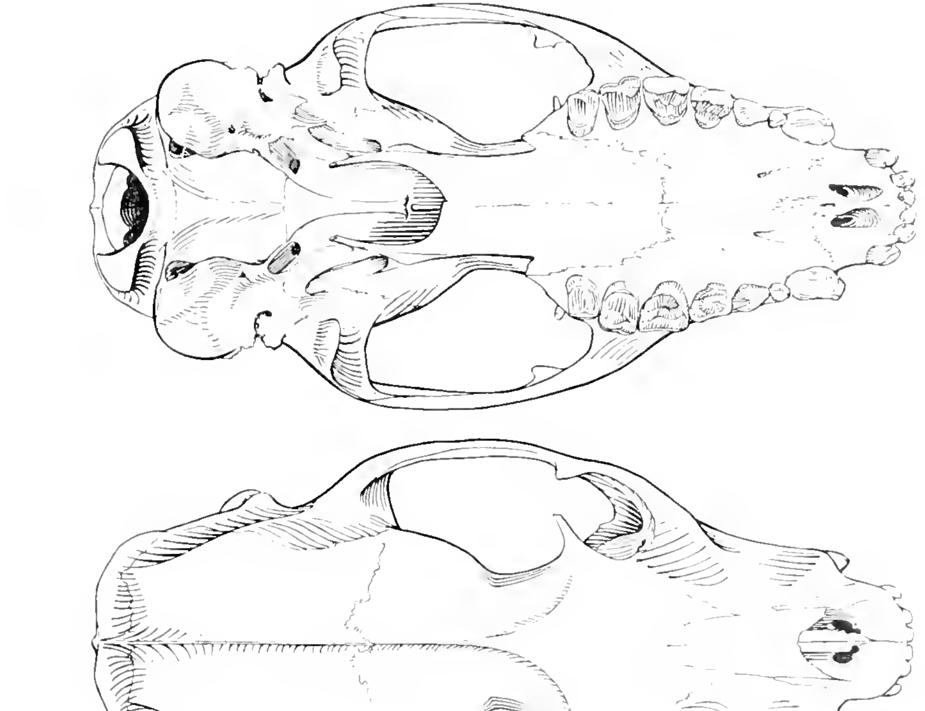


FIG. 43. *Galeriscus nigripes*: skull, B.M. No. 20.10.26.2, ♂, × 1; palatal & dorsal views

exceptionally strong and penetrating upper canines. Fish are, in this respect, a possibility; and their flesh is of a type that would be satisfactorily dealt with by the cheek dentition.

Nothing definite has been recorded about any other habits, including breeding; but in the course of collecting in the Cameroun forests, Gerald Durrell (personal communication) was never brought more than one juvenile at a time; and he was informed by various African hunters that they never found more than one young one in a nest. The adults, too, were said to be of solitary habit; nevertheless, those kept together in cages were not quarrelsome. From such judgment as can be made from the dates of capture of 3 juveniles, born between 2nd November and 9th January, the favoured mating time in West Africa would appear to be the early dry season. This is confirmed by the 3 young ones brought on different occasions to Durrell in the early part of the year, during the dry season. One black-footed mongoose has been known to live in

Table 20: Numerical data for *Galeriscus nigripes*

	nigripes (West Africa)
Vegetation	Forest
Number in mean	4
Condylobasal length	120·9
Basilar length	111·7
Palatilar length	67·2
Zygomatic breadth	61·5
Upper cheekteeth breadth	39·5
Nasals, length	27·2
Interorbital constriction	24·7
Postorbital breadth	17·5
Braincase breadth	37·6
Toothrow ($c—m^2$)	40·1
p^4 length	7·4
m^1 breadth	8·2
m^2 breadth	6·7
m_1 length	7·8
m_2 length	7·7
Head & body	640
Tail	365
Hindfoot	99
Ear	34
RATIOS (per cent)	
Tail/head & body	57
Zygom. br./condylob. l.	51
Braincase/condylob. l.	31
Braincase/zygom. br.	61
Palatilar l./condylob. l.	56
Interorb./postorb.	141
$p^4/c—m^2$	18·4

captivity for 40 months, but such a figure, of course, bears little relationship to longevity in the wild.

Taxonomy. The present author feels that *jacksoni* is specifically distinct; that eastern Congo *nigripes*, on the scores of size, some aspects of coloration, and pelage length, merits racial differentiation; and that West African specimens should therefore correctly be *Galeriscus nigripes nigripes* (Pucheran).

Genus **XENOGALE** J. A. Allen, 1919

Greater Long-nosed Mongooses

Xenogale J. A. Allen, 1919, *Jl Mamm.* 1: 26–27. Type species *Xenogale microdon* J. A. Allen, Akenge, Congo. This name was formed from the Greek *xenos* strange or foreign, and *gale* weasel, for a reason undefined but which may be guessed as referring to a set of characters regarded by Allen as unusual.

This genus, as at present known, embraces a single species occurring from the Cross River (south-eastern Nigeria) to north-eastern Congo, probably ranging throughout all of the central forest block north of the Congo River. In view of its monospecific nature more detail regarding distribution and all other matters relevant to the genus will be found in the account of this species which follows later. It is, however, first necessary to examine questions of taxonomy.

Taxonomy. The mongoose included here has been the subject of some confusion, even amongst expert taxonomists, and is still today a matter of dispute regarding its proper generic assignment. *Xenogale* was erected by J. A. Allen to accommodate a mongoose taken in eastern Congo which he considered not only to be a hitherto unknown species, named by him *microdon*, but also to present such "a singular combination of characters" as to call for a new genus. In taking this step Allen overlooked or disregarded a very similar animal from the Cameroun River which de Winton had some years earlier named *Herpestes naso*. There is little doubt that, as Hayman (in Sanderson, 1940) has pointed out, the two species are synonymous. The question therefore at once arises as to the correct generic assignment. This in itself is bound up with the conception of the breadth of *Herpestes*; whether this genus can satisfactorily cover not only the ichneumon of Egypt but a number of Asiatic species, large and small, the widespread slender African mongooses, and this bulky animal as well. Opinion is sharply divided. Hayman, in the place cited, thought that it was unnecessary to add a new genus to literature on account of characters that were no more diverse from typical *Herpestes* than those of certain oriental species generally today included therein. However, Simpson (1945), Grassé (1955) and Dekeyser (1955) all accord *Xenogale* recognition as an independent genus.

The question is certainly a very open one. Proposing *Xenogale*, J. A. Allen a little obscured the matter now under immediate discussion by drawing comparisons not only with *Herpestes* but with *Atilax* and *Ichneumia* as well. The differential characters he cited in support of his new genus in contrast with *Herpestes* alone amounted, externally, to a short thick tail compared with the attenuate tail of the latter species; and to more completely hairy palms and soles. These, by themselves, do not add up to anything very significant, and any valid distinction between the two genera must rest chiefly upon cranial and dental characters.

As regards these, Allen, admitting the relative size and general structure of the teeth in *Xenogale* to be as in *Herpestes* (*sensu stricto*), found the "braincase . . . very different in form from the braincase of *Herpestes*"—though he failed to support this view with any very precise account of the relevant distinctions. These are, in point of fact, largely differences of proportion; and, because it is in broadly the same size class, they are most readily seen in comparison with *H. ichneumon* though they hold, by and large, for Asiatic species too. The middle portion of the *Xenogale* skull is relatively very short; comparing it for example with *H. ichneumon*, the zygoma, measured from the infraorbital foramen to its posterior root, is almost exactly the same in the two skulls though the condylobasal length of the one is some 10 to 20 per cent longer than the other. On the other hand, the front portion of the skull, from the anterior rim of the orbit to the gnathion, is much longer, being in *Xenogale* almost one-third of the skull length but in *Herpestes* only a quarter or less. The rostrum besides being longer is broader and more inflated as well; as a rough measure of this it will be found that its breadth just posterior to the canine bulge is in *Herpestes* not much more than the external horizontal diameter of the orbital ring, whereas in *Xenogale* it is at least one-third as much again. The dentition is heavier, too, in this latter genus, the molars more strongly built; and the upper canines are proportionately bigger and somewhat of the compressed, flat-sided, sharp-edged *Galeriscus* type, unlike the more usual, smoothly rounded teeth of *Herpestes*.

There are several other distinctions between *Xenogale* and *H. ichneumon* but since they do not, or not so clearly, hold for Asiatic forms are not taken into account in this discussion. But several of these oriental forms have their own additional peculiarities of structure, such as an enlarged anterior chamber of the bulla. It seems to the present author that, taken all in all, the differences enumerated above justify Allen's separation of *Xenogale* from *Herpestes*.

A second taxonomic question concerns the species. There is no doubt that *Xenogale* skulls from the Cross River basin are appreciably smaller than those from the lower Cameroun and Spanish Guinea. Thomas observed this in connexion with a specimen from south-east Nigeria, to which he therefore gave the subspecific name *nigerianus* to distinguish it from the more southerly specimens, which he looked upon as typical *naso*. However, Hayman later (in Sanderson, 1940) drew attention to the fact that the type skull of *naso* did in most respects, in fact, more closely resemble the Cross River material than it did the specimens Thomas had taken as representing typical *naso*; and, further, that the locality from which it had come, Cameroun River, belonged essentially to the West African (*nigerianus*) region rather than to the central block south and east of the River Sanaga, whence these latter came. He therefore concluded that *nigerianus* and *naso* were, in truth, one and the same thing.

If this were so, the more heavily built, southerly, specimens that Thomas had mistakenly treated as typical *naso* were left without a name; and Hayman went on to adduce reasons for supposing that these, in fact, corresponded to the mongoose from Spanish

Guinea that had been described by Cabrera first as *Herpestes almodovari* and later as *Herpestes albicauda* var. *almodovari*. He concluded, moreover, that Cabrera was in error in this latter specific attribution and that, in the absence of proof to the contrary, it could reasonably be taken that the animal in question was not a variety of the white-tailed mongoose but identical with the southern form of *naso*, to which the subspecific name *almodovari* became, thus, appropriate. With this assessment the present author sees no reason to disagree.

Further confusion regarding this genus has been brought about by the strong external resemblance of *Xenogale naso* to *Atilax paludinosus* which has led to the former being taken for the latter, not only, and understandably, in the field but also, less excusably, by systematic zoologists. Lönnberg (1917) made this mistake and was followed in it by G. M. Allen (1939) who included both *naso* and *nigerianus* in his Checklist as races of *Atilax paludinosus*. Hayman records that Thomas, too, fell temporarily into this error, though not in print; and also (1915) shared Cabrera's mistake by assigning a specimen of *naso* (Christy No. 1202) to *Mungos* (*i.e. Ichneumia*) *albicauda*.

Skull (fig. 44). Some of the differential features of the *Xenogale* skull have necessarily been looked at above in the previous, taxonomic, section. A general description in so far as *naso* is concerned will be found later in connexion with that species.

XENOGALE NASO (de Winton) Greater Long-nosed Mongoose

Herpestes naso de Winton, 1901, *Bull. Lpool Mus.* **3**: 35, pl. 1, text-fig. Cameroun River. Type in the British Museum, No. 0.7.5.1, ♀; skin in good condition, and skull in good condition except that there is no trace of there ever having been a right upper canine. The name is from the Latin *nasus* nose, given in reference to the length of the muzzle.

Mungos naso nigerianus Thomas, 1921, *Ann. Mag. nat. Hist.* (8) **10**: 588–589. Niaji, 20 miles north-east of Oban, south-eastern Nigeria. Type in the British Museum, No. 10.6.1.14, ♀; skin fairly good, and skull good except for damage to the left side of the rostrum and consequent loss of the canine and first premolar.

Mungos paludinosus naso Lönnberg, 1917, *K. svenska VetenskAkad. Handl.* (2) **58** No. 2: 64.

Xenogale microdon J. A. Allen, 1919, *Jl Mamm.* **1**: 27; *Bull. Am. Mus. nat. Hist.* **47**: 199, pl. 27, text-fig. 58–60, 61 A & B. Niapu, north-eastern Republic of Congo. Type in the American Museum of Natural History, No. 51625, ♂. The specific name is made up from the Greek words *micros* small, and *odon* tooth.

Atilax paludinosus naso G. M. Allen, 1939, *Bull. Mus. comp. Zool. Harv.* **83**: 206.

Herpestes almodovari Cabrera, 1902, *Boln R. Soc. esp. Hist. nat.* **2**: 138–139. Cape San Juan, Spanish Guinea. This was named after the Duque de Almodóvar del Río, Valid as a race but extralimital.

Herpestes albicauda var. almodovari Cabrera, 1903. *Mems R. Soc. esp. Hist. nat.* **1**: 27–29. A specific re-attribution of the above.

Distribution. This is a rare, or at least very little-known, mongoose, the distribution of which in West Africa is very restricted. It is essentially a closed-forest animal. Its most westerly occurrence is the Cross River basin (*i.e.* south-east Nigeria and upper Cameroun); thence it ranges south to the equator and across to eastern Congo. It does not seem to be known south of the River Congo. Only 6 specimens exist in the British Museum from the area covered by this present work: 2 from the Oban district of

Nigeria; 3 from the Mamfe district of Cameroun; and the type from the Cameroun River. Specimens mentioned by Lönnberg (1917) from Cape Debundscha (Cameroun) would also appear to belong here; and Eisentraut (1963) obtained 2 on the north side of the Cameroun Mountain. Extralimitally, examples are known, on the western side of the continent, from Efulen (lower Cameroun), Benito River and Cape San Juan (Spanish Guinea); and, more centrally, from various localities in the upper Uele and Ituri River regions in eastern Congo. The total known specimens number about 30.

Description. *Xenogale* is a bulky mongoose, weighing about 3 kg and having a head & body length, in West Africa, of around 520 mm, and a tail of about 380 mm. Like the much smaller kusimanse (*Crossarchus*) this mongoose, too, has a long fleshy snout that prolongs the nose well beyond the usual limits determined by the bones and teeth—de Winton gives the extent which the nose of the type reached beyond the lower lip as 23 mm. This is an almost completely "black" animal, that is to say very dark all over; and, thus, both in size and superficial appearance it very closely resembles *Atilax*, for which it can therefore be easily mistaken in the field. There are of course, means of telling the two apart if specimens can be held in the hand; but to distinguish between them at sight, particularly as for the most part little more than a swift glimpse is possible, requires keen and practised eyes indeed. *Xenogale* has a narrower head with a sharper and longer muzzle; and the tail is about three-quarters of the head & body length whereas in *Atilax* it is not more than about two-thirds. Apart from these small points there is little that is at once certain and easily detectable. The coat in *Atilax* tends to be more evenly and finely speckled; that of *Xenogale* more of a mosaic of glossy black and pale patches; but in this matter, which in any case is difficult to detect in a poor light or at any distance, there is appreciable variation.

It has already been said that the overall impression of the coat of *Xenogale* is very dark. A good deal depends on the angle it is looked at from, but closer inspection reveals it to be a mixture of glossy black overlying paler colour, grey-brown or orangey-brown. In most specimens the dorsum is not speckled, though the head and neck always are; but in a few examples a speckling of deep yellow or orange covers the entire back. The pelage is very long, dense, loose and coarse. It consists of fine, slightly wavy underfur about 10 to 15 mm long, sometimes a little more, abundant but not tightly packed as in some mongooses. The colour is variable between different specimens, from a rather nondescript dirty-brown to greyish-brown or pale orange-brown. The tips are pale. In comparison with the very dominant top coat it plays a far more insignificant role than the underfur does in many species.

Amongst this underfur stand pretty abundant, very long, rather wiry bristle-hairs. These, on the lower back, measure 52 to 55 mm but occasionally reach as much as 60 mm. They are ringed with different colours; there are, of course, variations but an average bristle-hair has a pale base of 5 or 6 mm followed by a blackish zone about 10 to 12 mm long, and a pure or slightly yellowish white ring of 6 or 7 mm; then follows the long terminal part measuring some 28 to 32 mm, and this may be entirely shiny jet-black or be broken, a few millimetres from the tip, by an orange ring 2 or 3 mm wide. In some specimens this occurs in a high proportion of the bristle-hairs, resulting in a wholly speckled coat; but in the majority of specimens it is rare and detectable only on close inspection. In such coats the lower pale rings, and to a lesser extent the underfur, play their part in adding pale mottling to a coat otherwise chiefly notable for its glossy blackness.

The face to about the level of the eyes, the top of the head and neck always, and the shoulders sometimes, are speckled. The long nose to the large black rhinarium is plain dark brown. The chin has very short, very finely speckled, backwardly-pointing hairs which at its posterior limit come up against the longer, rather more coarsely speckled, forwardly-directed hairs of the throat. This forwardly-pointing pelage embraces also the chest and ends in two whorls in the region of the axillae where the normal backwardly-directed hair of the underside starts. Allen (1924) mentions abnormal direction of the fur in connexion with the dorsal pelage also of some specimens. The low, rounded, very broad ears are very finely and shortly haired on their inner faces, but they have a long tuft in front of them projecting upwards from near the base of the outer margin. The iris was recorded by de Winton as orange-brown.

The ventral pelage is a little paler than that of the back and somewhat sparser, especially over the belly itself. The tail is long-haired, very similar to the back in colouring; and it tapers evenly from the rather broad root to the tip. The very short legs are deep glossy brown, almost black. The feet are 5-toed, webbed between the digits up to the last joint, the claws long. The undersides of both fore and hind feet are completely hairy up to the pads, but the area surrounding these is wholly naked.

Skull (fig. 44). A few characters presumed of generic importance have already been looked at above; here follows a more detailed account as concerns the species: but since there are striking differences of build between the nominate race of *naso* found in West Africa and the extralimital one, here regarded as *almodovari*, the main emphasis is placed on the former. The latter is not only larger but is also in all respects more heavily built.

The typical *naso* skull is long and fairly narrow; the egg-shaped braincase terminates posteriorly in a broad, flange-like supraoccipital crest. In well mature specimens of both sexes there is generally a clear sagittal crest, though in the nominate race this appears unlikely ever to attain the great depth (6 mm) that it can in *almodovari*; and from one fully adult female it is entirely lacking. The postorbital constriction is always markedly narrower than the interorbital breadth. The whole frontal region is somewhat inflated and well rounded; the postorbital processes are long but do not quite join the almost equally long jugal processes (as they do in *almodovari*) to complete the orbital ring.

The rostrum is long and fairly narrow; longer and narrower in the type skull of *naso* than in that of *nigerianus* or of any other purely West African specimen. This is accounted for by Hayman (in Sanderson, 1940) by the absence, seemingly from birth or extreme juvenility, of the left upper canine, a defect that may have been responsible for unusual lengthening of the anterior part of the skull. Whatever the cause, this long rostrum brings the total skull length close to the range of the extralimital *almodovari*, though in almost all other respects this skull more nearly resembles the more slightly built northern animals. The zygomata are strong, deep in their anterior and middle portions but narrowing near the squamosal root. The postdental palate is

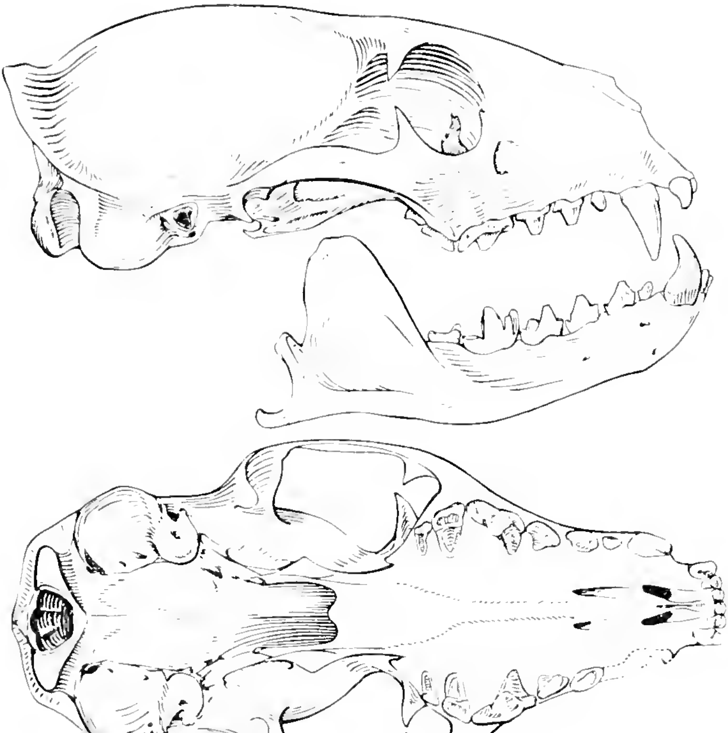


Fig. 44. *Xenogale naso*: skull, Type of *nigerianus*, B.M. No. 10.6.1.14, ♂, 1

about as broad as it is long. The anterior chamber of the bulla is relatively small compared with the posterior well-inflated portion. The lower margin of the auditory meatus is a deeply incised V. The coronoid process of the mandible is tall and fairly narrow.

The posterior outer corner of p^4 is situated near the posterior root of the maxillary process (fig. 33b). Normally there are 4 upper and 4 lower premolars on each side, the anterior ones being relatively very small; and this is the case in all the 5 known *n. naso* skulls except for the female that lacks a sagittal crest, which has only 3 lower premolars on one side. One extralimital, *almodovari*, male has had an extra posterior upper molar (m^3) on each side, now missing, but to judge from the alveoli they must have measured about 5 mm across; and another very old male from the same area has lost p^1 on each side, one alveolus having completely disappeared, the other almost. m^1 is always a pretty large tooth, about three-quarters of the bulk of the upper carnassial; m^2 is at least as large as the lingual section of m^1. In the front section of m_1 the anterior and buccal cusps are appreciably larger than the postero-internal one. The upper canines are only slightly curved; they are laterally somewhat compressed and nearly always display some sign of a narrow cutting edge on the posterior face, less frequently on the anterior one.

Habits. Almost nothing is known of the life and habits of the greater long-nosed mongoose. de Winton recorded that the original type specimen lived in the London Zoo for a year and "was at all times perfectly silent and somewhat shy, but soon became friendly with those whom it recognised . . .". It appreciated the gift of a sparrow or other small bird, which it quickly ate. The label on the type of *nigerianus*, on the other hand, indicates that it feeds on snails and young maize, and is reputed to be a scavenger. Nothing is known of mating or breeding except that J. A. Allen (1924) records 3 young in one litter; and one juvenile West African specimen was taken at the end of May. It seems likely that this mongoose would be a largely nocturnal species. R. W. Hayman has kindly supplied the following information regarding the species in north-east Congo. One specimen was found in a hollow log; and a young one still with milk dentition, and which, incidentally, swarmed with many more ticks than any other carnivore collected, was taken in a night trap near a small sandy stream. Indeed, tracks which appeared to be those of this species were frequently seen alongside other clear gravelly streams in the forest.

Taxonomy. Enough has already been said to make it clear that all the animals occurring within the limits covered by this work are in all probability *naso naso*; but it must be emphasized that this is based on the assumption that the type skull of *naso* is not, in fact, typical. The point cannot be proved until further collecting from the Cameroun River, as opposed to the Cross River basin, has shown this supposition to be well founded; and that no long and narrow rostrummed form intermediate between Thomas's *nigerianus* on the one hand and the heavy-skulled Spanish Guinea race believed to be *almodovari* on the other, in truth exists. It seems as though the eastern Congo animals correspond pretty closely to West African *n. naso*; and if this is so it gives the race a curiously distant east-west distribution contrasting sharply with its very limited north-south range, bounded as it is by the River Sanaga. But, as Hayman has pointed out, should these eastern animals eventually be shown to differ appreciably from the nominate race Allen's name *microdon* (which seems to have little etymological justification) is available for racial use.

Table 21: Numerical data for *Xenogale naso*

	naso, Type	*mgerianus*, Type	*naso naso*, Means	*naso almodovari*, means
Vegetation	Forest	Forest	Forest	Forest
Number in mean	1	1	5	5
Condylobasal length	109·7	100·8	103·7	112·9
Basilar length	101·6	92·4	95·3	104·7
Palatilar length	59·3	53·3	54·7	60·6
Zygomatic breadth	53·4	53·3	53·1	62·0
Upper cheekteeth breadth	33·0	32·4	32·6	35·6
Nasals, length	27·0	27·0	26·2	26·8
Interorbital breadth	21·2	20·5	20·5	24·1
Postorbital constriction	16·8	17·0	16·8	16·7
Braincase breadth	38·1	36·6	36·1	37·4
Toothrow (c—m^2)	40·6	36·9	38·3	40·9
p^4 length	9·5	9·8	9·7	10·2
m^1 breadth	9·3	9·2	9·5	10·0
m^2 breadth	6·2	5·8	6·0	6·7
m_1 length	9·2	9·0	9·1	9·1
m_2 length	5·6	5·6	5·8	6·1
Head & body	528	534	520	587
Tail	381	361	376	383
Hindfoot	103	98	95	107
Ear	30	33	34	38
RATIOS (per cent)				
Tail/head & body	72	68	72	65
Zygom. br./condylob. l.	49	53	51	55
Braincase/condylob. l.	35	36	35	33
Braincase/zygom. br.	71	69	68	60
Palatilar l./condylob. l.	54	53	53	54
Interorb./postorb.	126	121	122	144
p^4/c—m^2	23·4	26·5	25·3	25·0

Genus **LIBERIICTIS** Hayman, 1958

Liberian Mongoose

Liberiictis Hayman, 1958, *Ann. Mag. nat. Hist.* (13) **1**: 448. Type species *Liberiictis kuhni* Hayman, Liberia. This name is composed of the country of origin, Liberia, together with the Greek *ictis*, strictly regarded as the name for a weasel, but in modern zoological nomenclature often associated with a number of other small carnivores.

Since this is a monospecific genus about which nothing is at present known beyond the existence of eight skulls all relevant generic information can be gathered from the specific account which follows.

LIBERIICTIS KUHNI Hayman Kuhn's Mongoose

Liberiictis kuhni Hayman, 1958, *Ann. Mag. nat. Hist.* (13) **1**: 449–452. Kpeaplay, north-east Liberia. Type in the British Museum, No. 58.507, probably ♂, adult; no skin, skull in fairly good condition apart from being badly smoked and the loss of one upper and one lower incisor (i^3 and i_1) and both posterior upper molars (m^2). There were 7 paratypes. The species is named after its discoverer, Dr. Hans-Jurg Kuhn of Heidelberg University.

Distribution and general. This mongoose offers several points of interest. It is, firstly, somewhat astonishing that despite a good deal of systematic collecting in Liberia by a fair number of different workers from 1875 onwards it failed to come to light until 1958. Next, at the present time nobody outside a few hunters in a rather remote area of Africa has any idea of its external appearance beyond the fact that it must have a longer and very much narrower and sharper muzzle than any other known mongoose.* Finally, its teeth are so very much smaller and less carnivore-like than those of other herpestines that Hayman was amply justified in erecting for it a new genus.

The only known specimens, 8 skulls, all come from the closed high-forest of the upper Cess River, north-east Liberia, at Kpeaplay and Gaplay, roughly 6°36—7°08 N., 8°28—8°30 W. Apart from the type in London, the other specimens are lodged in Bonn and Saarbrücken. Hayman considered that *Liberiictis* was obviously related to *Crossarchus*; but there are 4 premolars above and below instead of 3. If Hayman's assessment of relationship is correct it is interesting to hazard a guess that, when discovered, *Liberiictis* will prove to be a mongoose twice the size of the kusimanse, with an even longer muzzle and nose, a dark, speckled, rather loose coat, and a relatively short tapering tail. The teeth, which in spite of the very much larger skull are only the same size as those of *Crossarchus obscurus* and not at all sectorial, would seem to indicate a soft, easily masticated diet, probably insects, millipedes, worms and the like, and possibly fish.

Skull (fig. 45). Comparisons of this figure with those of other West African mongooses shows at once the marked difference of form that clearly distinguishes this skull from the rest. Even at its widest point it is rather narrower than average, the zygomatic breadth being only some 48 per cent of the condylobasal length; and this narrowness is emphasized by the unusually long and exceptionally slim tapering rostrum, the whole structure having a very canine appearance. The length of the skull lying forward of the anterior rim of the orbit is about 60 per cent of that to the rear, whereas in other genera it is at most about 50 per cent and often much less.

Only one skull has been available for this present study, the type, its sex unknown. This has a low sagittal crest and the usual broad supraoccipital crest. In this specimen

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* Since this went to press Dr. Douane Schlitter of the Smithsonian Institute has kindly shown the author photographs of two specimens which he recently obtained in Liberia. These appear to accord well with the projected description given in this and the following paragraph.

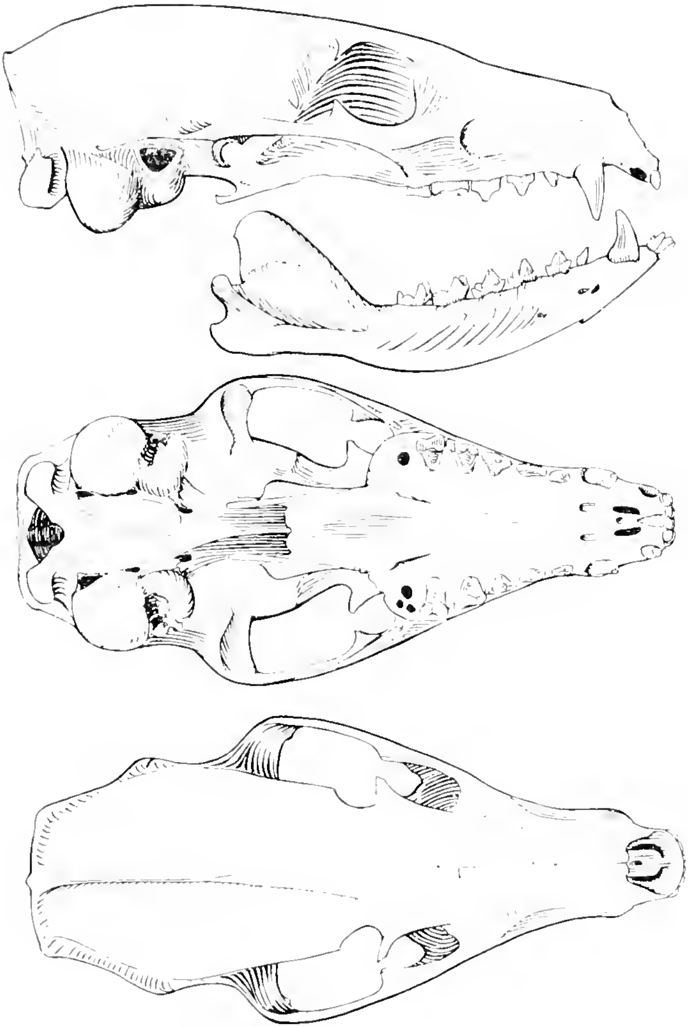


Fig. 45. *Liberiictis kuhni*: skull, Type, B.M. No. 58.507, sex ?, × 1

the interorbital breadth is precisely equal to the postorbital constriction; but Hayman (1958) examined the other seven known skulls and recorded that in all of these the postorbital constriction was very slightly the greater, the mean excess over the interorbital breadth being, however, only of the order of one millimetre. This latter breadth is appreciably greater than the width of the rostrum across the canines, a character true, amongst the other genera, only of *Crossarchus*. Hayman, as already mentioned, in his type description found that *Crossarchus* was the only other genus presenting a degree of similarity to *Liberiictis*. The West African species of that genus, *obscurus*, is of course very much smaller; but the extralimital *C. alexandri* (Congo) does more nearly approach the present genus in size, and in the dorsal aspect bears a fairly close general resemblance, apart from its appreciably shorter rostrum. The ventral aspect, however, at once reveals sharp differences in the number, size, form and disposition of the cheekteeth, and in the shape of the palate, both interdental and postdental. The postorbital processes, though well developed, remain well separated from the jugal processes; the zygomatic arch is relatively narrow throughout its length. The palate besides being narrow is longer than usual, the postdental portion being very slightly longer than it is broad. The anterior chamber of the bulla is considerably smaller than the highly inflated, domeshaped posterior chamber, and has a slight medial depression.

The cheekteeth, $\frac{4.2}{4.2}$, are remarkably small for the size of the skull. Hayman equated them to those of *Crossarchus alexandri* which, however, to the present writer seem appreciably larger. The upper carnassial, all of the first and half of the second molars

Table 22: Numerical data for *Liberiictis kuhni*

	Type	Means (from Hayman, 1958)	Range
Vegetation	Forest	Forest	Forest
Number in mean	1	8	8
Condylobasal length	94·2	93·6	91·8–95·7
Basilar length	85·6	—	—
Palatilar length	53·8	—	—
Zygomatic breadth	45·8	45·0	42·4–47·0
Upper cheekteeth breadth	26·0	—	—
Nasals, length	29·0	—	—
Interorbital breadth	17·4	17·4	16·6–18·0
Postorbital constriction	17·4	18·5	17·2–19·6
Braincase breadth	32·9	—	—
Toothrow (c—m^2)	32·5	32·7	31·7–34·5
p^4 length	5·4	5·2	4·8–5·7
m^1 breadth	5·8	5·7	5·0–6·0
m_1 length	5·5	—	—
m_2 length	5·0	—	—
RATIOS (per cent)			
Zygom. br./condylob. l.	49	48	—
Braincase/condylob. l.	35	—	—
Braincase/zygom. br.	72	—	—
Palatilar l./condylob. l.	57	—	—
Interorb./postorb.	100	94	—
p^4/c—m^2	16·6	15·9	—

are situated forward of the posterior root of the maxillary process. The cusps are low, the carnassials have little cutting ability, and the whole dentition is crushing and probably insectivorous rather than frankly carnivorous as commonly understood. The premolars and molars are both short and narrow, the upper carnassial occupies no more than about 17 per cent of the toothrow, c—m^2; and in terms of absolute size is no bigger than in the very much smaller animal *Crossarchus obscurus*. On the other hand, m^2 would seem from its now vacant alveoli to be almost as large as m^1; and m_1 and m_2 are certainly subequal. The antero-internal cusp is the largest of the three on the anterior part of m_1, very slightly exceeding the buccal cusp. The canines are relatively small; the upper incisors, though of more normal size, have the outer, slightly larger, ones (i^3) clearly separated from the rest and situated laterally rather than facing the front. In comparison with lower jaws of almost equal length in other genera, such as *Herpestes*, *Xenogale* or *Atilax*, the rami of *Liberiictis* are much more slenderly built and incapable of dealing satisfactorily with any very powerful prey.

Family **HYAENIDAE** Gray, 1869

Hyaenas

Distribution. This family is the smallest of the Carnivora and one of the smallest of all the Mammalia. Hyaenas are both Asiatic and African in distribution. As far as the former is concerned they range across Arabia, Syria, Iraq, Iran, southern Russia and Afghanistan to the northern and a good deal of the southern part of the Indian peninsula. In Africa they occur from the more inland regions of the Mediterranean countries to South Africa and South-West Africa to the latitude of about 28°S., though at both extremes they are becoming more and more scarce and have in fact withdrawn from a wider range which not so long ago extended from the north to the south coasts. Vegetationally they are essentially open-woodland animals, in West Africa from the Subdesert to the Guinea, the different species, however, having preferences for different zones. Normally they avoid the closed forest except as rare and transient visitors.

Taxonomy. The living hyaenids have long been recognised as forming an independent family, and this position is little questioned today. But the fossil record shows them to be derived from the Viverridae, furnishing remains of animals that could be regarded as representative of one family or the other.

Extinct forms apart, the animals included here are clearly separable into two divisions; either (Ellerman, Morrison-Scott & Hayman, 1953) as full families or (Simpson, 1945) as subfamilies. The former is probably justified but the latter's classification is nevertheless retained here pending a major classificatory revision of the African mammalia, the point being of little immediate moment in West Africa since only the chief of the two divisions occurs there. Simpson's subfamilies are the Protelinae and the Hyaeninae, both of Mivart, 1882. The former consists solely of the so-called aardwolf (*i.e.* Earth-wolf), *Proteles* I. Geoffroy, 1824, of southern and eastern Africa, which though it outwardly very closely resembles a small striped hyaena has dentitional and other characters that relate it to the Viverridae or, in the opinion of some, the mongooses in particular. The cheekteeth of this small, shy and weak-jawed carnivore are $\frac{3\cdot 1}{3\cdot 1}$ but are often partly missing besides being remarkably reduced in size and effectiveness. Moreover, it subsists largely on an insectivorous diet. With this animal this present work is not further concerned since only the Hyaeninae occur in West Africa. Nevertheless, it is interesting to note that support for its near affinity with *Hyaena* rather than the more distant one suggested by removal into a separate family is provided by the discovery of very closely related lice (Mallophaga) of the genus *Felicola* on both the aardwolf (*Proteles cristatus*) and the brown hyaena (*Hyaena brunnea*) (Ledger, 1968).

Subfamily **HYAENINAE** Mivart, 1882

Hyaenas

General description. Hyaenas proper are all animals of large or fairly large size which, although they are anatomically more closely allied to the Felidae, seem, in fact, in many ways far more dog-like than cat-like in general appearance. Possibly the most immediately noticeable peculiarity of these carnivores is the sloping line of the back due to a greater length of forelimbs than hindlimbs. Indeed, the whole front portion of the body is of appreciably heavier build than the rear, the shoulders, the thick neck, the massive head and large ears seeming overdeveloped in comparison with the hindquarters. Hyaenas are in consequence of clumsy rather than of elegant appearance. The deep jaw armed with huge teeth is extraordinarily powerful and capable of dealing easily with the thickest of bones—or even with tougher materials in need. In accordance with predominantly nocturnal activity the eyes have a very well developed *tapetum lucidum* which enables hyaenas to make full use of every glimmer of light. The ears, which may be pointed or rounded, stand up conspicuously above the head and have no bursa. The limbs are canine-like, terminating in thickly padded, broad feet which have 4 webbed digits and short, stout, blunt, non-retractile claws. These are in part concealed by very dense, stiff and wiry, curved bristles that cover the whole upper surface of the foot. The gait is highly digitigrade, the subdigital pads being both exceptionally deep and flattened on their anterior faces in accordance with this extreme verticality of the digits. The tail is short and bushily long-haired, either throughout its length or at least terminally.

The coat is fairly harsh, short-haired to very long-haired, with a crest that may be more or less confined to the back of the neck or extremely lengthy and run from head to tail. The pattern is of spots or transverse stripes—in an extralimital species the latter confined to the legs. The pelage, when not in moult, is composed of fairly abundant underfur that is sometimes very long and always wiry, not far removed in thickness and texture from the bristle-hairs of other families. Amongst this occur widely scattered, very long, terete or slightly flattened bristle-hairs, playing a relatively small part in the overall texture of the coat.

The scent glands are situated either side of the rectum, their external orifices lying deep in a hairless sac situated between the root of the tail and the anus. This pocket is surrounded by a soft, thickened, dilatable, naked rim, the upper and lower lips of which are parted when the tail is raised but come together when it is lowered, closing the pouch in an arch-like slit above the anus. The latter is thus, unlike in the mongooses, external to the sac; but the naked skin surrounding it is continuous with the naked lips of the pouch, the whole complex forming when the tail is raised and the pouch fully distended, a practically hairless subcaudal disc. The two external orifices of the main scent glands are sited on the floor of the sac a little distance to each side of its longitudinal axis; but between them lie, also, the pores of a number of lesser intermediate sebaceous glands.

Skull. This is of outstandingly powerful build. It is chiefly remarkable for its high sagittal crest that arises gradually, not abruptly, from the disproportionately narrow cranium and is projected far backwards beyond the usual limits of a skull in the form of a subpyramidal "helmet". The supraoccipital crest, that plays so prominent and constant a part in most skulls of the Viverridae is in this family relatively insignificant.

The zygoma is very strong, but the orbital ring is widely incomplete. The auditory meatus is bony and tubular.

The bullae are well developed: Pocock (1916c and 1928) drew attention to the fact that they are two-chambered despite the assertions of Flower (1869), Mivart (1882 a and b) and subsequent authors. The error arose from the more horizontal position of the septum, which divides an exceptionally large anterior chamber from a small posterior one, and which had hence been mistakenly assumed to be the actual roof of an undivided bulla. There is no external indication of the existence of two chambers, in the form of a depression in the wall of the bulla, as there is in the Viverridae. The paroccipital process is highly developed, completely enfolding the posterior aspect of the bulla, extending well below it in the form of a blunt point, and reaching laterally to the edge of the auditory meatus. Pocock also pointed out (1916f) that the same two authors were wrong in citing the absence of an alisphenoid canal as characteristic of the Hyaenidae since though it was usually absent it was sometimes present, at all events in *Crocuta*. Its apparent absence is due to the obliteration of its posterior orifice, the anterior orifice being mistaken for the foramen rotundum, which is, in fact, hidden within the alisphenoid canal, as observable by cutting away the outer wall of the latter. The mandible is massive.

The cheek dentition is $\frac{4\,1}{3\cdot 1}$, the upper molar being very much reduced by comparison with the huge carnassials and remarkably powerful remainder of the teeth; this is especially so in *Crocuta*, where m^1 is minute and sometimes lacking.

Differences of detail in the structure and proportions of the skulls of the two genera *Hyaena* and *Crocuta* have been very fully described by Buckland-Wright (1969).

Habits. Hyaenas have long had an unsavoury reputation as nothing better than cowardly scavengers, feeding on stinking carrion or, at best, slinking furtively in to finish off what remains of a carcass when the lions have killed and eaten their fill. It now appears that this picture is quite misleading, at least as far as the spotted hyaena is concerned, as described more fully below in the account of that species which recent observation shows to hunt and kill on its own account. However, there is no doubt that hyaenas do also scavenge, coming in to villages at night to take what offal they can find. If opportunity offers on these visits they steal sheep, goats or calves as well; and they have been known to take children too. As for their cowardice, it is true that they make little attempt to defend themselves but both kinds have been observed to drive off a leopard or a young lion from a kill. Their usual careful approach may be as much the outcome of excess of caution as of lack of courage.

These are chiefly nocturnal animals but are occasionally active during the day and especially in the early morning. As a rule during daylight hours they shelter and sleep in any cover, in aardvark holes, under boulders, or in dense vegetation; but they sometimes choose more open sites such as the shade of a tree. Though by nature not truly gregarious animals they do often live in family groups and frequently gather together in some numbers either at a kill or for a kill, as will be detailed later in the specific accounts. Since they are mainly night feeders they are not commonly seen except when the moon is full; but anyone who has been in the correct territory is very well acquainted with them through the hideous noise that they sometimes make throughout much of the hours of darkness. Both striped and spotted hyaenas do this; but the latter is somewhat louder and its rising whoops and cackle have made it famous to all as the "laughing hyaena".

Little is certainly known of their breeding habits. The maniacal laughter is thought to be made under the stimulus of sexual excitement. The females are capable of breeding at all seasons of the year. The period of gestation has been estimated as between 3 and 3½ months; there are mostly 2 to 4 in a litter. The young of the two genera are quite different: those of *Hyaena* resembling their parents in their markings; those of *Crocuta* displaying no pattern at all, merely a blackish-brown colour.

Taxonomy. No argument attaches to the separate recognition of this subfamily and that of the Aardwolf (Protelinae) apart from whether they are each of family or subfamily status. Within the subfamily itself, it was at one time customary to relate *crocuta* to *hyaena* as species within a single genus *Hyaena*; but there can be no doubt of their true generic independence, the nature of the teeth, the pelage and the sexual organs being very distinct.

KEY TO THE GENERA OF HYAENINAE

(previous key page 160)

Coat pattern of transverse stripes; a lengthy crest from head to tail; ears pointed; upper molar much more than 5 mm in transverse length . **Hyaena** (*page* 344)

Coat pattern of spots; if any crest present, relatively short and confined to the neck; ears rounded; upper molar very small, only about 5 or 6 mm across **Crocuta** (*page* 353)

Genus **HYAENA** Brisson, 1762

Striped and Brown Hyaenas

Hyaena Brisson, 1762, *Regnum Animale in classes IX distributum*, 2nd. edit.: 13 and 168. Type species *Canis hyaena* Linnaeus from Iran. This name is the Latin form of the Greek *hyaina*, itself reputedly derived from *hys* a hog, and *-aina* a feminine termination, and said to have been given in reference to the long spinal crest similar to that occurring, less exaggeratedly, in the European wild boar. The nomenclatural validity of Brisson's work has been questioned, the matter having been put before the International Commission in 1950 (*Bull. zool. Nom.* 4: 314) but no decision having yet been reached. Should this work be rejected the name *Hyaena* is still available from Brünnich, 1771, see below.

Hyaena Brünnich, 1771, *Zoologiae Fundamenta*: 34, 42 and 43. Type species *Canis hyaena* Linnaeus.

Distribution. This is the more widespread of the two hyaenid genera, being found over a good deal of two continents. It has been known for very many centuries from its chief species *hyaena*. This today occurs throughout much of the western half of the Indian peninsula, northwards as far as southern Russia, and thence across Iran, Iraq, Syria and the whole of the Arabian peninsula into Africa. In Africa the distribution is in two disjoined parts according to the two extant species. The striped hyaena, *hyaena*, which is also the Asiatic species, is to be found all around the Sahara, north as well as south, and as far east as the Red Sea and somewhat south of the Equator; the brown hyaena, *brunnea*, is confined, broadly speaking, to South-West Africa and a few scattered localities further east to Mozambique. In former eras the genus occurred in Europe.

General description. Hyaenas of this genus are externally characterized by much longer pelage than that found in *Crocuta*; and by a pattern of transverse blackish stripes, either on the flanks or at least, extralimitally, on the legs. The ears are pointed and pear-shaped, markedly different from those of the other genus; and the general bodily size is less. Further detailed description is reserved for the sole West African species, *hyaena*, below.

Taxonomy. There is little to add under the generic head to what has already been said. Clearly, in spite of former practice, it is correct to separate the spotted hyaena, *Crocuta*, generically from those now under consideration. It is equally clear that the genus covers two distinct, extant, species: *hyaena* of Asia and the northern part of Africa; and *brunnea*, with a different pelage pattern and a slightly larger skull and teeth, of the south, a specific distinction that has never been brought into question.

HYAENA HYAENA (Linnaeus) Striped Hyaena

Canis hyaena Linnaeus, 1758, *Systema Naturae*, 10th edit. **1**: 40. Type locality Benna Mountains, Laristan, southern Iran (*fide* Thomas, 1911, and Pocock, 1934: 809). Linnaeus' type is thought to have been the description, pp. 411–412, and plate (fig. 4) facing p. 407 in Kaempfer (1712) *Amoenitatum Exoticarum . . . Fasc. V. . . . Rerum Persicum et Ulterioris Asiae*. The derivation of the name has been given above under the genus.

Hyaena striata Zimmermann, 1777, *Specimen zoologiae geographicae etc.*: 366. A renaming of *hyaena* Linnaeus. Zimmermann's work was ruled unavailable in 1950 (*Bull. zool. Nom.* **4**: 547). The name *striata* is a Latin word implying marked with narrow bands.

Hyaena dubbah Meyer, 1793, *Systematisch-summarische Uebersicht der neuesten zoologischen Entdeckungen in Neu Holland und Afrika*: 94. Atbara, Sudan. This was entirely founded on the description by Bruce, J., 1790, *Travels to discover the source of the Nile . . .* **5**: 107–120, pl. Dubbah is the Arab name. Sometimes held to be of racial application in West Africa.

Hyaena orientalis Tiedemann, 1808, *Zoologie* **1**: 350. A renaming of *hyaena* Linnaeus. The name is the Latin word for pertaining to the east.

Hyaena fasciata Thunberg, 1820, *K. svenska VetenskAkad. Handl.* **1**: 59. A renaming of *hyaena* Linnaeus, This name is the Latin adjective meaning enveloped with bands.

Hyaena antiquorum Temminck, 1820, *Annals. gén. Sci. phys. Brux.* **3**: 51. A renaming of *hyaena* Linnaeus, this being the Latin word meaning of the ancients, since this was the only species known to the early classical writers.

There is a further fairly extensive list of synonymous names either exclusively applied to the species outside Africa or those of extralimital races.

Distribution. The striped hyaena has been known and been the subject of a good deal of far-fetched misinformation throughout south-western Asia and the Mediterranean region since ancient times. In Africa it occurs today all around the edges of the Sahara, and thence it ranges as far east as the Red Sea and, on that side of the continent, southwards to about 4°S. Within the desert itself it has to all intents and purposes disappeared, and it has become fairly rare around its northern borders, that is to say in the interior of Morocco and Algeria, though it is still not uncommon in southern Libya. It is essentially an animal of the arid zones, the Subdesert and the Sahel woodland, further south than which it occurs only sporadically as an occasional visitor. It can be expected anywhere within these two zones especially the latter far-spread belt of *Acacia raddiana* woodland, which extends in West Africa from Senegal to Lake Chad and thence across the continent eastwards to Somalia, turning south into parts of Kenya and Tanzania. Reputed occurrences outside this normal range in moister zones of vegetation are mentioned in the following paragraph.

In the right areas the striped hyaena is moderately common but is nowhere so abundant as the spotted hyaena may be in its optimum habitat. It is impossible to judge its numbers in West Africa from the British Museum material since this comprises only three specimens: one a skin complete with skull, but juvenile, from Manakaoki in Aïr; and two skins without skulls, one of them incomplete, in full moult, and almost certainly purchased from local hunters, the other from the London Zoo, where the animal had lived for 19 months, and so is probably not altogether typical. Both these latter skins come from Nigeria, the Zoo specimen without a locality, the incomplete one from Gwoza (11°05 N, 13°42 E), possibly in the Sudan zone but very near a tongue of Sahel. Two reasons probably contribute to this poverty of material: firstly, that *Hyaena* being almost purely a night animal is therefore rarely shot; and secondly, the arid zones of West Africa being far less stocked with game and with large game-killing carnivores such as the lion and the cheetah than other parts of the continent it is likely that the hyaenas are in consequence correspondingly few. Nor are there many reliable up-to-date records of observed occurrence. The species reputedly occurs as a rarity in the extreme north of Sierra Leone according to Stanley (in Goddard, 1925); and T. S. Jones (personal communication) heard of one shot by a Veterinary Guard near the northern border in 1954 which from a description must have been *hyaena*. A. J. Hopson, in a private communication, says the striped hyaena is to be seen occasionally on flats in the Yobe valley between Yo and Lake Chad; and another trustworthy observer reported a few years ago seemingly the most unusual of all occurrences when an African hunter shot a specimen near Nabardo, about 75 km from Jos on the Bauchi road (Nigeria), that is to say in Doka woodland some 400 km south of the normal range. Zimara (1935) recorded a specimen from Fort Archambault in the Sudan woodland.

Description. The striped hyaena (fig. 46) is the smaller of the two West African species, standing about 720 mm at the shoulder, or somewhat less, and weighing 35 to 45 kg. The sloping back, from high shoulders to low hindquarters, is very noticeable. The overall impression is that of a shaggy animal due to the generally long hair of the pelage accentuated by the extremely long and abundant crest running from head to tail. This crest, and indeed the whole pelage, is erectile. The colour of the coat varies between individuals and from region to region; and in the face of the paucity of specimens it is impossible to be very precise regarding its appearance in West Africa. In general the background colour ranges between pale grey and yellowish-buff, and on this, along each flank between the belly and the crest, are imposed a number (*c.* 6 to 8) of deep brown or blackish transverse stripes of very irregular length, breadth and continuity. The legs, too, especially the upper portions, bear similar dark transverse bands. For the most part the body stripes are some 10 to 15 mm broad at their widest, but usually taper at each end. They are formed by bristle-hairs that instead of being unicolorous as in the

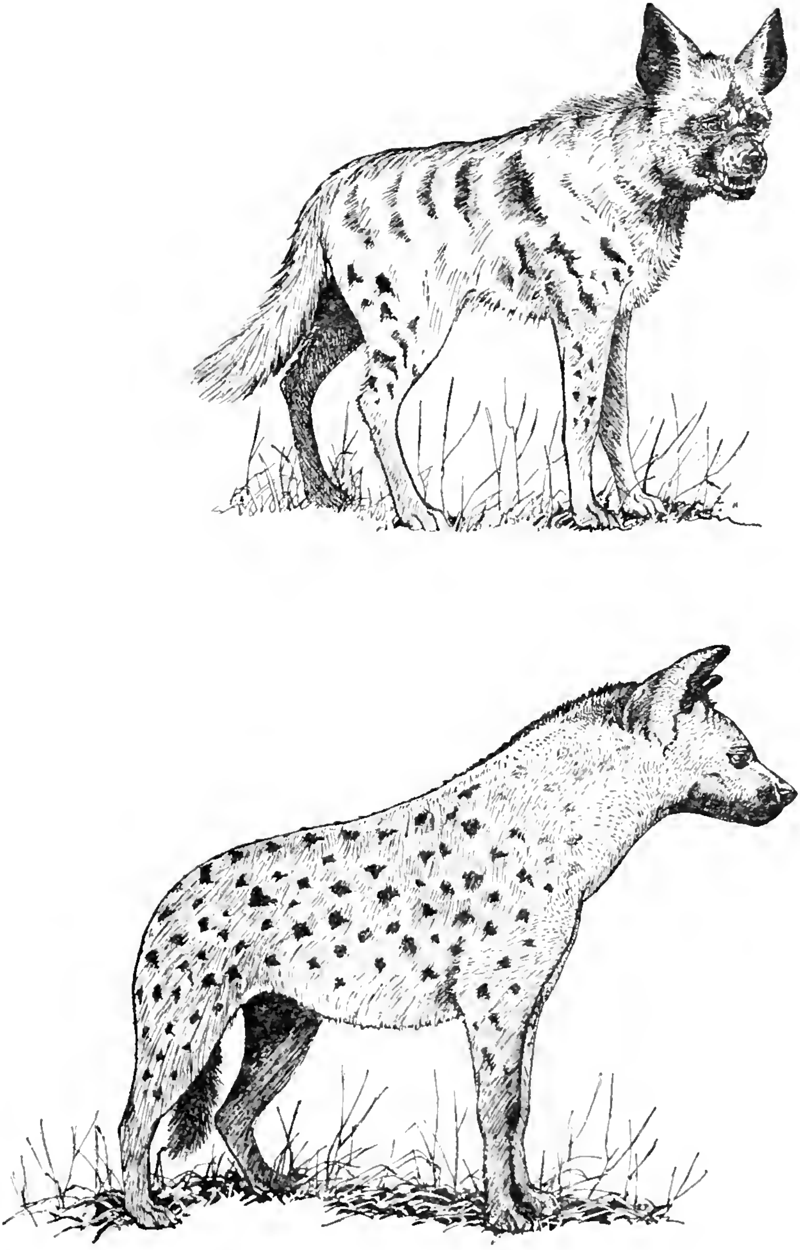


FIG. 46. Striped Hyaena (*Hyaena hyaena*)
Spotted Hyaena (*Crocuta crocuta*)

rest of the coat are blackened throughout all or a great part of their length. The spinal crest is composed of dense bristle-hairs that may reach well over 200 mm in length and are also blackened, though so much of the long pale basal portions shows as well that the general effect is parti-coloured black and buff. The throat, and sometimes a little of the chest, is black, this colour extending here and there to the sides of the neck.

The composition of the pelage is normally of moderately long underfur and much longer bristle-hairs. The lengths vary a good deal from specimen to specimen but an average is 25 to 30 mm for the underfur and 50 to 60 mm, sometimes more, for the bristle-hairs. In some cases, through moult, the underfur entirely disappears leaving a thin coat of bristle-hairs inadequate to conceal the skin. The tail is short, that is to say about a quarter or a little more of the head & body length, and very bushy with extremely long, coarse bristle-hairs similar to those of the crest, with which it is in a manner of speaking continuous. The long ears are pointed, and hence in sharp contrast to those of *Crocuta*. Another marked difference between the genera lies in the external sexual organs of the female, which in *Hyaena* are normal and do not bear that superficial resemblance to those of a male that has given rise in the other genus to stories of hermaphroditism. The supra-anal scent pouch has already been described above in the general account of the Hyaenidae. The female has three pairs of abdominal mammae.

Skull (figs. 47 and 48). This has been broadly described in the introductory account of the Hyaenidae, above. It differs from that of *Crocuta* partly in its appreciably smaller size and generally slightly less massive build. It is none the less a very powerful structure well adapted to the anchorage of an exceptionally strong muscular system. The posterior projection of the sagittal crest is much more rounded than in *Crocuta*. The most positive distinction between *Hyaena* and *Crocuta*, however, lies in the dentition. This, though in general smaller, differs in having a far larger upper molar which is by no means the smallest tooth in the head, its measurement transversely across the palate being of the order of 15 mm.

Habits. Because of its distribution, in the African Mediterranean countries, through Arabia to India, the very axis of the ancient world, the striped hyaena has been known, talked and written about for countless centuries, the source of horrific stories, wild beliefs and misleading information. Topsell (1658) in his indefatigable fashion compiled five or six closely printed pages crammed with fabulous beliefs and outrageous medicinal recipes gathered from Aristotle, Pliny, Galen, Albertus and a dozen other ancient authorities, information once a matter of most earnest acceptance though today almost wholly risible. Nor are these beliefs yet dead; for in Libya (Zammarano, 1930: 21) the local inhabitants still speak of this hyaena as of a legendary animal and attribute to it magical powers and fabulous medicinal properties. Harrison (1968) mentions a somewhat similar situation in Arabia. Despite a lengthy history of close association with man the plain fact is that by modern standards our knowledge of the way of life of this nocturnal and secretive creature remains extremely sketchy, still often amounting to little more than matters of hearsay since no set field study of the bionomics of *Hyaena* has yet been undertaken as it has for *Crocuta*.

Little that is up-to-date and supported by good evidence has come out of Africa itself. Few competent observers have written of the inhospitably arid zones in which this hyaena lives; and those that have mostly either failed to mention the animal or limited themselves to remarks regarding repulsive feeding habits and nocturnal howling. The behaviour of *hyaena* has always been tacitly presumed to be in every way precisely that of the rather better known *crocuta*; but while this may be so as regards the gross pattern it is in so far as the finer details of existence are concerned little more than an unconfirmed assumption. Even if we turn to India for information the results are still disappointingly meagre.

The striped hyaena is a more strictly nocturnal animal than the spotted hyaena, rarely emerging from its diurnal shelter before nightfall and returning to rest before daylight or soon after dawn. It is thus hardly ever seen except by moonlight; and this in part accounts for ignorance of the finer points of its habits and conduct. Further, unlike *Crocuta*, this hyaena does not as a rule join up with others into hunting or feeding parties but remains solitary or in pairs. Like the spotted species it is said to travel long distances in search of food. This last consists largely of carrion or, at least, the remains of carcases after other predators have finished with them. Almost nothing comes amiss, though Hilzheimer (1915) records that the flesh of vultures is scorned even by hungry hyaenas. Bones of all kinds and sizes are eagerly eaten, even those already denuded of all flesh by vultures. There is no difficulty regarding the breaking up of even those of large size. Nor is there about digestion; bones or the partly digested calcareous remains of them, in fact, form a high proportion of the droppings, which are very characteristic since they quickly dry to hard, pure white, subglobular masses.

Striped hyaenas are known to attack farm stock. The victims are commonly of the smaller or younger kind, sheep, goats and calves; but successful attacks are sometimes made on much larger animals up to the size of a donkey or a horse. The young of antelopes, or sick adults unable to defend themselves also fall to these hyaenas as occasion offers. Normally these predators ravenously and gluttonously get on with stuffing themselves with food as soon as they can safely get near the meal, and continue unremittingly until they are satisfied—sometimes consuming enormous quantities. At times, however, they carry food back to their dens, but whether this is as a further meal or for the purpose of feeding the young is not clear. Hilzheimer (1915) records that not infrequently a pair of tame hyaenas was, through lack of supplies, forced to go without eating for three or four days, and on one occasion eight days, without trouble or ill effect apart from eventual tremendous hunger. Something similar to this might well be a pattern in the wild. Flesh is without doubt their favourite meal; but in captivity they will eat other things, including bread (Hilzheimer, 1915) and fruit, for which latter Flower (1932) records an extreme partiality. Because they so readily scavenge anything available they can be easily trapped or poisoned. One of their more horrific reputations is the digging up of corpses. This has been positively asserted over and over again but occasionally writers have denied its truth. Both opinions probably have some justification: the story is almost certainly true in relation to hurriedly buried bodies lightly covered with sand; but seems less likely to be so of properly deeply interred corpses.

Striped hyaenas rest during the day in holes in the ground, such as porcupine or aardvark burrows duly enlarged when they are to form permanent breeding homes; or in cavities amongst rocks, or sometimes fairly narrow crevices. In so far as the last are concerned Zammarano (1930) relates a strange story of the bolder hunters of Libya worming themselves into the depths of such shelters in order to bind and drag out the occupant on a long rope; such performance being not altogether so dangerous as it might at first seem since the hyaena retreating head-first into the narrowest part of the crevice is unable to turn round to confront and bite its aggressor. Confirmation of this is given by Salez (1954) who states that in Algeria it is claimed that certain Arabs, going quite naked into a hyaena burrow, are easily able to capture the animal alive.

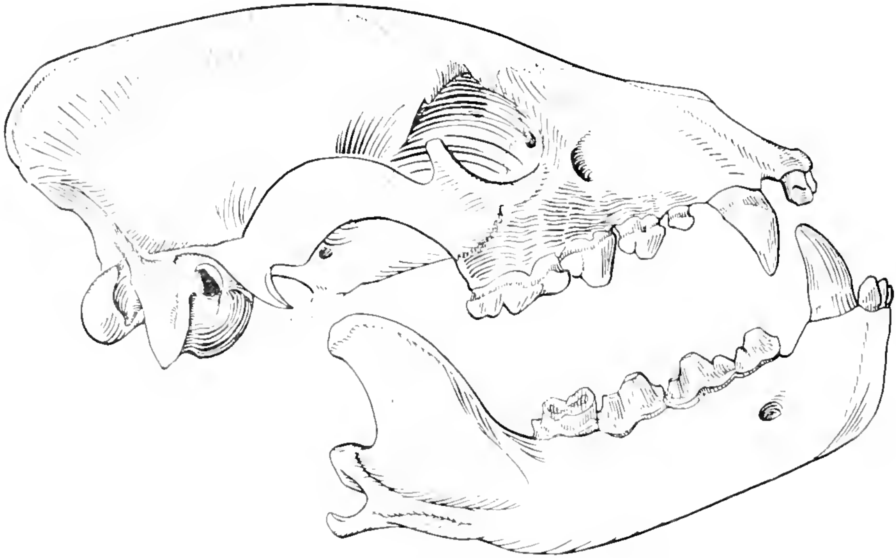


FIG. 47. *Hyaena hyaena*: skull, B.M. No. 23.1.1.78, ♂, × ½; lateral view

Breeding, also, takes place in these shelters. The period of gestation, according to observations quoted by Hilzheimer (1915) for the Leipzig and Berlin zoos, is probably 90 or 91 days, not 7 months as mentioned in Pocock (1941) which would seem to be far too long. Litter size is said to vary between 2 and 4, but observations are few and unreliable in spite of the fact that the species breeds readily in captivity (Crandall, 1964). The young differ from those of *Crocuta* in bearing a recognizable resemblance to the adult pelage pattern; the hair is short, silky and white but the transverse stripes on body and legs are clearly discernible; and the eventual spinal crest is indicated by a dark band. According to Pocock (1941) the newly born cubs have their eyes closed and their ears sealed down. If this is so it is in very marked contrast to *Crocuta* in which the young are born well developed and almost immediately active. Nothing is known of the course of development or of parental care; but as far as one aspect of the latter is concerned it is possible that the young are fed, after weaning, by regurgitation. At the other end of the scale, it is recorded that one of these hyaenas lived in captivity to an age of about

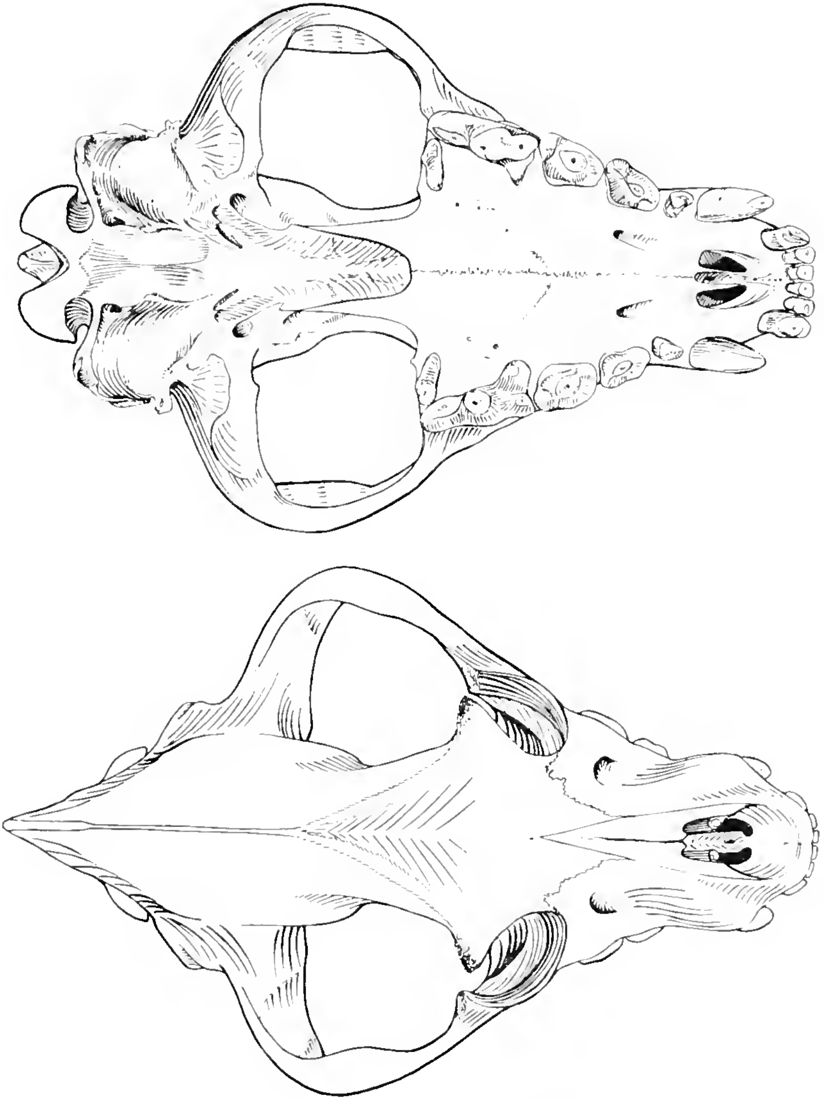


Fig. 48. *Hyaena hyaena:* skull, B.M. No. 23.1.1.78, ♂, $\times \frac{1}{2}$; palatal & dorsal views

24 years (S. S. Flower, 1931), still tame and friendly.

Strange as it may seem, these hyaenas can be fully trained. The younger the start is made the better; but Hilzheimer (1915) gives a long account of the domestication of a pair, still juvenile but seemingly past their babyhood. These were difficult at first until complete domination had been established by strong-arm methods; but they eventually came to conduct themselves like well-trained dogs and even exhibited obvious affection. It is interesting to note that this last was displayed in its highest form, as an excited welcoming, by the opening and eversion of the supra-anal pouch, the tail being held stiffly erect. However, no mention is made by this author of any objectionable odour from these glands, then or at other times; but a curious use of the scent for criminal purposes is recorded by Salez (1954). This author relates that the odour of the striped hyaena is so feared by dogs that they freeze with terror and flee without uttering any sound; and this effect is made use of in parts of Algeria by bandits who, furnished with a hyaena skin or themselves anointed with the scent, can thus without raising an alarm from the watchdogs enter settlements and drive off herds, later to be restored in return for the payment of ransom. Whether the odour of striped hyaenas really does have such a terrifying effect on dogs is unconfirmed, though Bruce (1790) discovered that his normally brave greyhounds refused to hunt them. On the other side of the picture, both Bruce and Hilzheimer relate that these hyaenas are extremely keen on the flesh of dogs and will display considerable audacity in carrying them off. Pocock (1941), however, mentions hyaenas in India shamming dead when attacked by dogs; and also a case of a tamed hyaena living in perfect amity with several dogs. The vocalizations of this species of hyaena are somewhat similar to those of *Crocuta* but less noisy.

Taxonomy. A good many races of the striped hyaena have from time to time been described, five being currently recognized, 3 in Asia, 2 in Africa. None has ever been named for the area dealt with in this present account. Authors have depended for subspecific distinction very largely upon colour, with or without some other attribute of the coat, and occasionally on the size of the teeth especially the upper carnassial, p^4. Pocock (1934) went into the question of the races of *Hyaena* in great detail, carefully examining the evidence for all the named forms. He came to the conclusion, at least in so far as tropical Africa was concerned, that colour could not be regarded as a basis for subspecific separation, many of the distinctions claimed as of taxonomic importance being merely seasonal or individual. Re-examination of the British Museum specimens confirms this view. The plain fact is that the material is too meagre and of too scattered origin to form a properly sound basis of argument; but there can be very little doubt that in any given locality there is an appreciable individual variation, of coat colour and marking, apart from any differences attributable to age, moult or season. It must not be overlooked, too, that these hyaenas are great wanderers and travel many miles in search of food. Those fortuitously gathered together in any one place at a kill may, in fact, have come from appreciably different backgrounds; and the existence of any strictly "local" race is open to doubt, the more so as the wandering habit renders breeding contacts very wide.

Pocock reached the conclusion that two races could be recognized in Africa: *barbara* Blainville confined to north-west Africa, and *dubbah* Meyer covering all those forms named for the eastern side of the continent. The latter was held to be characterized by a smaller skull and teeth as indicated by p^4; but the evidence for this seems pretty slender, and Pocock himself admitted a link between the two races afforded by specimens from

Darfur. Since the publication of his paper it has become customary to assume that West African hyaenas are also assignable to *dubbah*. Bruce's description of this form (*i.e.* the original English of the German translation used by Meyer) is of a vast animal with a head & body length of 1750 mm, a tail of 530 mm to the end of the hairs, and weighing some 50 kg—as Pocock remarked, an exceptional giant amongst striped hyaenas. The pelage colour was given as yellowish-brown, the head and ears lighter; both the tail and the spinal crest were of a reddish-brown colour "without any rings or bands of blackness upon the points". Certainly nothing like this is so far recorded from West Africa, the only known skin closely corresponding to this colouring coming from Uganda. Pocock himself made no attempt to assign the only West African specimen then to hand, an immature skin and skull from Manakaoki (Aïr), either to his widely variable *dubbah* or to any other form. Since his detailed review further West African material has become available but as this comprises only two skins unsupported by skulls, the one a zoo animal reputedly from Nigeria, the other incomplete and in full moult without underfur from Gwoza (Nigeria), it is quite insufficient as the foundation of any reasonable judgment. The first two are densely haired and basically buff; the last almost hairless, what little there is of the thin top-coat being white.

The present author sees no virtue in pretending to a degree of accuracy implied by the attachment of a third name, either *dubbah* or anything else, to West African specimens on the basis of the present available material.

Genus **CROCUTA** Kaup, 1828

Spotted Hyaenas

Crocuta Kaup, 1828, in Oken's *Isis*, **21**: column 1145. Type species *Canis crocuta* Erxleben. This name was really preoccupied by *Crocuta* Meigen given to a two-winged fly in a paper published in 1800. Although Meigen's pamphlet was declared available in 1944 by Opinion No. 152 of the International Commission on Zoological Nomenclature it was, in 1962, suppressed by the same body under Opinion 678. The name is derived from the Greek *krokotos* meaning saffron-coloured, with reference to the pelage.

Crocotta Kaup, 1829, *Skizzirte Entwickelungs-Geschichte und naturliches System der Europäischen Thierwelt* . . . **1**: 78. Type species *Canis crocuta* Erxleben. A re-spelling of the above.

This genus differs from the last in being purely African in its present distribution; but in late Tertiary times it was an inhabitant of Asia and Europe, at least as far north as England, where caves are known containing abundant remains. Though, in its heavy forequarters and sloping back, *Crocuta* bears a broad resemblance in bodily form to *Hyaena*, the general pelage pattern and character are quite different, consisting of spots, not stripes, and being much shorter in length, lacking any marked spinal crest. The rounded ears are also quite distinct; and there is an important difference in the dentition. Since the genus is monospecific there is no need for further generic description.

CROCUTA CROCUTA Erxleben — Spotted Hyaena

Canis crocuta Erxleben, 1777, *Systema Regni Animalis* . . . Classis I, Mammalia: 578. In this work the range was given as Guinea, Ethiopia, to the Cape of Good Hope; but Cabrera, 1911, in *Proc. zool. Soc.*

Lond.: 95 argued that the type locality was most probably Senegambia. The derivation of this name has been given above under the genus.

Hyaena maculata Thunberg, 1811, *Mém. Acad. Sci. St. Petersb.* **3**: 302. Type locality South Africa. The name is the Latin adjective meaning spotted.

Hyaena capensis Desmarest, 1817, *Nouveau Dictionnaire d'Histoire Naturelle etc.*, Nouvelle edition, **15**: 499. Type locality Cape of Good Hope.

Hyaena rufa Desmarest, 1817, *Nouveau Dictionnaire d'Histoire Naturelle etc.*, Nouvelle edition, **15**: 499. Type locality Cape of Good Hope. The name *rufa* is the Latin for reddish, referring to the pelage coloration.

Hyaena croacuta A. Smith, 1826, *A Descriptive Catalogue of the South African Museum, Part* **I**, *of Mammalia*: 12. A misspelling of *crocuta*.

Hyaena encrita A. Smith, 1827, *Trans. Linn. Soc. Lond.* **15**: 461. A misprint for *crocuta*.

Hyaena cuvieri Boitard, 1842, *Le Jardin des Plantes*: 233. Type locality Cape of Good Hope. This was named in compliment to the great naturalist Baron Cuvier.

Hyaena (*Crocotta*) *thierryi* Matschie, 1900, *Sber. Ges. naturf. Freunde Berl.*: 30. Type locality Sansanne Mangu, Togo. This was called after its collector Oberleutnant Thierry.

Hyaena (*Crocotta*) *togoensis* Matschie, 1900, *Sber. Ges. naturf. Freunde Berl.*: 31. Type locality Kete Krachi, Togo.

Hyaena (*Crocotta*) *noltei* Matschie, 1900, *Sber. Ges. naturf. Freunde Berl.*: 215. Type locality Yoko, upper Sanaga, Cameroun. Named after Oberleutnant Nolte, who collected it.

Distribution and general. It may be broadly said that the spotted hyaena is spread through Africa south of the Sahara with the exception of the closed forest. It is true that occasional occurrences in this last zone are reported but these mostly refer to places that are not far distant from the open grass-woodlands or at least from clear-felled farmlands; and, in West Africa at any rate they are very exceptional. One such visit is mentioned later in this account. On the western side of the continent *Crocuta* occurs in Senegal but apparently not so far north as Rio de Oro. From this extremity it ranges across the continent in the Subdesert zone (but not the desert itself) Sahel, Sudan, Doka and Guinea woodlands to Eritrea and Somalia; thence down the eastern half to parts of South Africa, South-west Africa and Angola. It is known to ascend to an altitude of about 3500 metres. Its distribution, thus, in western Africa in parts overlaps that of the striped hyaena, chiefly in the Sahel zone. Although it occurs outside them the spotted hyaena is most at home in the Sudan and Sahel woodlands, though rarer in the latter than the former. Its appearance further south in the Doka and Guinea zones is to a large extent a matter of season; for in these, especially the latter, it is impossible to see and not easy to progress through the tall dense grass that normally covers them. When this is burnt in the dry-season, however, large stretches of the country become wide open, the newly sprouting green grass attracts antelopes, and the zones become for a few weeks a profitable hunting ground. In parts of eastern and southern Africa the spotted hyaena is exceedingly abundant; in West Africa this is not so, though in certain areas of the Sudan zone it is not uncommon. An interesting comment on the relative importance of the two hyaenas in that zone in West Africa is provided by the fact that whereas the Hausa-speaking peoples have only one or two terms for the striped variety they have nearly a score of names and epithets for the spotted one. In Sierra Leone it was formerly common in the open woodlands of the north; and, in fact, these animals proved a pest in Kabala town between 1924 and 1930, coming down at night from the rocky hills to steal cattle hides pegged out to dry. T. S. Jones (1966) noted that the species was well-known and common in the wilder parts of Bombali and Koinadugu; he found (personal communication) that the numbers had been greatly reduced and that it had become localized in hilly areas away from towns. Yet further west, Monard (1940) recorded that it was then abundant in Portuguese Guinea; and G. S. Child says (1971, private communication) that it occurs but is not common in the Borgu Game Reserve (extreme west Nigeria).

However, as far as the whole region covered by this present work is concerned *Crocuta* is very poorly represented in the British Museum, study material comprising merely 2 skins and 4 skulls, half of each being juvenile. These come from Gambia and north-east Sierra Leone. It is certain that in recent years the species has become less plentiful in West Africa. This is due in part to increase in human population and extension of agriculture, resulting in less and less game; but in some measure it is more directly due to a policy of poisoning, the Bauchi (Nigeria) local government, for example, a few years ago offering a bounty of £2/10/- a skin, resulting in near extermination (Sikes, 1964b). Poisoning has also been carried out from time to time in Sierra Leone by the Veterinary Department in response to complaints from Fulani cattle owners that their calves were constantly stolen. Some of T. S. Jones's specimens in the British Museum are the outcome of such control in the Gberia area where about 20 hyaenas died, several in their subterranean holes. It is possible that widespread destruction has similarly been carried out throughout the length and breadth of West Africa. Nevertheless, Matthews (1939a) found that although in Tanzania *Crocuta* was mercilessly killed at every opportunity, and sometimes in large numbers, it remained superabundant. The difference is without much doubt attributable to the very disparate availabilities of food.

Description. *Crocuta* (fig. 46) is a far larger, more heavily built animal than *Hyaena*, rather clumsy in appearance in fact. This greater size is succinctly conveyed by its weight which normally lies between 65 and 75 kg, and may be more, as compared with 35 to 45 kg in the other species. It can stand 750 mm at the shoulder. Like the striped hyaena its forequarters are far more heavily developed than the hindquarters, and the forelegs longer than the others so that the back is in consequence similarly sloping from neck to tail.

Colour is widely variable and these differences have been used as the basis of several local races, as discussed later. But speaking in broad terms the pelage has a ground coloration of pale greyish-brown or yellowish-grey on which is superimposed an irregular dorsal and lateral pattern of dark, roundish spots. These, mostly very distinct, may be reddish, deep brown or almost blackish, and are of variable size, in the same skin as well as between specimens, but are commonly of the order of 20 mm diameter. This maculation is continued, though sometimes less distinctly, on to the legs and belly but not the throat and chest. On the back and sides of the neck the spots are often replaced by five, paler, not sharply defined longitudinal bands; but these markings are sometimes so obscure as to be virtually absent. The broad medial band on the back of the neck is nearly always lengthened into a slightly forwardly directed crest sometimes broad enough to constitute a small mane; and it is very often continued posteriorly as a spinal crest, rather shorter in length and less forwardly pointing. It usually fades out somewhat to the rear of the shoulders; and it is nowhere in any way comparable in length and importance to the crest of *Hyaena*. It is mostly a lively red-brown, and this colour consequently in the majority of specimens dominates the back of the neck to the crown. But it is sometimes darker, and sometimes so short as to be virtually lacking. It must be emphasized that the foregoing description is a general one applying to a large proportion of specimens; but all kinds of variation of colour and coat length are met with, including one in which the whole dorsum is dominated by a bright red-brown, and the spots are indistinct and ill-defined.

Although generally adequate to conceal the skin the pelage is relatively sparse and is composed of two types of hair; moderately fine underfur which is so long that it may be mistaken for bristle-hairs, and longer, stouter, flat-sectioned bristle-hairs themselves. The components vary in length between specimens and under different conditions, but average figures are in the region of 15 to 20 mm for the underfur and 30 to 40 mm for the bristle-hairs. These latter may be black throughout or merely with long black ends; and they are comparatively widely dispersed, the main coat being formed by the long underfur. Here and there are scattered much longer, flat-sectioned black bristles; and the hairs of the nuchal crest may run up to 80 mm in length. The fur feels mostly slightly harsh but if properly cleaned becomes in fact, soft to the touch.

It has already been said that these hyaenas seem disproportionately heavily built anteriorly. Part of this effect is produced by the long, very thick neck, a highly muscular structure that complements the powerful cutting and ripping attributes of the massive jaws. The head, too, is wide and flat, the muzzle deep and blunt, the naked rhinarium broad. The crown and upper part of the face is brownish, of the same tone as the back, except for a whitish band above each eye; but in front of the eyes the area around the rhinarium, the upper and lower lips, and the anterior portion of the chin are all blackish. The ears are in marked contrast to those of *Hyaena*. They are unevenly elliptical, with a well curved outer margin and a rather straight inner one; and they are more rounded at the apex than those of the other genus.

Both fore and hindlegs are spotted; but the large feet are plain coloured, lighter or darker brown, sometimes blackish. They are clad, particularly on the upper surface, with a dense covering of very stiff, curved bristles. The four digits are webbed, the non-retractile claws stout, blunt and short; the pads very broad and flat, the whole under surface of the foot around them naked. The tail is short for the size of the animal, of the order of 300 to 350 mm to the end of the hairs. It is narrow in the basal half and there relatively short-haired, brownish like the back at the root but with a small whitish or greyish area distally of this; the whole posterior half of the tail is occupied by a very long-haired, black or almost black, bushy tuft. Except at occasions of excitement, that is to say while standing about or while merely trotting from place to place, the tail is usually held downwards; but under the spur of keen interest it is curved over the rump, the terminal black bush well feathered out, especially towards the rear. Juveniles are entirely deep blackish-brown in colour, without spots, all over except for rather hairless patches in the axillae and groins. The claws, as yet unworn, are slender, curved and sharp.

The scent glands in the adult, both male and female, situated either side of the rectum and discharging in a sac sited between the tail and the anus, have been more fully described under the family heading. This hyaena is chiefly remarkable for the structure and appearance of the female genitalia, which have given rise to misunderstandings and fables throughout many centuries. The male organs are normal. Those of the female have been described by several authors but the most detailed recent account is that of Matthews (1939c). Clear illustrations are also to be found in Davis & Story (1949). Very briefly the position is this. In a female that has not yet reached sexual maturity the resemblance of the sexual organs externally to those of a male is so close as to be indistinguishable. This decreases considerably during the later stages of life. The likeness is brought about by a stout peniform clitoris, free anteriorly for a length of some 50 mm, 25 to 30 mm in diameter at its base, and sited in the precise position normal to the male organ and equally capable of erection. Through this runs the urinogenital canal, finding its exit at the tip in a narrow slit exactly as in a penis. The visual correspondence to the male engendered by this structure is strengthened by the occurrence of low, paired swellings closely simulating a scrotum, positioned as in the male just forward of the anus. This overall parallelism is increased by further correspondence of detail not entered into here.

As puberty is approached changes take place and resemblance to the male sex, while still existing, starts to become less remarkable. This is occasioned by the necessity for both penetration by the male and ultimate parturition to take place through the peniform clitoris. As the urinogenital meatus as described above is a minute slit only some 2 to 3 mm in length it is obvious that considerable enlargement of this must come about. With the onset of puberty progressive widening of the preputial orifice takes place until it is capable of extension to some 35 to 40 mm, though normally contracted by its elastic walls. Other changes, not relevant to the present brief account, also take place, to a greater or lesser degree affecting the proportions and overall appearance of the prepubertal clitoris. With parturition yet further stretching occurs and the organ loses a good deal of its original peniform aspect. A slack-walled and reduced prepuce, with an enlarged orifice which has come to lie ventrally and the lips of which tend to hang apart, eventually bears but a limited resemblance to a penis. It is this very marked alteration of appearance that gave rise to the very lively and persistent belief that the hyaena is hermaphrodite or changes its sex from year to year.

The lactating female has two large abdominal nipples but there are also two small non-functional ones a little posterior to these. A similar pair of rudimentary nipples occurs also in the male.

Skull (figs. 49 and 50). A description of the main features of this was given above under the generic heading. The *Crocuta* skull differs from that of *Hyaena* partly in its markedly greater size. The posterior projection of the sagittal crest is much narrower and less rounded than in *Hyaena*. Several other differences of detail between the two genera have been described by Buckland-Wright (1969). The most immediately characteristic distinction is to be found in the teeth, the upper molar being the smallest tooth in the head, only some 5 mm across, and often lacking on one or both sides, giving a false impression of the true dental formula. Taking size into account the *Crocuta* skull is relatively amongst the most powerful of all carnivores. The enormous anchorage for muscles provided by the enlarged sagittal crest, the deep zygomata and the massive mandible; the siting of the carnassials far back in the jaw at a point of high mechanical efficiency; and the fact that these teeth are little smaller than those of the vastly bigger lion all contribute to this. It may be mentioned here that at various times authors have claimed that differences in proportions between various parts of the skull constituted valid bases for subspecific differentiation. Matthews (1939b) as the result of very detailed investigation found this not to be so.

FIG. 49. *Crocuta crocuta*: skull, B.M. No. 59.272, ♀, (missing posterior detail filled in from B.M. No. 61.41, sex ?), × ½; lateral view

Habits. The spotted hyaena, like its striped relative, has an unsavoury and unlovable reputation. It is almost universally regarded as a cowardly, skulking scavenger, of unclean habits, unclean in itself, feeding only on the vilest refuse and carrion or at best the scraps left after more worthy creatures such as the lion have killed and eaten their fill. All men's hands are against it as one of the most ignoble and undesirable of all existing mammals. But while there may be an underlying element of truth in all this it now emerges that the overall picture must be very much revised. Recent studies show

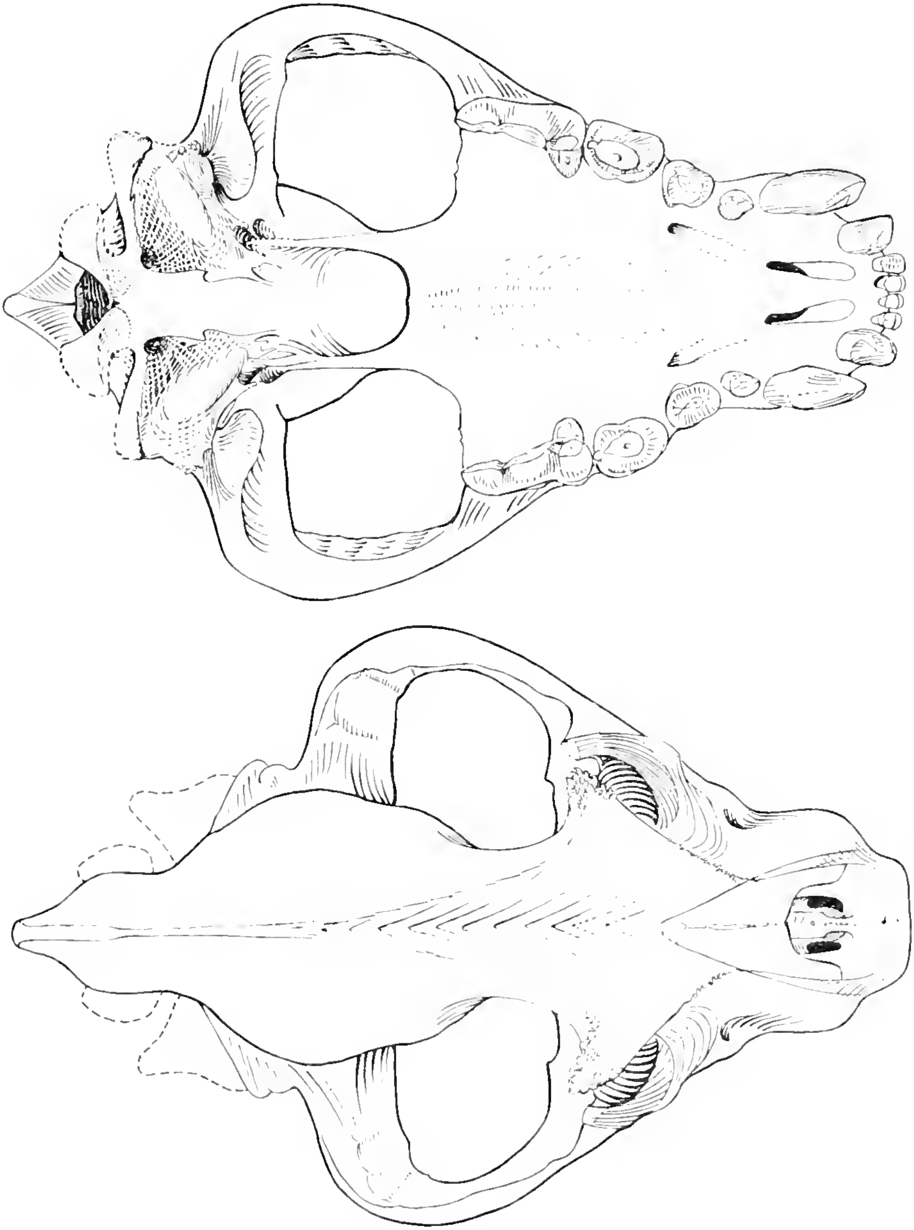


Fig. 50. *Crocuta crocuta*: skull, B.M. No. 59.272, ♀, (missing posterior detail filled in from B.M. No. 61.41, sex?), × ½; palatal & dorsal views

that *Crocuta*, in fact, commonly kills on its own behalf, eating warmly fresh flesh; that it is the lion that is very often dependent upon the hyaena, not *vice versa*; and that by its scavenging it serves a very useful purpose, and by its predation upon the ungulates does much to preserve a healthy balance of nature.

In comparison with the striped hyaena, as well as with a high proportion of the other animals dealt with in this work, the mode of life and general behaviour of the spotted hyaena are now relatively well known as the outcome of investigations by competent field workers directed entirely or largely to this end alone rather than merely from random gleanings incidental to travel. Chief among such research workers in recent years are Matthews (1939 a, b and c), Kruuk (1966 a and b, 1967, 1968, 1970) and the van Lawick-Goodalls, whose astonishingly intimate picture (1970) of day to day life amongst the hyaenas goes far to dispel the unsavoury repute in which these creatures are held and to engender an understanding of their true character. It is no exaggeration to say that absolutely nothing has been recorded of the habits of the spotted hyaena in West Africa and it is therefore necessary to rely almost completely on the findings of these workers in East Africa to build up the account which follows. But here it is necessary to utter a caution. One of the many interesting points emerging from Kruuk's investigations is the rather surprising fact that the habits of spotted hyaenas vary quite appreciably with the circumstances of their environment. His observations were made in two areas of Tanzania, not far removed from each other but very different in effective character. The Ngorongoro crater is to all intents and purposes a walled-in plain only some 250 square kilometers in extent, the animal inhabitants of which have limited intercourse with those outside and must learn to fashion their existence to relatively restricted circumstances. It is, in effect, a self-contained ecological unit. The Serengeti National Park on the other hand is wide open to movement, migration and contact with other animal populations over a vast area. *Crocuta* displays somewhat different patterns of behaviour in these two diverse sets of conditions; and it is therefore by no means sure to what extent observations made extralimitally are applicable to the region dealt with herein.

Yet another circumstance must be taken into account. It has emerged, largely from the work of Kruuk, that the two favourite objects of predation by spotted hyaenas in East Africa are firstly wildebeest and secondly zebra, each of which is commonly deliberately selected for hunting, each in somewhat different fashion. The fact that neither of these ungulates occurs in West Africa postulates one prime difference in behaviour pattern. However, it may be supposed that this hyaena's third favourite choice of prey in Tanzania, Thomson's gazelle, provides some indication of its feeding preference in West Africa. In this latter area this antelope, which is absent therefrom, may reasonably be regarded as represented by the not very distantly related red-fronted gazelle. It is also possible, or even probable, that wildebeest are substituted by hartebeest. But there is one considerable difference, that of quantity and concentration. In eastern Africa Thomson's gazelle is common and occurs in sizeable herds; in the west, red-fronted gazelle are by comparison few and far between and live, at most, in small bands of a dozen or much less. Similar numerical disparity applies to hartebeest and wildebeest. This fact, and indeed the entire situation in West Africa with its virtual lack of large ungulate concentrations of any kind, argues a different mode of life for the hyaena from that uncovered on the eastern side of the continent. Possibly nomadic Fulani herds of cattle, from which calves and, less often, incapacitated adults are commonly stolen constitute a more important food factor in West Africa than in the eastern parts of the continent more abundantly furnished with wild species. The suggestion has also been made that, anyhow in some respects, the behaviour of the species in southern Africa is at variance with that in Tanzania (*Rep. Brit. Mus.* (*Nat. Hist.*), 1966–1968). Quite obviously a profitable field of study of comparative behaviour between *Crocuta crocuta* in western and eastern Africa is opened up. With these cautionary observations it is now possible to review some of the main habits of this hyaena revealed by recent field studies as indicating the kind of habits and behaviour that may be critically looked for in West Africa.

Better knowledge of *Crocuta* than of *Hyaena* is in part due to the former's greater abundance in Africa, and in some measure to the fact that it is less restrictedly nocturnal, being not infrequently seen by day. But although it shows itself and can thus at least be more clearly observed than by moonlight it is at these times often atypically inactive, lying about resting or on the watch. Kruuk (1970) in fact accounted this hyaena, by reason of its almost nocturnal activity, a very frustrating subject of study, the acquisition of even the simplest information demanding a disproportionate expenditure of time. For most of the information regarding behaviour it is necessary to rely on brilliant moonlight or to hold these animals in the headlights of a car, pursuing them across country if they are on the run. However, a good deal about domestic behaviour can be picked up in better light in the vicinity of breeding dens (Goodall, 1970).

Except occasionally, spotted hyaenas are not solitary; nor, on the other hand, are they truly gregarious as, say, the banded mongoose is. The fact is that habits in this respect vary according to different factors. Basically these hyaenas hold together in small units, possibly single family groups; but these at times become associated into loosely knit communities, depending upon season, availability of territory or of prey, and to some extent sex, the males being more given to wandering than the females. Although some individuals may be observed during the day, for the most part *Crocuta* seeks shelter while the sun is up. For this purpose use is made of holes in the ground, gaps between rocks, sheltered hollows, or dense undergrowth. At times the shade of a tree suffices; and any shallow pool of water or of wet mud—even that self-made by urinating—is welcome during the heat of the midday and afternoon sun. In rocky country a plentiful supply of hyaena dens is available ready-made in the form of fissures or, sometimes intricate, series of gaps between boulders; but elsewhere, where the soil is sufficiently soft, the favourite and commonest refuges are holes in the ground. Some few of these may have started as aardvark burrows or deserted termite mounds that have subsequently been greatly altered and extended; but the majority are self-excavated by the hyaenas, probably continually enlarged over a number of years. Such lairs may stand more or less alone but with others at short distances; sometimes they are constructed close to one another in the form of a warren, though apparently not intercommunicating under ground. Kruuk (1967) observed that during the breeding season a central denning site was formed, at one such there being 30 cubs playing round. In illustration of how loosely knit such communities really are, Kruuk noted that, unlike the hunting dog (*Lycaon*), each female tended only her own offspring.

Matthews (1939a) investigated a large warren of dens covering an area of over 30 × 15 metres, honeycombed with burrows. These excavations proved to be surprisingly large. The general form is that of a tunnel with a spacious end chamber used for sleeping or breeding. Matthews found the former to measure up to 2 metres in width, the height being rather less; the latter, which were roughly oval in shape, were approximately 3·5 × 2·5 metres in length and breadth. This particular warren lay in the vicinity of a dry river bed with deep banks into which entrance had probably originally been effected. One such adit was sited at a depth of about 3·5 metres below ground level; but the tunnel sloped upwards fairly sharply, soon rising to within 2 metres of the surface, and at 9 metres from the entrance being only 1·2 metres below. Mostly the burrows are not so far beneath the surface, lying at a depth of some 60 to 90 cm. Where such excavations get too near the surface they are liable to collapse leaving a plan of their whereabout in the form of depressions. The walls of the craters thus left by the large end-chambers become conveniently available fur further horizontal adits to new dens. But entrance is by no means always in a horizontal direction and must, in fact, over the general run of country be by a vertical shaft turning into a horizontal gallery. Not all tunnels are of the large diameter described by Matthews; or if their adits are wide they soon narrow.

On the surface, entrances may be quite close to one another; and, below ground, so may chambers; but although a chamber may have three or four tunnels leading to it there does not appear to be any intercommunication between different units in a warren making the burrows into a really communal complex. But the tunnels themselves may fork; and Sutcliffe (1970) mentions a chamber which had at least ten exits situated around it. No description of a chamber in actual use as a breeding nest has been given, as to whether it is lined in any way or left bare, as seems most probable. However, studies have recently been made in East Africa of the contents of burrows. These established that bone fragments are found around and inside the entrances to burrows and also in some quantities within the tunnels but, to all intents and purposes, never in the chambers. A wide variety of prey was found to be concerned: zebra, buffalo, wildebeest, kob and other antelopes, baby hippopotamus, donkey, cow, dog, and human skulls and bones looted from a hospital burial ground 4 km away, which subsequent examination shows to be regularly visited. Only very few remains of hyaenas themselves were found to occur and those juvenile. The conclusion arrived at was that, while adult hyaenas mostly feed where they have killed or otherwise found a meal, they sometimes bring food back to the nesting site and the young may then carry it below into the tunnels but not as a rule into the chambers (Sutcliffe, 1970). It is of interest to note here that the reason for this special investigation of hyaena dens in caves and burrows was to discover the habits of these animals with regard to bone storage in their lairs in order to cast light on the now disputed origin of large concentrations of splintered bones, principally of *Crocuta*, found in caves in England, until recently believed to indicate that these sites had therefore been hyaena dens (*Rep. Brit. Mus.* (*Nat. Hist.*) 1966–1968).

Any food that is brought back by adults to the breeding site for feeding the young is mostly of easily digested parts; yet around the warren are found piles of very much more resistant materials. These are accounted for thus. Adult spotted hyaenas can readily splinter all but the most solid parts of the largest bones; and they do not hesitate to swallow large chunks of these and other hard matter. Digestion is for the most part extremely efficient and rapid. Nevertheless, certain parts of the carcass do prove intractable—hair, hoofs, teeth and very stout bone fragments—and these are, after digestion of the rest, regurgitated in masses around the burrows. One of the less endearing facts of the hyaena's existence is that as soon as regurgitation takes place the animal performing it, or others if they can get to the spot quick enough, roll heavily in the expelled matter and pick out from it such fragments of bone as can be reswallowed (Goodall, 1970).

It is interesting to note that this animal so widely regarded as the pattern of filthiness takes care not to foul its lair. Only most exceptionally is any sign of droppings discovered within the burrow; and these hyaenas, like so many other wild mammals, have in fact set latrine areas. Sikes (1968), however, found that attempts at house-training a young *Crocuta* were fiercely resisted, and it is therefore possible that such deposits as do sparingly occur in dens are those of juveniles who have not yet learned to make use of the correct site. Spotted hyaena latrine areas are readily recognisable by the gleaming, dead-white, dried droppings scattered over them. When evacuated these are green; but they quickly dry out to hard calcareous lumps composed largely of partially digested bone mixed sometimes with undigested fragments, and with hair or feathers.

Much has already been said above, incidentally, regarding feeding habits in the spotted hyaena. There seems to be no record of its eating fruit or other vegetable matter as so many other carnivores do; nor is there much to suggest that reptiles, amphibians or insects play much of a role, if any, in its dietary, though it may be supposed that a good-sized snake, if dead, would not come amiss; and Pitman (1931) records that one has been observed digging up and eating crocodiles' eggs. For the fact is that, though these animals more commonly kill and eat fresh flesh than has in the past been supposed, they are still in a very large measure scavengers and when beset with hunger will take not only carrion but anything with any faint suggestion of flesh or blood in it. It has long been known that they will steal and eat boots or harness or any other leather articles left lying conveniently about; but the following would seem to be new. Some years ago a forest officer paid a visit to the Mamu Forest Reserve some 35 km south of Ibadan (Nigeria), using a kit-car and spending the night in the rest-house. Next morning he discovered that his tyres had been badly savaged and eaten. Only *Crocuta* would have the strength of jaw and the possibility of the urge to effect the degree of damage that was done. But this posed two problems. Why was rubber attacked; and what was a spotted hyaena doing in such a high-forest locality? As regards the latter, it was first thought that the animal was most likely an escape from an itinerant Hausa showman such as from time to time toured the country with one or a pair of muzzled hyaenas; but it is now known that these animals occasionally visit the closed forest, though admittedly this was a matter of 50 km from the nearest grass-woodland. In so far as the first point is concerned, it was supposed that, it being the rainy season, a large number of frogs had been run over, and in consequence the tyres were well covered with their blood and other remains. Nothing can be proved but there seems to be no other likely alternative explanation of this incident. The Goodalls (1970) record that hyaenas attack, or savagely play with, exterior fittings of cars, and also their interiors; but no mention is made of tyres; and, indeed, if such an urge were common their close-up observation of these animals from stationary motor vehicles would have been a matter of yet greater difficulty.

In spite of their reputedly cowardly nature spotted hyaenas are bold enough to rest on the outskirts of villages by day and prowl about their streets by night. They will even enter houses; and children or incapacitated adults have certainly been badly bitten or killed and carried off by day as well as by night. In cleaning up the offal and other offensive matter from compounds and village rubbish heaps these animals, of course, fulfil a very desirable and useful purpose, though the same can hardly be said of their propensity for disposing of buried humans, a practice recently confirmed by Sutcliffe (1970). This last habit has usually been associated only with shallow, hastily dug graves; it is therefore interesting to note that Abel Chapman (1908) mentions the removal by hyaenas of a corpse buried at a depth of 2 metres, the hole not only filled with earth but topped with stones as well. In the light of the now known deep burrowing habit of these animals such a feat arouses little surprise. Several writers (*e.g.* Johnston, 1886) make it clear that the profanation of graves is in various parts of Africa nonchalantly regarded as an everyday matter of course. Pitman (1931), indeed, refers to the spotted hyaena as that "loathsome body-snatcher".

Such actions, together with the patient and servile waiting for the lion to feed before rushing in to gourmandize such second-rate matter as may then remain, are those for which the spotted hyaena is most widely famous. But in recent years attention has become more sharply focussed on this animal's behaviour as a constant and very active predator in its own right. It also transpires that it is not so utterly pusillanimous as commonly believed. This is very largely due to the field work and writings of Hans Kruuk (1966 a and b, 1967, 1968, 1970) and the Goodalls (1970). In spite of its common notoriety as merely a scavenger it has long been recognised that the spotted hyaena is something more than that and quite regularly kills for itself. Mostly its reputation in this respect was in connexion with the theft of farm stock or attacks on children or sleeping men; but nearly a century ago Johnston (1886) drew attention to the fact that it was much more of a predator than was commonly supposed; and Matthews (1939a) recorded being reliably informed that these hyaenas combined into packs to hunt and kill zebra. However, Kruuk (1970) has in recent years made nearly a thousand first-hand observations of hyaena kills involving not far short of 8000 participant hyaenas, apart from analysis of many hundreds of droppings, and the hunting, killing and feeding habits of *Crocuta* have now passed out of the hearsay stage and are the subject of concrete figures and statistical analysis casting valuable light on the precise role these animals play in controlling the numbers of game and so forth. But these observations do, nevertheless, derive from East Africa and, as pointed out in the introduction to this section, are of doubtful application elsewhere and certainly, since they mainly involve zebra and wildebeest, not the region now under review. Interesting as Kruuk's results are, only their main points, together with the often more intimately domestic observations of the Goodalls, can be usefully glanced at here, and those very briefly, not as having any positive application to West Africa but as pointers to lines of field study that might be carried out into comparative behaviour under a dissimilar set of conditions.

When dusk falls the really active life of *Crocuta* begins. Animals emerge one by one from their daytime shelters and walk about carrying out lengthy greeting ceremonies with others of their clan until a gathering numbering from a few to twenty or even more builds up. Eventually they all move off in a common direction, though giving the impression of being, unlike hunting dogs, not so much a unified pack as a collection of individuals. Somehow or another the prey for the night seems to have been predetermined, whether it be zebra or wildebeest; and once this has been done alternative species are passed by even though they may be much more conveniently at hand. Numbers probably have something to do with this; for large gatherings of hyaenas set out after zebra; wildebeest are hunted when only two or three predators are co-operating—though others quickly join the feast once the kill has been effected; and single hyaenas seek out gazelles. The method with the larger game is to chase a herd at a steady pace, though working individually rather than as a pack, keeping up sufficiently close for each pursuer to make repeated bites into legs and hindquarters until one of the hunted animals can take no more and sinks to the ground. Whereupon the whole gathering of hyaenas breaks off the hunt, falls upon the victim and devours it, ripping up the belly and starting with the soft internal organs while the victim is still alive. The chase may last some minutes and extend over a couple of miles; but once an animal has been brought down every trace of its existence, even of so large a creature as a zebra, may disappear within half-an-hour or less. When in full career these hyaenas can cover the ground at about 60 km an hour, or somewhat more, head and stout neck up and strained forward, tail down. When merely seeking out prey they lope along at some 15 km an hour, or, finally, make a stealthy walking approach. Eloff (1964) records three instances of very long distances covered by hyaenas either in actual chase or, at any rate, to secure prey. In one case a pack was observed to have followed a gemsbok for rather more than 22 km; and on another occasion for about half this distance. Lastly, a few goats having been killed in a compound one night, the tracks of the hyaenas which caused this damage were followed for 40 km back to the pack's resting holes; from which it was inferred that the raiders must have travelled 80 km in one night.

Such hunts are always carried out at night; but killings of another sort sometimes take place in rather better light. Often hyaenas lie hidden on the fringes of herds patiently watching for stragglers they may pounce upon; or they steal up close to females with new-born young in the hope of being able to snatch the latter; and this they may sometimes attempt with quite large animals, the size of a rhino. A mother, of course, will do her best to drive off the sneak-thief, sometimes successfully; but she may be taken unawares; she may be tired out by repeated attempts; or if two attackers are concerned the second can snatch her baby whilst she is dealing with the first. Killing of new-born calves is carried out by shaking in the mouth and biting, not by ripping up the soft underparts. It is surprising how closely hyaenas are able to approach their prey, a herd of zebra, for example, not taking fright until their aggressors are within 4 or 5 metres.

Stress has already been laid on the fact that behaviour differs amongst spotted hyaenas according to differing circumstances. This is nowhere more apparent than in the matter of territories. Where the total area of land available is restricted, as it is to all intents and purposes in the Ngorongoro crater, territories are limited and well defined, though how clan boundaries running across a featureless plain are immediately recognisable is not easy for human beings to comprehend. Clans, 8 in number and varying in strength from 20 to 80, are there each limited to an area averaging roughly 30 square kilometers. This they determinedly defend against intrusion, and over this they hunt. Should a chase lead a clan into a neighbouring territory, finishing up with a kill there, and should the owners of that territory become aware of the fact, a tremendous quarrel ensues, sometimes involving as many as 70 hyaenas, leading to the retirement of the invaders with loss of their prey and sometimes, though not often, with loss of life. In the much more spacious conditions of the Serengeti, although the clan system exists, the population is more mobile and there is but limited insistence upon territory and upon its defence.

Boundaries of territories are not altogether stable. Loss of area may take place by unobserved encroachment by a neighbouring clan or in the face of defeat in the course of dispute; in which case the boundary may fluctuate back and forth. But, taken all round, clan limits are well recognised, any threat to them being hotly resisted. Females seem to be more clan conscious than males; and, indeed, cases have been observed of young males attempting to be, and at least in some measure succeeding in being, members of two clans simultaneously. Boundaries across a featureless plain seem incomprehensible to the human eye; but they are well defined by scent-marking readily picked up by sensitive noses. This is carried out on tufts of grass by straddling them with the hindlegs and dragging the extruded supra-anal scent sac across them. Elsewhere, trees or stones may be similarly marked. This registration of ownership is carried out throughout various parts of a territory while the clan is on the search for prey; but there may also be special boundary marking expeditions led by the dominant female.

One reason why females adhere more firmly to a territory than males do is that they are more tied by nature to a definite denning site for the long period which it takes to bring their young to independent maturity. Another reason possibly lies in the fact that the hyaena's is quite plainly a matriarchal society, the top females leading in the hunts, dominating the males at the succeeding meals, and generally keeping them at a respectful distance at other times. Unquestionably there is, as well, a well-recognised and always-respected order of precedence in both sexes, but that of the females is the more important since those of high rank, and especially the leading matriarch, control the day to day life of the community. Being of high rank makes a good deal of practical difference to life; for first and foremost those possessing it always have the chance of fully satisfying their hunger with the choicest food. Being born to a high-ranking mother is, likewise, a considerable advantage, for such a cub at all time receives assured protection and, moreover, is taken hunting at a younger age, sheltered from harm during this and the subsequent feeding under the dominant personality of its parent. It thus gains earlier experience of the rough and tumble of life, gets better fed, from the relative richness and abundance of its mother's milk and from its privileged participation in meat meals, with consequent more rapid growth (Goodall, 1970).

Hunting and feeding habits must ultimately be in a very great measure dependent upon the availability of potential prey. Under certain circumstances the spotted hyaena is not primarily a scavenger; quite the reverse; but where game is relatively difficult to come by these animals must depend in a much higher degree on what they can glean from other sources. In Ngorongoro there is a large resident population of ungulates to some extent restricted in its movements by the walls of the crater; and the hyaenas, though they may on occasions have to travel 15 km or so in search of food, can in general operate over a relatively limited area. Outside this exceptional locality the herds of antelope habitually range over long distances seeking fresh pasturage, and the hyaenas with other beasts of prey must necessarily follow suit. Marked individuals were, in fact, found by Kruuk to have moved up to 100 km in six weeks. As a direct consequence of these differing conditions, in Ngorongoro no less than 82 per cent of hyaenas were observed to feed on prey they had killed themselves; in Serengeti only 55 per cent. It is also interesting to note that gazelles—three species of which occur in West Africa—formed in Ngorongoro less than 1 per cent of the meals; in Serengeti 13 per cent. Most of the remaining percentages were made up of the two animals absent from the West African fauna, wildebeest and zebra. Though they form no part of Kruuk's published studies it is worth inserting here in connexion with feeding habits though not involving active hunting, that it is known that given the right opportunity *Crocuta* will regularly prey upon recently born hippopotamus calves.

T. S. Jones (personal communication) thinks that in Sierra Leone spotted hyaenas may, in the past, well have lived largely on Buffon's kob, once in plentiful herds, besides bushbuck and duiker; but that today they probably subsist to a much greater extent on domestic cattle, in the numbers of which there has been in recent decades a very large increase, and from the herds of which there is a constant theft of calves. There are also dead cows necessarily left lying by constantly roving Fulani herdsmen, as well as such other corpses as dead dogs thrown out of villages, and inadequately buried humans. A source of supply which formerly did not exist is civets, mongooses and other animals now killed with some regularity on the road by fast-moving lorries.

The success rate for hunting is not very high; for no matter what the quarry only about one in three pursuits results in a kill. It is, moreover, almost certain that, in selecting which herd-member shall be singled out for hunting, hyaenas, like many other beasts of prey, keep a sharp watch for any signs of ill-condition, wounding or other weakness, and that it is only animals which, for such reasons, hold promise of an easier kill that are followed (Estes, 1967 pt. 2). Attacks on calves are upon more or less stationary animals; but no attempt is made upon more mature prey without first setting the herd in motion, probably for the express purpose of being able thus to detect infirmities.

Other interesting matters emerge from the intensive field studies made by Kruuk and others. Although lions very often kill for themselves Kruuk thinks that they as often, or more, depend upon the hyaenas to do this, subsequently driving them by reason of their superior strength from the carcass. Nevertheless they do not always win in such a dispute, hyaenas if in sufficient numbers being courageous enough to join issue and scare off the invaders. On the other hand, as part of this very complex affair of meal-winning, Estes (1967) thinks that hyaenas may, at least at times, make use of lions to effect an easier kill, though only partial evidence for this is so far available. This they do by following closely behind a pride stalking its prey. When at length the dominant lioness springs upon the neck and shoulders of her selected animal and starts to claw and bite it as it gallops off the hyaenas close in and fasten onto the victim's hindquarters, gashing and tearing out flesh. This unexpected interference so upsets the lioness that she abandons her purpose and leaps off, leaving a now badly wounded beast to be followed and quickly killed and ripped up by the hyaenas before the pride can gather themselves together and close in.

Hyaenas have been observed to employ parallel tactics with hunting dogs, watching them and following them to their kill, which they can by reason of their greater size take forcible possession of. Neverethless, if the dogs are present in sufficient numbers they can as a unified pack drive off hyaenas, which are individualists without much co-operative pack sense (Estes, 1967). *Crocuta* and *Lycaon* seem to have a natural aversion from each other. On the other hand hyaenas appear to tolerate jackals so long as the latter do not presume too greatly. Jackal burrows occur amongst those of spotted hyaenas; and so long as these small scavengers keep well in the background and only rush in for a quick snatch from a carcass hyaenas make little attempt to drive them away. Vultures are kept at a distance; but there is, none the less, some interdependence between the two, for hyaenas watch the vultures in the sky for any sign of their dropping down to carrion, and the birds closely follow the movements of hyaenas in the hope that they will snatch a calf or sick animal. These, of course, are only incidental daylight events since deliberate hunts by hyaenas take place only at night when vultures are at rest.

It will be seen, then, that feeding in *Crocuta* is not a simple and straightforward matter of patiently waiting for the left-overs of lions, as popularly supposed, but that these animals play a complex role in a highly involved activity. They do in part serve a useful purpose as scavengers; but, since their numbers are very high, their appetites voracious and their digestion rapid, the total effect of their predation on the large concentration of ungulates in East Africa is considerable, much greater in fact than that of the larger but less abundant felids. Whether they have the same impact in West Africa is another matter. Owing to the greatly different circumstances with regard to game animals they may there be little beyond village scavengers and pillagers of domestic stock. This remains to be determined.

That the motions of vultures in the distant sky can be watched and analysed demonstrates that *Crocuta* has excellent vision; the senses of smell and hearing are also well developed. As regard the last, hyaenas listen for and react at once to calls of their own kind and those of other animals at considerable distances. By playing a tape recording of hyaenas at a kill Kruuk found that he could assemble as many as 60 *Crocuta* at a place where, in fact, no kill had taken place, so that neither smell nor sight had any part in this response. Lions, too, respond to this call, demonstrating clearly that they are not above seeking a free meal from the despised hyaena without the necessity and uncertainty of themselves hunting. The range of calls and other vocalisations of the spotted hyaena is wide, and not all are understood. The cry for which it is most famous is the spine-chilling "maniacal laughter", impossible to transcribe in print but broadly described as a high-pitched and rising cackle. This is only uttered under special circumstances, which are sexual stimulation and, possibly, when excitement over feeding rises to an exceptional degree. A more common noise is a series of chuckles, often rising in intensity uttered whilst feeding. There is also a whooping call, perhaps the commonest hyaena sound, often repeated several times; and there is a softly-intoned warning vibrant grunt drawing attention to possible danger. Besides these there are loud growls and yelps made when actually fighting. Another sound characteristic of hyaenas that receives little mention in accounts of these animals is the thud of their broad feet as they pound the hard ground, especially as, in the night, they canter round and round a camp or compound.

A few other general matters may be added here. These hyaenas are quite at home in water. They very much like lying partially submerged in it to keep cool during the heat of the day; but they will if occasion demands dive into it and submerge themselves. This happens when some prey animal mortally wounded and exhausted not infrequently plunges into a stream or pool and gets drowned. The hyaenas then, or later, set about salvaging it, either, by an unusually co-ordinated effort, dragging the whole corpse from the water or securing such parts of it as they can rip off by diving below the surface. As for longevity, Goodall (1970) mentions 30 years as a likely old age; and, certainly, a spotted hyaena is known to have lived to 25 years in captivity. Not all, of course, reach this. Kruuk, over 2 years, found a rate of mortality steady at 16 to 17 per cent. This is probably due, apart from old age, to fighting with other clans and to unfortunate clashes with lions or other large felines; but some of the ungulates themselves can cause grievous bodily harm leading to immediate or subsequent death.

Despite the attention which *Crocuta* has drawn to itself by its hideous laughter reputedly uttered under the stimulus of sexual excitement, and in spite of the concentrated study devoted to this species in recent years little is definitely known of courtship and mating. It would seem (Goodall, 1970) that at least as an early preliminary a good deal of "bowing" by the male to the female is carried out, in which he repeatedly lowers his head to the ground. Beyond this, little is clear.

Some details of the growth of the young in captivity have been published by Pournelle (1965), and these are supplemented by the observations of young animals and their parents made by Goodall (1970). The gestation period is reputedly about 110 days, though little accurate study has in fact been devoted to this matter, and figures given by Golding (1969) for observations in Ibadan University zoo would seem to argue up to about 10 days longer. The number in a litter more certainly lies between

1 and 3, being most commonly 2. The cubs are born with their eyes open and their ears erect, and they evince immediate reaction to both sound and movement. They look completely different from their parents being entirely covered with deep chocolate-brown underfur, their short spiky tails being similarly clothed. The weight is a little under or a little over $1\frac{1}{2}$ kg. The cubs are remarkably active almost from birth, dragging themselves along by their forepaws. Indeed, Pournelle observed one to stand on all four legs on its 2nd day. Incisors and canines are fully erupted, but the cheek teeth do not start to appear until about the 31st day. The new-born young apparently remain hidden below in the breeding chamber for about 10 days; they were observed at the mouth of the burrow, still unsteady on their feet, on the 10th day (Goodall, 1970). Thereafter, suckling always takes place on the surface in the vicinity of the den, and at any sign of danger the cubs hastily retire or are pushed into the burrow.

Replacement of the juvenile pelage begins at about 6 or 7 weeks as an ashy patch above the eyes. This spreads over the face and cheeks and extends gradually onto the throat, chest and forelegs, and the pattern of spots becomes apparent in these areas at about 9 weeks. Change of pelage continues slowly in a backwards direction, leaving a dorsal stripe and the hindquarters till last. The moult is completed by about the 18th week except for the spinal stripe, which persists for several months; but Golding (1969) gives a period of just half this.

Suckling is a prolonged business, lasting 18 months or more until the young hyaena is able to take a determined part in the day to day competition for food. It is supposed (Goodall, 1970) that this lengthy nursing is rendered necessary by the fact that, unlike *Lycaon*, hyaena mothers do not normally take their offspring out hunting, nor do they regularly bring back food for them to subsist on. Golding (1969), however, records juveniles brought up in a zoo taking small quantities of meat at the age of about 2 months. When the cubs are young suckling is carried out by frequent feeds of short duration; but as they get older a suckling period may last for as much as an hour and a half. Since female hyaenas develop only two functional mammae twins are convenient; but a litter of three must give rise to a great deal of difficulty and lead to some insufficiency of nourishment. There is good evidence, indeed, that single cubs develop better than twins, and certainly that the offspring of dominant or high-ranking, and hence more abundantly fed, mothers grow faster and bigger than those less well-born. Weaning of practically adult offspring can often be a trying period of displays of bad temper on the part of both mother and child, especially the latter as it finds its long-enjoyed rights harshly denied. When danger threatens, or for other less well defined reasons, young relatively helpless cubs are carried by the mother to another den; and older cubs may themselves move home to share with others. The father takes no part whatsoever in the upbringing. He and other males are kept at a distance or at least sharply watched by the mothers. At Ibadan zoo a second litter was produced by a pair of adults after an interval of 12 months; this consisted of a single cub of less weight and much more backward in every way than the first litter of two (Golding, 1969).

The home and family life of spotted hyaenas, as so vividly and intimately described by the Goodalls (1970), is full of affection, playfulness and good humour; it is therefore not surprising that they have proved to make amusing and unexpectedly intelligent pets, provided they are obtained sufficiently young. One such animal has been described by Sikes (1964b). This was found to be very responsive to affection and training, and to get on well with other captive animals, though it did on one occasion at the age of about six months kill a muscovy duck. It was able to digest meat from a very early age. It showed itself remarkably fond of water, to lie, bath or play in; and it gave no sign of any offensive body odour. What is perhaps most interesting of all is that after a year's separation, and being then an inhabitant of a zoo, this animal still recognised his original human foster parents, chuckling with joy and allowing them to romp with him in his cage, even to the extent of allowing them to put their hands inside his mouth, nibbling at them gently.

Taxonomy. Little serious doubt has ever been raised regarding the monospecific nature of the genus, though in 1900 Matschie gave 6 "geographical forms" specific status; and Cabrera in 1911 described 4 more. These and a few others have long been regarded as subspecies at most, totalling, in all, 20; and it remains here merely to examine the validity of such as have been held to apply to West Africa. These are 3 in number, all of Matschie's creation: *thierryi* from Sansanne Mangu, northern Togo; *togoensis* from Kete Krachi, Togo; and *noltei* from Yoko, upper Sanaga, Cameroun.

It has already been pointed out that the material available from West Africa is so scant that it would be impossible to determine from it the existence or validity of any of these described forms. It therefore remains to examine the matter from another standpoint. Matthews (1939b) investigated the question of races of *crocuta* in Tanzania in greater thoroughness, and having at his disposal a larger amount of uniformly collected study material, than for any other African mammal. Local forms have all been described on inadequate data, colour being one of the favourite diagnostic criteria, others being distinctness of pattern and length of pelage, besides various cranial and dental characters embracing both absolute size and relative proportions. Matthews studied all these in relation to a series of 103 skins and skulls, all collected in the same locality within one month, adding to these the material then existing in the British Museum amounting to 66 skulls and 58 skins from various parts of Africa. He reached the conclusion that there was "only one character by which specimens can be allocated to the appropriate geographical race, namely, the locality label". The range of variation in the spotted hyaena was shown to be so very wide that it was obviously impossible to attempt to divide the species subspecifically without comparable long series from various localities. The 20 described forms could all be matched by specimens from a single area in Tanzania. It therefore seems to the present author that it is idle to pretend that any racial name can usefully and meaningfully be attached to any West African specimen.

Practically nothing is available in the way of measurements of West African specimens; the following data are therefore derived mostly from other sources and are given merely as a guide.

Table 23: Numerical data for the family *Hyaenidae*

	Hyaena hyaena Darfur, Sudan	*Crocuta crocuta* Sierra Leone	*Crocuta crocuta* Tanzania (Matthews, 1939)	
			largest ♂	largest ♀
Vegetation	Sahel	Guinea	Sahel type	Sahel type
Number in mean	2	1	1	1
Condylobasal length	217	(260)	—	—
Basilar length	199	(240)	—	—
Palatilar length	106	124	—	—
Zygomatic breadth	151	177	—	—
Upper cheekteeth breadth	85	108	—	—
Nasals, length	63	57	—	—
Interorbital breadth	45	62	—	—
Postorbital constriction	37	46	—	—
Braincase breadth	66	80	—	—
Toothrow (c—p^4)	88·4	104·6	—	—
p^4 length	31·6	37·3	—	—
m^1 breadth	14·1	—	—	—
m_1 length	20·8	30·0	—	—
Head & body	1125	—	1295	1333
Tail	332*	—	267	296
Hindfoot	209	—	234	234
Ear	146	—	127	133
RATIOS (per cent)				
Tail/head & body	29	—	21	22
Zygom br./condylob. l.	70	68	—	—
Braincase/condylob. l.	34	31	—	—
Braincase/zygom. br.	44	45	—	—
Palatilar l./condylob. l.	49	48	—	—
Interorb./postorb.	121	135	—	—
$p^4/c-p^4$	35·8	35·6	—	—

*This figure is high by comparison with East African specimens, which average about 280.

Family **FELIDAE** Gray, 1821

Recent and Fossil Cats

Subfamily **FELINAE** Trouessart, 1885

Cats

Distribution and general. The family Felidae comprises a single subfamily of extant cats and two or more subfamilies covering a large number of fossil genera. The Felinae, or modern cats, exist as wild species over the greater part of the globe with the exception of the West Indies, Madagascar, New Zealand, Australia, New Guinea and the Pacific Islands; but they do not occur further north than about 70°N. Nevertheless, the group is represented in all these places, for domestic forms of one kind or another have, of course, been carried to almost every part of the world where man is found. In the continent of Africa indigenous wild species are to be found from the Mediterranean to the Cape, in all vegetation zones, including the Saharan region. The subfamily, being a well-defined and fairly homogeneous unit, is one that has for a long time attracted a good deal of interest and become the subject of considerable study, with consequent divergence of opinion. This will be dealt with more fully in the taxonomic section.

The cats are often looked upon as the most typical of carnivores. In several ways this is true. Their patience and agility in pouncing upon and, with a very high success rate, capturing living prey; their peculiarly lithe and muscular bodies supremely well suited to this end; their specialized feet almost uniquely armed with cruelly sharp and efficient claws; their powerful teeth totally adapted to firmly holding a struggling victim and to flesh-cutting alone; and their very limited interest in all foods other than vertebrate flesh all contribute to this view. The cats without doubt fulfill an important function in the balance of nature; but since they are relatively rare, often solitary, sporadically occurring animals the sum of their importance in this respect is possibly not so great as that of other more numerous members of the Suborder. Their most important effect lies probably in the control of creatures of large size beyond the capacity of lesser predators.

In view of the taxonomic disagreement that exists, to be dealt with later herein, differing figures are given for the number of genera constituting the Felinae, but there are in the world something in the nature of two dozen clearly distinguishable species of wild cats. Of these, 8 occur in West Africa, one or more in every zone of vegetation from the Subdesert to the High Forest. Two others are found in Africa beyond the limits set for this present account: The swamp cat (*Felis chaus*) of the lower Nile valley and delta, and the black-footed cat (*Felis nigripes*) of South and South-West Africa.

General description. There is a very wide diversity of size amongst the Felinae, ranging from animals of about the bulk of the domestic cat to that of the lion, that is to say from a weight of the order of 5 kg to one as much as 200 kg or sometimes more. Yet, all in all, there is a remarkably strong fundamental resemblance between all the various species and the veriest layman could scarcely fail to recognise any member of the subfamily as a true cat. First and foremost of the distinguishing characteristics comes the rounded, subglobular head with its very short, broad muzzle quite unlike anything found in the dogs, hyaenas, mongooses, genets or other carnivores. This is topped by upstanding ears, mostly set high on the head but always prominent, generally rounded but occasionally pointed and apically tufted. There is always a large bursa, the top end of its posterior flap arising behind the pinna, the anterior flap deeply notched. It is a remarkable fact that the backs of the ears of a number of the subfamily carry a pattern of black, with or without a white patch, varying from species to species but quite typical of each. The muzzle terminates in a naked rhinarium that scarcely overshoots the level of the lower lip, and differs from that of the Canidae and most other fissipedes in being more restricted in area, there being little more than a narrow naked strip dorsally and very little in the way of lateral spread below the nostrils. The serval, however, forms a notable exception in these respects. In the Felidae, as in the Canidae, the upper lip carries a central, longitudinal naked strip capable of sideways distension and with a medial groove that is continued upwards into the lower part of the front face of the rhinarium. The mystacial vibrissae (the "whiskers") are very well developed; and so are those above the eyes, the superciliary vibrissae; but a tuft that is present in other fissipedes, that situated on the hinder part of the chin between the branches of the lower jaw, is uniquely absent in this subfamily. The eyes, which are provided with a well-developed *tapetum lucidum*, have in many species pupils that expand in the form of a vertical ellipse, which in the most typical cats is capable of closing to a mere slit; but in others of the subfamily the pupils may be round or at most capable of closing only to a relatively broad vertical ellipse.

The body is also very characteristic being long, narrow, very muscular but extremely flexible. The legs may be very long or fairly short. They terminate in roundish, almost always soft-padded feet, the soles being entirely hairy between the pads. There are always 5 digits on the front and 4 on the back, the 1st digit of the forefeet being far removed from the remainder, and of the hindfeet lacking. These are armed with extremely sharp, highly curved, laterally compressed claws, except in *Acinonyx* in which they are straighter, blunt, altogether more dog-like. In all cases the claws are retractile, disappearing, once again with the exception of *Acinonyx*, with a greater or less degree of completeness into protective sheaths of skin growing as bilobed pockets from the upper surface of the toes. Retraction is controlled by ligaments which draw the terminal claw-bearing joint up and alongside the penultimate phalanx, the whole being thus enfolded within the cutaneous receptacles. It is commonly stated that the claws of *Acinonyx* are incapable of retraction. This is not so, the difference between this genus and the rest lying in the complete absence of cutaneous outgrowths, the claws thus remaining exposed (Pocock, 1916 i). The object of withdrawal into sheaths seems to be purely one of protection against wear on hard ground, it being essential to maintain the rather delicate points in a needle-sharp state for sinking into the often tough hide of the prey in an immediate and secure positive grip and for ripping it and the flesh. In a way the terminology in general use though convenient is misleading. The claws are not so much retractile as extensible, their normal muscular at-rest position being withdrawn into the sheaths, and the act of extending them being a deliberate one which at the same time forms the foot into a tensely firm and powerful weapon. Posture of the foot in progression is digitigrade.

The tail may be either very long, practically as long as head & body, or short, less than half the head & body length. When long, it is a very flexible, highly mobile structure very expressive as well as useful; for not only is it of great importance as a balancing organ but its motions, also, closely reflect the emotional stresses to which the animal is subject. It is well-clothed with hair which is mostly loosely standing, of moderate and even length according it a narrow cylindrical outline quite distinct from the bushily long-haired tail found in the dogs and most of the mongooses; but the lion is an exception in being tightly short-haired with a terminal tuft. In the Felinae there are no perineal or anal scent glands. Females commonly have 4 pairs of mammae, 2 abdominal, 2 pectoral, though not all are always equally developed; the cheetah has 6 pairs or more.

The pelage displays a very wide variety of colour and pattern ranging from pale sandy to deep sepia-grey, plain or spotted in diverse ways or, extralimitally, striped. Melanos are not uncommon in certain forms but wild albinos seem to be unknown or extremely rare. In texture the fur may be soft or somewhat harsh; it may be very short and close-lying or moderately long and loose, there being often a range of length within a single species depending on environmental factors. The male lion develops an abundant mane of very long hairs on the neck and chest; the cheetah a dense but relatively short nuchal crest. In general the pelage is made up of hairs of three different types: fine underfur which is usually, but not always, very abundant; bristle-hairs, which are of terete or slightly flattish section and fairly stout throughout most of their length; and sub-bristles, which may be as long as, or even longer than, the bristles but which consist for about the basal half of their length of a very narrow colourless stalk, the distal portion being a flat-sectioned, fusiform, coloured blade terminating in a slender black point. In the lion and the leopard, however, the pelage comprises underfur and sub-bristles alone.

Skull. The distinguishing character of this lies firstly, more especially as regards the smaller members of the subfamily, in its round shape due to a highly curved profile, a domed braincase, a very short, broad rostrum and widely bowed zygomatic arches. The nasals, except in the lion and to a lesser degree the leopard, curve down steeply, sometimes very steeply, from their junction with the frontal bone. The relative widths of the interorbital and intertemporal regions vary very considerably from subequal to widely disparate, the former being in some cases much less than half the latter. Except in the lion and leopard the braincase is broad and often subglobular. A sagittal crest is for the most part lacking save at the posterior extremity of the braincase where a short flange meets the always well developed supra-occipital crest in a T or a Y; but in the golden cat, the lion and the leopard a narrow keel extends the entire length of the cranium. The zygomatic arch is deep and strongly built to anchor very powerful jaw muscles; it consists in a large measure of a long jugal bone connecting a very short maxillary process to a squamosal process that stands away perpendicularly from the braincase before curving abruptly forward at nearly a right angle (fig. 55). The orbit is very large, but the circumorbital ring incomplete. The infraorbital canal is short, sometimes very short, the oval foramen small to moderate, or in *Acinonyx* narrow.

In the ventral aspect, the palate is short and broad, often of nearly equilateral shape, though rather narrower than this posteriorly in the leopard. There is a short medial postdental extension, in the smaller cats divided from the main palate by deeper or shallower emarginations. The anterior palatal foramina, elliptical in shape and of fair size, are situated between the canines; the very small posterior foramina are sited in the lateral margin of the palatine. The bullae are, in the smaller species, large or very large, the furrow marking the division of the smaller anterior chamber from the highly inflated posterior chamber sometimes not very clear or even impossible to detect. There is no alisphenoid canal. The mandible is short and strong, the coronoid tall, the short, blunt angular process twisted inwards, the anterior extremity of the rami bearing the canines and incisors sharply upturned.

The dental formula in the Felinae is $\frac{3\ 1\ 3\ 1}{3\ 1\ 2\ 1} = 30$ or $\frac{3\ 1\ 2\ 1}{3\ 1\ 2\ 1} = 28$. The teeth are all highly specialized and adapted to capturing and securely holding struggling living prey as well as to efficiently severing its flesh. The incisors form a firm, continuous, straight, transverse row, the outermost ones being somewhat, or much, larger than the inner ones. The canines, which are shallowly and sometimes obscurely grooved, are exceptionally long, strong, slightly curved and sharply pointed, well fitted to sinking deep into flesh. Their depth of penetrating and holding power is increased by the existence, in all but *Acinonyx*, of a post-canine gap created by the lack of the 1st or 1st and 2nd upper and 1st and 2nd lower premolars, aided by the sharp upward curve of the mandible anterior to p_3. The gap thus formed, which is clearly evident when the jaws are closed, serves to accommodate a roll of flesh as the canines anchor themselves deeper and deeper into the victim.

The cheekteeth are all laterally compressed into sharp-edged, and often sharply-cusped, blades well adapted to shearing but having about them little or nothing suited to a grinding function. It is of interest to note that although p^1 is normally lacking in the Felinae there is one West African specimen of *libyca* in which it exists as a minute peg on one side. p^2, which is present in all species covered by this work except *caracal*, is always small, mostly very small, singly rooted, and fulfils no practical function; p^3 is 2-rooted and has a tall triangular crown with small subsidiary cusps situated anteriorly and posteriorly at the base of the main triangle, except in *Acinonyx* where the cuspidation is more complex. The upper carnassial, always the largest tooth, similarly has three cusps set in line; the anterior one small, about equal to the posterior cusp of p^3; the central one tall and triangular; the posterior one lower but long and blade-like. This tooth is the only one in the head to have an internal cusp, situated at about the level of the anterior external cusp and furnished with its own root, making the whole tooth 3-rooted; in use it bears against the posterior cusp of p_4. The upper molar is always very small, its long axis set transversely in the skull roughly at right-angles to p^4, in use closing against the posterior face of the lower carnassial. In the mandible the two premolars are broadly similar to p^3, consisting of a large triangular median cusp with smaller anterior and posterior cusps basally. The lower carnassial,

m_1, is quite different in profile from the other subtriangular cheekteeth since it consists of two compressed blades, its anterior and posterior margins parallel and upright, the superior, cutting, edges inclined inwards towards each other (fig. 2).

Although it is not strictly a part of the skull one small portion of the skeleton closely associated with it must here be mentioned since it has been given unusual taxonomic importance in its use by Pocock (1916g and 1917b) and subsequent authors for the separation of the genus *Panthera* from *Felis* and *Acinonyx*. This is the hyoidean apparatus; but as it is of practical use only to those with the facilities and inclination to make a careful anatomical dissection it is not employed in this present account. Briefly, therefore, without going into unnecessary detail the hyoidean apparatus consists of a chain of small bones, known collectively as the suspensorium, passing from the bulla, on each side, to further small bones at the root of the tongue and embracing the top of the windpipe. In most of the cats this apparatus, except at its cartilaginous extremities, is fully ossified and the larynx is thus held up firmly to the base of the skull and limited in its movement; but in *Panthera*, that is to say in West Africa the lion and the leopard, part of the suspensorium remains unossified and elastic and is much longer, allowing greater freedom of movement. Clear detailed illustrations are to be found in Pocock (1916g, 1917b and 1939) and Mivart (1881).

Habits. The Felinae are by nature very largely nocturnal or crepuscular, a fact which is basically true of the domestic animal as of the wild species, though the exceptional, atypical circumstances of life in close association with man tend to mask it somewhat in this case. But no species is exclusively active at night, and although in the wild much of the daylight hours may be spent in sleep, all cats can at least occasionally be seen during the day prowling around with no apparent purpose, or feeding, or training their offspring, or grooming their coats, or, if young enough, playing. Nevertheless it is not until evening draws in and darkness approaches that the important business of life, the hunting and killing of prey and the finding and coupling with a mate, commences in earnest. In these matters, as in several others, the cheetah seems to form an exception to the majority of felines since its pursuit of prey, at least, takes place in fuller daylight. Because of their predominantly nocturnal habits details of the behaviour of many species remain obscure and in some cases virtually unknown. The majority of cats, also, are solitary except at mating time or when a mother is followed by her litter; but lions live together more permanently in small bands and so, to a lesser extent, do cheetahs, which at least often congregate together for hunting.

The cats, unlike the dogs, make little use of confined shelters either for their daily rest or for breeding. Sometimes they will make a temporary home in a cave or in a large cavity amongst boulders, but they rarely make use of holes in the ground, a cover of dense vegetation generally serving all their needs. As the vast majority of them are excellent climbers rest and safety is often found in the lower branches of trees, curled up in a crook against the trunk or stretched out along a stout bough; and possibly some of the smaller forest species may use a convenient hole in a trunk, either at ground level or higher up, for giving birth or shelter to the young during their early babyhood. Singularly little is known about the sex lives of the cats. Observations have been made on some species in captivity but on few under natural conditions. So far as present knowledge goes it would seem that in most species the male and female remain together for only the limited period of coupling or of raising one specific litter. In view of the great disparity of bulk occurring in the felines no general figure for gestation or for size of family can be given, though as regards the latter the cats rarely produce at a birth the large numbers which from time to time are born to some canid mothers, two or three being a common issue and nine probably an exceptional maximum. The young are known variously as kittens in the smaller species or as cubs in the lion and leopard. They are always born in an incomplete state of development, mostly requiring 10 days or so for the eyes to open completely and yet more for them to become fully functional as regards focussing; further, new-born kittens need one to two weeks to become properly mobile and steady on their legs; and considerably longer for their teeth to erupt.

The very sharp curved claws possessed by all cats except the cheetah, aided by their very powerful leg muscles and relatively light bodies, enable most species to climb trees and other fairly vertical rough surfaces with considerable ease and speed. Even in the cheetah the young, before the claws become worn and blunt, are quite good climbers; but in the lion, possibly owing to its greater bulk and general massiveness of build, climbing ability is more limited and ascents are normally restricted to the lower branches of smaller trees, and those often with sloping trunks that can be readily walked up. Yet, that actual weight has little to do with limiting the ability to climb is shown by the extraordinary power of the leopard to ascend vertically for a considerable distance carrying in its mouth a heavy antelope—a vivid demonstration of the immense muscular power of the jaws, neck and legs found in the Felinae. The power of the legs is shown in another way, for the typical cats have the facility for making prodigious standing jumps, sometimes employed for the initial stage of a vertical climb or for getting onto and over obstacles, but more importantly for leaping suddenly onto prey.

Various gaits are used by the cats according to circumstances. The commonest is a leisurely saunter with tail outstretched or sometimes raised. When prey is being deliberately stalked a similar action is used but very much more slowly and with the body in a crouched position. When more purposefully on the move from place to place than implied by the usual idle stroll all the cats, but especially the bigger ones, engage in a springy trot; but when it is necessary to move really fast they bound over the ground both fore and hindfeet more or less coming together then stretching fully apart as the body flies through the air, one forefoot next touching the soil a little before the second, the hindfeet then being brought forward together again to close proximity on the ground with the forefeet.

A diversity of vocalizations is to be heard in the subfamily from the well-known mew of the domestic cat, through the snarl of the leopard to the roar of the lion, the latter's louder calls being made possible by the far greater freedom of the larynx due to the form and less ossified structure of the hyoidean apparatus in *Panthera* as compared with *Felis*. In the latter genus some of the larger wild species utter sounds not much removed from a "mew"; and most of them in alarm draw back the lips to expose the teeth and "spit". In several members of the subfamily a vibrant sound related to the contented "purr" of the domestic cat is uttered, though not always expressive of serenity. However, between the lion and the domestic cat little has, in fact, been clearly recorded of feline utterances, and they are probably more difficult to express verbally than those of dogs or hyaenas without the use of specially coined onomatopoeic words such as "mew" and "purr".

The Felinae, whose diet is possibly more completely derived from the flesh of mammals and birds than that of any other section of the fissipedes, fulfil an important function in preserving the balance of nature though since they are less numerous than other members of the suborder their total effect may in sum be slighter. However, the lion, leopard and to a smaller extent the cheetah exercise an influence in an otherwise untouched quarter as they are able to kill fully adult ungulates of a size beyond the powers of lesser carnivores with the possible exception of a pack of hyaenas. The essential part these animals play in a balanced countryside has not infrequently been overlooked, with disastrous results; as, for example, when the offer of a bounty for destruction of leopards as "vermin", or their overkilling in plain greed for their valuable pelts has led in the course of time to a marked increase of baboons with consequent severe depredation of agricultural produce by vastly larger troops of these notorious and wasteful crop thieves. By what, in turn, the numbers of felines are kept in check is less apparent. There is always, as just mentioned, man out to kill unwelcome predators to protect himself and his property; or in search of warm and often highly ornamental skins for his own use or for sale. Man apart, without doubt the smaller carnivores are preyed upon by larger members of their kind besides forming meals for hawks, eagles and snakes; but when it comes to holding in reasonable check the lion and the leopard the position is not so clear. However, it must be remembered that even the largest and most powerful animals are very vulnerable whilst juvenile. There are many hazards between birth and safe maturity. There is first the uncertain temperament of both mother and father which sometimes leads to abandonment and not infrequently to destruction and cannibalization of their own young; there is always the chance of theft by hyaenas; there is disease or injury resulting in inability to survive. Finally, as regards a species as a whole, there is the vital question of the sufficiency, or even availability, of food. No area can support a greater number of predators than there is sustenance for, surplus to the maintenance of a stable population in the food species itself. In any struggle to obtain meals from a marginal or inadequate source of food the weakest and less efficient predators soon die off. This factor is of considerable moment in much of West Africa where over vast areas, owing to expansion of human populations and of agriculture, conditions for the survival of prey species, of all except the smallest kinds, are now much deteriorated from what they were even 50 years ago and are annually worsening.

Taxonomy. As a group the cats have excited a great deal of interest and attention and in consequence, as Simpson (1945) has pointed out, not only is the literature enormous but there have as well arisen "irreconcilable differences of opinion regarding the phylogeny, and hence the major taxonomy, of the felids . . .". It would be pointless to attempt to discuss here more than a very small part of what has been written. What follows is merely a brief resumé of the position in so far as the existing cats of West

Africa are affected; and it at the same time affords some key to the conflicts of views and nomenclature that may be encountered in the literature.

There is little or no dispute regarding the identity and individuality of the various units which make up the group under discussion but only as to the taxonomic level to be assigned to them; and in this matter there are two widely divergent schools of thought. At one time all the cat-like creatures were included in the single Linnaean genus *Felis*; but it is now pretty generally agreed that two major separations from the typical cats can and should be made: firstly, that the cheetah, by reason of points of external form, notably the absence of digital sheaths into which the claws can be withdrawn, is clearly generically distinct and assignable to *Acinonyx*; and secondly, that the lion and leopard (together with certain other extralimital large species) should, on the score of the form of the hyoidean apparatus, noticed above under the description of the skull, be ascribed to the separate genus *Panthera*. Common practice today is therefore to divide the existing cats into three genera, *Felis*, *Panthera* and *Acinonyx*.

It is with the first of these genera that disagreement starts; for in 1858 Severtzov gave almost every known species subgeneric rank, to the number of nearly two dozen; and though the majority of recent authors have continued to treat these mostly monospecific units as nothing more than subgenera Pocock (1917b) in his classification of the Felidae and in two subsequent major publications (1939 and 1951) has insisted on giving full generic status to 14 names of Severtzov and other authors. In this he had a subsequent measure of support by J. A. Allen (1919a). Largely in consequence of his attitude towards *Felis* and these others as cognate genera Pocock felt the need to emphasize the distinction between this group and those of *Panthera* and *Acinonyx*, and this he brought about by raising all three to subfamily rank as the Felinae, Pantherinae and Acinonychinae. Pocock specialized to a large extent on the Carnivora and more especially on the cats, his last published work being an uncompleted monograph on the Felidae (1951). His experience was unusually wide and in some ways unique since he had, over many years, close acquaintance with living captive animals and the dissection of newly deceased specimens as well as with abundant museum material. His views, therefore, cannot be dismissed lightly; yet the general consensus of opinion today, led by Simpson (1945), and with the single exception of Ognev (1962), is that his taxonomic ratings are at too high a level and that the numerous genera of Severtzov, Gray and others are best relegated to the position of subgenera of *Felis*, and that Pocock's new subfamilies are unnecessary. This view of classification is adopted in this present work.

It may be added that Hopwood (1947) from examination of skulls came to the conclusion that the lion was the most primitive of the great cats and probably merited separation from the leopard and others to a genus of its own. The whole situation is complex and, in truth, not very well understood, the present fluctuating classifications of the Felidae being based on differing individual evaluations and interpretations of characters derived often from quite inadequate museum material and without taking into account patterns of behaviour or vital information derivable only from living animals. Until an obviously sounder based concept of the Felidae has emerged from a study of the group in depth involving not only considerably better material but a far wider range of valid taxonomic characters as well there seems little point in tinkering piecemeal with a classification and nomenclature which is widely understood and works practically though phylogenetically possibly capable of improvement.

As a matter of convenience the keys which follow deal with individual forms, treating genera, subgenera and species alike without attempt to set them forth in their correct taxonomic grouping. External characters are rendered difficult by phasal or developmental changes in pelage colour and pattern.

KEYS TO THE SPECIES OF FELINAE

(Previous key page 160)

A. Cranial characters

1. Total length of adult skull over 180 mm 2
 Total length of adult skull less than 180 mm 3
2. Total length of adult skull less than 270 mm; length of p^4 under 30 mm **P. pardus** (*page* 439)
 Total length of adult skull over 270 mm; length of p^4 over 30 mm **P. leo** (*page* 460)
3. Upper premolars 2 only; nasals descend very steeply from the inflated frontal (fig. 54) . . . . **F. caracal** (*page* 402)
 Upper premolars 3; nasals do not descend so steeply 4
4. Total length of skull less than 110 mm 5
 Total length of skull over 110 mm 6
5. Bulla length approximately equal to the width of the rostrum across the canines . . . . **F. libyca** (*page* 384)
 Bulla length markedly greater than the width of the rostrum across the canines . . . . **F. margarita** (*page* 395)
6. Nasals broad posteriorly (about 20 mm) not very tapering; total adult skull length about 160 mm . . . . **A. jubatus** (*page* 493)
 Nasals narrow posteriorly (about 6 mm) sharply tapering; total adult skull length not more than about 145 mm 7
7. Postorbital constriction about 50 per cent greater than the interorbital breadth; p^2 small; total skull length about 125 mm . . **F. serval** (*page* 412)
 Postorbital constriction not much greater than the interorbital breadth; p^2 extremely small, total skull length about 140 mm **F. aurata** (*page* 425)

B. External characters

1. Head & body length of adult not more than about 600 mm; tail little more than half as long; ears without any black pattern on their backs . . 2
 Head & body length of adult at least 750 mm; ears (except *aurata*) with some black on their backs 3

2. Ears set fairly high on the head, pointed and with a small apical tuft; tail with two or three subterminal black rings and usually a black tip **F. libyca** (*page* 384)

   Ears broadly rounded and set low on the side of the head; tail without, or only ill-defined, black rings . . . . . . **F. margarita** (*page* 395)

3. Tail at least half as long as the head & body 4

   Tail well under half the length of head & body 6

4. Tail tapering, clad with very short, close-lying, pale brown hair, unspotted in the adult but always with a contrasting blackish terminal tuft **P. leo** (*page* 460)

   Tail clad with relatively loose upstanding hair, subcylindrical in shape or slightly broader towards the end; spotted 5

5. Spots of the body pattern aggregated into "rosettes", *i.e.* 3, 4 or 5 black spots grouped in a ring round a pale centre . . . **P. pardus** (*page* 439)

   Black spots of the body pattern randomly scattered; claws incapable of withdrawal into sheaths . . . . . . **A. jubatus** (*page* 493)

6. Ears sharply pointed, their backs wholly black or at least deep grey, and with a pronounced black apical tuft . . . . . **F. caracal** (*page* 402)

   Ears rounded, not wholly black on the back, and without any apical tuft . 7

7. Ears large and set high on the head, their backs with a black apical area surrounding a white, or yellowish, patch; legs long and slender; body black-spotted on a pale brown ground-colour . **F. serval** (*page* 412)

   Ears not set high on the head and without black on their backs; legs short and stout; pelage of various hues from rich red-brown to dark sepia-grey, unspotted or spotted but the spots never black . **F. aurata** (*page* 425)

Genus **FELIS** Linnaeus, 1758

Cats

Felis Linnaeus, 1758, *Systema Naturae*, 10th ed. **1**: 41. Type species *Felis catus* Linnaeus, the domestic cat. This name is from the Latin *feles* applied to cats and other small carnivores.

Caracal Gray, 1843, *List of Mammals in the British Museum*: 46. Type species *Caracal melanotis* Gray (= *Felis caracal* Schreber). The name is derived from the Turkish words *qarah* black, and *qulaq* ear, from the colour of the hair on the back of this structure. Valid as a subgenus.

Profelis Severtzov, 1858, *Revue Mag. Zool.* (2) **10**: 386. Type species *Felis celidogaster* Severtzov (= *Felis aurata* Temminck). This name is coined from the Latin *pro*, a preposition of various meanings but in this case most probably implying instead of, together with *Felis*, as above. Valid as a subgenus.

Urolynchus Severtzov, 1858, *Revue Mag. Zool.* (2) **10**: 389. Type species *Felis caracal* Schreber. This is derived from the Greek *oura* tail, and *lynx*, *lynchos* a lynx, with reference to the somewhat longer tail than in the common or European lynx.

Leptailurus Severtzov, 1858, *Revue Mag. Zool.* (2) **10**: 389. Type species *Felis serval* Schreber. The name is a combination of the Greek words *leptos* small or slender, and *ailouros* cat. Valid as a subgenus.

Chrysailurus Severtzov, 1858, *Revue Mag. Zool.* (2) **10**: 389. Type species *Felis neglecta* Gray = *Felis aurata* Temminck. This is from the Greek *chrysos* gold, and *ailouros* cat.

Serval Brehm, 1864, *Führer durch den Zoologischen Garten zu Hamburg*, 6th ed.: 53. Type species *Serval maculatus* Brehm. This name is said to be derived from the Portuguese *lobo-cerval* for a lynx.

Galeopardus Heuglin & Fitzinger, 1866, *Sber. Akad. Wiss. Wien*, Math. Nat Cl. **54**, sect. 1: 557. Type species *Felis serval* Schreber. The name is from the Greek *gale* weasel, and *pardos* leopard, given with reference to the smaller, more slender form.

Servalina Grevé, 1894, *Nova Acta Acad. Caesar. Leop. Carol.* **63**: 76. Type species *Felis serval* Schreber. This is a dimuntive of *Serval*.

Eremaelurus Ognev, 1926, *Ezheg. zool. Muz.* **27**: 356. Type species *Eremaelurus thinobius* Ognev (a race of *Felis margarita* Loche). This name is compounded from the Greek words *eremia* desert, and *ailouros* cat.

General. *Felis* in its widest sense is a large genus covering some three-quarters of the living species constituting the Felinae; but, as already said, it has, more for convenience than by reason of any compelling taxonomic characters, been divided into many subgenera, of which four concern this present work. The distribution of the genus in so far as its wild forms go is to all intents and purposes that of the subfamily as given on page 373; but if the domestic cats are taken into account it may be reckoned as world wide. But though the genus is so far-flung and so catholic in its ecological demands as to embrace all kinds of vegetation from rain-forest to desert, and from intense tropical heat to the snow-line, it is in point of actual numbers not very large. For the cats, though so widely occurring are for the most part solitary creatures, each ranging over a fairly large territory and therefore, though by no means rare, relatively sparse on the ground, in pronounced contrast to many of the ungulates, rodents, bats or even primates.

Little purpose would be served by attempting to give here any general sketch of the genus *sensu lato*. It has already been pointed out that throughout the entire subfamily, that is to say including the other genera, there runs a close and unmistakable superficial resemblance that renders difficult any attempt to differentiate *Felis* from the rest in general terms. Morphologically and taxonomically—and with extreme succinctness—*Felis* differs from *Panthera* in the form of the hyoidean apparatus in the throat; and from *Acinonyx* in the somewhat less obscure character of retractability of the claws. In respect of the genus *Felis* itself, though it is often of considerable ease to tell many of the cats apart at sight this is by no means always so with some of the smaller, extralimital, kinds; and to translate such differences of size and appearance as do exist, even at their widest, into terms of valid taxonomic distinction at higher than specific level seems sometimes, if not always, a matter for some hesitation. The points that separate *Felis sensu stricto* from the other three reputed subgenera occurring in West Africa, *Caracal*, *Profelis* and *Leptailurus*, are in some measure evident in the keys given above and will become somewhat clearer from the individual accounts which follow.

Subgenus **FELIS** Linnaeus, 1758

True Cats

As far as West Africa is concerned the most typical cats, that is to say those species which externally bear the closest resemblance to the type species, the house cat (*Felis catus*), are smaller than those of the other subgenera. One of the two species with which we are here concerned, though considerably variable in colouring, does in fact bear in some of its forms a very passable likeness to a domestic pussy, though in its nature and behaviour very different. Both the two West African species are most typically inhabitants of the drier zones, one not uncommon, the other rare. Two other species of the subgenus occur extralimitally in Africa: the jungle cat (*F. chaus*) in Egypt, and the black-footed cat (*F. nigripes*) in the southern part of the continent.

FELIS LIBYCA Forster African Wild Cat

Felis lybica G. Forster, 1780, in Buffon's *Naturgeschichte der Vierfussigen Thiere, etc.* **6**: 313. Gafsa, Tunis. The name seems to have been based on a not very clear description furnished by the explorer James Bruce. Forster's spelling of the specific name is an obvious *lapsus* since the country from which it was derived has from ancient times been written as Libya (see Ellerman & Morrison-Scott, 1951).

Felis lynx lybiensis Kerr, 1792, *The Animal Kingdom etc.*: 156. Capsa, Libya (= Gafsa, Tunis).

Felis cristata Lataste, 1885, *Act. Soc. linn. Bordeaux* **39** (*i.e.* (4) **9**): 229. Not of Falconer & Cautley, 1836. The name is the Latin for crested.

Felis haussa Thomas & Hinton, 1921, *Novit. Zool.* **28**: 2, 3. Zinder, Niger. Type in the British Museum, No. 21.2.11.16, ♂; skin good, skull in fair condition but with the frontal region and bullae partly smashed. The name is derived from that of the people inhabiting the region of West Africa whence the specimen came. Valid as a race.

Felis lowei Pocock, 1944, *Proc. zool. Soc. Lond.* **114**: 68. Jebel Marra, 1200 m, Darfur. Type in the British Museum, No. 23.1.1.66, ♂; skin and skull both in good condition. This was named after the collector Willoughby Lowe.

Felis lybica lynesi Pocock, 1944, *Proc. zool. Soc. Lond.* **114**: 68. Collected 56 km north of El Fasher, Darfur. Type in the British Museum, No. 23.1.1.65, ♂; skin good, skull with right upper canine area smashed and missing, and one ramus of the mandible lacking. This was named in honour of the collector Rear-Admiral Hubert Lynes.

Felis lybica foxi Pocock, 1944, *Proc. zool. Soc. Lond.* **114**: 71. Kabwir, 820 m, Nigeria. Type in the British Museum, No. 12.11.7.5, sex ?; skin fair, with paws lacking, no skull. This was named after the collector Dr. J. C. Fox. Valid as a race.

Felis libyca savannicola Dekeyser, 1950, *Bull. Inst. fr. Afr. noire*, **12**: 704, 705. Messirah, south Senegal. Type in the Institut français d'Afrique noire, No. 48–5–38, ♀; skin and skull. The name is coined from savanna and the Latin *colo* meaning to inhabit.

Distribution and general. The African wild cat (Plate 10) has an extensive distribution. In Africa itself it is to be found over most of the continent from the Mediterranean to the Cape with the exception of the closed forest block. It occurs also in a restricted area of Southern Europe, that is to say in Italy and on the islands of Majorca, Sardinia and possibly Corsica; and beyond this it ranges east across Palestine, Arabia and Persia to Turkestan and northern India. With such a distribution, embracing an exceedingly wide range of vegetation, it follows that there is an equally varied degree of external appearance. This renders any general description difficult; but colour and distinctness of maculation apart there are certain characteristic markings all or at least some of which are, with greater or less degree of clarity, always exhibited. These are detailed below.

Five races have been attributed to the region covered by this present work; but this point is more fully discussed in the later taxonomic section. It is natural that the abundance of this cat should vary from locality to locality throughout its wide range according to local circumstances, food supply, predators and the degree of severity of general existence; in regard to West Africa, study specimens are fairly rare though the species is known, by repute, to occur from the extreme west to the extreme east, and broadly speaking is not at all uncommon in the Sudan and Sahel zones. It is also known from well into the Subdesert zone at Tchsiderak in Aïr; another form occurs chiefly in the Doka and, apparently more uncommonly, in the Guinea woodland. The species is almost certainly absent from the high-forest. The most southerly specimen in the British Museum is from near Obubra on the Cross River; but this would seem to be exceptional.

Recognition of *libyca* is sometimes made doubtful by two facts. Firstly, that it is not unusual in Africa for domestic cats to go feral and, by force of circumstances in a highly competitive environment, to lose all trace of their normal placid nature and become so uncompromisingly aggressive in behaviour as to give the impression of being unquestionably members of the true indigenous fauna. In the second place, *libyca* does from time to time cross with domestic cats, the offspring sometimes displaying the markings of the one and the character of the other. Within the experience of the present writer there was some years ago a house cat in a station in Bornu (Nigeria) which clearly exhibited the key markings of *libyca* but had the passivity of temper associated with an ordinary domestic pussy.

Description. This (Plate 10) is one of the two smallest of West African cats though, so far as can be judged from the few study specimens with any live data, of pretty diverse size from 400 to over 600 mm for head & body length, and a weight usually quoted as of the order of 4·5 to 5·5 kg though one reliable collector in West Africa has given a figure as low as 2·7 kg for an animal said to stand 320 mm at the shoulder, which is big for a cat. It has already been pointed out that the pelage colour and general body pattern of *libyca* are extremely variable, ranging from greyish to reddish, with or without markings of small spots which when present may or may not tend to run into transverse stripes. In known West African specimens this body pattern is absent or very obscure; but in some extralimital races it is a pronounced feature. In Asiatic forms the spots are independent and very strong giving a quite different overall impression from the more typical African animals, the appearance recalling rather that of a small serval.

In accordance with the arid terrain most commonly favoured by this cat the pelage colouring is often basically of a sandy or buffish nature, the belly mostly whitish; but animals from the rather damper woodlands are distinctly more rufous. Despite this overall variety of colouring and pattern there are seven points of recognition of the species no matter where it occurs throughout its wide range, at least four or five of which are always detectable in any given specimen. These are, roughly in their order of constancy and importance:

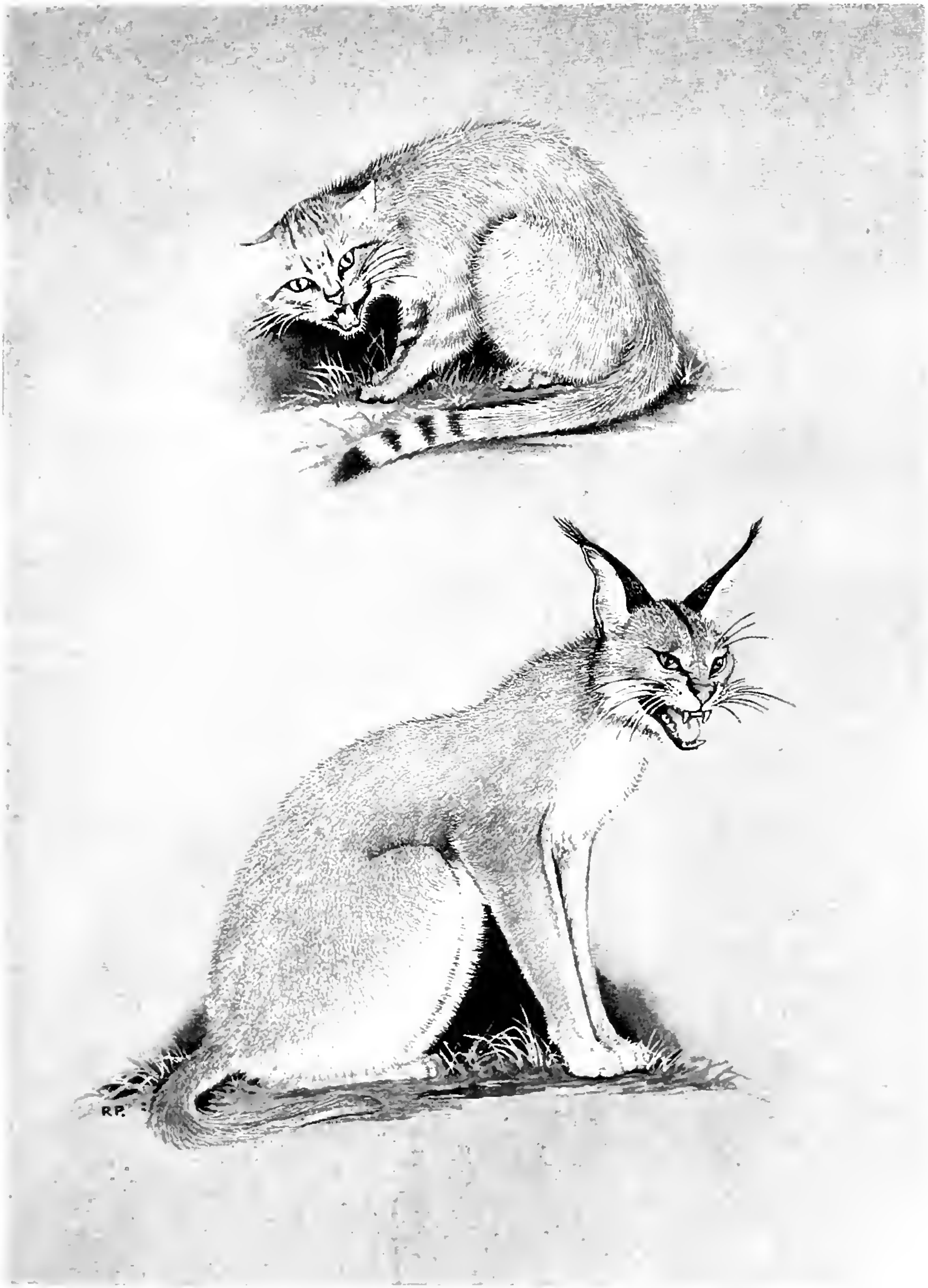
Tail	There are always a short black tip and two, sometimes three black subterminal rings or partial rings. Its length is usually roughly two-thirds of that of the head & body.
Feet	These are entirely hairy below except for the actual pads; and they are always black below, this colour being sometimes limited to the plantar area but, on the hindlimbs, often extending some or all of the way to the heel.

Ears	These are subtriangularly pointed and always plain red or ochre on their backs and mostly with a short apical tuft of the same colour.
Face	This is marked with a narrow, mostly ginger, line from the outer corner of the eye towards the angle of the jaw, and with a similar, shorter one from the inner corner of the eye to the rhinarium. There is often, but not always, a third line nearly parallel to the first of these and running lower down across the cheek.
Forelegs	At maximum development there are two complete black rings ("bracelets") encircling the arm, one near the top, one about half-way down; but these show various degrees of fading, being sometimes visible only as half-rings on the inside of the limb, or sometimes one or both lacking; and the colour may decline from black through blackish-brown to ginger.
Throat	This exhibits two, mostly ginger-brown, narrow transverse bands, of which the anterior may be indistinct or lacking, but the posterior nearly always perceptible.
Spine	From just posterior of the shoulders to the root of the tail there is generally a band of more pronounced, mostly golden-brown colour, never very sharply defined and sometimes very obscure.

One of the many factors that are inconstant in the African wild cat is the length of the coat which, apart from increasing from youth to maturity, varies in accordance with differing seasons as well as with general ecological conditions. In Pocock's accounts of the different races (1951), for example, he quotes extremes of pelage length of 22 to 44 mm on the flanks and 34 to 55 mm for the spinal crest. The texture of the fur as well as its overall appearance varies with this length from moderately soft and loose to slightly harsh and close. The pelage is composed of three types of hair: very fine, fairly long, dense underfur; lengthy flattish-sectioned bristle-hairs which are of constant diameter throughout all their length except for the tapering tip, and which by reason of their much greater stoutness and pure white or very pale basal regions stand out prominently when the coat is turned back; and almost equally long sub-bristles with appreciably finer proximal portions than in the bristle-hairs but expanded distal regions. The bristle-hairs are markedly more abundant in the spinal band than on the flanks.

The coloration varies considerably, of course, from race to race; but in general terms, and as far as West Africa is concerned, the underfur, which is of the order of 14 to 17 mm long on the flank and 20 to 25 mm in the mid-dorsum, is white or pale-coloured for the majority of its length but has a short terminal zone of slightly more intense colour, and occasionally a faint intermediate band. The underfur is not entirely concealed by the longer and stouter bristle constituents of the pelage. Average ranges of lengths for these latter in West African forms are: for the bristles 30 to 35 mm in the spinal band, 21 to 27 mm on the flanks; the sub-bristles 2 or 3 mm shorter. The coloration of these two types of hair is very similar: there is always a slender black tip 4 to 8 mm long; subterminally there is a pale band, often narrowly golden yellow

PLATE 10



African Wild Cat *Felis lybica*. Caracal *Felis caracal*.

fading into white or pale yellowish and 3 to 7 mm in length; this is succeeded proximally by a black or deep-brown band 2 to 3 mm wide; and this passes into a long white base. In extralimital greyish forms the subterminal white bands accord a "frosted" look to the fur; but this is not apparent in the generally more buffish or sandy West African animals though it does account for the "ticked" appearance of the pelage in these.

Skull (figs. 51 and 52). According to Pocock (1951) there is no constant difference between the skulls and teeth of *libyca* and those of the European wild cat, *F. silvestris* Schreber. The profile is very rounded, falling away from an inflated frontal region just posterior of the postorbital processes, the nasals descending very steeply to a short, blunt rostrum, the length of skull lying in front of the infraorbital foramen being only a quarter, or less, of that lying posterior to it. There is no sagittal crest except for a short and usually not very highly developed posterior section joining the supraoccipital crest. Only in a very occasional extralimital specimen is there any sign of development of a crest across the main part of the cranium. The supraoccipital crest is variable, being always present; but the posterior portion of the cranium is in some specimens much more deeply excavated than in others. This is partially, but not entirely, to do with age; no conclusion can be reached with regard to sex. Apart from this backward extension the braincase is broad and subglobular. The postorbital processes are long but never join with the very well developed jugular processes to form a complete ring. The orbit itself is very large. The interorbital distance is narrow for the general width of the skull; the postorbital constriction relatively broad and inconspicuous, usually though not invariably at least twice the former.

The zygomatic arch is strong, the anterior, suborbital, portion much deeper than the posterior half. The palate is almost equilateral in form; there is a short postdental extension divided from the main area by broad emarginations which reach at least as far forward as the level of the posterior edges of the carnassials, and generally rather more, its posterior border double-concave with a small medial spine. The mesopterygoid fossa is wide, parallel-sided, the posterior processes of the pterygoids (hamulars) very narrow and sharp. The bullae are large, the anterior chamber much smaller than the highly inflated domed posterior portion; the paroccipital processes pronounced and spreading over the posterior aspect of the bulla wall but not, or scarcely, fused to it.

The dental formula is nominally $\frac{3\cdot1\cdot3\cdot1}{3\cdot1\cdot2\cdot1} = 30$, but there are occasional aberrations: in some specimens (3 out of 9 available West African skulls) p^2 is lacking on one or both sides having been shed and the alveolus closed over, an occurrence that can be observed in process in some skulls. In one specimen p^1 is also present on one side, of minute size closely approximated to p^2. When present, p^2 is always very small, no bigger, sometimes less, than the outer incisors. p^3 is a narrow but much bigger tooth, subtriangular in lateral profile, with a pronounced cingulum, a main cusp usually slightly taller than the carnassial, and a very small posterior cusp but no anterior one. The antero-internal cusp of the upper carnassial is small, sometimes very small, and sharp; m^1, which lies at right-angles to p^4, is always small or very small, generally about the size of p^2 but in some examples rather larger.

Habits. Very little indeed is known of the life of this cat either in the wild state or in captivity. Like most cats it is extremely secretive in its habits, the difficulty of study being added to by the fact that it is very largely nocturnal in its activities, though not entirely so for it may from time to time be seen on the move, or at least awake lying along a branch, during daylight. Normally it likes to shelter in a hole of not too large size, either in a tree or amongst rocks or in a small burrow made by some more fossorial animal, not too far below the surface where the soil is warmed by the sun. In Pocock (1944) the burrows of fennecs receive particular mention. Like all cats *libyca* seeks good protection from the rain, and a semi-open sleeping-place on the surface amongst grass is thus not much favoured, as such sites often are by the wild dogs or hyaenas. Since practically no field study has been carried out upon these cats it is unknown how constantly any shelter may be occupied; except, of course, that at breeding time a permanent secure home is absolutely essential for a few weeks. Most of the time, apart from the short period of actual mating or for the few months when a mother is accompanied by her kittens, these cats appear to lead entirely solitary lives.

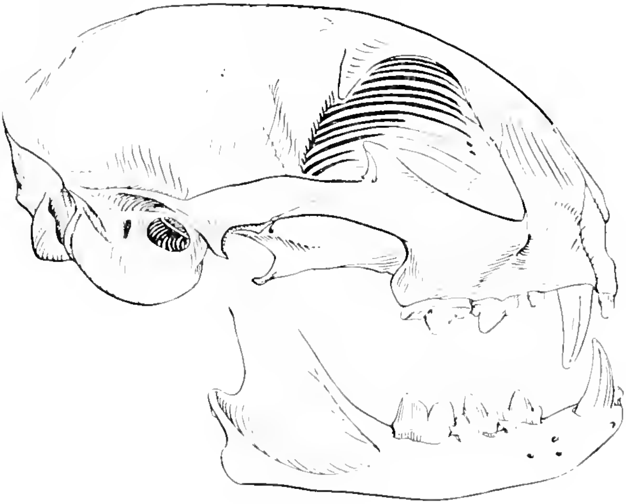


FIG. 51. *Felis libyca foxi*: skull, B.M. No. 13.2.5.3, ♂, × 1; lateral view

The African wild cat feeds upon rats, mice, gerbils, hares, birds of small to medium size (up to francolins), and lizards. It has been said in the southern part of the continent, where the species often attains considerably greater bulk than in the west, to tackle larger prey such as antelope fawns, or domestic stock such as lambs and kids; and it is reputed to be a continual threat in poultry yards. Like other carnivores it will probably, on occasions of need or when good opportunity offers, turn its attention to large insects or swarms of plump termites; but whether it will eat snakes, as sometimes claimed, seems never to have been clearly established.

Nothing appears to have been recorded of courtship and mating; but these animals certainly often frequent the outskirts of human habitations and couple with domestic cats to the accompaniment of a good deal of vocal outcry. The period of gestation is usually held to be normally 56 days, though the longer period of 63 days is sometimes quoted, and the reputedly conspecific *silvestris* (see the taxonomic section below) has twice been observed to take 68 days (Cocks, 1876). The litter consists of from 2 to 5 kittens, born with their eyes closed. No details of development appear to have been published.

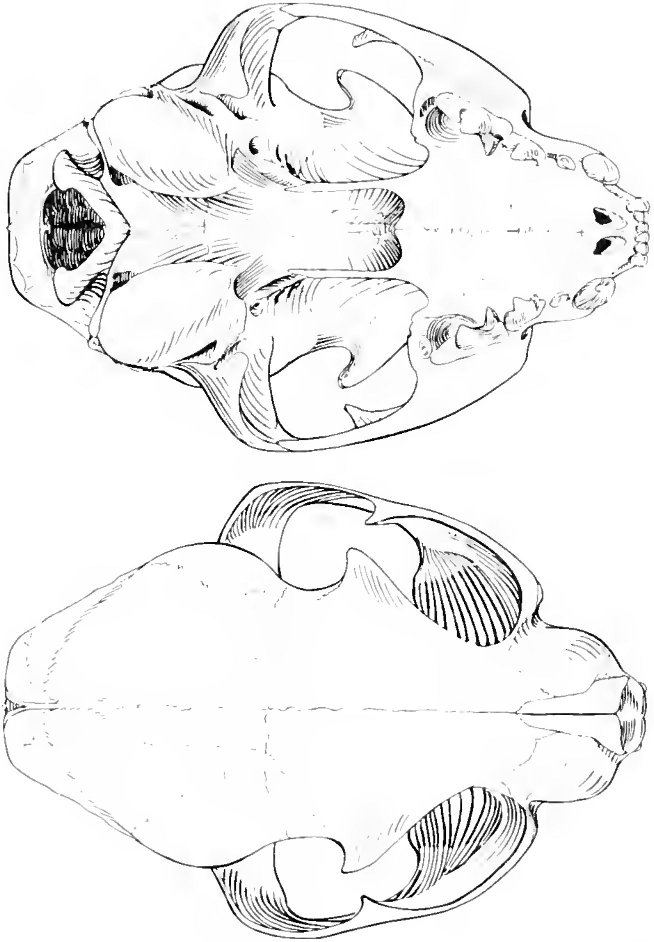


Fig. 52. *Felis libyca foxi*: skull, B.M. No. 13.2.5.3, ♂, × 1; palatal & dorsal views

Felis libyca is certainly of a fierce disposition and it is often stated to be quite untameable; but it is pretty clear that it was, in fact, tamed in ancient Egypt and became the chief ancestor of modern domestic cats, being carried thence eastwards to Asia, and westwards and northwards to Europe, where it appears to have interbred with the local wild cat, *silvestris*, and given rise in this way to at least one of the two pattern-forms of the common household animal (Pocock, 1911 and 1951).

Johnson & Lester (1929) reported finding one of these wild cats, under the then commonly used name *Felis ocreata*, at Sherifuri (11°58 N, 10°08 E) to be infected with *Trypanosoma brucei*.

Taxonomy. The taxonomy is involved and, like that of the Felidae in general, the subject of much disagreement and consequent abundance of literature. The trouble stems from the fact that, while there is a strong fundamental resemblance current throughout the entire subgenus that unites it and renders it a matter of ease to perceive that any member can only be a *Felis*, there are a number of basic pattern-forms that on the one hand appear to establish sound points of separation yet which in the sheer abundance of their variation furnish such stages of intergradation between widely diverse forms that it becomes difficult to know where to draw distinctions or whether such distinctions have any real validity.

The problem starts at specific level. Haltenorth (1953) and authors following him now consider that the African wild cat, *Felis libyca*, is not a true species but nothing more than a race of the European wild cat, *Felis silvestris* Schreber. Pocock (1951), on the other hand, while admitting the close relationship of the two, held that they are nevertheless taxonomically distinct. The fact is that on the existing evidence it is impossible to be definite. If accepted in the wide sense now claimed for it, *silvestris* embraces extremes of such vastly diverse appearance, between those of northern Europe, southern Africa and central India, that it becomes difficult to credit that they could belong to a single species, though there is admittedly a considerable degree of intergradation. Pocock, nevertheless, with no apparent hesitation accepted half of this proposal, including the spotted cats of Asia with the grizzled cats of Africa in the one species *libyca*; but while conceding that there is no constant difference between the skulls of that species and *silvestris* he considered that the two are always clearly separable by features of the pelage pattern and the nature of the tail; and, what is much more, that this separation is specifically valid. Such characters are indeed slender as the basis of specific distinction; and the two forms certainly breed with one another as Pocock himself (1911) practically demonstrated. The two are in fact held to be the common ancestors of one pattern of the domestic cat, the blotched tabby or *catus*-phase, presumed to have been brought about by the infusion of something from *silvestris* into the basic striped tabby or *torquatus*-phase derived directly from *libyca*. Data concerning the occurrence at the present time of the two reputed forms of wild cat, *silvestris* and *libyca*, in the same localities in southern Europe or the Mediterranean islands, with the consequent possibility of crossing in the wild, is sketchy and inconclusive.

It is strange that Pocock, with his very great interest in and deep knowledge of cats, should in his last, detailed and most mature monograph on the Felidae (1951) have offered not the slightest hint of the possibility that *libyca* and *silvestris* might be one and the same species, though the probability of this had been suggested in the literature for some years (Schwangart, 1928: 28 and 1932; Haltenorth, 1941). He apparently did not think the suggestion merited mention even in the paragraph in which he stated the two species to be closely allied and that there was no constant difference between their skulls and teeth. Nor have others, for example Ellerman, Morrison-Scott and Hayman (1953), thought fit to unite the two groups, Without doubt there is a not inconsiderable case for such a union; but the matter is still every bit as much one of opinion as the case for the opposing view, and on the existing data is beyond proof. Such a problem, in common with similar ones elsewhere can yield only to the application of more sophisticated and positive taxonomic techniques than mere estimation from morphology and pattern, accompanied, perhaps, by a clearer definition of species. Meanwhile, there seems no incontrovertible reason for the rejection of a convenient as well as possibly correct classification; and *libyca* is therefore herein treated as a species in its own right.

Attention must now be directed to the question of subspecies. Pocock (1951) accepted and furnished very detailed descriptions of 25, of which 16 are African, apart from a number of specimens which he did not feel able to place with certainty. There is little doubt that some of these named forms could reasonably and advantageously be synonymised. Once again the difficulty arises from a wide range of individual variation leading to a multitude of forms and intergradation with consequent doubt as to what degree of difference merits a fresh name. This, of course, must always remain purely a matter of opinion. Study of Pocock's subspecific descriptions clearly shows a remarkable degree of variation, both of colour and marking, admitted by him to a single form; and many of the taxonomic diagnoses specifically state that there is intergradation with one or more other forms. One is left with the impression that without knowing the provenance of a skin it would very often be difficult if not impossible to assign it with confidence to any particular race. J. A. Allen (1924) also made it clear that a series of 15 from a single locality (Faradje, Congo) presented such a wide range of colour variation irrespective of age or sex that the material helped to show the uncertain basis of forms founded on single specimens, there being two extremes, one distinctly grey, the other rufescent, intergrading through intermediate stages. It is fair to add that Pocock (1951) considered that this series may have been nothing more than pure or half-bred feral house cats, though the fact that the skins were gathered together over a period of many months, partly as freshly collected animals by the expedition and partly from local African hunters would, if this were so, seem to be stretching coincidence a long way. Dorst (1950), also, found a wide range of colour from red to grey in a very useful series of 15 from a restricted collecting area 6 to 16 km north of Lome (Togo). This series also demonstrates that there is considerable range of size in a single population of these cats.

The practical value of the attachment of a third name in such circumstances becomes questionable. There are indubitably recognisable distinctions: between the wild cats of Mediterranean Africa and those of the temperate south; between those of the arid tropical pre-Saharan zones and those of the moister and denser Guinean woodlands; but to multiply such distinctions until they become so slender as to be incapable of more precise definition than at present achieved seems to lack point. Dekeyser (1950) made some attempt to relate races of the African wild cat more or less to definite faunal zones as defined by Chapin (1932: 90), and it seems that some such scheme is a reasonable basis for the recognition of subspecific forms, at least for West Africa. As far as this latter region was concerned he postulated three: one in what is now known as the Sahel and the northern portion of the Sudan woodlands, reaching eastwards to the Nile and beyond; one in the southern portion of the Sudan, the Doka and the Guinea woodlands as far east as roughly the Benue and the western shore of Lake Chad; and one in the same zones but continuing east of this limit as far as the north-eastern Congo. Enough has been said about intergradation to make it clear that no precise boundaries are likely between forms; but recognisable breaks are more probable in a north-south direction between different ecological zones than east-west within an unaltering vegetational continuum. From examination of West African specimens it seems to the present writer that they fall conveniently into two groups, one occupying the northern Sudan, Sahel and Subdesert zones, and the other southwards of this. The former, in which the basic dorsal tone is whitish-grey or buff, and whatever red there may be in the pelage—and there is sometimes a good deal—is confined to the spinal band and to any pattern of spots that may be developed, is *haussa*. In this the belly is fundamentally white though often marked with pale red, sometimes heavily. The second group, *foxi*, is appreciably darker in tone, and red can be seen to suffuse the entire dorsal and flank pelage, the spinal band and any spots being correspondingly deeper. All but one of the British Museum skins are locally purchased and incomplete so that it is difficult to be positive about the belly colour, but this too seems to be dark and reddish rather than basically white as in the other group. These matters are entered into in more detail in the following accounts of the two forms.

Felis libyca haussa Thomas & Hinton — Hausa Wild Cat

Distribution. This is mostly found in the Sudan and Sahel woodlands, but three specimens were obtained by Angus Buchanan in Aïr in the Subdesert zone. The places in West Africa from which specimens exist in the British Museum are:

Sudan zone: Farniso, Dan Kaba (Nigeria)
Sahel zone: Zinder (Niger, type); Fort Lamy (Chad)
Subdesert zone: Tchsiderak (Aïr, Niger).

There is also a skin from an unspecified locality in Ghana; and a skull from the Gombe River (Bauchi, Nigeria; Sudan zone); as this is without a skin it is subspecifically indeterminable, but from its provenance should belong here, though this is discussed later. This gives a total of 9 skins and 8 skulls, of which 6 match, 1 being very juvenile.

Taxonomy. Pocock (1951) divided these specimens between *haussa*, *lynesi* and *lowei*, the two latter with some uncertainty. The present writer questions the worth of the distinctions of colour, pattern and size drawn. A good deal has already been said of the capriciousness of the two former characters; scarcely any two existing specimens are precisely alike, and in these circumstances, with no real knowledge of normal population range, comparing a maximum of three skins from one locality with even less from others, drawing fine distinctions between shades of buff in the coat, or the amount of red along the spine, or black on the feet, or the precise tint of the ears seems to be straining after a precision that the existing material does not in fact warrant. The same applies to pelage length; for though valid differences may well exist between the coats of temperate, Mediterranean, animals and those of warmer regions attempts within the latter zones to make taxonomic deductions from this character, which is variable in response to season, age and moult as well as temperature and humidity, by the comparison of single specimens are unconvincing.

The form *haussa* was distinguished by Pocock from *lynesi* and *lowei* solely by its smaller skull. On the face of it, from the figures given for total length, there is some support for this view; but once again we have no idea of the normal range of size, and examination of the table given below on page 400 shows that the means of most of the other cranial and dental measurements of such limited study material as exists are fairly close and there seems no very strong reason at present for separating *haussa* from the outwardly very similar *lynesi*. Turning to the suggested form *lowei* which Pocock erected from a single skin from Jebel Marra and to which he provisionally assigned a West African (Fort Lamy) skin, the type is certainly a shade darker and greyer than the *haussa-lynesi* material; but it nevertheless belongs to the grey-buff group, not to the red phase, and the erection of a separate subspecific name for it is of doubtful justification.

If the reputed differences between supposed forms were eventually found to hold true for long series from the given localities there might be sounder support for a multiplicity of names; but there is an at least equal chance that more abundant study specimens would demonstrate the futility of attempting to draw an excess of minor distinctions. Meanwhile it seems most satisfactory to regard all the wild cats of the transcontinental dry Sudan and Sahel woodlands, as well as those from the yet more arid Subdesert areas, as belonging to a single race, *haussa*.

Description. In view of the range of variation no more precise description can be furnished than that the overall impression is one of a palish cat, basically buffish or light-greyish and with a little red mostly in the spinal band or such faint pattern of spots or lines as may in different cases be developed. The whole underside from chin to anus is long- and loose-haired, fundamentally white but sometimes faintly spotted or suffused with very pale red.

The skull from the Gombe River (mislabelled Gonebe River) mentioned earlier as, vegetationally, presumably belonging here is nevertheless, as the table on page 400 shows, in several cranial and dental respects appreciably larger than any of the identifiable *haussa* group of specimens, and much more nearly corresponds to *foxi*. Without a skin it is impossible to know whether this indicates a wider range of size for *haussa* or that *foxi* spreads deeper into the Sudan zone than hitherto supposed.

Felis libyca foxi Pocock — Mid-belt Wild Cat

Distribution. The Doka zone may be regarded as the centre of distribution of this form which, however, ranges a little farther north into the southern part of the Sudan zone and, apparently less commonly, south into the Guinea woodland. Seven specimens, all from Nigeria, exist in the British Museum but constitute a very unsatisfactory set of study material consisting of five skins without skulls and two skulls without skins. Of the former only the type appears to have been obtained at first hand by the collector, and that is in only fair condition; the others are mostly incomplete and give the impression of having been purchased from African hunters or in local markets, their exact provenance being thus open to some doubt. Three of the seven specimens here attributed to *foxi*, the type and the two skulls all from Kabwir, originate from the Doka/Sudan interchange zone; one, said in general terms to be from Zaria district, is probably from the Doka zone; two others from the Kode area 24 km N.-E. of Lau (on the R. Benue) and from Langa 24 km N. of Lau, would thus come from the Sudan woodland; and one from Mkpani, Obubra. This last is somewhat of a surprise and has the interest of being by a very long way the most southerly of all known West African examples. This village is nominally in the high-forest belt but lies opposite, across the Cross River, a large expanse of Guinea-type woodland. It is presumably from this last that the specimen, part of Sanderson's collection but obviously of local purchase, may well have come—if, indeed, it did not enter the area from a distance by way of trade along a well-established route, the river. Of this set Pocock dealt only with the Kabwir skin and two skulls, and the Zaria district skin, referring them all to *foxi*, the last somewhat hesitantly. There seems little doubt that this was the form that Dekeyser must have had in mind when he, apparently unaware that *foxi* had already been erected, described *savanicola* from Messirah, Senegal, in Guinea woodland vegetation, and projected its range from Senegal to Lake Chad.

Description. The external character that differentiates this race from *haussa* is the deeper, sometimes much deeper, red colour which suffuses the whole coat. There is, however, the usual variety of tone and pattern. The type shows no pattern of spots whatsoever, the only distinct mark on an otherwise plain ticked coat being the deep red spinal band. The other specimens all exhibit spots in a greater or less degree, tending to coalesce into transverse bars, this fusion being complete in the Zaria district skin. The underside is paler than the back but in no sense fundamentally white, as in *haussa*, being at most a light brown. It will be seen from the table on page 400 that the skull and teeth of *foxi*, as deduced from the two Kabwir skulls devoid of skins, are both quite appreciably greater than those of *haussa*.

The two skins from near the Benue north of Lau present some difficulty. They are incomplete lacking the heads and parts of the legs, feet and tail; but though they have all the appearance of pelts originally inexpertly prepared they have subsequently been soft-dressed and their places of origin given with some precision by the collector—of whom no particulars beyond the bare name have been discoverable. The two localities lie within a few kilometres of each other and can with some certainty be regarded as lying within a uniform biotope; but the skins differ fairly markedly in colour. That from Kode is not very dissimilar from the Cross River skin; the one from Langa is of a distinctly paler tone, though still much redder than any *haussa* specimen. The undersides, too, are different, though in the incompleteness of the skins it is impossible to be precise. The darker, Kode, skin has the chest and at least the after part of the belly pure white; the paler, Langa, skin appears to have very little white. It was the whiteness of some of J. A. Allen's reputed *rubida* specimens that caused Pocock to suggest that they were pure or hybrid feral house cats; and similar considerations may be applied to the two Benue animals. The series of 15 skins from north of Lome (Togo) reported on by Dorst (1950) obviously belong to *foxi*; but they demonstrate that there is a considerable range of colour in animals from a small uniform area; and Dorst concluded that it is the greater intensity of pigmentation rather than actual colour that distinguishes *foxi* from *haussa*.

A problem of a somewhat different nature is presented by the skull from the Gombe River, cited above under *haussa*. This locality lies some 100 km further north than the area from which the two skins just discussed came, rather deeper into the Sudan zone. It might thus be assumed to have come from a *haussa* type animal; but, as the measurement table shows, it is of a size much more representative of *foxi*. However, Dorst (1950) came to the conclusion that size was an unreliable taxonomic character in these cats since there was wide variation in specimens of apparently equal age; and all his Togo skull material of *foxi* was more comparable in this respect to *haussa* rather than to the type of that race. The skull is illustrated in figs. 51 and 52.

Other forms. Finally, Dekeyser's suggestion that the West African Guinea form (which he called *savanicola*) is replaced eastwards of Benue-Chad by the north-eastern Congo *rubida* Schwann must be examined. This latter is a red form in the type skin of which the pattern is not only unusually clear but also consists, exceptionally, of spots that show no tendency to coalesce into transverse bands. Pocock suggested that this was probably nothing more than an individual idiosyncrasy; but other skins with the same peculiarity have since come to light from the southern Sudan. The only other skins in the British Museum collection attributed to *rubida* by Pocock are all too young to be properly comparable. J. A. Allen's (1924) series of reputed *rubida* from the north-eastern Congo, on which Pocock cast doubt as possibly pure or half-bred feral house cats, shows that the form is widely variable and that one cannot take any particular colour or pattern as narrowly representing the race. Taking this much less restricted attitude than that adopted by Pocock there is little doubt that *rubida* closely resembles some of the West African skins herein considered to be *foxi*, and there is a considerable possibility that a single variable, constantly intergrading form—but not a cline—ranges across the continent in the Doka-Guinea zones from Senegal to the north-eastern Congo; and that *foxi* in consequence may eventually prove to be nothing more than a synonym of *rubida*. This last position is not adopted in this present work because there are factors of uncertainty: the material from both sides of the range is quite inadequate; the lacunae in collecting localities great; and such figures as exist for cranial and dental measurements—two skinless skulls from the west and Allen's slightly doubtful series from the east—indicate that *foxi* might be appreciably larger.

FELIS MARGARITA Loche Sand Cat

Felis margarita Loche, 1858, *Revue Mag. Zool.* (2) **10**: 49–50, pl. 1. Near Négousa (misprinted Négonça), Algeria. The type has in all probability been destroyed (Haltenorth, 1953: 63 f.n.). The spelling of the specific name as given here is retained in order to avoid confusion in view of its long and wide usage. Nevertheless, it seems to the present writer that it was clearly originally a *lapsus* on the part of the author or, more probably, a printer's error. The species was dedicated to Commandant (subsequently Général) Margueritte to whom Loche went to some length to express his gratitude for constant aid as well as the hope that natural-scientists would always preserve this helper's name. It is thus unthinkable that Loche would have insulted a high-ranking soldier and friend by deliberately attaching a feminine forename to an animal which he hoped would lastingly commemorate this officer's kindness. It is unfortunate that yet a second error crept into Loche's description when one of the 't's from Margueritte's name was dropped later in the text; this, however, is no sanction for the spelling *margarita* or *margueritei*, and only Trouessart (see below) eventually grasped and recorded the author's true intention. Jean-Auguste Margueritte published a work on hunting in Algeria and earned fame as a general in the Franco-Prussian war; it is to be regretted that mischance and convenience of usage deny to his name the honourable position that Loche obviously desired.

Felis marginata Loche (Gray, 1867, *Proc. zool. Soc. Lond.*: 275. Printed in error for the above).

Felis caligata margaritae Loche (Trouessart, 1897, *Catalogus Mammalium*, **1**: 363. An emendation of Loche, putting the name in the more usual genitive case rather than simply in apposition).

Felis libyca margueritei Loche (Trouessart, 1904, *Catalogus Mammalium*, Supplement: 273. A supposed correction of the alleged spelling by Loche "*margaritae*", made in conformance with Loche's second mis-spelling when citing Margueritte's name in the text of the original description).

Felis ocreata margueritti Loche (Trouessart, 1905, *Caus. scient. Soc. zool. Fr.* **1**: 386–387. A correct emendation of spelling in accordance with Loche's original intention of honouring Commandant Margueritte).

Felis ocreata margaritae Loche (Antonius, 1928, *Der Zoologische Garten*, Neue Folge, **1**: 375).

Felis lybica margaritae Loche (Koller, 1930, *Annln naturh. Mus. Wien*, **44**: 1).

Felis margarita airensis Pocock, 1938, *Ann. Mag. nat. Hist.* (11) **1**: 472–476. In-Abbangarit, West of Aïr, 260–300 metres. Type in the British Museum, No. 1939.1673, ♀; skin and skull both in good condition except for the left upper canine half broken. Valid as a race.

Felis margaritei Loche (Dekeyser, 1955, *Les Mammifères de l'Afrique Noire*, 2nd edit.: 279).

Distribution and general. The sand cat, or General Margueritte's cat as it is alternatively known, may be reckoned a rare species since its habitat is restricted to desert or near-desert conditions. So far as present information goes this animal occurs from the Sahara (Algeria to the north, Aïr to the south), across Sinai and the southern and eastern Arabian peninsula to the Turkestan region of southern Russia and further south in West Pakistan; but the distribution within this wide range is by no means continuous, only remote unpopulated desert areas being suitable. Relatively few specimens have been collected, there being no more than five in the British Museum, of which one alone is West African in the sense adopted in this work. This last came from In-Abbangarit, west of Aïr (Subdesert zone); but there is a second specimen from rather further north, just extralimital to this present account at Touaret, northern Niger, 20° 17′ N., 7° 08′ E., in the Desert zone.

Description. To judge from the few British Museum specimens there is a considerable diversity of size, the West African example, an adult female, being very considerably smaller than a male from the Algerian Sahara and no bigger than an average sized house cat. To give a body weight, therefore, can be nothing more than a wide approximation, but it may be indicated for the purposes of general comparison as of the order of 3 kg. However, when well developed the sand cat is in appearance very like a plump domestic pussy, the plump appearance being fostered when the animal is lying down by the very big square-looking head which seems over-large in relation to the body. One of the most noticeable features is the very broad ears set far apart well down on the sides of the head, pointed, with no apical tuft but well protected in the front view by a dense growth of long white hairs directed outwardly from the head across the opening and continuing along the inner margin to the apex. The backs of the ears at once distinguish *margarita* from *libyca*, in which they are unicoloured, by reason of a blackening at the tip, this varying in extent from a small dark mark chiefly on the outer edge to a deep black area embracing the whole apical region but with an ill-defined proximal limit. The eye pupil closes to a vertical slit.

The pelage is variable in length and colour. As regards the former, the West African animal has an appreciably shorter coat than the Algerian one, slightly harsh to the touch. It consists of very dense fine, long underfur and fairly abundant longer, black-tipped, flattish-sectioned bristles, together with fine-stalked sub-bristles with a wider distal region. In the West African specimen the underfur is buff in colour, 20 to 25 mm long, and only partly concealed by the other two elements. The bristle-hairs are 30 to 35 mm long, all white except for black tips of 2 to 11 mm in length; the sub-bristles are a little shorter, with the expanded terminal section measuring about 16 mm. The overall colour differs from specimen to specimen but, as far as the few available study specimens go, is with one notable exception less variable than in *libyca*. The West African example is pale greyish-buff dorsally, but there is a darker spinal band from the mid-back to the root of the tail bordered by two rather ill-defined narrow black lines.

The underside from chin to anus is densely clad with long, loose, pure white hair which together with a good deal of white on face and limbs caused the collector, Buchanan, to comment on the animal's snowy appearance in life. On the posterior half of each flank about half-a-dozen faint but clear pale-brown narrow transverse stripes are discernible, better defined in this and the Touaret skin than in those from elsewhere. The pelage of this latter, just-extralimital, skin is very markedly lighter in tone than the In-Abbangarit, or any other, specimen, being in no sense greyish but golden-sandy in colour.

There are in *margarita* certain fairly constant markings, some of which correspond to those of *libyca* but some of which serve as points of distinction. Chief of the latter is perhaps the black tip to the ear already mentioned. The face has a brown line running from the outer corner of the eye towards the corner of the jaw but lacks the second subparallel one of *libyca* across the cheek. There is a less well-defined area of similar colour between the inner corner of the eye and the rhinarium, of variable extent and not necessarily reaching to the nostril. On the back of the neck are 3 to 5 dark, narrow, always obscure and sometimes indistinguishable, longitudinal lines. There are two more or less well-defined "bracelets" on the forearm, one of which at least is always very clear as a patch on the inside face of the limb, and apparently always quite black, even in the pale red Touaret skin. The outsides of the hindlimbs have from 2 to 5 dark, mostly black, half-rings. The feet are chiefly notable for their undersides being densely clad with long fairly stiff hairs which to a large extent conceal the pads and doubtless aid progress on loose sand. These hairs may be blackish-brown but the underside of the foot is not otherwise black along much of its length as it is in *libyca*. The tail, as in this latter species, has a black tip and 2 or 3 rather ill-defined blackish subterminal rings. It is somewhat more than half the length of head & body. The readiest dis-

FIG. 53. *Felis margarita airensis*: skull, Type, B.M. No. 1939.1673, ♂, 1

tinguishing points of *margarita*, therefore, lie in the width and low position of the ears, with their black apical mark; and in the soles of the feet.

Skull. There are certain clear differences between this and the skull of *libyca*, as comparison of figure 53 with figs. 51 and 52, together with measurements given in Table 24 on page 400, show. Comparison is most profitably made with *libyca haussa* since this comes from a similar sort of arid habitat and is of the same order of size, rather than with the moister-zoned and appreciably larger *l. foxi*. It is sometimes said that the braincase of *margarita* is broader than that of *libyca*; but both visual and mensurational comparison show that, for West Africa at least, this is not a good character. The zygomatic breadth, on the other hand, is, both in absolute and relative terms; for it measures somewhat over 79 per cent of the condylobasal length as compared with 75 per cent in *libyca*. The nasals provide a good point of recognition; for not only are they longer in *margarita* but are also of a different shape since they are almost parallel-sided throughout a great part of their length, only tapering abruptly posteriorly; whereas in *libyca* in almost every case they decrease in width continuously throughout their posterior half and so are narrower and more wedge-shaped. In the palatal aspect, the palate itself is appreciably shorter and, as the measurement across the cheekteeth shows, somewhat narrower posteriorly. But the dominant feature of this aspect is the bullae, which in *margarita* are much larger both in length and breadth; and because of this last the space between them is, in West African specimens, only some 4 or 5 mm as compared with 6 to 8 mm in *libyca*. The auditory orifice is, like the bullae, also exceptionally large, complementing the broad external ears.

As regards dentition, the upper toothrow from the canine to the molar is in general shorter in *margarita*; and as the carnassial (fig. 2) is of the same order of length as in *libyca* it consequently occupies some 40 per cent of the toothrow as contrasted with about 36 per cent in the latter species. Both m^1 and m_1 are very small, much smaller even than in *libyca*.

Habits. It will be readily appreciated that in view of the remote habitat and limited collecting of this animal that has taken place there is very little known of its habits. It can only be surmised that these follow the general pattern of all small cats. The food is mainly gerbils and jerboas but hares, ground-squirrels, lizards, small birds and insects are also from time to time taken. It probably never drinks. Fortunately we have one field note from West Africa concerning the sort of shelter favoured; for Angus Buchanan observed the animal which subsequently became the type of *haussa* to enter a hole in a sand dune, from which it was then dug out. Since these cats are always inhabitants of deserts it would seem likely that this is a general habit; and, indeed, Russian specimens have likewise been taken alive from sand dunes. The only breeding note is also Russian (Ognev, 1962): that a captured female gave birth to 4 kittens, two of which were immediately torn to pieces by the nearby male, the others subsequently eaten by the mother.

This animal is not difficult to capture and several specimens have been kept in zoos. One from Arabia lived in the London zoo for 7½ years until it was killed by accident. From the present writer's observation this animal had a constant surly look, and though not actually aggressive always flattened its ears and spat if any attempt was made to

Table 24 Numerical data for species of subgenus *Felis*

	libyca							***margarita***	
	haussa sensu stricto	*lynesi*	Tchsiderak specimens	*lowei*, type	Extended *haussa* group	*foxi*	Gombe River specimen	*airensis*, type	Touaret specimen
Vegetation	Sudan Sahel	Sahel	Subdesert	Sahel	Sahel Subdesert	Doka Sudan	Sudan	Subdesert	Desert
Number in mean	3	2	3	1	9	2	1	1	1
Condylobasal length	77·0	82·6	82·9	82·0	80·7	87·8	91·6	76·9	81·0
Basilar length	69·0	74·4	75·3	74·0	72·8	78·7	83·4	70·0	73·3
Palatilar length	30·1	30·3	32·7	31·9	31·3	35·1	34·5	26·5	28·2
Zygomatic breadth	59·0	60·9	62·5	61·3	60·8	66·8	68·6	61·1	64·1
Upper cheekteeth breadth	33·5	35·5	35·0	33·5	34·3	38·2	36·5	31·4	32·2
Nasals, length	22·3	22·6	24·7	23·0	23·2	26·6	24·9	25·4	25·4
Interorbital breadth	14·5	15·8	16·3	16·4	15·6	18·3	18·4	15·4	16·3
Postorbital constriction	31·1	34·2	34·0	33·3	33·0	33·5	32·9	32·7	32·1
Braincase breadth	41·3	43·3	43·5	42·4	42·6	45·0	44·8	41·6	42·0
Bulla length	20·2	20·5	20·7	21·0	20·5	21·5	21·5	23·0	23·4
Toothrow (c–m^1)	26·8	28·3	29·2	28·8	28·4	30·8	30·3	25·4	26·7
p^1 length	10·0	10·5	10·2	9·9	10·2	11·7	11·0	9·8	10·7
m^1 breadth	2·9	3·3	2·9	3·4	3·0	4·0	4·0	2·1	2·6
m_1 length	7·7	8·1	8·0	7·4	7·9	9·0	8·8	6·9	7·2
Head & body	434	507	452	559	465	660	—	390	420
Tail	258	330	325	336	302	292	—	245	270
Hindfoot	107	128	120	124	117	—	—	100	110
Ear	55	57	58	55	57	48	-	52	70
RATIOS (per cent)									
Tail/head & body	59	65	72	60	65	44	—	63	64
Zygom. br./condylob. l.	77	74	75	75	75	76	75	80	79
Braincase/condylob. l.	54	52	52	52	53	51	49	54	52
Braincase/zygom. br.	70	71	70	69	70	67	65	68	65
Palatilar l./condylob. l	39	37	39	39	39	40	38	34	35
Interorb./postorb.	47	46	48	49	47	55	56	47	51
p^1%c–m^1	37·3	37·1	34·9	34·3	36·0	38·0	36·3	38·6	40·1

handle it. During its captivity it developed little real response to domestication though it would allow its head to be scratched and closed its eyes in satisfaction while this was being done; but it would never voluntarily approach with the object of receiving such attention as a domestic cat, or some captive animals, would.

It is interesting to note that the dense mat of hairs covering the soles completely obscures the pad marks in the sand so that the spoor is nothing more than the plain outline of a cat's foot, claw marks only showing when the claws have been deliberately extended prior to making a spring.

Taxonomy. *Felis margarita* seems fairly clearly to be a species in its own right, the differences of external form between it and *libyca*, concerning the ears and feet, as well as of the skull and teeth being of a specific rather than racial order. Nevertheless, it does in a degree share some of the pelage markings of *libyca* and it has been suggested that it is, in fact, nothing other than a subspecies of this—itself often held to be only a form of *silvestris*; but this view is not much favoured today, though *margarita* may well be a specialized desert derivative of *libyca*. Animals at the eastern end of the known range, in Turkestan, have not only been placed in a different species, *thinobia* Ognev, 1927, but also in a separate genus, *Eremaelurus* Ognev, 1927; but while Haltenorth (1952) accepts the species, but not the genus, both Ellerman & Morrison-Scott (1951) and Pocock (1951) regarded this as nothing more than a race of *margarita*. The point is of no particular concern to West Africa.

Regarding subspecies, since the type of *margarita sensu stricto* from Algeria is unknown it is difficult to say whether Pocock's proposed *meinertzhageni*, also from Algeria, is materially different and therefore valid as a race. But while this is of little direct moment to this present work it seems evident from the single specimens available, that is to say the two types, that *airensis* is sufficiently distinct in size and colour from *meinertzhageni* to merit separate recognition. The West African animal should therefore be referred to as given below.

Felis margarita airensis Pocock — Aïr Sand Cat

The form, which is known only by the type skin and skull in the British Museum from In-Abbangarit, on the extreme northern edge of the Subdesert zone, has been sufficiently dealt with above. A second skin from 300 km further north, from Touaret (northern Niger) in the Desert zone, might also be looked upon as belonging to this race; but it is not only paler but also of a very much more lively light red colour.

Subgenus **CARACAL** Gray, 1843

Caracals

This monospecific subgenus differs from *Felis sensu stricto* partly in its larger size but chiefly in the possession of relatively much longer, very pointed, long-tufted, blackish-backed ears and a very short tail measuring little more than a third of the head & body length. The webs between the toes are also markedly shorter. The skull differs in having only two upper premolars, a third anterior one being only exceptionally developed. In addition to this the nasal branch of the premaxilla is a narrower and longer bone than in *Felis*, wedging much further between the nasal and the maxilla so that contact between these two latter bones is very much shorter and sometimes almost non-existent, the premaxilla practically abutting onto a narrow tongue of the frontal. This feature is, however, shared with *Leptailurus*. *Caracal* is of wide distribution through most of Africa and much of western Asia.

FELIS CARACAL Schreber — Caracal or Desert Lynx

Felis caracal Schreber, 1776, *Die Säugethiere* . . ., pl. 110; 1777, text **3**: 413 and 587. Type locality Table Mountain, Capetown, South Africa. The priority of this over Müller's identical naming, which follows below, and a similar one that has wrongly sometimes been attributed to Gueldenstaedt (1776) has been fully discussed by J. A. Allen (1924: 279–281). Allen's conclusions were either unknown to or ignored by Pocock (1939) who continued to follow Matschie (1912) in citing Müller as the prior author; but they were at a later date accepted by Ellerman & Morrison-Scott (1951). The derivation of this name has been given above in the generic synonymy.

Felis caracal P. L. S. Müller, 1776, *Des Ritters Carl von Linné* . . . *Natursystem* . . . Supplement: 30. Type locality given as Arabia but was more probably Constantine, Algeria.

Caracal melanotis Gray, 1843, *List of the specimens of Mammalia in the collection of the British Museum*: 46. A renaming of Schreber's species on transferring it from *Felis* to a new genus *Caracal*. The name is a combination of the Greek *melas, melanos* black, and *ous, otos* ear, with reference to this diagnostic character.

Caracal caracal poecilotis Thomas & Hinton, 1921, *Novit. Zool.*, **28**: 3–4. Type locality Mount Baguezan, Asben, Niger. Type in the British Museum, No. 21.2.11.19, ♀; skin in good condition, skull good except for the left i^1 and p^4 missing and *c* broken. This name is derived from the Greek *poikilos* varicoloured or pied, and *ous, otos* ear, from the "frosted" nature of the back of the ear in this form.

Distribution and general. Outside Africa the caracal ranges across the Arabian peninsula, Palestine, Syria, Iraq, Iran and Turkestan as far east as northern India. In Africa itself its distribution once embraced the greater part of the continent from the Cape to the Mediterranean with the exception of the closed forest block and central Sahara; but while it has never been a common animal it has now like so many other mammals in the face of advancing development become much rarer than it used to be and is now absent from the southernmost parts of the continent and is fairly unusual in Morocco, Algeria and other north African countries. However, it still occurs widely, though sparsely, in the tropical open woodlands and is at its most plentiful in the eastern territories. In West Africa it manages to retain a foothold but in many areas this is now very tenuous. The only material from this region in the British Museum consists of 6 skins, mostly incomplete and without skulls, from Gambia, Lake Chad, Ghana (Gambaga) and Nigeria (Kode and unspecified); one skull without a mandible from Nigeria; and a single matching skin and skull, the type of *poecilotis*, from Mount Baguezan, Aïr. In so far as can be judged from the localities cited, the vegetational zones which these specimens inhabited were the Sudan, the Sahel and the Subdesert; but the Gambia animal may have come from the Guinea woodland; and G. S. Child (private communication) says that it occurs in the Borgu Game Reserve, which lies in the Doka zone.

Besides this museum material there is a very interesting record supported by a photograph (*Animals*, Jan. 1970) of two cubs taken from a cave near Ado Ekiti (Ondo, west Nigeria), a place which lies close to the high forest; but it is now largely open woodland, and being rocky country offers attractive refuges. The literature contains several generalised statements asserting occurrence of this animal in most of the West African territories from Senegal to the Central African Republic without citing particular specimens; but Frade (1949) published a definite record for Bafatá, Portuguese Guinea, apparently in the Guinea woodland.

Description. *Felis caracal* (Plate 10) is a medium-sized cat, that is to say it is appreciably larger than *libyca* and *margarita* but very considerably smaller than "the great cats"—in Africa, the lion, the leopard and the cheetah. There is, however, some considerable range in size though satisfying figures for this are difficult to come by. Only one West African specimen has any collector's measurement data. These relate to a fully adult animal, the type of *poecilotis*; but since this is both female and an inhabitant of difficult subdesert terrain it is expectedly of less than average size. Nevertheless, the dead weight given by the careful collector, Buchanan, 5·9 kg is vastly inferior to that indicated by Shortridge (1934) for South-west African animals, 18 kg, or even that given by Wilson (1968) for Zambian specimens, 12 kg for a female to 14·5 kg for a male. Buchanan's type was recorded as having a shoulder height of 400 mm, from which Shortridge's range, 406 to 457 mm is not so widely remote.

Colour, too, is a matter of considerable variability. There are dark specimens with a good deal of black mixed into the fur, palish sandy-grey specimens, and those of a lively red. Shortridge (1934), indeed, speaks of the intensity of colour varying within the same district. No albino seems to have been reported; but, as in a good many other of the Felinae, melanos are known; there are two Kenya skins in the British Museum; Pitman (1949) recorded one for Uganda; and one of the two cubs from west Nigeria referred to in the previous section was, from the colour-photo, very dark though apparently not a true melano. With these reservations the caracal can be described in general terms as dorsally of a more or less uniform greyish-sandy or reddish colour from the crown to the end of the tail. There is usually a faint and very ill-defined, slightly darker spinal band. Much of the upper side is often "frosted" to a greater or less degree, this feature showing up better on the darker, redder coats than on the pale, buffer ones. The "frosting" is due to longer or shorter subterminal regions on many of the bristle-hairs and sub-bristles, interesting in that they are not really complete encircling bands as in most "ticked" mammals but are pure white on their upper sides and of the normal pelage colour below. The dorsal pelage, as exemplified by the few West African specimens, is variable in texture, density and length, possibly as much according to age, moult and season as to locality. In some the fur is moderately long and soft, in others short and rather harsh. It consists of abundant long or fairly long underfur which is colourless or very pale brown with darker tips and amongst which are scattered bristle-hairs slightly oval in section, with long white bases and black tips; and there are also less frequent sub-bristles with long very fine petioles and flat-sectioned blades. Average lengths for these components are: underfur 9 to 11 mm, bristle-hairs 13 to 20 mm, and sub-bristles 13 to 18 mm, the petiole measuring 10 to 12 mm, the flattish blade 4 to 6 mm.

The flanks are somewhat paler than the back. The belly, chest and sometimes the throat are pure white or whitish and bear, especially on the belly, pale red spots which vary in their distinctness, their abundance and the amount of the underside they cover according to different specimens. There are distinctive facial markings, one being a fairly pronounced dark line from the inner corner of the eye to the rhinarium. Above the inner corner and below the whole of the eye are white patches which are sometimes sufficiently extensive to give the impression of a complete encircling ring. There is also a prominent white patch either side of and below the rhinarium, continued posteriorly along the edge of the upper lip, at first narrowly and partially interrupted by a blackish patch from which the mystacial vibrissae arise and then expanding onto the cheek. The lower lips are wholly white. The eyes are greenish, the pupil an upright ellipse which never narrows to a mere slit as in the typical cats.

Fig. 54. *Felis caracal*: skull, Type of *poecilotis*, B.M. No. 21.2.11.10, × 1; lateral view

The ears are very characteristic. They are of a tall triangular shape, quite different from the rounded pinnae of the serval or rather squat triangle of the wild cat; and they carry at the apex a long pencil of hairs, by far the longest tuft of all the felines, measuring about half as long as the pinna itself. The backs are covered with very short close-lying hair, their colour often sweepingly stated, as a diagnostic character, to be black. Yet this last is true only in a general sense, the overall impression in sharp contrast to the otherwise sandy pelage being broadly of that colour; but a closer look shows that there is invariably some white mixed with the black, and in a large number of cases a con-

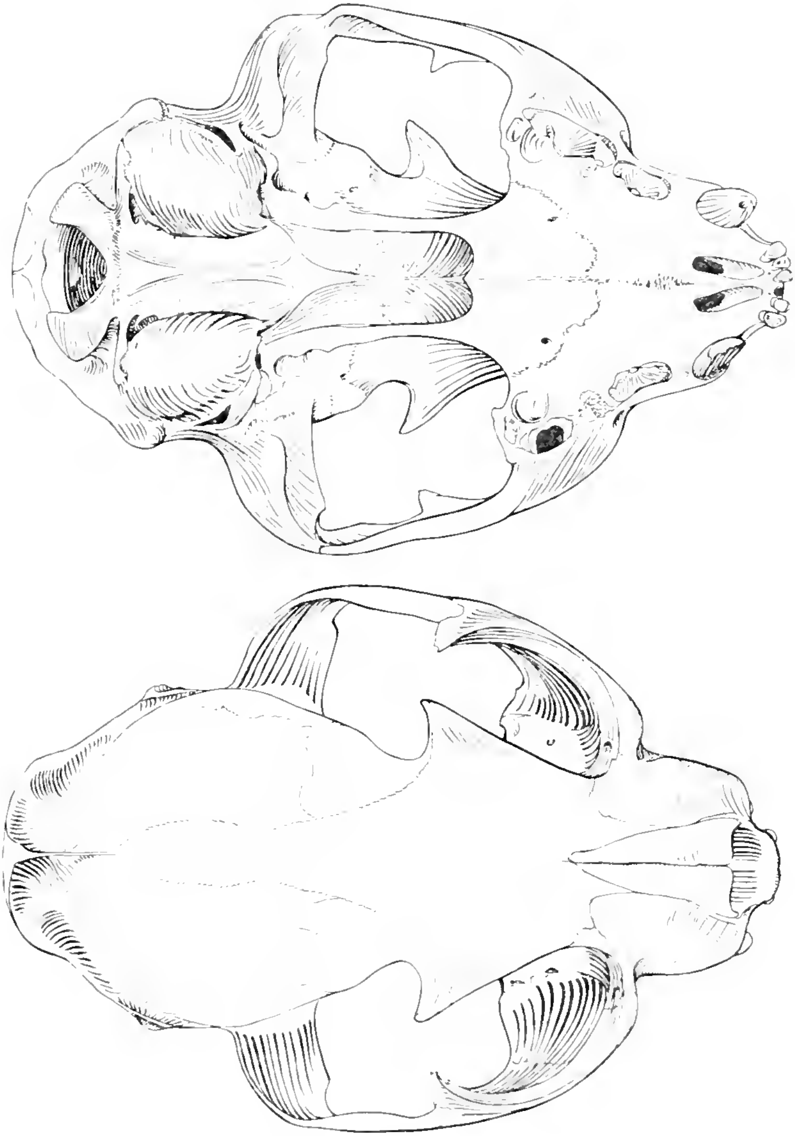


FIG. 55. *Felis caracal*: skull, Type of *poecilotis*, B.M. No. 21.2.11.19, ♀, × 1; palatal & dorsal views

siderable amount, until at its extreme the colour becomes more silvery than black. This latter character was largely relied on by Thomas & Hinton for the differentiation of the West African race *poecilotis*; but it is by no means so uncommon as the description of that form might lead one to suppose. The base of the pinna together, often, with a small surrounding area on the head, is of a more intense black which not uncommonly shows up very conspicuously from the side and behind in the living animal. It is interesting to note that the greying on the backs of the pinnae shows up most prominently in melano animals where it forms the only contrast to an otherwise wholly black pelage. In all cases, except melanos, the extreme edges of the ears are narrowly white; the front face carries a growth of upwardly directed long white hairs along the inner margin, and shorter white hairs along the outer margin; and there is a tuft of similar hairs arising from the head and obscuring the orifice. The apical pencil may be pure black or, more usually, have a greater or lesser mixture of white hairs with it. In older animals when the ears are not being actively pricked their tips together with the apical pencils hang down in tassel fashion and waggle when the pinnae are twitched —as they can be independently.

The tail is remarkably short being merely about a third of the head & body length, reaching only to about the hocks when the animal is standing and the tail hanging. It is subcylindrical, the hairs coming to a slight point at the tip, a little darker above than below but devoid of black rings or other markings. The legs are moderately long but relatively stout compared with those of the serval, the hinder ones rather longer than the front ones, so that the rump stands higher than the shoulders, the whole hindquarters being somewhat more heavily built than the forequarters. The feet are abundantly hairy below between the pads but do not carry that dense mat of stiff hairs characteristic of the sand cat. The interdigital webs are short; the claws retract into sheaths in the normal cat fashion.

Skull (figs. 54 and 55). This is of rounded but irregularly curved profile, being most elevated across the frontals at the interorbital constriction, falling away gradually posteriorly but sharply anteriorly, the nasals descending abruptly to the short blunt rostrum. The frontal region itself is slightly hollowed medially. The nasals are, in comparison to the most typical *Felis*, broad, parallel-sided at about their mid-length, tapering to a short blunt point posteriorly. Attention has already been drawn above to the narrow and intrusive nature of the nasal branch of the premaxilla which reduces the length of contact between the nasal and the maxilla to a short, or sometimes extremely short, distance—though this reduction is not very marked in the type of *poecilotis*, shown in the figure. The posterior part of the sagittal crest, joining the broad, sharp supraoccipital crest in a T, is always well-developed; anterior of this there is sometimes a low continuation across the main body of the cranium even in females. The orbital ring is never complete. The bullae are fairly large, the exterior chamber occupying a quarter or less of the whole. The post-dental palate is short and wide; the mesopterygoid fossa also broad and open, the hamulars curved and sharply pointed, the external wings of the pterygoids well-developed. The main palate itself is short and broad, its posterior margin shallow open curves, not narrow notches as in typical *Felis*.

The mandible is strongly built, the rami deep, sharply upcurved anteriorly, the posterior blade deeply excavated and ridged to accommodate powerful muscles. The coronoid process is tall and narrow; the angular process short and blunt, incurving.

The dentition is powerful. The cheekteeth are $\frac{2 \cdot 1}{2 \cdot 1}$, p^1 and p^2 being normally lacking, though the latter may exceptionally be developed. With the loss of these teeth the jaw has become shortened and the distance between the back of the canine and the front of p^3 is unusually short. There is, nevertheless, a clear, if narrow, post-canine gap. Both upper and lower carnassials are large; p^3 has a small anterior as well as a posterior cusp but it is very often worn away and undetectable. m^1 is not only very small but transversely orientated and bears against the posterior face of m_1.

Habits. Some observations of the habits of caracals in captivity have been recorded but not much is postively known of their very secretive lives in the wild. Without question they are solitary animals associating in the adult state only for brief periods of courtship and mating. Even the nature of their nocturnal or breeding shelters is not clearly known. For this purpose they certainly take advantage of natural caves, fissures in rocks or cavities amongst boulders; but relatively little country providing refuges of this kind exists in West Africa, and though caracals are very good climbers and no doubt often rest and possibly sleep in trees such locations are wholly unsuited to raising a family and it seems probable that holes in the ground, originally excavated by other animals, are most commonly resorted to as homes.

It is obvious that small to medium-sized mammals and birds form the staple diet; rats, gerbils, hares, dassies, monkeys, young baboons, francolins, guinea-fowl and the like. But these very active cats also kill small antelopes and snatch the fawns of larger ones; Bothma (1965) records the remains of a Grimm's duiker found in stomach contents. Caracals also have a reputation for raiding domestic stock and poultry, and for this reason they are accounted vermin in South Africa. They are such accomplished climbers that they are difficult to fence out. Whether these cats regularly take other kinds of prey than mammals and birds does not appear to have been clearly observed in the field; but Shortridge (1934) mentions that a specimen in an Asiatic zoo killed and partly devoured a cobra that had entered its cage. As in other carnivores, a certain amount of vegetable food is taken; Bothma (1965) notes that in South Africa grapes were found in a stomach, and a small quantity of green grass.

Caracals may be on the move at night but chiefly hunt by day. Two methods of capturing prey are employed: running it down or leaping upon it by surprise, a method that must most especially be used, of course, for birds. With regard to the former, the caracal has some reputation for speed over short distances, though in this it can hardly be in the same class as the cheetah. Indeed, with its not particularly long, rather solidly built legs it is difficult to see how it could establish itself as an outstanding runner; yet, nevertheless, it was up till recent times tamed and kept by Indian princes for the hunting and capture of small game, and Vigne (1842: 42) who witnessed such hunts considered that its speed "was quicker in proportion than that of the chita". The kill in the case of larger animals is made by a bite in the neck severing the jugular vein.

The caracal's real ability, however, lies in its leaping capacity, its powerfully built hindquarters enabling it to make jumps of surprising range. These are most spectacularly performed in the killing of birds, the caracal making a standing jump of as much as a couple of metres clear into the air to bring down its victim with a clap between its two front paws. Almost every detailed account of this animal refers to the statement attributed to Blyth, the prime mid-19th century authority on Asiatic mammals (original reference not traced), that Indian potentates customarily pitted their tame caracals against one another, wagering on the number of birds that would be killed by each when the competing animals were allowed to leap into a flock of feeding pigeons. A skilful caracal could knock down nearly a dozen on the ground and in the air before the remainder could make their escape. This deliberate act of "sport" with its resultant fluttering confusion must with little doubt be the true origin of the expression to "put the cat amongst the pigeons"—a saying that has, however, somewhat unaccountably come into common use only in very recent years.

The habit of stalking and leaping upon a flock of birds is illustrated by an experience of the late J. T. Davey (personal communication). While he was travelling in a lorry in northern Nigeria in the early morning the driver sighted a flock of guinea-fowl in the road ahead and, as the custom is in such circumstances, accelerated rapidly in the hope of killing one or two. At that moment a fully-grown caracal leapt from the grass at the roadside and seized a bird, with the consequence that both it and the guinea-fowl were immediately killed by impact with the vehicle. Either the animal's concentration upon its prey must have been so intense as to render it unaware of the clatter of the approaching lorry, or it failed to connect such a noise with danger. A young caracal's attitude towards motor-cars was noted by the same observer on another occasion. When a caracal cub emerging from the bush first sighted his car parked at the side of the road it hastily hid behind a tree, from which position it played "peep-bo" for about ten minutes, repeatedly peering cautiously round the edge of the bole and withdrawing again until it was satisfied that no danger existed, when it came out into the open, examined the vehicle and finally trotted off.

Most cats are of an independent nature but the caracal has a stern aloofness of look and bearing that sets it apart even from the others. There is no doubt that it is not only very self-sufficient but also of an extremely fierce disposition, becoming a formidable antagonist if cornered. Some authors, indeed, flatly assert that it is quite untameable; but though this may often be the case it is not always so; for animals, as humans, differ in their temperaments and adaptability and, apart from caracals formerly habitually domesticated in India, there are more modern well-authenticated cases of complete taming (*e.g.* Petzsch, 1939). In its natural surroundings the caracal is one of the most briskly active and nimble of cats, with its short bursts of high speed sprinting, its prodigious leaps and its facile climbing. So powerful is it in the last that, like the much bigger leopard, it is said by Roberts (1951) to carry its kill up into the forks of a tree. There does not appear to be much range of vocalisation beyond alarm notes consisting of a low growl, that sometimes amounts to little more than a hard outward breathing, and the usual feline hissing. Kralik (1967) noted, however, that if a male and female are kept in adjacent cages they communicate with each other by "peculiar barking signals".

Observations on breeding and the raising of young in captive animals have been recorded by Kralik (1967), Krishne Gowda (1967) and Cade (1968). These differ slightly in some of their findings but present the following general picture. Coupling according to Kralik is carried out at night, but Cade says the act is performed several times a day, the male gripping the female in the back of the neck with his teeth. There is some preliminary play, and coition lasts for about 10 minutes. The period of gestation has not been determined with great accuracy but appears to be between 69 and 78 days, the former of these probably being more nearly correct. As the time of parturition approaches the female eats more and at length prepares a nest for herself of hair and feathers obtained from her prey; but she does not feed on the final day of her pregnancy. The litter may be of from 1 to 6 cubs but 2 or 3 are the commonest numbers. The newly-born young are closely similar to the adults in appearance with the normal sandy or slightly reddish fur, unspotted except perhaps on the belly, black-backed, tufted ears and the usual facial markings. They are born blind, the eyes opening on the 9th to 10th day—though Cade records that in his litter they began to open on the 4th day and were fully open by the 6th. The cubs start to crawl at the age of about 3 days, begin to learn to walk as soon as their eyes are functional about the 9th day, and become steady on their feet at about a fortnight from birth. A week later they regularly leave the nest of their own accord and start learning to chase moving objects; and when a month old they can run fairly rapidly. However, at this time they are still suckling though just learning to take solid food. They eat meat regularly at about 1½ months and are weaned about a month later. During babyhood they indulge in lively play. What happens in the wild state is quite unknown; but in captivity if the male is near and unrestrained he at once attacks and devours the newly-born cubs; and unless she has an atmosphere of quiet security free of all disturbance the female also may eat her young, even up to a couple of weeks after birth (Petzsch, 1939). Krishne Gowda's pair of adults produced a second litter 7 months after the first; but Petzsch records an interval between births of just over 3 months. According to the dates given by Krishne Gowda his caracals bred at the age of little more than 6 months; but Cade found, from his own and communicated records, that females can be expected to become sexually mature at about 2 years old. As for longevity, Flower (1931) cites a pair of caracals each of which attained an age of between 16 and 17 years in the Dublin zoo, though the normal expectancy of life in captivity is more usually of the order of 8 or 9 years.

Taxonomy. There is no question concerning the validity of *caracal* as a species, it being amply different both externally and cranially to distinguish it clearly at this level from all other felines. Subspeciation is, however, another matter. The variations in colour found amongst study specimens have inevitably given rise to the erection of a number of presumed races; but the relatively few skins that exist from any one locality give little or no idea of what might be regarded as a normal range of variation within a single population. This does not apply solely to West Africa; Ognev (1962), indeed, drew attention to the fact that the material at present available in collections was extremely poor and did not permit the drawing of any conclusions. The trouble starts, as so often, with the proper determination of the nominate race. In this case there are two contenders for that position: Schreber's animal from South Africa and

Müller's from the opposite end of the continent, Algeria (*vide* the synonymy above). It is difficult to say, therefore, how or how much any suggested forms differ from that which might be regarded as the typical race.

Only one race has been ascribed to West Africa, *poecilotis*. All other named forms concern either northern or southern Africa except one, *nubicus* (J. B. Fischer, 1829) which, from its name alone, must be assumed to have its origin in or near the Nubian Desert, Sudan. Fischer's diagnosis is without any value whatsoever. As far as West African specimens are concerned there appear to be, from the 7 skins available, two extremes of colour, at one end very red, at the other only slightly so, these being basically more buffy-grey, less warm in tone. The two categories, however, do not appear to relate to particular vegetation zones. Considering the greyer material first, this includes the type of *poecilotis* from Mount Baguezan, in the Subdesert, and a skin reputedly from Kode, 24 km north-west of Lau on the Benue (Nigeria), situated in the Sudan zone, but from its history and appearance quite possibly bought in a local market. This, a poor specimen, is very little darker or different from Thomas & Hinton's "desert-coloured form", the ears perhaps a shade less silvered. There is also one of two skins purchased in Kano market (No. 71.758) which, though belonging to this category, is very noticeably darker than the others, appreciably different, in fact, from any of the rest by reason of a plentiful admixture in the pelage of bristles with much longer black tips, giving a deeper greying to the basic buff. The blackening is extended onto the upper surface of the tail. It resembles skins not only from Sudan but from Ethiopia and Algeria as well; and though it might be local it could just as easily have travelled across the desert by one of the many camel trains which regularly come to Kano market.

The remaining 4 skins of warmer tone come from Gambia (locality unspecified but possibly Guinea woodland), Gambaga (Ghana, Sudan woodland), Lake Chad (ex-Zoo, almost certainly Sahel woodland) and a second skin from Kano market (No. 71.757, real provenance uncertain). These are all fundamentally of similar colouring, contrasting in their red tone, to a greater or lesser degree, with those dealt with in the previous paragraph, being, moreover, essentially different from anything else in the collection. They vary amongst themselves both in the intensity of their redness and in the amount of "frosting" on the coat brought about by white subterminal regions to the bristle-hairs. The least intense in its redness is the Kano skin; the Gambia skin is several shades redder and also has the greatest amount of frosting. The remaining two skins are both of a richly warm colouring, differing from each other only in the somewhat greater frosting to the Lake Chad pelage.

The 7 West African skins all differ from each other in some degree. At the very minimum it would seem admissable to allot them to four different forms. But in view of the poor quality and incompleteness of the material available, the doubtful provenance of most of the specimens and our virtual ignorance of normal population variance the drawbacks of adding further burdens and uncertainties to the nomenclature seem to outweigh any possible slight advantage. Nominal differentiation of these putative races is therefore postponed till further, better documented and more complete collecting has adequately demonstrated that the creation of new names is justifiable and beneficial.

Table 25: Numerical data for *Felis caracal*

	poecilotis, type	Nigeria specimen
Vegetation	Subdesert	?
Number in mean	1	1
Condylobasal length	105·7	113·0
Basilar length	94·3	101·6
Palatilar length	43·4	42·8
Zygomatic breadth	81·4	83·6
Upper cheekteeth breadth	49·4	50·5
Nasals, length	33·8	—
Interorbital breadth	22·0	23·5
Postorbital constriction	30·0	27·7
Braincase breadth	49·9	50·3
Toothrow (c—m^1)	37·1	39·4
p^4 length	15·1	14·4
m^1 breadth	4·2	(4·6)
m_1 length	11·5	—
Head & body	594	—
Tail	254	—
Hindfoot	155	—
Ear	76	—
RATIOS (per cent)		
Tail/head & body	43	—
Zygom. br./condylob. l.	77	74
Braincase/condylob. l.	47	45
Braincase/zygom. br.	61	60
Palatilar l./condylob. l.	41	38
Interorb./postorb.	73	85
p^4/c—m^1	40·7	36·6

Subgenus **LEPTAILURUS** Severtzov, 1858

Serval Cats

Taxonomy. This is another subgenus most often now considered to be monospecific though at one time it was commonly held to comprise two species. This latter view was due to there being two apparently distinct pattern forms, one, the typical serval cat (*serval* Schreber), in which the black spots are relatively large and relatively few, and the other, commonly called the servaline cat (*brachyura* Wagner, *servalina* Ogilby) in which the maculation consists of innumerable very small spots. Disbelief in the specific disunity of the two forms was expressed by Elliot as long ago as 1883; but the controversy really centres round Pocock who in 1907, having gone into the matter at some length, at first accepted that the two forms represented separate species. Ten years later (1917b) he had become convinced that this was not so. This change of view was brought about by a statement made at a meeting of the Zoological Society of London in 1915 (*vide* Proceedings: 154) to the effect that in Sierra Leone kittens of the two diverse forms had been brought by a local African to the speaker "almost certainly from the same litter", thus showing the pattern to be dimorphic in a single species. J. A. Allen (1924) was, with justification, somewhat scathing about the scientific value of this "evidence", which was in fact nothing more than a supposition. Nevertheless, Pocock retained the same monospecific standpoint, and in what was practically his last paper dealing with the Felidae (1944: 696 f.n.) asserted that since he had first expressed his conviction of the two forms being but a single species "considerably more evidence in confirmation of that conclusion has come to hand", though he omitted to indicate what this evidence was. It must, however, have been very largely that contained in Pitman (1934) where a specially assembled collection of *Leptailurus* skins is described as showing "every stage of variation in size of spots between the large spots hitherto considered as typical of *serval serval*, and the (almost) pin spot typical of *serval servalina*". Other, less important, notices of the wide variability of maculation have also been published and the synonymy of the two reputed species is now generally unquestioned. The incontrovertible evidence indicated by Pocock himself (1907) as desirable "the occurrence of the two types in the same litter of kittens known to be the progeny of parents resembling each other in pattern" is, however, still not forthcoming.

General description. *Leptailurus* is clearly distinct from all other African members of the genus *Felis* and is only possibly to be confused by the inexperienced with the cheetah (*Acinonyx*) because both, typically, have a pattern of single, smallish, jet-black spots on a sandy ground. It is this coloration and pattern that immediately distinguishes the serval from the other West African felines, the wild cat, the sand cat, the caracal and the golden cat. Other quite characteristic features are found in the very prominent ears. These are very tall and large, oval, not triangular, in shape with broadly rounded apices, and sited unusually close together at the top of the head; and on their backs their distal half is black enclosing a somewhat elongated white patch. The head is small for the general size of the animal, the legs exceptionally long, and the tail short, only a quarter to a third of the head & body measurement. The skull is very similar to that of *Caracal* including, in a number of instances, the long, narrow intrusion of the premaxilla between the maxilla and the nasal. The bullae are generally rather larger; but the most immediately observable difference between the two skulls is the presence in *Leptailurus* of a small anterior premolar, in the upper jaw very largely filling the space between the canine and p^3.

Distribution. The subgenus is solely African in its distribution, ranging from Algeria to southern Africa, now to only about 30°S. though once much nearer the Cape.

FELIS SERVAL Schreber Serval Cat

Felis serval Schreber, 1776, *Die Säugethiere in Abbildungen* . . ., pl. 108; 1777, text **3**: 407 and 587. Cape of Good Hope. This name is supposed to be derived from the Portuguese *lobo-cerval*, a lynx.

Felis capensis J. R. Forster, 1781, *Phil. Trans. R. Soc.* **71**: 4, pl. 1. Cape of Good Hope.

Felis galeopardus Desmarest, 1820, *Encyclopédie Méthodique . . . Mammalogie*, **1**: 227. No type locality.

This was based on "Le Serval" of F. Cuvier (1818); J. A. Allen (1924: 269) found it to be indeterminable and hence unavailable either as a valid species or as a prior name for *senegalensis* Lesson, as has sometimes been argued. The term was coined from *gale* the Greek for a weasel, and the Latin *pardus* leopard, referring to its similarly spotted coat but relatively insignificant size.

Felis senegalensis Lesson, 1839, *Magasin Zool. Paris* (2), classe 1 Mammifères, **1**: pl. 10 and two pages of text. Banks of the River Senegal. Preoccupied by *Felis leo senegalensis* Meyer, 1826.

Felis servalina Ogilby, 1839, *Proc. zool. Soc. Lond.*: 94. Sierra Leone. Preoccupied by *Felis servalina* Jardine, 1834, = *Felis libyca ornata* Gray, 1830, (*vide* Cabrera, 1910: 426). This name is a diminutive of *serval* given with reference to the smaller spots.

Felis brachyura J. A. Wagner, 1841, in Schreber's *Die Säugethiere*, Supplementband **2**: 547. A substitute for *Felis servalina* Ogilby preoccupied by *F. servalina* Jardine. The derivation of this name is from the Greek words *brachys* short and *oura* tail.

Felis ogilbyi Schinz, 1844, *Synopsis Mammalium*, **1**: 469. Sierra Leone. A renaming of *Felis servalina* Ogilby, 1839, preoccupied.

Felis serval pococki Cabrera, 1910, *Boln R. Soc. esp. Hist. nat.* **10**: 427. Senegal. A replacement for *Felis senegalensis* Lesson, preoccupied. This was called after R. I. Pocock who had first demonstrated the true position of Lesson's naming.

Felis (*Serval*) *togoensis* Matchie, 1893, *Sber. Ges. naturf. Freunde Berl.*: 109–110. Bismarckburg, Togo.

Distribution and general. Since there is only a single species the distribution of the serval is that already broadly indicated for the genus, that is to say, it is wholly African, ranging in the north from some of the Mediterranean countries to southern Africa, where it once occurred not far from Capetown itself but has now been forced to withdraw much further north. At the other extreme of its range it is also losing ground; but it may still be encountered in the northern parts of Tunisia (Gouttenoire, 1954), and it was, at least until recently, to be found in Algeria. The species is known to exist in all West African territories, inhabiting all zones from the Sahel to the closed forest, being recorded even from a coastal island; and it ascends to moderate altitudes into the mixture of forest, open woodland and pure grass characteristic of hilly parts of the region at about 1000–1500 metres. The serval appears to avoid the desert; indeed, it demands two conditions, dense cover and fair proximity to water. This means that while it may be at home almost anywhere in the forest or Guinea zones, in the drier sorts of grass-woodland, the Sudan and the Sahel, it finds suitably dense vegetation only near the banks of rivers or marshes where there is sufficient tellurian moisture to support lusher growth. Nevertheless, as this is a predominantly nocturnal animal it will, of course, in order to hunt emerge into scantier vegetation under cover of dusk or darkness.

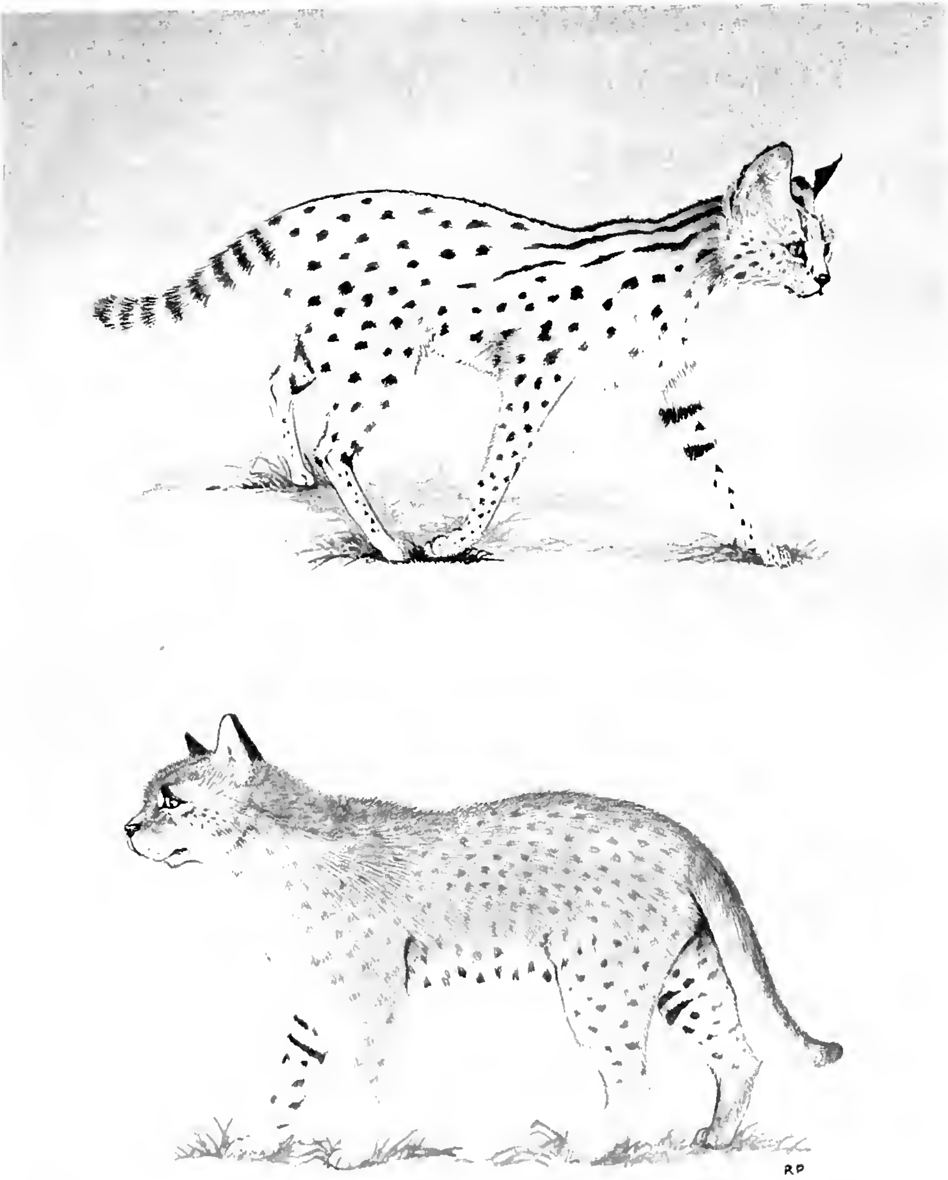
The serval is a not uncommon animal; there are, in fact, 34 West African skins and 12 skulls in the British Museum as contrasted with only 7 caracal specimens. Yet as it is only exceptionally on the move during the day, and then mostly skulking in undergrowth, it is very rarely seen save in car headlights or by night hunters with powerful lamps. Of the British Museum material, 9 specimens come from Senegal, including Thiès and Bakel; 9 from Sierra Leone, including Makali, Makeni, Karina, Nerekoro, Bonthe, Gberia Timbako and the River Moa; a single skin from Liberia, 80 km inland of Monrovia; 5 from Ghana, including Ejura and a site 48 km west of Juaso; a skin from an unnamed locality in Togo; 8 specimens, but with only 2 skulls, from Nigeria between nearly the coast and Lake Chad—Gombe River, Zo 32 km north-east of

Lau, 48 km east of Bauchi, 20 km south-west of Jalingo, Petico 24 km north-west of Lau, near Sapele, and an unspecified locality at Lake Chad (ex-Zoo); two examples from upper Cameroun at Njawbaw and Olulu both situated in Assumbo north of Mamfe; and one skin from Fort Lamy. It is also reliably reported (in personal communications) by A. J. Hopson as occasional near Lake Chad, one having been killed in a compound at Malamfatori; by the late J. T. Davey as common in Macina (Mali); and G. S. Child as occurring in the Borgu Game Reserve (west Nigeria). Published records are: the environs of Timbuctu (Zimara, 1935); and three places in Portuguese Guinea, Catió (Frade, 1949), Contubo-el and Pitche (Monard, 1940). This is an extremely wide range and varied habitat, from mangrove and coastal scrub (Bonthe), or dense high forest (Sapele), to widely open Sahel-type woodland not very far from the Sub-desert though in swampy conditions near the Niger or a lake. However, the position with this apparently abundant London study material is not very satisfactory since only 6 skins are matched with adult skulls; and not a single skin carries any field measurement—a point held in common with the vast majority of British Museum specimens from anywhere in Africa, there being, all told, only some 3 or 4 bearing such data. A very high percentage, in fact, appear to have been purchased from African hunters. Only 7 specimens have the sex indicated; and a quarter have no precise locality, and, indeed, even the broadly named provenance of some of the older material is suspect. Such of the British Museum specimens as can be determined show that 3 specimens come from the Sahel zone, 5 from the Sudan, 11 from the Guinea, 6 from the forest, 1 from mangrove and scrub, and 1 from mountain forest and grass.

Description. Because of the existence of very diverse types of maculation in this species the account which follows deals initially with points of morphology and those few markings which are completely common to the various forms, leaving description of the pelage and its distinctive patterns to the end. The serval (Plate 11) is a much more elegant cat than the caracal being more slimly built, narrow from side to side, and with longer far more slender limbs, which differ from the other species also in that the forelegs are longer than the hindlegs. Although it is of the same order of size as *caracal*—both being in the category of "medium-sized cats"—and actually stands higher at the shoulder, that is to say between 500 and 550 mm as compared with 400 to 450 mm, its weight, at 10 to 13·5 kg, tends to average out at rather less. Like *caracal, serval* is somewhat more heavily built in the hindquarters than in front, and the long slender neck and disproportionately small head serve to exaggerate this inbalance. In comportment the serval is a fine upstanding, alert cat, not one given to cautious slinking; and even when it sits up on its hindquarters it holds itself erect and looks very tall. In this position the two parallel black bars on the inside of the upper end of each foreleg are very conspicuous; and, also from the front, a narrow black line or row of spots can be seen forming a "necklace" across the lowest part of the throat—though this is mostly very obscure in the small-spotted forms.

The front view of the serval, however, is dominated by the remarkable upstanding ears which are so large that they measure from base to summit almost as much as the distance from the base to the large rhinarium. Apart from their size they have several other notable features. They are set unusually high on the head and when actively

PLATE II



Serval *Felis serval* African Golden Cat *Felis aurata*

pricked are brought exceptionally close together. They are ovoid shell-like in form, the pinnae being deeply concave, broad at the base with the margins rising with very gradual narrowing to a broad arc at the apex. There may be a slight apical fringe but no tuft. The front aspect carries a dense cover of white hairs; the back is quite characteristic with a black distal half wholly or partially transversely divided by a broad pure white patch. This very noticeable mark forms one of the most immediately conspicuous features of the living animal seen from the rear or the side. Facial markings consist of a dark patch at the inner corner of the eye reaching some way towards the rhinarium; and a solid or broken line, generally much fainter, from the top of each eye to the crown. There is a broad white streak under the eye, and a shorter white patch above towards the inner angle. There is an area of white, sometimes considerable, to the side of the rhinarium continuing narrowly along the upper lip and spreading somewhat onto the cheek posteriorly. The lower lips and chin are wholly white.

Irrespective of the size of maculation on the back and flanks the outsides of the upper parts of both fore and hindlimbs are prominently marked with large black spots, which abruptly diminish into small black spots below. The inner faces of the limbs are white, mostly black-spotted, the foreleg with two very conspicuous black bars. The soles of the feet are densely clad between the pads with longish, deep blackish-brown hairs; the claws are fully retractile, that of the pollex being appreciably larger than the rest. The interdigital webs on the forefeet are fairly extensive reaching to about the bases of the claws. On the hindfeet they are somewhat narrower. The serval is one of the short-tailed cats, the tail measuring little more than a third of the head & body length. It is of the common feline subcylindrical form, of the basic pelage colour with black rings, or partial rings since they do not always join below. There are generally about 6 or 7 of these, and the tip is always black. There is also, very clear in some specimens, obscure in others, a black line, continuous or interrupted, running down the upper side of the tail to about the second ring from the end. In the eye, the iris is golden, the round pupil contracts to a broad upright oval.

Turning now to the pelage, this is fairly soft and of moderate length, its composition of the usual three elements: very abundant, long, fine underfur, mostly very pale buff with coloured tips; stoutish bristle-hairs of terete section, either all black or black-tipped with or without a subapical band of gold; and sub-bristles with a fine petiole and expanded flat-sectioned distal region which is mostly golden-yellow with a black tip. The lengths of these components vary with different specimens but generally fall within the following limits: underfur 20 to 26 mm; bristle-hairs 27 to 31 mm; sub-bristles 27 to 35 mm, the flat blade measuring some 7 or 8 mm. The black spots are composed of similar elements which from pale bases become distally progressively darker, passing through sepia to black.

In large-spotted, "serval", specimens there is a good deal of variation in pelage colour in animals from different areas or sometimes from the same or closely proximate localities. The general ground-colour is mostly some shade of sandy-buff, a little lighter, a little darker; but skins from the closed forest exhibit a much richer red colour. Whatever the colour it is almost invariably a trifle more intense down the spine, and usually a little paler on the flanks. On this ground-colour is imposed, in the "serval" form, a bold black pattern of continuous lines and independent spots, variations in the size, shape and number of both of which have been the source of subspecific naming.

The longitudinal pattern of continuous, or almost continuous, lines follows the following basic scheme. It starts at the back of the head as four slender lines; these all fan out over the back of the neck, the two inner ones remaining fine, the two outer becoming rather broader and bolder. At the base of the neck the divergence continues rather more sharply, the inner pair of lines becoming as bold as the outer. The latter curve round the shoulders toward the flanks where they peter out as continuous stripes and become the flank spots; the middle pair also break up into the innermost row of dorsal spots at about the same level. Before they do so a third pair of narrow lines appears between them, sometimes with the faint indication of a central spinal line, and these after slight initial divergence continue back in sub-parallel fashion and often slightly broken almost to the root of the tail, with the faint medial line between them soon becoming equally pronounced and sometimes itself closely dividing into two posteriorly. Over the main part of the body, either side of the medial striation, is a pattern of roundish, oval or oblong spots not very precisely disposed in longitudinal lines. So far as they can with any accuracy be determined there are at the posterior end of the body commonly about 6 such rows either side of the spinal lines; but there may be one more or less. All this pattern, in the matter of continuity of the stripes and, most especially, the size, shape and number of spots, is subject to wide variation, though its main features are always clearly observable. As for the underside, the chin is white with a chain of small spots across it posteriorly; the throat buffish, mostly also with a chain of spots, sometimes confluent, across it; the chest and belly white, or to a greater or less extent suffused with buff, well-covered with long and loose hair, and mostly, but not invariably, marked with rather obscure dark spots.

In the small-spotted, "servaline", forms the whole dorsal ground-colour becomes dulled so that there is little or nothing of the bright buffy or sandy hue of the typical serval. This seems to be due to a more general spread of dark pigment, which instead of being intensely concentrated in small areas, giving black spots on a pale ground, diffuses throughout a high proportion of the hairs of the back so that the underfur together with the petioles of the sub-bristles become a dull sepia instead of whitish or pale buff. Extralimitally, the fur may even assume a grey tone rather than buffish. The size of the black spots is very much reduced and their number vastly increased; but in at least one known example the reduction is carried to the extreme of complete disppearance of any dorsal maculation whatsoever. In all cases any trace of the distinctive pattern of continuous lines so characteristic of the large-spotted animals completely, or almost completely, vanishes. The underparts, however, together with both inner and outer aspects of the limbs remain much the same in both phases.

This slight suffusion of the dorsal pelage with dark pigment is a long way from intense general melanism—which, as in other felines, is not uncommon in this species too, though no specimen has so far been recorded from West Africa.

Skull (figs. 56 and 57). In size and overall appearance this is very similar to that of the caracal, though the profile does not descend so abruptly over the nasals. Comparison in this lateral aspect (e.g. in figs. 54 and 56) clearly shows that the zygomatic arch is considerably flatter in its curvature; that the suture between the jugal and the maxillary process is more nearly parallel to the line of the teeth instead of ascending sharply; and that the anterior edge of the latter bone projects further forward in the serval and overhangs the infraorbital foramen. The premaxilla intrudes narrowly between the maxilla and the nasal as it does in *caracal*, but on the average not quite so far as in that species though in some young skulls it nearly reaches the long forward angle of the frontal. The sagittal crest is as in *Caracal*, developed only posteriorly; but differences to be observed in the dorsal aspect are that the serval skull is narrower in that the zygomatic width is relatively rather less; the difference between the interorbital and postorbital widths is more marked, the former being somewhat less than in *caracal*, the latter appreciably more, this last according the whole braincase a rather larger appearance. One Sierra Leone skull (No. 50.2042 from the coastal scrub of Sherbro Island) affords a striking exception to the general run in this character: in it the postorbital processes are much longer than usual, there are well-developed postorbital ridges that markedly overhang a postorbital constriction that measures only 110 per cent of the interorbital width instead of the usual 160 per cent. This skull is in all other respects typical and is accompanied by a normal large-spotted serval skin.

In the palatal view the bullae in *serval*, though somewhat variable in size in different specimens, are in general clearly larger than in *caracal*; the mesopterygoid fossa is markedly wider—14 mm or more as compared with 12 mm; and the lateral wings of the pterygoids are broader. In the mandible the coronoid process is not so tall; the condylar process less strongly built; the rami are not quite so deep, the jaw thus giving the impression of being rather less powerful. Anteriorly, the rami do not curve up quite so steeply; and this together with the lesser angle of descent of the nasals brings about a rather less blunt rostrum.

The cheekteeth formula is $\frac{3\cdot1}{2\;1}$ there being 3 premolars on each side of the upper jaw instead of 2 as in *caracal*; 30 skulls examined furnished only a single exception to this, one young skull having the anterior premolar lacking on one side. The carnassials both above and below are noticeably smaller in *serval* than in *caracal* and *aurata*, and the toothrow, in spite of the extra premolar, is shorter; p^3 has both a posterior and anterior cusp, the latter mostly quite distinct but sometimes rather obscure. Most of these points of comparison of the skulls of the species are brought out in the tables on pages 411, 423 and 436, in so far as it is possible to judge from such limited data as the few available specimens provide.

Habits. The serval is one of those animals which are rarely seen and whose habits have in a large measure been deduced from occasional and sometimes fleeting observations. This is mainly due to the species being nocturnally active; and even if these cats are awake and alert during daylight they are more often than not hidden from observation by the density of the undergrowth in which they take cover. Even though they may possibly start their nightly round of foraging before darkness has properly set in they rarely seem to emerge into really open country where they could be easily seen. The difficult task of making a set field study of the life of these secretive animals in the wild has not yet been attempted; and though servals have commonly been kept in captivity very little of a detailed nature has been published relating to them.

The precise nature of the ground vegetation in which these cats find shelter is immaterial, whether it be forest undergrowth, grassy tangle or palustrine reeds; but all observers are agreed that the proximity of water seems a desirable factor; and it is of course true that it is near water that the ground cover is generally most dense, especially in the drier vegetation belts. If necessary, the serval shows itself to be an efficient climber but it is predominantly a terrestrial animal. For breeding purposes it resorts to holes, not made by itself since its digging powers are nil but those originally excavated by aardvarks or porcupines, or at the bases of termitaries, or in hollow logs, or amongst rocks. Whether such places as these are used at other times as ordinary day to day refuges or whether these animals are normally content to sleep curled up in ground vegetation has not been determined.

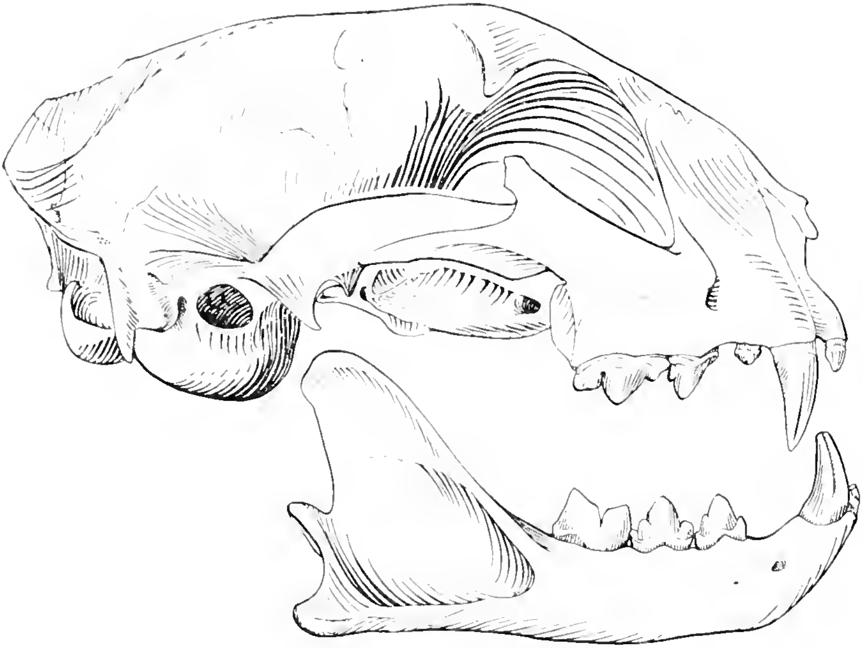


Fig. 56. *Felis serval*: skull, B.M. No. 99.10.23.3, ♂, × 1; lateral view

Since hunting or at least the greater part of it is carried out at night good nocturnal vision is indicated as in most cats; but from the enormous external ears backed by unusually large bullae it may be inferred that hearing also plays a prominent role in this animal's activities. The prey sought after is that common to all these small and medium sized cats: rodents of all kinds, including the larger ones such as the cutting-grass (*Thryonomys*) and the giant rat (*Cricetomys*), squirrels and hares. The smaller

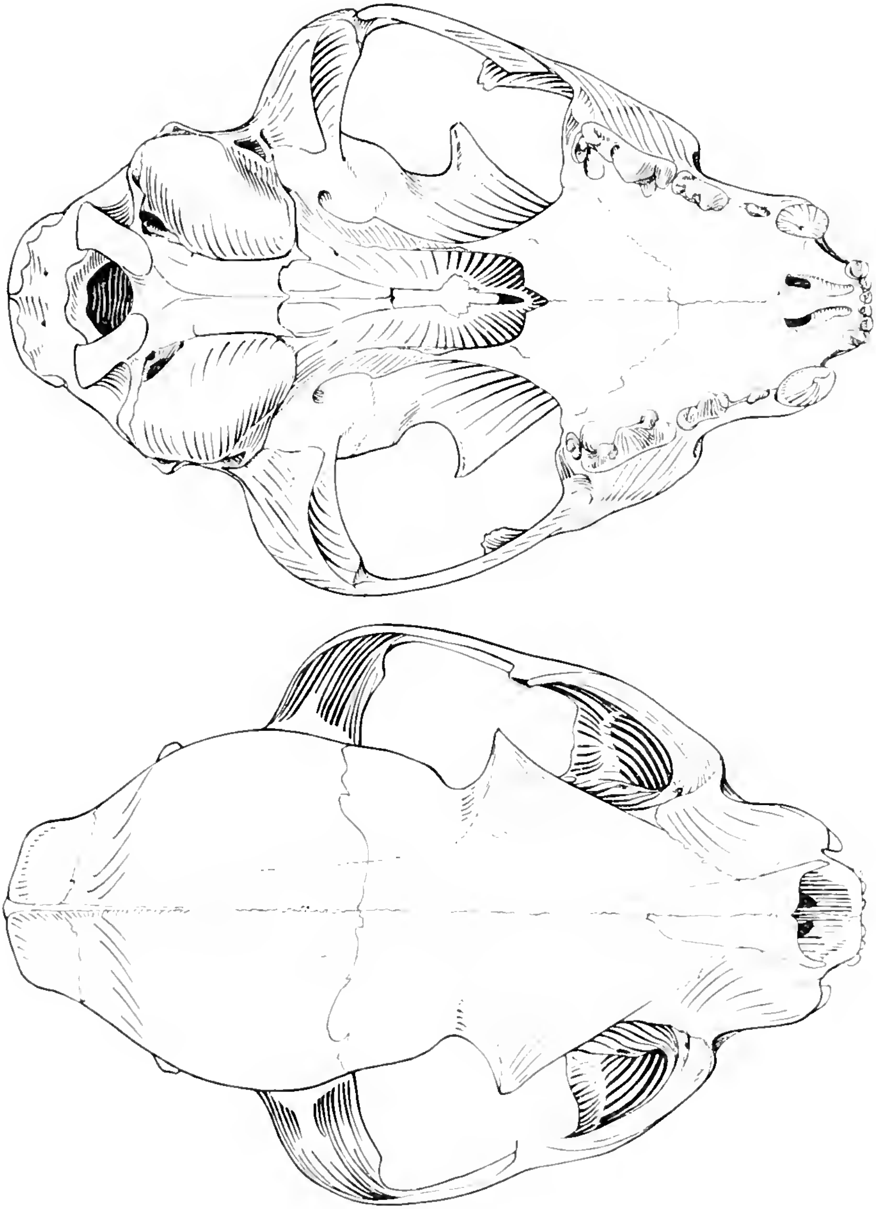


Fig. 57. *Felis serval*: skull, B.M. No. 99.10.23.3, ♂, × 1; palatal & dorsal views

antelopes are also taken and ground-nesting birds. Doubtless near the water's edge these predators frequently come across resting birds of the larger kinds: herons of various sorts, storks and so forth. Whether servals eat reptiles and amphibians does not appear to have been clearly recorded; but it is possible that the preference for the neighbourhood of streams may have some connexion with fishing since it is known that servals are not afraid of water or of getting their feet wet (Lousada, 1956), and one Kenya specimen in the British Museum, though shot at some distance from the river, was nevertheless found to have its stomach full of crabs.

Like other cats servals prowl at a slow pace; but when they are purposefully on the move along a road or a path they proceed at a trot. In view of their exceptionally long legs one would suppose them to be capable of high speeds and to employ this facility in the running down of prey in the manner of a cheetah. Yet nobody seems to have witnessed such a chase, or at any rate to have furnished a first-hand account of it. Such pursuit postulates not only open country but, in a nocturnal animal, a sufficiency of light to be able to follow the course of fast-moving prey at some distance. However, unconnected with any specific hunting activities, Lousada (1956) records of young captive animals that they could run very fast and that when, as a consequence, out of breath they panted like a dog. Without doubt the commonest method of securing a meal is by pouncing suddenly upon the victim and biting it in the neck. Such leaps are often made from considerable distances, for the serval's powers of jumping are as great as those of the caracal, and it has been said, like that animal, to kill birds by springing at them in mid-air. Servals, in common with many other carnivores, are held responsible for raids upon poultry yards and other farm stock of the smaller kinds. Certainly they have been killed at night in compounds in suspicious circumstances.

As with the majority of animals, inherent diversities of temperament influence the response of different individuals to attempts at taming; but if taken young enough the majority of servals would seem to respond excellently to domestication and become interesting and sometimes very affectionate pets which will follow their owners like dogs and even display complete confidence in strangers. They are extremely playful, amusing themselves for long periods with each other, or some such toy as a ball, or even their own tails; and they are clean about the house, soon learning to go outside to defaecate, for which purpose they select little natural hollows in the soil (Lousada, 1956). They have, however, one very great disadvantage. Their playfulness and great activity combined with their astonishing powers of leaping—not only onto chairs but onto tables, the tops of the highest cupboards and onto curtains as well—lead them into deeds of unintentional destruction that is difficult to tolerate in the average home. Servals utter several different sounds. In contentment they purr like an ordinary domestic cat only more loudly, and this they will happily continue for some time while being nursed and stroked. An anxiety call is an oft-repeated, rather high-pitched and slightly raucous miaow, which has been expressed as a nasal "*mwa-mwa*" slowly reiterated six or eight times. There is also a kind of complaining moan ending with a low purring growl which, uttered as a warning note in the presence of food, often becomes not so much a snarl as a loud hiss.

Apart from kittens having from time to time been taken from aardvark holes no other information relating to breeding in the wild is available and all that is known of this aspect of their lives is derived from observations on captive animals. The species, indeed, takes readily to captivity and breeds freely, the young being easy to rear. Accounts have been furnished for Basle by Wackernagel, 1968, and for Jersey by Bloxam, 1969 and Mallinson, 1970. The first of these observers records that the female may come into season several times during a single month, the oestrus period mostly lasting only for a day though occasionally extending to 3 or 4 days; and in one case copulation was repeated over a stretch of 10 days. The period of gestation lies between 66 and 77 days, with a mean of about 74 days. At Basle 47 young were produced by 3 females in 20 litters, the sexes of these being about even; at Jersey a single pair produced 6 litters in 4 years, totalling 13 kittens, of which at least 11 were females. The range of litter size is from 1–4, 2 or 3 being the commonest numbers at a birth. There may, thus, be more than one litter in a year, the shortest period recorded between births being 184 days. The newly-born young have not been described, but they soon exhibit a pelage closely resembling that of the parents except for being rather looser in texture. Wackernagel found the eyes to open on the 9th day; but in Jersey (Mallinson) a kitten was noted to open one eye on the 12th day and both on the 13th. The permanent dentition is fully acquired by the time the kittens are just over 6 months old. However, they will begin to take solid food from an early age, about 2 to 3 weeks old. In zoos the young babies can be given sophisticated diets; but those faced with the bringing up of a serval kitten under less ideal circumstances and when there is no domestic cat in milk available may care to know that Lousada (1956) successfully reared one on unboiled milk strongly laced with cod-liver oil; from an early age scraped beef was given, later changed to minced beef. After a time there is no difficulty since young servals will take a wide variety of commonly available foods. Lousada's animal drank little water, possibly because it remained on milk for a long time. The mother often carries the kittens from place to place in her mouth, and they do not become wholly independent of her until they are about 3 months old. There are no accounts of the young having been killed and eaten by the parents, so commonly recorded of other carnivores. Lousada's young servals attained a shoulder height of 460 mm and a total length, nose to tail, of 1120 mm at the age of 9 months. Servals can live for a long time; a female in the Basle zoo reached an age of nearly 20 years, having her last litter when she was 14 years.

Taxonomy. The question of whether there is one or two species in the genus has already been sufficiently dealt with above. There is very little doubt in the minds of taxonomists today that the small-spotted servaline and the more common large-spotted serval are one and the same animal; and this being so, the name *brachyura* has no specific standing or application other than possibly to designate a small-spotted Sierra Leone form, to which it was originally applied.

The matter of subspecific division is less readily settled. Without question *serval* occurs in quite distinct forms not only as regards pattern but in respect of colour and perhaps size as well, all of which characters could possibly be, and indeed have been, the basis of racial naming. But if, as now generally accepted, two extremes of maculation can occur in a single litter they cannot logically be distinguished by subspecific names since they are merely phasal. In the days when it was believed that the species was straightforwardly dimorphic, occurring in two sharply differentiated forms (Pocock, 1917b) it was legitimate to refer to the serval-phase and the servaline-phase. But it is now known to be polymorphic. As the outcome of a special investigation Pitman (1944) found, and the British Museum specimens go a long way to confirm, that skins "show every stage of variation in size of spots between the large spots hitherto considered typical of *serval serval*, and the (almost) pin spot typical of *serval servalina*". Such differences of maculation are brought about by the specific concentration or random scatter of dark pigment in the dorsal pelage; and this scatter can result in an infinite variety of maculation dependent upon no other factor than genetic chance. It may be recorded here that one skin in the British Museum, No. 47.641 from Karina (Sierra Leone) exhibits no distinguishable dorsal maculation whatsoever, thus carrying the breakdown of pattern to its extreme, hitherto noted only, in *liposticta* Pocock, as affecting the forepart of the back alone.

This being so, there can be no practical value in attaching names to any particular forms of pattern that may come to hand. Their chances of exact repetition or of clear distinction from other forms are equally slender. It may be a matter of descriptive convenience to continue to speak in broad terms of "a large-spotted form" or "a small-spotted form"; but to attempt greater nomenclatural precision based on this character seems to furnish no gain beyond a purely fancied accuracy.

This leaves two factors as the possible basis of a more meaningful racial naming, colour and size. Dealing with the latter first, the amount of study material at present available is quite inadequate to provide dependable data: no body measurements for West Africa exist, and only 7 skulls, 4 of which belong to a single group, the other 3 from scattered localities, only 2 of the whole set being sexed. Certainly 2 skulls, males, give some indication of larger size, with condylobasal lengths of 112·5 mm and 115·5 mm as compared with the mean of 105 mm for Senegal: and zygomatic breadths amounting to 77 per cent and 75 per cent of these lengths in place of the more general 69 per cent. But these are single specimens from the widely diverse localities of Sherbro Island (Sierra Leone) and Togo, and it would be unwise to base deductions on such slender evidence. The former of these, moreover, is that referred to above in the skull section as being remarkable for its exceptional postorbital structure.

As regards colour, there is some evidence that, as might be expected, animals from the forest have a richer, deeper pelage tone. The skin from the dense rain-forest of Sapele (Nigeria), No. 35.2.20.1, is of a rich reddish hue not exhibited by any other British Museum specimen. The nearest approach to it, though not so intense, is No. 50.2042 from the coastal Sherbro Island, referred to in the previous paragraph. The vegetation of this locality, however, is not high forest but mangrove and scrub. Another dark skin, though not so red, is from the moist hilly country of Assumbo to the north of Mamfe, a mixture of forest and grassland. At the other extreme of coloration the palest, buffest, skin, No. 56.225, does not come from the driest zone but from 20 km south-west of Jalingo on the Benue, that is to say from the Doka/Sudan zone border. This is one of 4 skins from the same general areas as this last, covering about 150 km of pretty uniform Sudan woodland which, nevertheless, display clear differences of both colour and maculation. A more closely located set is 3 skins, Nos. 1938.7.25.2 to 4, from about 50 km north of Juaso (Ghana), their biotope recorded as "savannah close to forest edge"; these differ somewhat from each other in colour but this is due in great measure to the variety of maculation which ranges from few large spots in one skin to many of pretty small (but not the smallest) size in another. However, a skin, No. 35.10.22.74, from about 60 km away at Ejura, with almost precisely similar vegetational conditions, has more red in it.

Looking at the skins as a whole there is a wide variety of background colour further complicated by the breakdown of spots and the consequent greater or lesser diffusion of dark pigment. So far as can be gathered from the skins mostly of scattered provenance currently available there is no obvious constancy of colour to be associated with a given locality or set of conditions. The extremes are clearly distinguishable; but there lie in between, even amongst the relatively limited British Museum material, so many forms that to attempt to provide each with a distinctive name is unthinkable, and to furnish a selected few with such labels, as has been done in the past, is pointless. It is therefore recommended that nomenclatural subdivision of the species be avoided.

Table 26: Numerical data for *Felis serval*

	Senegal	Bonthe (Sierra Leone)	Togo	Kenya
Vegetation	Guinea	Scrub	?	
Number in mean	4	1	1	2
Condylobasal length	105·3	112·5	115·5	—
Basilar length	95·8	102·5	105·7	—
Palatilar length	42·7	45·8	47·9	—
Zygomatic breadth	72·9	86·2	86·3	—
Upper cheekteeth breadth	42·4	46·0	48·5	—
Nasals, length	31·5	32·7	33·3	—
Interorbital breadth	20·5	23·0	24·4	—
Postorbital constriction	32·4	25·8	36·0	—
Braincase breadth	48·4	50·0	53·2	—
Toothrow (c—m^1)	35·6	36·5	37·9	—
p^4 length	13·9	12·9	14·8	—
m^1 breadth	4·5	4·5	4·7	—
m_1 length	10·4	9·2	11·3	—
Head & body	—	—	—	756
Tail	—	—	—	274
Hindfoot	—	—	—	178
Ear	—	—	—	82
RATIOS (per cent)				
Tail/head & body	—	—	—	36
Zygom. br./condylob. l.	69	77	75	—
Braincase/condylob. l.	46	44	46	—
Braincase/zygom. br.	66	58	62	—
Palatilar l./condylob. l.	40	40	41	—
Interorb./postorb.	63	89	68	—
p^4/c—m^1	39·0	35·4	39·1	—

Measurements. Those of 6 of the 7 available skulls are given in the table on page 423. These are divided into a Senegal group of 4, mostly from Thiès but one of more doubtful provenance; and 2 exceptionally large specimens are shown separately, one of them of unusual postorbital narrowness. The seventh skull, from Sierra Leone, accords fairly closely with the Senegal group, but being rather younger is slightly smaller. As there are no body measurements recorded for West African specimens the mean of 2 Kenya animals, of skull size corresponding to the Senegal group, is given as a guide.

Subgenus **PROFELIS** Severtzov, 1858

Golden Cats

Distribution and general. This is another subgenus that has an extra-Ethiopian distribution, also to Asia but in this case not as a single widely but continuous ranging species, as *caracal*, but as two distinct and geographically disjoined species, *aurata* Temminck in Africa and *temmincki* Vigors & Horsfield, 1827, in Tibet, southern China, extreme north-east India, Burma, the Indo-Chinese peninsula, Malaya and Sumatra. Pocock (1907: 662) had no doubt of the close relationship of *aurata* to *temmincki* and, further, that the two fell into a natural group together with the central and southern American *Felis* (*Leopardus*) *pardalis* Linnaeus, the ocelot. Despite their present distributional isolation he considered that there was nothing extravagant in claiming this close affinity, dispersion having taken place from an ancient Euro-Asiatic centre across land bridges that formerly connected the continents. These relationships are, of course, at present pure conjecture; but there are, without question, considerable cranial and dental resemblances between the Asiatic and African species, less so with the American. Much the same may be said with regard to external appearance.

Profelis is, especially in Africa, despite a considerable number of skins in museums a very little-known genus. The majority of the African study material has been purchased from local hunters or pelt dealers. It is therefore devoid of skulls, its exact provenance is uncertain, and there is little or no first-hand observation of the animal in the field. The external appearance of the African golden cat is highly variable since it can occur in any of four main varieties of colour and pattern, apart from intermediates. These are, broadly, either golden-brown or sepia-grey, each colour phase with or without a marked pattern of dorsal spots.

Description. There is little possibility of confusion with either of the two other African cats of similar, medium, size (Plates 10 and 11). Apart from differences of pelage pattern the ears are a great deal smaller than in both the serval and caracal, almost wholly black on the back but bluntly pointed and untufted. The fur also displays a unique feature in that the hair on the back of the neck, from just forward of the shoulders to the crown, is orientated forwards. Where the change of direction takes place, at the shoulders, there are two lateral whorls or sometimes a single medial one; and where this contrary-directed fur abuts the more normally directed coat, that is on the crown and at the sides of the neck, there are slight ridges along the opposing lines of contact. This is not a feature of Asiatic *Profelis*, though there are interesting parallels in changes of pelage direction on the face and sides of the neck.

This is another short-tailed cat, the tail in the African species measuring not much more than a third of the head & body length. The claws are fully retractile; the soles densely haired between the pads; the interdigital webs, so far as can be judged from dried skins, appear to be extensive. Cranial and dental characters which distinguish this subgenus in Africa from the other two medium-sized cats, *Caracal* and *Leptailurus*, are detailed below in the account of the single African species *aurata*.

FELIS AURATA Temminck — African Golden Cat

Felis aurata Temminck, 1824, *Monographies de Mammalogie, etc.*: 120. The date is usually quoted as 1827, that on the title page of the completed volume; but the section in which this name was given appears, in fact, to have been published in 1824, *vide Isis, Jena* **20**: 273, and *Bull. Sci. nat. Géol.* **4**: 89. No locality of origin was stated since it was unknown, the type specimen having been purchased from a dealer in London: van Mensch & van Bree assume it to have come from Lower Guinea between the Cross River and the River Congo, and (1969: 251) officially fix this as the type locality. The type, a mounted specimen, is now in the Rijksmuseum van Natuurlijke Historie, Leyden, (Jentink, 1892, in which it is distinguished by the single letter *d*; but it has now been given a new number, 19.633, *fide* van Mensch & van Bree, 1969, who furnish a photograph of it). The name is the Latin adjective meaning golden.

Felis celidogaster Temminck, 1824, *Monographies de Mammalogie, etc.*: 140. Regarding this date see the remarks above under *aurata*. The type locality was thought to be the coasts of Chile or Peru; but the specimen had been exhibited alive in a London menagerie and, after death, as a mounted specimen in Bullock's Museum, from which it had eventually been purchased. It is still in the Rijksmuseum van Natuurlijke Histoire, Leyden, cited by Jentink (1892) under the letter *c*, but now given a new distinguishing number, 19.632 (*fide* van Mensch & van Bree, 1969, where there is a photograph of it. Temminck (1853) redescribed the species from a specimen of Pel's from "Guinea", meaning Ghana, with very little change of his 1824 wording. This specimen, which Lydekker (1906) wrote was "now generally accepted as the type" is also in the Rijksmuseum, mounted but lacking head and tail according to Jentink (1892) who cites it under the letter *b*, subsequently renumbered 19.631. The name was derived from the Greek words *kelis, kelidos* spot, and *gaster* belly. Possibly valid as a subspecies.

Felis chrysothrix Temminck, 1827, *Monographies de Mammalogie, etc.*: 251. This date is correct, *vide Isis, Jena* **21**: 92. This was a substitute name provided by Temminck for his *aurata*, 1824, under the mistaken impression that this latter was invalidated by the prior use of *Lynx aureus* by Rafinesque apparently for a form of the North American bobcat, now *Felis rufa* Schreber. The name is a compound of the Greek *chrysos* gold, and *thryx* hair.

Felis chalybeata Hamilton Smith, 1827, in Griffith's *The Animal Kingdom* **2**: colour plate facing p. 473. This was a drawing made by Smith himself of the animal in Bullock's Museum which subsequently became the basis of Temminck's *celidogaster*, drawn some time before the publication of this plate while the specimen was actually on exhibition and thus before Temminck had acquired it at the sale of Bullock's effects. The two "species" therefore had the same type. The name implies a steely-grey colour, derived from the Greek *chalyps, chalybos* steel.

Felis neglecta Gray, 1838, *Ann. Mag. nat. Hist.* (1) **1**: 27. Sierra Leone. Type in the British Museum, No. 38.4.16.325, sex unrecorded; skin without head, no skull. This specimen was not actually cited by Gray but has subsequently been labelled as the type. The name is a Latin word meaning neglected or omitted.

Felis rutilus Waterhouse, 1842, *Proc. zool. Soc. Lond.*: 130. Sierra Leone. Type in the British Museum, No. 47.3.12.1, sex unknown; skin without head or feet, no skull. The name (which should properly have been *rutila*) is the Latin adjective for golden-red.

Distribution and general. There has been considerable doubt and confusion about this animal owing to the fact that it occurs in a number of different phasal or subspecific forms several of which have in the past been regarded as independent species and accordingly named. This matter will be looked at more fully in the taxonomic section which follows but must be briefly mentioned here in order to set forth certain points clearly. Basically there are two colour phases: one reddish, at its extreme a lively golden-red not inappropriately termed the golden cat (Plate 11); the other greyish or sepia-greyish, sometimes called in contrast, but not so aptly, the silver cat. There are various intermediate colour forms between the extremes, in some cases not easy to place certainly in one category or the other. Further, either colour phase may occur with or without dorsal maculation, the spots when present being either fairly large (10–15 mm diameter), distinct and relatively few; or numerous, small and often obscure.

This cat must be presumed, from the specimens occurring in museums, to be comparatively abundant in the field. Van Mensch & van Bree (1969) examined no less than 186 skins from various sources; and in the British Museum there are 35 skins from West Africa alone, apart from extralimital material. When these numbers are considered in comparison with other species it is seen that the golden cat is either relatively plentiful or relatively easily snared, or both. Nevertheless, it has rarely been seen, at least by European collectors; for nearly all the London material, which is probably fairly representative, has obviously been acquired from African hunters or market stalls. Only 5 of the 35 West African skins are accompanied by skulls, 1 alone of these being both complete and adult; 2 of them are from zoo specimens of imprecise provenance, indicating that the animals had most probably been trapped young and brought in for live sale by hunters. It looks, indeed, as though trapping was the commonest method of obtaining this animal, few of the skins showing signs of bullet holes. Measurements and field observations are restricted to a single skin, and that extralimital, shot near the Benito River, Spanish Guinea, by G. L. Bates, who thus appears to have been possibly alone among collectors ever to have come face to face with the golden cat in nature.

The favoured habitat seems to be the high forest, the vast majority of specimens having come, so far as can be judged from labels, from localities in that kind of vegetation. A few are related to places in the Guinea woodland, though there have doubtless been islands or fringes of closed forest in the neighbourhood. This last probably applies also to coastal scrub or strand and mangrove areas from which two or three specimens are said to have emanated. It must be repeated that the majority of skins appear to have been purchased and their exact provenance is therefore open to some doubt. This is very obviously so in the case of three skins from Kano market in Nigeria. It is extremely unlikely that the animals from which these came can have lived within a considerable distance of Kano; and it is a matter of common knowledge that goods are brought into this international market from far and wide, not least saleable pelts since there is a very active tanning section amongst the traders. The question of provenance becomes of considerable importance when we later come to consider a main point of taxonomy.

British Museum West African specimens are labelled with the following places of origin: Senegal, 2 from unspecified localities; Sierra Leone, 4 unspecified, 1 from Zimmi (Makpelli); Liberia, Mount Barclay and Cavally River, 1 each; Ghana, 2 unspecified, 1 each from Ashanti, Accra, Oda, near Kintampo, Sukusuku, Koforidua, and 3 from

Foso (Cape Coast district); Dahomey, 1 unspecified; Nigeria, 3 from Kano market; Cameroun, 5 from Mamfe, 2 from Kumba, and 1 each from Kesham (Mamfe), Nkambe market and Wum. The two last places are interesting in that they are situated in the Bamenda highlands in country which is predominantly Guinea woodland but has patches of relic or intrusive forest. Kuhn (1965) furnishes a considerable list of places in Liberia from which specimens have been recorded. Van Mensch & van Bree (1969) also give a very long list of all the localities throughout the species' range from which they have examined examples or in which specimens have been said, in literature, to occur. Extralimitally to this present work *aurata* is known to range down the western side of Africa to north Angola and across the continent to north-east Congo, Uganda and Kenya.

Before entering upon a description of the golden cat it is first necessary to consider points of taxonomy.

Taxonomy. Questions of taxonomy revolve, as might be expected, about the two variable characters of colour and pattern. The almost complete lack of corporal measurements and dearth of skulls in the past have very largely prevented size from being taken into taxonomic account, and no other useful characters have suggested themselves. The two original forms described by Temminck embraced two extremes, *aurata* being a bright red-brown cat with no dorsal spots but the flanks bearing small, indistinct maculation somewhat darker than the ground-colour; and *celidogaster* being of a uniform mouse-grey marked on back and sides with clear spots of chocolate-brown colour, those along the spine somewhat oblong, the rest round. It has for long been agreed that Gray's *neglecta* is indistinguishable from *celidogaster*, and Waterhouse's *rutila* from *aurata*, and that all are, in fact, one and the same species. This synonymy was first suggested by Eliot (1871) as the result of careful comparison of the types in Leyden and London. This notion had a divided reception; but Pocock (1907) came down firmly on Eliot's side, adducing further evidence that the red and the grey cats were nothing more than colour phases of a single species. Pocock had at that time available to him in London only 10 skins; there are now very many more, in London and elsewhere, enough to establish beyond reasonable doubt that colour in this species has no taxonomic significance whatsoever. One of the arguments adduced by Pocock was that an animal in the London Zoo had,indeed, changed colour from rufous to grey in about four months from its arrival. The skin of this young animal, a plain deep grey, is now in the British Museum, No. 30.3.3.9, ♀.

This gave rise to the speculation that the two phases might in some way be connected with season; but van Mensch & van Bree (1969), have, with the aid of 186 skins, closely investigated the question of colour and come not only to the conclusion that it has no specific significance but also that it has no connexion at all with season, age, size, sex, locality or climate. The source of the great majority of the British Museum material being, as already pointed out, African hunters or market stalls, information relevant to all of these factors is almost entirely lacking, and exact localities of origin must also be suspect; but so far as can be judged it is true that both red and grey phases can occur in the same area; and, from the 3 West African and 4 extralimital sexed examples, in male and female alike.

Whether maculation is equally independent of all these factors and merely phasal is another matter. Pocock (1907) reached the conclusion that, irrespective of colour, two subspecies were validly recognizable: *a. aurata* with no dorsal maculation but with numerous small spots on the flanks; and *a. celidogaster* not only with distinct dorsal maculation but with the flank spots few, large and clear. As a result of their recent investigation van Mensch & van Bree (1969) have come to very much the same conclusion. They recognise four pattern forms, the main distinguishing characters of each being in brief:

A. Spotted all over
B. Spots on the neck and back indistinct
C. No pattern on the neck or back; lower flanks distinctly spotted
D. Virtually no pattern whatsoever except on the belly.

These, they claim, "have an approximate geographical value", A and B being found in the western part and C and D in the eastern part of the African tropical rain forest region. Owing to a paucity of specimens there is considerable doubt regarding the position in the middle part of the continent; but they believe that two subspecies can be distinguished, a spotted form (A + B) in western Africa, and an unspotted form (C + D) elsewhere, the dividing line between their distributions being possibly the Cross River.

Examining this as regards West Africa in the light of British Museum material the following points emerge. The four categories of van Mensch & van Bree stand up well to practical test apart from one or two very slightly doubtful cases respecting C or D. The material is found to fall conveniently into two groups: that from Senegal to Nigeria, and that from upper Cameroun (to which may be added extralimital Cameroun, Spanish Guinea, central and east African examples). The former group comprises 22 skins, from which must be deducted the 3 from Kano market as being of exceptionally doubtful provenance, leaving 19 specimens ranging from Senegal to Dahomey, there being nothing certainly originating in either west or east Nigeria. Of these 19, 15 are clearly spotted (14 category A, 1 category B). The upper Cameroun group comprises 10 skins all of which are unspotted (7 category C and 3 category D); and with these can be taken into account for the purposes of the present argument the 7 extralimital skins from a little further south, of which 6 are unspotted (4 of C and 2 of D) and 1 alone a border case, probably category B; and 10 central and eastern African examples, all plain. This is substantial support for division into 2 subspecies, vitiated by the existence of 4 plain coats out of place in the west and 1 spotted skin in lower Cameroun. It is therefore necessary to look more closely at these 5 anomalous specimens.

Two are reputed to have come from Senegal, collected in 1863 by Winwood Reade. This is an unlikely habitat for the golden cat; but, apart from this, the provenance of these specimens is open to considerable doubt on other grounds—a matter that has been mentioned earlier in connexion with *Herpestes ichneumon*, page 277. Winwood Reade went out to Gaboon specifically to investigate Du Chaillu's credibility as a field naturalist in relation to his specimens and stories of gorillas. On his way back from this territory Reade visited various other African countries, finishing his West African journeys in Senegal; but, as his works clearly show (1864 and 1873) he was far more interested in people than in animals, which receive scant mention; and it is a not altogether unjustifiable assumption that while he was on Du Chaillu's track in Gaboon and groping for evidence he collected skins there, just as Du Chaillu had done, but that when he had satisfied himself regarding the questionable nature of Du Chaillu's integrity his interest in animals waned and he did little collecting in the places subsequently visited. When he finally brought his specimens to the British Museum it is very possible that the erroneous impression was obtained that they came from the country from which he had just returned, namely Senegal. Similar mistakes have occurred much more recently; but in 1863 the matter would not have been closely investigated or regarded as of vital interest, for the whole of western Africa was at that time apt to be looked upon as a single faunal region. Something of this same zoogeographical imprecision may very well explain also another of the unspotted West African specimens, which was registered even earlier, in 1855, as coming from Sierra Leone. The last of the aberrantly unspotted skins is somewhat more difficult to account for since it is better documented. This is the animal that changed colour in the London Zoo (Pocock, 1907) and which was deposited there in 1906, also as coming from Sierra Leone, dying a few months later though its remains were not taken into the British Museum collection until 1930. The origin of this specimen would therefore seem to be less open to doubt; but in 1906 Freetown still was, as it had by reason of its harbour long been, one of the chief trading centres of West Africa, to which goods found their way from far afield through the medium of very active coastal shipping both large and small. Within the present writer's experience, some years later, it was possible to buy animals that had obviously been brought long distances, and, at least until recently, there was a flourishing export trade in animals and birds, not all of which were of strictly local origin. It will therefore be seen that, though nothing can be proved, there are at least good grounds for questioning the provenance of all these unspotted reputedly West African skins.

The dividing line between dorsally spotted and dorsally plain animals appears to lie, if it exists at all and in so far as it is possible to determine in the absence of any authentic material from Nigeria, somewhere in upper Cameroun. It has been suggested (*vide* van Mensch & van Bree, 1969) that the Cross River is the probable boundary. This might be so as regards the high-forest, plain specimens existing in the British Museum from Kumba (4°39 N, 9°26 E), Mamfe (5°46 N, 9°17 E) and Kesham (5°53 N, 9°17 E); but this river is unavailable further north, outside this zone in the relict forests of the Guinea woodland of the Bamenda area (Cameroun), whence similarly unspotted specimens are known from Wum (6° 23 N, 10°04 E) and Nkambe (6°38 N, 10°40 E). These Cameroun specimens together project a purely artificial boundary at about longitude 9° E, that is rather further east than the Cross River. Certainly 16 of the 17 skins in the British Museum from east of this line are unquestionably of van Mensch & van Bree's categories C and D. The odd specimen, though not prominently spotted like those from the West African forest block, is nevertheless category B rather than C.

On the whole, therefore, the British Museum material gives considerable support for the east- and west-forms theory; but van Mensch & van Bree themselves mention 4 dorsally spotted skins from the Middle Congo, which if they are authentically from that area serve to upset it. But no definition of these specimens is given and it is possible that they, too, are native skins which have travelled some distance to their final market. The authors also point out that there is a very large region in the middle of the continent which has been very poorly collected as far as this species is concerned. Nevertheless, on the face of it there is fairly good reason to believe that in the true West African forest block, that is to say from the Dahomey gap westwards, all golden cats are dorsally spotted; and that from Cameroun east and south, somewhat less certainly, they lack such maculation. If this is in truth so then there are two races, *a. celidogaster* west and *a. aurata* east; but the evidence at present is too beset with suppositions to make it wholly acceptable.

One other point of interest may here be put forward. Between 9° E and the lower Cross River lie the dense and thinly populated forests of Oban in which P. Amaury Talbot formerly collected a large variety of mammals, failing, however, to procure the golden cat. Had this species been present, and certainly if, though secretive, it were as common and as frequently trapped as it appears to be in the rest of the forest zone, this persistent resident collector must without doubt have come across skins, been impressed by their unusualness, and brought some back to the British Museum. That he did not, together with the complete lack of specimens from the whole of the rest of Nigeria, leads to the interesting speculation that there may, in fact, be a physical gap between the two forms, a stretch of territory from Dahomey to about 9° E from which both are absent.

Description. It will be at once appreciated from the above that it is not possible to give a general description of the golden cat as regards pelage colour and pattern enabling any specimen to be instantly recognised in the field. But, appearance of the coat aside, there are certain characters common to all forms of this species. It is, to start with, one of the medium-sized cats (Plate 11). Measurements from newly-killed animals are scarce and erratic; but judging from those furnished by van Mensch & van Bree (1969) an adult might be expected to have a head & body length of approximately 850 mm, more or less, with the short tail in addition running to some 30 or 40 per cent of this. This is a little larger than either of the other two medium-sized cats, but the general resemblance of *aurata* in its proportions is more to *caracal* than to *serval*, the build being stocky with nothing of the long-legged slender elegance of the latter. The shoulder height is, in fact, in the nature of 400 mm, that is about that of the caracal and far less than the 500 to 550 mm of the serval. The body weight of a well-grown adult golden cat is some 12 kg or possibly more. The whole structure is very sturdy, the legs not only short but stout and strong; the round head appears rather small, as in the other two cats, but differs from them most markedly in the very short ears which have a height of only about 55 mm as contrasted with 75 to 85 mm in the other species. Their outline is rather roundly triangular with a blunt tip which has no tuft; and they are almost wholly shiny black on the back except for a greyish patch at the lower outside edge.

There are small white or whitish patches above the eyes, especially at the inner corners; and the lower part of the cheeks is also white; but there are otherwise no very obvious facial markings. The iris is brown; the pupil upright spindle-shaped. The tail, which is soft-haired, smoothly subcylindrical or slightly tapering in form, has a dark dorsal line throughout its length and a number of more or less obscure transverse, similarly coloured bands, sometimes very ill-defined. The extreme tip, when present, is dark. The structure possesses the typical feline mobility. The feet are densely long-haired between the pads; the interdigital webs broad; the powerful claws fully retractile into sheaths.

Whatever the colour and marking of the dorsum the pelage always exhibits certain pretty constant characters. The underparts are in a varying degree white or whitish: the chin and throat are mostly pure white, but at the anterior end of the latter are often to be detected one or more faint transverse chains of very small spots; the lower throat may be white or more often suffused with ground-colour and spotted; the chest and at least the medial part of the belly white, the sides of this last frequently being suffused with colour; and the whole chest and belly is always heavily spotted with large blotches. On the dorsal surface, throughout all the various forms, the coat always displays a very distinct and characteristic reversal of direction between the shoulders and the crown, the hair in this area pointing forwards. The change is marked at shoulder level either by a single medial whorl or two lateral whorls; and by low crest-like ridges along the sides of the neck and on the crown just anterior to the ears where opposingly directed hairs meet.

The dorsal area is subject to so many variations of colour and pattern that it is pointless to attempt to give a detailed description of any particular form or forms. Pelage texture, too, is inconstant. The coat may be either short, close-lying and rather harsh, or fairly long, loose and soft; and there are no data reliably relating such differences to any particular factor, whether age, season or climate. The fur is composed of the three usual elements, underfur, bristle-hairs and sub-bristles. The underfur is always dense and very fine; in some cases it is wholly concealed by the abundant bristles, in others only partly so. The bristle-hairs are of slightly oval section and broad to the base; the sub-bristles have long fine petioles. When the fur is turned back it is seen that the coat colour resides mostly in its distal part, the base being pallid or even pure white. The underfur is usually either very pale or wholly white but may occasionally have faintly coloured tips. The bristles are always dark-brown tipped: in reddish skins this apical zone may occupy only some 3 to 4 mm and be succeeded proximally by a narrow orange zone and a faintly brown ring, the rest being white; in sepia-grey skins the terminal zone may measure 9 to 11 mm, the whole of the remainder being white. How variable coat length is, is illustrated by the fact that in some animals the underfur is only 10 to 12 mm long, the bristle-hairs 15 to 16 mm; while in others the underfur is 16 to 18 mm and the bristle-hairs 22 to 23 mm.

The overall colour ranges from a bright marmalade-orange-red to a deep dusky sepia-grey; but there are many intermediate shades both of red and grey, and it is sometimes difficult to say to which basic colour category a skin belongs. Some of the greys are cold, some tinged with a warmer hue. The dorsal pattern is also highly variable, not only as regards its presence or absence but in the size and character of the maculation as well. In the most typical West African form—the subspecies *celidogaster* according to van Mensch & van Bree—the dark spots are mostly large, roundish and clear, whether the general colour be red or grey; but they may be smaller or of elongated shape and sometimes rather obscure though unquestionably present. Largish flank spots are always clearly observable. Over the back of the neck, in the area of reversed pelage, the spots become very narrow and long, medially often joined into more or less uninterrupted lines. These stripes are not always clearly separated but are approximately four in number, apart from spots lateral to them. Between the shoulders and the root of the tail there is a dark spinal band; and through this, in the majority of cases, about three of these slender nuchal, yet darker, stripes extend backwards as far as the rump. In the Cameroun, central and east African form—reputedly the nominate race *aurata*—there is no purely dorsal or nuchal pattern of spots, but the dark spinal band exists. Flank spots may or may not occur; but the belly and other underparts are always spotted as described earlier.

FIG. 58. *Felis aurata*: skull, B.M. No. 25.10.7.13, ♂, $\frac{13}{10}$; lateral view

Melanos are known, in West Africa as well as extralimitally. In black forms of all cats there is sometimes some difficulty, owing to obscurement of the pattern, in determining the species; *aurata* presents an immediate means of recognition in the reversal of pelage direction on the back of the neck.

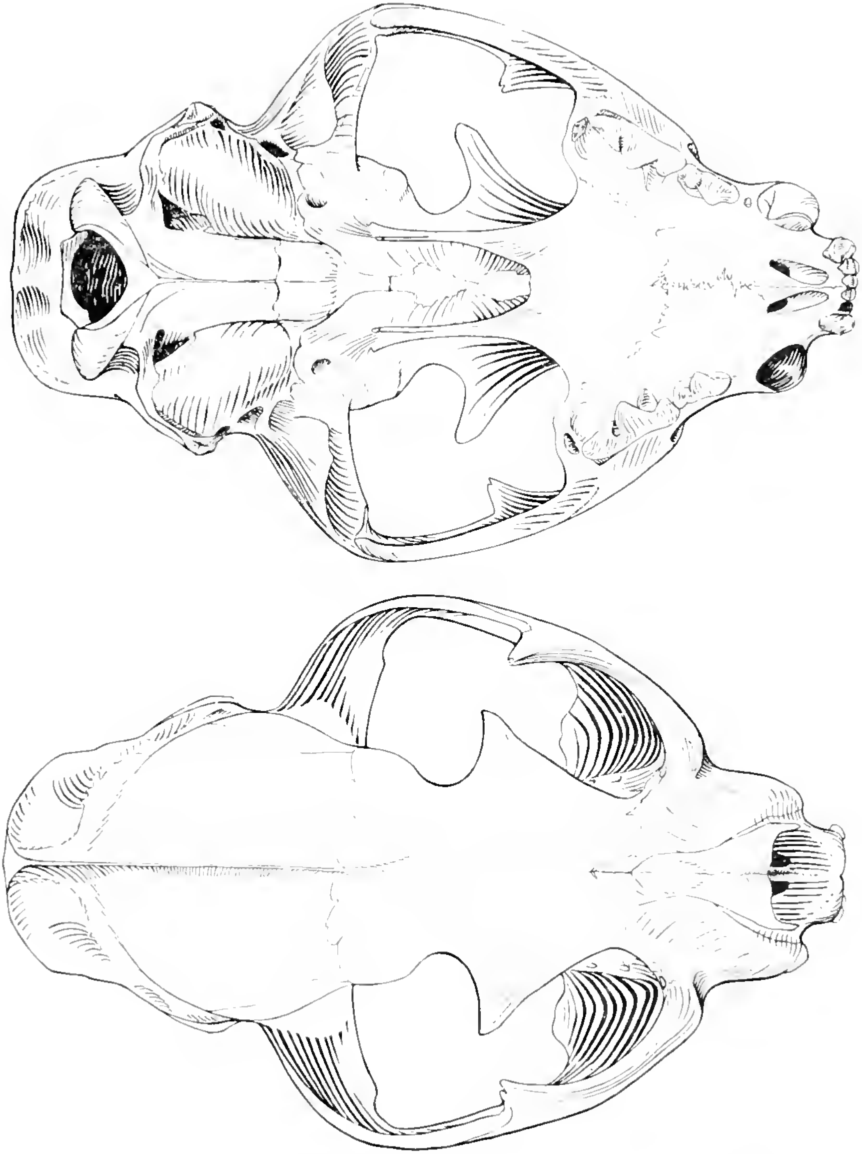


Fig. 59. *Felis aurata*: skull, B.M. No. 25.10.7.13, ♂, × $\frac{9}{10}$; palatal & dorsal views

Skull (figs. 58 and 59). This is very like that of *serval* and therefore not readily distinguishable though on the whole slightly larger. Van Mensch & van Bree (1969), who examined 46 skulls from all over Africa, cite a number of characters serving to differentiate between the two species; six of these are cranial or dental measurements expressed as percentages of the condylobasal length; but the differences mostly seem to be too slight to be meaningful and in some cases run counter to those emerging from this present investigation of West African material. From the very wide size ranges given it would seem likely that they must have included immature skulls, the proportions of which notoriously differ from those fully adult. It also seems to the present author from an examination of all the British Museum African specimens concerned that some of the characters from time to time quoted by authors to differentiate between subgenera of *Felis* are not constant and therefore unreliable—such as the shape of the posterior margin of the postdental palatal extension, and the exterior wings of the pterygoids.

Table 27: Comparative data for *F. caracal*, *serval* and *aurata*

	caracal	*serval*	*aurata*
Interorb./Postorb. widths	*c.* 75–85 per cent	65 per cent	*c.* 80–90 per cent
Maxillary process	only slightly overhangs the infraorbital foramen	sharply overhangs the foramen	sharply overhangs the foramen
Infraorbital foramen	medium; broadly elliptical; max. diam. 5–6 mm	small, rather straight-sided and oblong; max. diam. 4·0–4·5 mm	large, more narrowly elliptical; max. diam. usually well over 5 mm, mostly *c.* 6·7 mm
Jugo-maxillary suture	rises very steeply anteriorly	rises only a little	rises very steeply anteriorly
Depth between jugo-maxillary suture and alveolar line at the level of the foramen	usually not more than 14 mm	11–12 mm	*c.* 16 mm
Length of maxillary process from the foramen to its posterior edge	generally 18 mm or less	18–19 mm	20 mm or more
p^1	lacking	3–4 mm front to back	a mere peg, 2 mm
p^3	small anterior cusp, sometimes worn away	small anterior cusp	no anterior cusp, (or very small)

In profile the cranium curves evenly posterior of the postorbital processes whereas in other species it mostly dips slightly at about the level of the fronto-parietal suture, especially in older skulls. There is in *Profelis* often, but not always, a fairly well developed sagittal crest extending from the postorbital constriction to the broad supraoccipital crest, at any rate in the males, there being no females in the British Museum by which to judge this character in that sex. However, one old male as well as one medium-aged male show no sign of a crest except posteriorly. The orbital ring is incomplete. The zygomatic arch is of flattish curvature as in *serval*; the jugo-maxillary suture first dips down forming a distinct angle and then rises sharply anteriorly, the height of the maxillary process above the teeth being markedly greater than in the two other genera;

and it is also longer from the foramen to the posterior edge. As in *Leptailurus* this process sharply overhangs the infraorbital foramen, which is largest in this genus with a long diameter usually of 20 mm or more. The premaxilla intrudes narrowly between the nasal and maxilla but almost invariably leaves a long margin of contact between these two latter bones. The nasals are fairly broad, often more or less parallel-sided posterior to their suture with the premaxillary or tapering only slightly, their junction with the frontals bluntly triangular or even rounded.

The bullae are fairly large to large; the mesopterygoid fossa relatively narrow (about 12–13 mm), its anterior margin generally an even elliptical curve; the lateral wings of the pterygoids broad as in the serval. The anterior end of the mandible is appreciably less abruptly upturned than in *caracal*, the gap between the canine and first premolar longer; posteriorly it is deeply excavated externally, leaving a broad flat shelf for the accommodation of muscle. In this it differs quite clearly from *serval* and also, though less markedly, from *caracal*. There are 3 premolars in the upper jaw, the anterior one being a mere peg, of 2 mm or less from front to back.

Table 27 gives a comparison of various characters in fully mature skulls of *caracal*, *serval* and *aurata*.

Habits. Of this animal next to nothing is certainly known and not a great deal can be inferred. In the wild it leads a highly secretive and obscure existence. It has already been pointed out that a very large proportion of museum specimens have been purchased from African hunters or traders, and that few, if any, competent field naturalists can ever have seen this cat alive in its natural surroundings. It is true that a few golden cats, probably less than half-a-dozen in all, have been taken alive and eventually exhibited in zoos; but this tells us almost nothing of their daily way of life, and, moreover, regrettably little of the habits of these few in captivity has been recorded.

It would seem that the golden cat not only secretes itself in dense forest growth but is also very strictly nocturnal so that the chances of ever seeing it are slender, the more so as there is no doubt that its colour and pattern, whatever form these may take, are effectively cryptic. This difficulty applies as much to African hunters as to European collectors, and it seems likely that the majority of these animals killed have either been trapped, poisoned or shot with the aid of head lamps—seen only as glowing eyes in the dark. Only a single field note refers to a living animal having been seen at all, one of Bates's specimens having been chased up a tree by a dog and shot there; and even this is not explicit as to whether it was seen by the collector himself or by one of his hunters; or whether the sighting was by daylight or by lamp at night.

It is not, indeed, clear whether this is primarily a terrestiral or arboreal cat. Its short, powerful legs are ideally suited to climbing, the very reverse of the terrestrial serval's long, slender limbs. Basilio (1962) professes a greater knowledge of this animal's habits in the wild than any other author. He says that it spends its day hidden in the lower branches of shady trees, and at night sets out to capture its favourite prey, birds such as Guinea-fowl and francolins which also sleep in the lower branches, as well as small mammals from rodents to little antelopes. This may well be so. Blonk (1965), who recently kept a golden cat in captivity, found that, although it was not fastidious about food, it ate birds eagerly, always plucking them first, however. A point which seems to favour a largely arboreal life is the fact that nobody seems ever to have found a breeding shelter in this species; for, unlike most other animals, there are no juvenile specimens in the collection; and T. S. Jones, in a wide and varied field experience, has never been brought kittens by African hunters. One would suppose that if the nesting refuge were a hole in the ground or other commonly used terrestrial site it would from time to time have been come across, as in the case of other ground-breeding mammals. On the other hand, if it is hidden high in trees, and if the kittens never descend to the ground until they are well-grown this would account for the lack of juvenile specimens.

Accounts of this animal's behaviour in captivity are limited. Eliot (1873) recorded that a specimen exhibited in the London Zoo could be handled by its keeper even while feeding. Blonk (1965), on the other hand, though characterizing his animal as relatively tame found that it would not ever allow itself to be touched. This latter author also noted that no attempt was made by the cat to cover up its droppings in the manner of

Table 28: Numerical data for *Felis aurata*

	West Africa	Lower Cameroun, etc.
Vegetation	Forest	Forest
Number in mean	4	3
Condylobasal length	115·4	126·6
Basilar length	104·4	113·8
Palatilar length	46·5	50·3
Zygomatic breadth	86·7	90·3
Upper cheekteeth breadth	51·1	49·8
Nasals, length	33·8	35·6
Interorbital breadth	22·9	24·2
Postorbital constriction	27·7	27·9
Braincase breadth	50·6	52·7
Toothrow (*c*—m^1)	39·5	43·1
p^4 length	16·2	16·0
m^1 breadth	4·8	5·6
m_1 length	12·1	12·2
Head & body	657	860
Tail	349	300
Hindfoot	164	155
Ear	54	55
RATIOS (per cent)		
Tail/head & body	53	35
Zygom. br./condylob. l.	75	71
Braincase/condylob. l.	44	42
Braincase/zygom. br.	58	58
Palatilar l./condylob. l.	42	40
Interorb./postorb.	83	87
p^1/*c*—m^1	41·0	37·1

other species; there was only a slight scratching with the hindfeet before defaecation or urination. This, too, would seem to postulate arboreal rather than terrestrial habits, for if defaecation generally took place from a tree branch there would be no point in, or possibility of, covering up the droppings.

Measurements. The table on page 436 is derived from 4 West African and 3 closely extralimital specimens (1 skin only of each); that is to say, broadly, *a. celidogaster* and *a. aurata*. The measurements given by van Mensch & van Bree (1969) do not widely depart from these, except that external bodily measurements in their table reach a markedly greater size.

Genus **PANTHERA** Oken, 1816

Leopard and Lion

Panthera Oken, 1816, *Lehrbuch der Naturgeschichte*, Part 3, Zoologie, sect. 2: 1052. Type species disputed: on page 1052, the first mention of the name, it is given as *Felis colocola* (*sic*)—the South American pampas cat, not now considered to belong to *Panthera*; its first association with the leopard is on page 1058. Oken's work has been rejected for nomenclatural purposes by Opinion 417 of the International Commission on Zoological Nomenclature (1956); for the present continued use of this name see the discussion which follows this synonymic list. The Latin word *panthera* for a leopard was itself related to the Greek *panther* for the same animal.

Leo Oken, 1816, *Lehrbuch der Naturgeschichte*, Part 3, Zoologie, sect. 2: 1070. No type was specified; taken, by tautonomy, as *Felis leo* Linnaeus. The same objection applies to the use of this name as to *Panthera* Oken, above. The name is the Latin *leo* (Greek *leon*) for a lion.

Leo Brehm, 1829, *Isis, oder Encyclopädische Zeitung, von Oken*: 637. Type species *Leo asiaticus* Brehm. *Felis leo* Linnaeus (designated by Swynnerton & Hayman, 1951: 335).

Pardus Fitzinger, 1868, *Sber. Akad. Wiss. Wien.* **58**, 1: 459. Type species *Felis pardus* Linnaeus. This was the Latin term for a male leopard.

Leonina Grevé, 1894, *Nova Acta Acad. Caesar. Leop. Carol.*, **63**: 60; as a subgenus of *Felis* Linnaeus, type species *Felis leo* Linnaeus.

Taxonomy. With this genus we are from the outset faced with an important nomenclatural difficulty in that there is wide disagreement regarding its correct name. There is no question but that officially *Panthera* Oken does not exist. It was unequivocally rejected, in common with other of Oken's names, by Opinion 417 of the International Commission on Zoological Nomenclature published in 1956. It is equally certain that to all intents and purposes no other name has for well over half a century been employed for the leopard and the lion in scientific and semi-popular literature alike. Despite the embargo laid on it by the International Commission it is still regularly used in the Zoological Record to which reference is constantly made by practising mammalogists; and to introduce any other name now for the great cats would, without doubt, be to unstabilise a stable position and to introduce at least a measure of confusion.

For this reason Morrison-Scott (1965) submitted to the International Commission a proposal for the official conservation of *Panthera* Oken, 1816. This brought forth a great deal of detailed argument in the Bulletin of Zoological Nomenclature of considerable interest but too lengthy to do more than summarize here. Hershkovitz

(1960a), who had previously (1949) expressed uncompromising objection to the nomenclatural use of Oken's *Lehrbuch*, very strongly opposed the suggestion on several grounds, including the opinion that no preservation of the name was called for since it was taxonomically unnecessary, the genus *Felis* Linnaeus correctly including the great cats as well as the small. With this view Hemmer (1967a) joined issue in considerable detail showing that Hershkovitz's arguments were faulty and that there were several valid taxonomic reasons for subdivision of the felids at even higher than generic level; and he therefore strongly supported Morrison-Scott's application for the conservation of *Panthera* Oken. Later, Leyhausen (1969) adduced further reasons for disregarding the all-embracing conception of *Felis* advocated by Hershkovitz; but since far-reaching research was then in progress which, though still a long way from completion, seemed likely to revolutionise ideas on inter-relationships in the cats he recommended that no binding nomenclatural changes should be made until the work at the moment in hand had established a sure foundation for a lasting classification of the Felidae.

With this view the present writer has considerable sympathy; which, together with the opinion that it seems ridiculous to abandon a strongly established nomenclature on theoretically justifiable but practically confusing grounds, leads to the continued use in this work of the name *Panthera* Oken contrary to the ruling of the International Committee. If ultimately *Panthera* is irrevocably ruled out it must, if not sunk in *Felis* Linnaeus, be substituted by *Leo* Brehm, which conveniently replaces *Leo* Oken, which also, like *Panthera*, stands rejected by the Commission.

The main anatomical character which the great cats of this genus have in common and which in Pocock's view (1916g) separates them taxonomically from both *Felis* and *Acinonyx* is the fact that part of the suspensorium, mainly the epihyal, of the hyoidean apparatus remains unossified and elastic (see pages 377 and 380); but Leyhausen (1969) says that there is evidence that this feature is linked with body size rather than with kinship. Whatever its significance this modification has one notable practical result in that the freedom of movement it affords to the larynx permits these large felids to roar or at least to utter very much more sonorous vocalisations than the mewing sound characteristic of the small cats and even the cheetah.

The scope of the genus, as so many other points of taxonomy in the family, is disputed. It is commonly held to cover the lion, leopard, tiger and jaguar, but sometimes the snow leopard and clouded leopard as well. These are each often accorded subgeneric rank. Pocock, however, was completely opposed to such subdivision, maintaining, at least in so far as the lion, tiger and leopard were concerned (1929a, b & c), that at their extremes of pattern, coloration and form of the skull distinguishment became obscure and they could not, therefore, logically be separated at higher than specific level. Notwithstanding this, the differences between the two animals with which the present account is concerned, the lion and the leopard, appear to the writer to be of a greater degree and, following Ellerman & Morrison-Scott (1951), the two species are assigned to separate subgenera, the former to *Leo* Brehm, the latter to *Panthera* Oken. It must, however, be added that Leyhausen (1969) has foreshadowed a possible fundamental reorganisation of the Felidae embracing a larger number of genera but in which subgenera find no place.

The two West African species, lion and leopard, are so well known that it is scarcely necessary to enter here into the differences which distinguish them; nevertheless, certain key characters of pelage and skull will be found on pages 381 and 382.

Distribution. The range of the genus, though for many years now contracting before the advance of civilisation, is still very wide though as regards continuity and numbers on the ground far more sporadic and sparse than formerly except in parts of Africa. In that continent the southern limit of the genus is now roughly about 30°S but occasional stragglers are from time to time reported much nearer the Cape. Thence northwards the genus occurs over practically the whole of tropical Africa except the deserts, becoming extremely rare in Egypt and extinct in Algeria and Tunisia. On the west side of the continent it is still to be found as far as the south of Mauritania but is absent from Rio de Oro and exists only in remote corners of Morocco. Outside Africa it is widely spread across almost all the southern part of Asia, south of about 45°N; from Asia Minor and the Caucasus through southern Russia to China; and south through the Indian peninsula to Ceylon, Burma, Indo-China, Malaya and the larger East Indian islands.

Description. No useful purpose would be served here by attempting a general description of a genus extremely diverse in external appearance and size. The skulls are, in the adult state, larger than those of *Felis* but bear a general resemblance, constant diagnostic differences between the genera not existing. The structural character on which separation of the two depends lies in the hyoid chain as explained above.

Habits. These vary a good deal between the different species. They have, however, one thing in common. Through the great size of these cats, combined with their bold predatory natures, they all constitute a high potential danger both to man himself and to his domestic stock.

Subgenus **PANTHERA** Oken, 1816

The characters of this monospecific subgenus are those of the species below.

PANTHERA PARDUS (Linnaeus) Leopard

Felis pardus Linnaeus, 1758, *Systema Naturae*, 10th ed., **1**: 41. Type locality originally indicated as India but this was queried by Thomas (1911) who fixed it as Egypt; the probability of this was subsequently brought into question by J. A. Allen (1924) who designated Algeria as the more correct locality. The name *pardus* was the Latin for a male leopard.

Felis panthera Schreber, 1775, *Die Säugethiere in Abbildungen nach der Natur* . . ., **3**, pl. 99; and 1777, text, **3**: 385. Africa and the warmer parts of Asia. Schreber wrongly attributed this name to Buffon since his plate 99 was a direct copy of the latter's plate 12 captioned simply, La Panthère femelle, as acknowledged in the text, **3**: 586. Buffon used no Latin names. Schreber himself **3**: 384, synonymised this name with *Felis pardus* Linnaeus. The derivation has been given above under the genus.

Felis leopardus Schreber, 1775, *Die Säugethiere in Abbildungen nach der Natur* . . ., **3**, pl. 101; and 1777, text, **3**: 387. Africa from Senegal to the foothills of the Cape of Good Hope. This name was similarly wrongly attributed by Schreber to Buffon since it was an acknowledged copy of the latter's plate **14** captioned Le Leopard. *Leopardus* was late Latin for a leopard, ultimately from the Greek *leon* lion, and *pardus* "pard", between which animals it was considered to be a hybrid.

Felis leopardus A. Smith, 1826, *A Descriptive Catalogue of the South African Museum* . . . pt. 1. Of Mammalia: 7. Southern Africa. Not of Schreber, 1775.

Panthera pardus reichenowi Cabrera, 1918, *Boln R. Soc. esp. Hist. nat.*, 18: 481. Yoko, Cameroun. This was called after a well-known German ornithologist, Dr. Anton Reichenow, then Director of the Berlin Zoological Museum. The type, *fide* Dobroruka (1965), was destroyed in Madrid in 1936 during the civil war.

Distribution and general. Not only is the leopard one of the best known animals in the world, at least as far as its name and general appearance are concerned, but it is also one of those with the widest distribution, ranging over a very great deal of Africa and across southern Asia from Asia Minor to Manchuria in the north and Malaysia and Java in the south. In Asia the alternative name panther is often used and there is a mistaken belief that the two animals are different. The leopard was once to be found in the whole of Africa except the heart of the deserts but its northern and southern limits have now contracted and it is almost certainly extinct in Algeria, probably extinct in Tunisia, and at most extremely rare in Egypt. It is said (Merion, 1954) still to exist in Morocco amongst wooded hills; but it does not occur in Rio de Oro. In a southerly direction it is a regular member of the fauna as far as about 30° S, but is also still an occasional or very rare wanderer almost to the southern tip of the continent. In West Africa it may occur anywhere from Senegal to Cameroun in forest and open-woodland alike, even to the edges of the Sahara, though owing to persecution it is far less numerous than it used to be. It has been recorded on the Cameroun Mountain both in the forest and well above the tree-line; but it is now probably much less numerous than formerly (Eisentraut, 1963). As the leopard though wary, is also coolly audacious it not uncommonly turns up in unexpected places, even in large towns. Widespread as it is, the leopard, being predominantly nocturnal, is not often seen. Nevertheless, it can sometimes cause surprise and some alarm by strolling, seemingly quite unconcerned, out of cover onto a path or road during daylight. When it is lying at rest it is difficult or even impossible to detect owing to the disruptive pattern of its spots, which blends perfectly with the light and shade of the vegetation. This ability to remain completely concealed enables it often to avoid death by shooting. But its very boldness is a main cause of its destruction since being little hesitant of exploring man's habitations in search of a meal it commonly, with the same audacity, enters traps baited with goats or sheep. Formerly occasionally destroyed chiefly because of its predation, the leopard has in recent times become an extremely profitable source of revenue to hunters through the tremendously enhanced value of its pelt in the fur trade, and hence a subject of persistent pursuit. Thirty or forty years ago it was possible for the traveller in the remoter parts of West Africa to purchase skins with some ease for £1 apiece, or less; in response to an insatiable market and progressively decreasing supply the price some years ago rose to many, many times this amount. This onslaught on the leopard from the trade angel was to some extent simultaneously encouraged by the attitude of public bodies who regarded large predators as vermin inimical to both domestic stock and herds of game under protection in reserves. The emphasis in wild life protection was, in the past, almost inevitably slanted toward the elegant antelope, of sentimental appeal, overlooking that prime factor in natural history, the balance of nature. As any competent farmer well knows, it is fatal to attempt to graze more than a limited amount of stock on a given area; and unchecked and expanding herds of antelopes can quickly bring about the impoverishment of their own habitat, especially when the region over which they can wander is, unlike earlier times, restricted to the relatively small extent of a national park. The essential role which the large carnivores play in maintaining a healthy balance in these circumstances, as well as in holding in check such farm pests as baboons, is now realized and the leopard has in many parts been elevated from a public enemy to a protected animal. But this is none too soon as it was in considerable danger of eventual extermination.

By reason of its large size, its striking coat and, possibly beyond all else, its dreaded ability to kill human beings the leopard from early times made an overwhelming impact upon the minds of peoples who lived within the shadow of its power. This was especially so in the deep forest regions of western Africa, within the eerie dimness of which the solitary traveller, returning as night fell from market or farm, was in constant fear that he might be leapt upon from some overhanging bough, cruelly clawed and bitten to death. The leopard consequently figures largely in folk-lore. More importantly, it has been the inspiration of numerous status clubs and powerful secret societies. The latter, in former days, might even constitute a major basis of some kind of administration (Forde, *et al.*, 1956); but, more sinisterly, in certain areas, notably Sierra Leone, south-eastern Nigeria and the Congo, they from time to time occasioned ritual murders. These, at least sometimes, involved the use of artificial leopard's claws fashioned in iron, whose purpose was perhaps not so much to give the impression that the victim had been pounced upon and savaged by a real leopard as to act as the visible seal of the society and engender terror of its power—as it undoubtedly did (Kingsley, 1897; Talbot, 1912). Two sets of these iron claws exist in the ethnographical department of the British Museum. Such ritualistic killings, possibly never very frequent, grew less and less with the spread of education and increased urbanization; but nevertheless occurred at intervals up to relatively recent historical times.

In lesser ways the leopard was regarded as possessing magical properties. Its gall was held to be particularly potent and to cause death if taken in food or drink (Talbot, 1912). Perhaps strangest of all was the fact, widely recognized by trophy hunters earlier in this century, that when a leopard had been killed its whiskers would surreptiously disappear during skinning, or subsequently, unless a close and constant watch was kept upon the pelt. This was because they were widely believed to confer ascendency over one's enemy and to bring about his death—by irritation of the gut?—if chopped up and scattered in his food. This respect for the power inherent in the whiskers was observed, too, by Mary Kingsley (1897); and it is a fact that out of 25 West African skins in the British Museum only one has its full complement of whiskers, and in 22 they are completely missing except for short cut off stumps.

An attempt is from time to time made to revive an ancient collective noun for a number of these animals—a leap of leopards. This expression dates from 1486, when it was first printed in what is now known as The Book of St. Albans, an account of heraldry and cognate matters. To define a formal group of leopards painted on a shield in the deliberately picturesque terminology of the 15th century such a noun may well be justifiable; but to pretend that it has any validity as a modern term for living animals that are notoriously solitary seems nothing more than an inexcusable exercise in preciosity.

Description. The leopard is the largest of the spotted cats in Africa. Elsewhere it is only approximately equalled, or occasionally exceeded, by the neotropical jaguar. Of the two other faintly similar cats, both Asiatic, the snow-leopard never reaches quite the same size as the largest leopards; and the clouded leopard is yet smaller. But the leopard itself, even when fully adult, is of widely variable bulk; and there is a very marked difference between males and females, the latter being always appreciably smaller. Sexual distinctions apart, adults may range from a total length, nose to tail tip, of 200 cm, or somewhat less, to 290 cm. It may be added that skins stretch quite considerably in preparation and it is therefore unwise to judge the living size of an animal from a dressed specimen. There are, in fact, few records of actual living measurements of West African leopards; but a total length of 250 cm would represent a fine male specimen. Of this, some 150 cm would be head & body, and 100 cm the tail. The largest recorded specimens are reputed to have reached a weight of some 90 kg, but West African animals are much less than this and the weight of a well grown male might be of the order of 50–55 kg; but females would run only to 30–35 kg. Sizes in East Africa appear to run somewhat higher, the record overall length in Rowland Ward (1969) being 292 cm; but Mary Kinglsey (1897) records a Gabun skin measuring 290 cm from nose to tail tip. It has sometimes been held that Indian animals, especially "panthers", are larger, but this is not so.

The black markings of a leopard's coat, though at once recognisably belonging to a single, quite distinctive pattern, are nevertheless highly variable from specimen to specimen; so much so that almost any general statement may in some measure be faulted. Each unit of the pattern can be regarded in one of two ways: either as built up of separate spots, or as the outcome of the breakdown of larger markings. Description is commonly based upon the former concept; but that which follows uses the latter. It is immaterial, and possibly neither is wholly correct. Basically the marks are very approximately circular or elliptical in shape; but, with few exceptions, the centres have been lost, the black being replaced there by fur that is very often of a shade redder tint than that of the general pale background colour on which the maculation is imposed. There is thus left a black annulation which, however, is further complicated by being almost invariably itself split up into spots or curved stripes so that the ring is, in fact, never or very rarely complete. The entire composite marking is commonly referred to as a "rosette". The New World jaguar has a very similar pattern which differs in having a small black spot in each central area; but such a mark may occur also here and there in the leopard (fig. 60b). Within the context of this general design there are very wide differences, not only from specimen to specimen (fig. 60) but perhaps also in different areas of a single skin. The normal maculation may, indeed, be sometimes entirely disrupted and almost unrecognisable as that of a leopard; Pocock (1935) records a remarkable disintegration and rearrangement of pattern in a Somaliland skin in which,

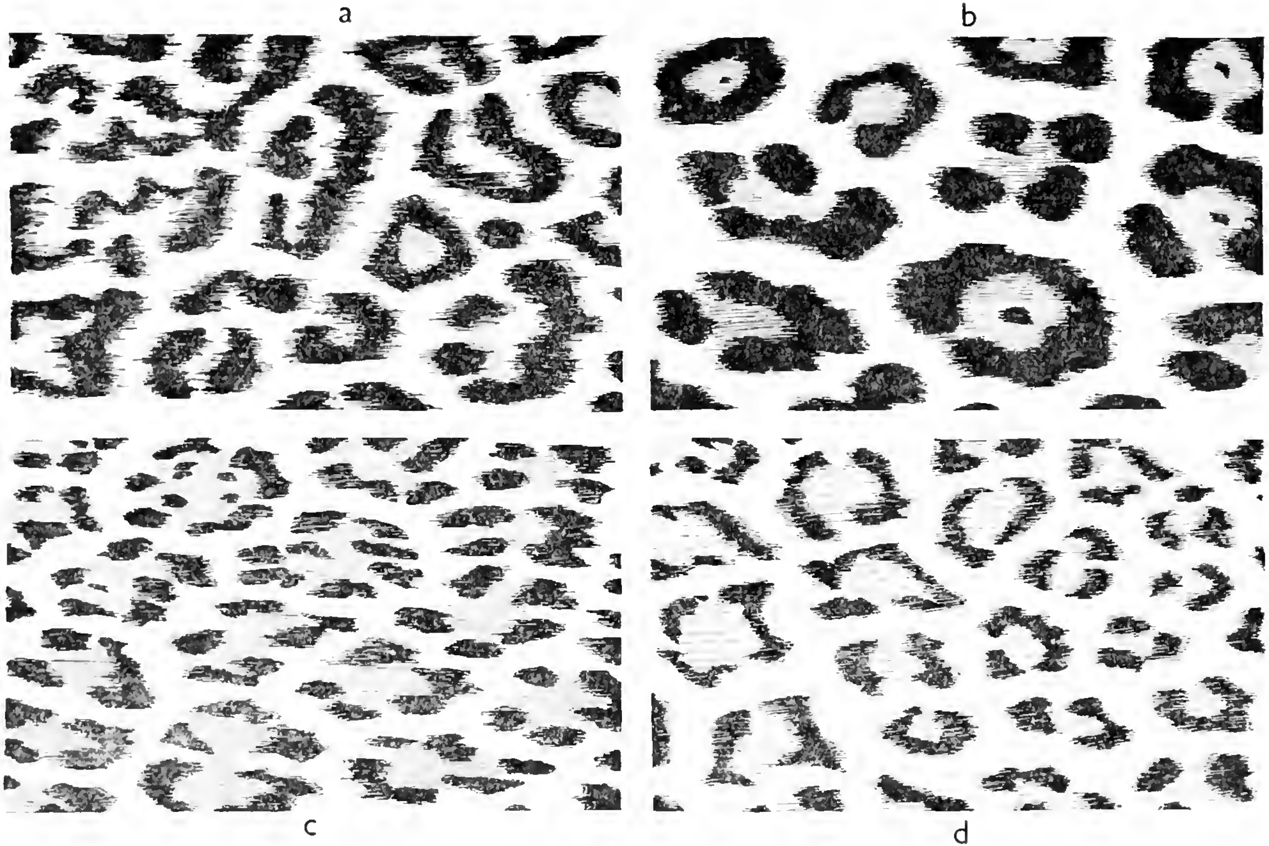


Fig. 60. *Panthera pardus*: pelage patterns, $\times \frac{1}{2}$

a. B.M. No. 48.766, ♀, Mamfe (Cameroun): forest.

b. B.M. No. 1938.7.25.1, sex ?, Juaso (Ghana): forest.

c. B.M. No. 1939.1648, sex ?, Bornu (Nigeria): Sudan woodland.

d. B.M. No. 7.12.12.2. sex ?, Bornu (Nigeria): Sudan woodland.

amongst other aberrations, "the pattern of the shoulders, flanks and thighs is a maze-like mass of coiled, twisted and looped black stripes . . . scarcely a trace of the original typical rosettes being detectable". The spots always grow smaller anteriorly in the region of the neck; but this apart, in the main dorsal and flank area their overall diameter ranges, in different specimens, from about 10 mm to 60 mm or more. Further, the width of the spots or lines forming the rings may be as little as 5 mm, and in places even less, or as much as 15 mm or sometimes more. There are, thus, relatively lightly spotted coats or massively marked ones; but in the former the maculation is mostly more abundant.

"Rosettes" cover nearly all the body from the crown to the basal part of the tail; but down the spine, especially posteriorly, the spots tend to be elongated and form fairly clear longitudinal lines. The proximal parts of the limbs also carry rather elongated rosettes which distally pass into single progressively smaller spots. The pattern on the tail is variable and often somewhat confused. Proximally there are rosettes which, however, may be composed of very elongated spots; in the distal half, which is basically white, the markings tend to become heavy, solid blobs or, near the end, partial rings. The extreme tip is black above, white below. All the underparts from chin to tail, together with the insides of the limbs, are white but none the less spotted. On the face the spots are simple and small and run in longitudinal lines; on the throat they form transverse rows, there being sometimes a well-marked one dividing it from the chest. The backs of the ears are black in the bottom half. The feet are broad and strong, the claws powerful and retractile.

The basic background colour of the pelage varies a good deal in different specimens, being either very light buff, buff, red of a pale to medium intensity, or rather greyish-yellow. The tone is deepest near the spine, fading on the flanks until it becomes white on the underside. This basic coloration has widely been considered to be related to ecological conditions, dark leopards in West Africa inhabiting the closed forest, pale ones the more arid regions. This broad generalization is examined in more detail in the taxonomic section below. However, it must be pointed out here that in the few cases where more than one specimen exists from a locality the skins exhibit clear differences both of colour and pattern.

In some extralimital areas the pelage grows to more than ordinary length and abundance in response to prevailing temperature or season; but in all the known West African skins it is short, close-lying and slightly harsh. It is composed of very fine underfur together with sub-bristles having long fine petioles and a flat blade. The underfur in an average coat is 10 to 11 mm long, and colourless except that the longest sometimes have yellow tips. The sub-bristles are 18 to 22 mm long, of which 8 to 10 mm is the fine, colourless petiole, and the remainder the flat-sectioned blade, which is yellowish or gold with a black tip or entirely black. In the pattern spots the sub-bristles and underfur are deep brown through much of their length, the jet-black of the maculation lying only in the distal parts.

Skull (figs. 61 and 62). A large cheetah skull may attain roughly the size of a youngish female leopard; but when the latter species is well developed, in either sex, the skull, with condylobasal length of 170 mm or more, is considerably larger than anything previously dealt with in this work and is exceeded in West Africa only by the lion. Apart from its size the leopard skull is extremely solidly built, with strong anchorage in both upper and lower sections for powerful jaw and neck muscles. This is especially so in the male, where a marked sagittal crest, virtually lacking from the female, is present. The measurement table at the end of this section shows that there is a clear disparity in size between the sexes, and also between forest and open-country animals.

There is, in fact, quite a difference in overall appearance in leopard skulls according to whether they are male or female, forest or open-country, and any general description may thus possibly to some extent be misleading. However, the braincase is always relatively narrow; in *Felis* and *Acinonyx* it measures between 42 and 47 per cent of the condylobasal length whereas in *pardus* it is less than 40 per cent. There is an interesting distinction between the sexes in the frontal region: in the 3 West African males examined there is a long postorbital waist, and the postorbital constriction measures less than the interorbital breadth; in all the females, on the other hand, the postorbital region is not lengthened and its width is greater than that of the interorbital breadth. The zygomatic breadth is also proportionately somewhat less than in the smaller felines, notably as regards both the caracal and cheetah. The arches, nevertheless, are very strongly built. Because of the lengthening of the postorbital region the profile of the male skull has a longer and somewhat more angular appearance than that of the females. In either sex its highest point lies sometimes between the postorbital processes and sometimes to the rear of them. The rostrum is much less blunt than in *Acinonyx*. The postorbital processes are pronounced but generally short and triangular without any finger-like extension; and they are well separated from the long, sharp jugal processes. The upper branch of the premaxilla protrudes narrowly and mostly for only a short distance between the nasal and the maxilla; but it may exceptionally have a very long, very fine posterior extension. The anterior nares are wide but none the less comparatively much less open than in the cheetah. The palate is appreciably longer than in both *Felis* and *Acinonyx*, measuring some 46 to 48 per cent of the condylobasal length as compared with 38 to 41 per cent in those genera. The posterior palate, with gently converging margins, is also appreciably longer; the mesopterygoid fossa is wide but by no means so wide as in *Acinonyx*; the bullae are well inflated.

The mandible is very strongly built, with deep, solid rami, well excavated posteriorly for the accommodation of powerful muscles. There is a remarkably long diastema between the canine and anterior premolar; but though in the upper jaw this interval is short the premolar there is so small, and both the jaws curve away behind the canines so much that there is, in sum, when the jaws are closed a very large postcanine gap.

In all the West African specimens examined the premolars were constant at $\frac{3}{2}$, the upper anterior one (p^2) being considerably smaller than the others, blunt crowned and functionless for biting purposes. The blades of the premolars, top or bottom, do not exhibit the trifidy of *Acinonyx*; the upper carnassial, though a long tooth, in fact occupies somewhat less of the toothrow (c–m^1) than in the smaller cats.

Habits. Although the leopard is one of the most widespread of mammals and was not so long ago almost ubiquitous in Africa, knowledge of its way of life is much less detailed than might be supposed. This is largely because, besides being an animal both difficult and dangerous of approach, it is a mainly nocturnally active one. However, no animal abides unremittingly by a fixed programme, and local circumstances, dull weather or hunger due to failure in the previous night's forage may induce this normally nocturnal hunter to seek and kill in daylight. Schaller (1972b) observed leopards to go after prey in daylight on no less than nine occasions. Leopards do, in fact, generally become active before darkness falls; and, since they move extremely silently through the bush, they may sometimes in the late afternoon or evening without warning emerge from the undergrowth. Leopards of the forest appear to be markedly more secretive in their habits than those of more open country; and this may be so in direct response to the sombre nature of this environment—though, on the other hand, the impression may be nothing more than the erroneous one arising from the more complete and constant cover afforded by the dense vegetation.

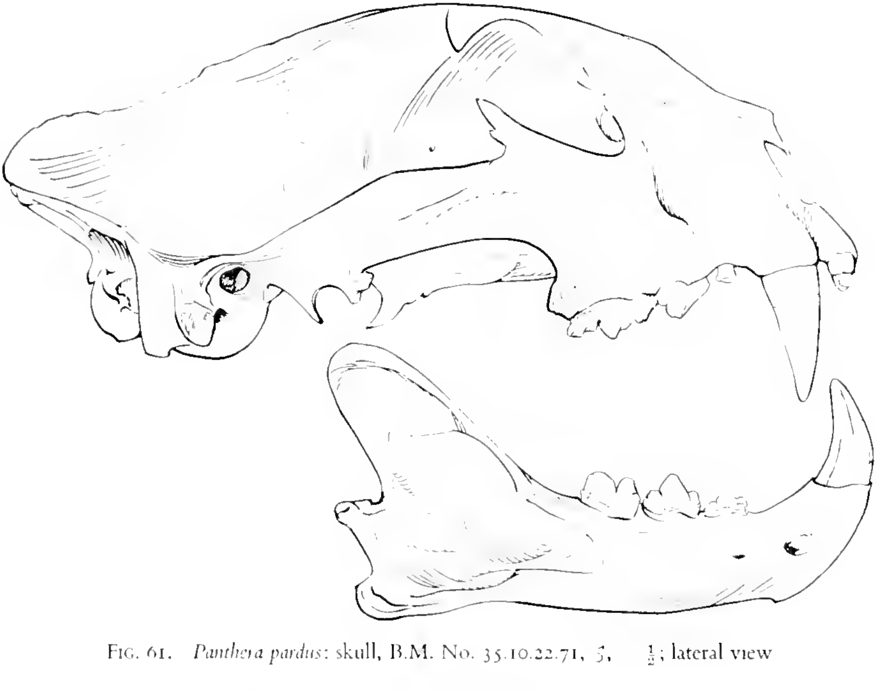


FIG. 61. *Panthera pardus*: skull, B.M. No. 35.10.22.71, ♂, ½; lateral view

Most of the daylight hours, however, are generally devoted to rest, the animal sleeping or at least lightly dozing with closed eyes. This may take place on the ground in a conveniently secluded spot in thick undergrowth, in cavities amongst rocks, in a cave, or up a tree. The last situation involves a fine sense of balance; for the leopard does not curl up, safely supported in a crutch but lies at full length along a branch with

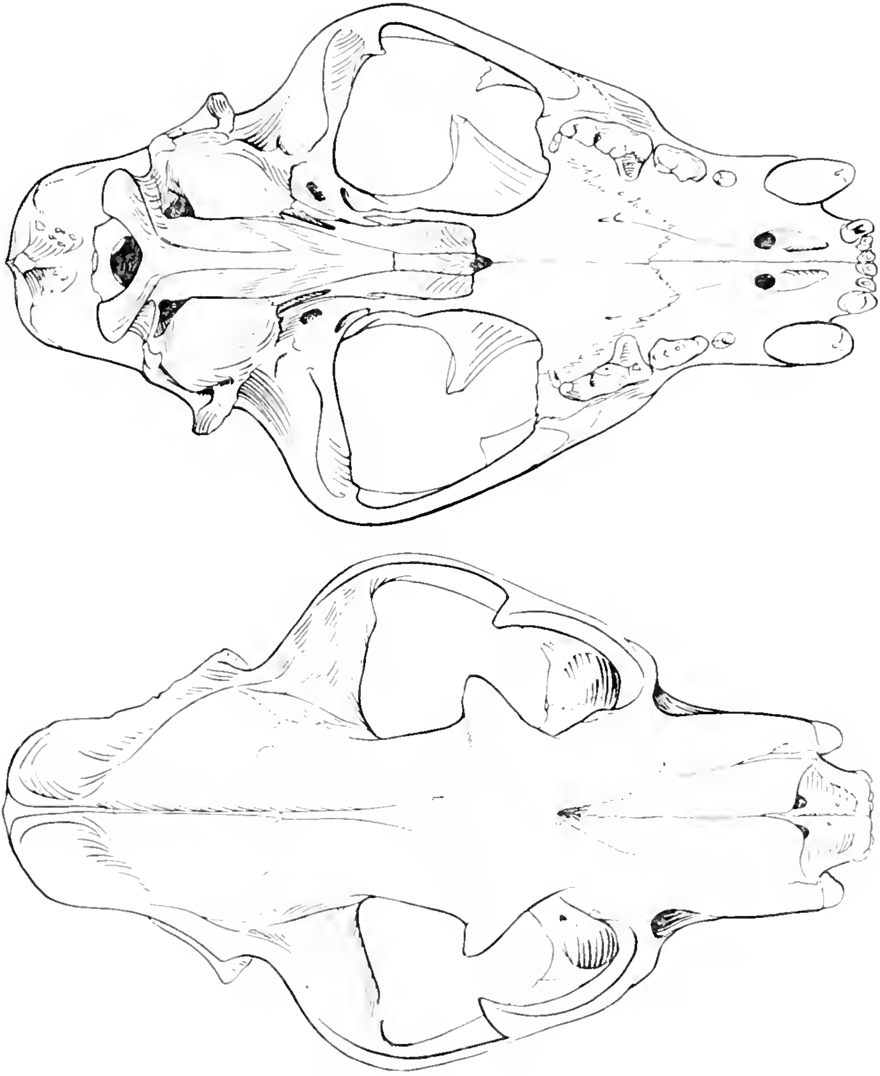


FIG. 62. *Panthera pardus*: skull, B.M. No. 35.10.22.71, ♂, × ½; palatal & dorsal views

its legs, or at least the hind ones, dangling down either side. In such a situation a mother is sometimes accompanied by her cubs, all stretched out along the same branch, the young ones in front of her where she can keep an eye on them. Fey (1964) describes two contrasting resting places in undergrowth, used by the same leopard as occasion demanded. The one was a thicket partly open to the sky, admitting patches of sunlight; the other, for use in inclement weather, was beneath a rainproof roof formed of a dense tangle of interwoven creepers. Leopards often lie in dappled sunlight; for not only are they fond of warmth but such situations are ideally suited, too, to their cryptic coloration. They will occasionally, in remote areas where the risk of disturbance is small, bask in full sunshine. This is necessarily carried out on rocky slopes or in short grass clearings, but there is always some fairly dense cover near at hand; for though leopards are often compelled to secure their prey in fairly open country they are, in general, averse to exposing themselves any longer than absolutely necessary, being by nature forest or semi-forest animals, at ease only in thick undergrowth or leafy trees. So long as a leopard has secure cover to operate from or to which it can at once retire it displays little fear, and it will loiter for many weeks on the edges of human settlements, even large towns, boldly at night raiding compounds and at times entering houses.

Little detailed study has been given to the leopard's behaviour. There is no obvious hunting pattern such as exhibited by the cheetah, the lion or the hunting-dog. It is all largely a matter of lurking in promising places such as paths or drinking holes, or of stealthy approach, a quick spring or swipe with the paw. The leopard's hunting technique appears often to hinge upon careful observation and memory—the knowledge that suitable prey will be in such and such a place or pass along such and such a route at a known time, and then of lying patiently in wait until the moment comes. Such predation is incomparably more passive than the very active behaviour of the other species just mentioned. Some, perhaps a good deal, of meal-finding is fortuitous, victims being flushed or encountered by chance in the course of noiseless prowling. The leopard moves very silently on its broad, softly padded paws; and though it has a rank smell this may be carried away by the breeze or, especially in the still density of the forest floor, not spread sufficiently far in advance to afford prey adequate opportunity of escape.

Prey is varied. An adult leopard is said to be willing to tackle animals up to about twice its own weight, that is to say, in West Africa, an almost fully grown hartebeest or a half-grown waterbuck; but normally it is content with smaller species, the duikers, oribi, reedbuck, bushbuck or gazelles, together with the fawns, adolescents or weakened adults of the larger antelopes. Pigs commonly fall prey to leopards, red river-hog in the forest, warthog in the open woodlands; and the larger rodents often provide a satisfying meal, that is to say the giant Gambian rat (*Cricetomys*), the cane rat or cutting-grass (*Thryonomys*) and the two porcupines, the brush-tailed (*Atherurus*) in the forest, the crested (*Hystrix*) elsewhere. Porcupines, with their harsh quills, may seem very unpromising subjects to be attacked and eaten; but leopards very frequently do so. What a leopard has recently fed on can be gathered from the abundant fur and other remains found in its droppings; such evidence of porcupine meals has time and again been reported. Sonia Jeffreys in Ghana (private communication) found the faeces of one leopard to consist of nothing else but *Atherurus* quills. Such prey, nevertheless, especially the crested porcupine, has its dangers. Leopards have been found dead with quills penetrating their livers and other organs; and many have been recorded with quills in their pads, sometimes (Jobaert, 1960) the animal in an extremely emaciated condition, its paws so riddled as to render hunting impossible.

Other favourite meals are baboons (*Papio*) in open country and drills (*Mandrillus*) in the forest. This is partly because of their size which ensures a good meal; but smaller primates are also taken, especially the more ground-haunting species, the green and red grass monkeys (*Cercopithecus aethiops* and *Erythrocebus patas*). These two are open-woodland species; but Sanderson, writing of the Cameroun forests, records a leopard with the remains of two *Cercopithecus* monkeys in its stomach. It is also recognized that immature chimpanzees are carried off; and Pitman (1931) says that young gorillas, too, are taken. Many other kinds of animal are readily consumed. One of Sanderson's specimen's contained part of a genet; and it is known that civets also are seized. So, too, are aardvarks and possibly pangolins; hares, dassies and, rather surprisingly, many of the smaller mice form very welcome articles of diet. There is little record of reptiles being eaten; Kruuk & Turner (1967) mention a python; but no one seems to have recorded the capture of a monitor lizard, an animal that is large and meaty enough to form a very satisfactory meal.

The larger kinds of birds that spend at least part of their time on the ground are often killed by leopards: such are Guinea fowl, francolins, bustards, secretary birds, storks, ducks and geese. Moreover, these large carnivores are also not above taking insects: they have been observed to eat locusts; and Fey (1964) watched one turning over buffalo droppings in order to pick up dung beetles, which it conveyed to its mouth with its paw. As for the leopard's relationship to man in respect of food, farm stock is from time to time raided, goats appearing to be the most desirable prize, though sheep, calves, foals of donkeys and occasionally of horses are also taken. But of all domestic animals dogs seem to be the most sought after, leopards brazenly stealing them at night from bedsides, or from gardens or verandahs even though numbers of people may be close at hand. In more natural conditions wild species of *Canis* correspondingly constitute much favoured prey, Estes (1967) recording that one leopard took no less than 11 jackals in three weeks. Coming nearer home, there is no doubt that from time to time, though infrequently, leopards, for unknown reasons, adopt a man-killing habit; but apart from some mutilation of the face whether they go in much for actual man-eating is open to dispute. There seem to be authentic records of babies having been carried off; and of women rather than men being attacked. Usually solitary travellers, or single stragglers at the rear of a file homeward bound from market are selected as victims. There seems to be no record of leopards eating fruit as other carnivores are known to do. They drink perhaps every two or three days, but there is little observation concerning this.

One of the least expected foods for a leopard is fish. Frechkop (1943) recorded that leopards in the region of Lake Edward (Congo) occasionally fed on catfish (Siluridae) that came out of the water onto land, as these fish from time to time do. Fey (1964) relates the case of a leopard on a small island in the Kariba lake on which three antelopes had also been trapped by the rising water. These latter were, unexpectedly, left quite unharmed, the leopard regularly lying on the bank in the heat of the day and with its paws flipping large fish (*Tilapia*) out of the water and consuming them. The same author points out that some leopards, at least, seem to have food preferences; this one for fish; but another he knew of lived for 8 months almost exclusively on bushpig (*Potamochoerus*), as clearly shown by the droppings. The 11 jackals referred to in the previous paragraph might be similarly accounted for. However, things are not necessarily always what they seem; and such limitation of menu may possibly be the result not so much of deliberate and active exercise of preferred taste as, more passively, the fortuitous outcome of the leopard's common strategy of observation and memory, referred to earlier in this section, leading it to haunt routes regularly taken by the same prey species day after day.

Killing is reputedly effected by a bite in the back of the fore-end of the neck, behind the ears of an antelope, severing the jugular veins; but Estes (1967) and others have observed that leopards also often kill by seizing the throat and suffocating the victim after the manner of a cheetah. They do not always kill their prey outright; the same author observed a leopard to play with jackals it had caught before giving them the death bite. The first thing that a leopard does when it has killed by severing a jugular vein is to drink the blood, continuing to suck it or to lick it up until the flow ceases. This taste leads it sometimes to kill many of a flock of goats at a single marauding visit merely to suck their blood rather than carry off their flesh. After this preliminary course of blood a leopard then disembowels its victim and buries the entrails beneath a pile of earth and leaves before proceeding to eat the liver, lungs, and heart, these being followed with the muzzle, tongue and ears (Jobaert, 1960). As a rule leopards eat the skin and fur together with the flesh, as evidenced by their droppings; but they have sometimes been observed to pluck off the fur before starting to eat. Bartlett & Bartlett (1961) saw one clean an area of fur round the shoulder of a hartebeest before tackling the flesh; and others have recorded the complete plucking of small mammals such as genets (Hamilton, 1947).

In one important respect the leopard differs clearly in behaviour from the other cats. It does not kill merely to take a single meal, leaving what is left over for the jackals and vultures or other scavengers, but it continues to feed off the carcass, at intervals, until it is finished—and sometimes, in the case of large animals, pretty rotten. There is some evidence that a leopard does not necessarily feed off the carcass every day, and, indeed, that these predators can, if occasion arises, go for some days without eating. This pattern of behaviour necessitates protecting the kill from any number of thieving species only too ready to dash in and secure a free meal. Sometimes the leopard achieves this by dragging the carcass to a secluded place and lying near it a day or two; but more spectacularly it carries the body up into a tree and lodges it in a fork where it is secure from most pilferers. This is usually at some 4 or 5 metres above ground; but there is one record of a leopard carrying a carcass up about 10 or 12 metres and laying it out on the very topmost branches as on a platter. Tremendous strength and climbing ability are called for to effect this, which involves not only leg muscles but the power to hold perhaps 50 kg or more—that is, getting on for a hundredweight—firmly in the mouth and support it erect with the neck alone. Indeed, much heavier burdens than this, young zebras or young giraffes in East Africa, have been reported, one of the latter estimated as weighing nearly 100 kg (Hamilton, 1947). Bartlett & Bartlett (1961) observed a leopard carrying out this feat. A dead gazelle was dragged to within about a metre of the base of a tree; the leopard then straddled it and with a tremendous leap, the gazelle in its jaws, lifted it some way up the bole, anchoring itself into the bark and then clawing its way up to the first fork where it rested the carcass. During this climb the dead antelope was held between the trunk of the tree and the leopard's body, entirely supported by the jaw and neck muscles. The ascent was then continued to the next branch. Sometimes instead of lodging the carcass in a fork it is balanced across a branch, but it is there, of course, less secure. Indeed, the stable instalment of a carcass in any part of a tree may call for repeated deliberate adjustments on the part of the leopard, as noted by Schaller (1972b). In descending a tree a leopard comes down head foremost from branch to branch, ending with a bound from the lower trunk to the ground.

Leopards are far from sociable. They are, indeed, habitually solitary except for a brief period at mating time, when a male and female may be seen together; and over a more extended length of time during which a mother is accompanied by her young. Joint hunting, as in lions or cheetahs, is rare. Nothing is known in this species regarding territorial claims or the systematic demarcation of range boundaries. The fact is these animals are so secretive and wary that it is almost impossible to observe their behaviour except when they cannot avoid publicising themselves by making a kill. Up to that moment they nearly always conceal themselves and avoid crossing open ground except by accident when it cannot be helped. Although a leopard may have no demarcated territory it is often very local in its habits, remaining in one area for several months. Fey (1964) records one that stayed in the same locality for 8 months; but hunting may, nevertheless, be carried out at some distance from the favoured base; and leopards always seem eventually to move off permanently elsewhere.

The leopard's daily life gives the impression of being one of quiet indolence save for a single short burst of fierce energy. When it is not asleep it lies and silently watches; and when it does get on the move it is almost always at a slow, casual walk, its shoulder blades conspicuous above the general level of the spine. During this prowl it may flush suitable prey, which if small and near enough it may strike with its paw or, otherwise, leap upon. If, however, it becomes aware of the possibility of game at a slight distance it sinks into a low crouching posture, its belly to the ground, and slinks forward thus foot by foot, its whole attention, especially its ears, concentrated on the vital spot where its intended quarry is, until near enough for a kill to become possible. The final stage may be a short, very swift dash or, more commonly, a single powerful spring. Anything more than this is unusual, though Kruuk & Turner (1967) once witnessed a longish chase. The leopard can, indeed, abandon its normal leisurely gait and trot when in a hurry or run rapidly over a short distance. It is also a good swimmer. The tracks are known as "pug marks" or simply "pugs". Each foot-print measures, in the adult male, some 9 to 10 cm from front to back; it consists of four regularly oval subdigital pad marks in front with a spread of about 8 cm, and a posterior mark some 6 cm across and of a broad equilateral triangular shape with rounded angles. There are no signs of claw marks except just as the animal is about to spring, when it extends the claws from the retracted position in order both to obtain a firm take-off for its leap and to land on its prey ready to effect instant anchorage in the flesh.

From a standing spring a leopard usually aims to land on its victim's back and bite it in the neck; but when a dash after the quarry is involved it often, cheetah-like, knocks the prey off its balance, rolls it over and seizes the throat. An attack does not always succeed. The intended victim may move just as the aggressor springs and thus avoid the full weight of the assault; or an inexperienced leopard may make an attempt on something which proves stronger or more ready to defend itself with its horns or tusks than expected. Mostly, however, leopards are far too cunning to tackle anything that can put up a good defence, such as a well grown antelope, a warthog boar in its prime, or a fully-developed male baboon, which with its almost equally fearsome set of teeth can give a very good account of itself. Leopards, nevertheless, are very fond of eating baboons and kill large numbers of them; and where there is a baboon-haunted rocky outcrop a leopard will, often enough, be found to lurk in the neighbouring bush. Attacks on this prey are generally by night when the baboons are sleeping; for, large males apart, a troop may well co-operate to repel a marauding leopard foolhardy enough to attempt a theft while they are yet awake. Leopards have, too, more active enemies, apart from man. Pitman (1931) records one killed by a crocodile while at the water to drink; spotted hyaenas will combine to rob leopards of their kill, unless it is safely stored up in a tree; and even in that situation lions have been known to steal from such a "larder". When driven to bay a leopard will turn on its attackers, adopting a crouching attitude ready to spring, its ears laid flat, its lips drawn far back exposing its powerful teeth, the whole posture highly intimidating. At the same time it utters a threatening snarl. The most famous, and perhaps most often heard, leopard sound is the husky cough, ending with a low vibrant growl, characteristic of an animal on the hunt. This cough is repeated at short intervals of about a second and has been compared by some to sawing wood. The leopard utters a grunting growl, too, as it springs upon its prey. When content after a meal it makes a low purr.

Such knowledge of breeding behaviour as we possess is largely the outcome of observation of captive animals. Leopards probably become sexually mature at the age of from 2½ to 4 years. They have an oestrus cycle of 27 to 58 days with a mean of 47 days, each period of heat lasting 6 to 9 days. These figures are given by Maddock (1968) who describes also the actual act of mating and characterises it as "a noisy and almost violent spectacle". The female in season makes advances to the male, swinging her hindquarters towards him and sometimes dragging her posterior along the ground. The male eventually mounts her, and when coupled growls loudly and bites and pulls at her neck, whilst she struggles and moves forwards, also growling. Copulation then proceeds in silence, and after some 15 to 30 thrusts the male suffers an orgasm and again growls and bites his partner's neck. They then break, sometimes with a short scuffle, both rolling excitedly on the ground. Coupling takes place every 5 or 10 minutes.

The period of gestation has been variously estimated, the minimum and maximum figures differing widely. Dobroruka (1968) quotes a number of observations extending from 90 to 105 days, and in one exceptional case of a leopardess in Prague Zoo 112 days. Something in the region of 95 to 98 days would seem to be the normal. In the case of twins in the Jersey Zoo (Maddock, 1968) there was an interval of 19½ hours between the first and second birth; but this period might have been longer but for an injection given to the mother, the second cub being still-born. In nature birth takes place in a well secluded retreat, sometimes above ground, often in a convenient hole, perhaps one made by a large burrowing mammal, or at the base of a tree, in a hollow log, or amongst rocks. Litter sizes of from 1 to 5 have been recorded but 2, or occasionally 3, are commonest. The cubs are born with their eyes closed and in a very helpless condition, not more than about 15 cm long. Their death-rate is said to be high. According to Jobaert (1960) they do not quit the nest until they are 3 or 4 months old. At this latter age the mother feeds them on regurgitated flesh; and at about one year they accompany her hunting. Nothing is known of parental training, of play or other juvenile behaviour; but since baby leopards tame well and for a year or so make tolerable and amusing pets it may be assumed that their pattern of childish play and other behaviour is, in nature, much as in other felines. Whether there is any favoured breeding season is not known, but in view of the swiftly repeated oestral periods seems unlikely. A leopard has been known to live in captivity for 21 years.

Taxonomy. The last classic paper on the taxonomy of *Panthera pardus* in Africa was that of Pocock (1932). To this he later (1936) added further information and views in respect of West Africa. Since in the 1932 paper Pocock reviewed his own investigations in the light of suggestions made in previous accounts by Cabrera (1918 and 1928) and J. A. Allen (1924) it is only necessary for the purposes of this present work to examine his conclusions, more especially those reached in the section specifically devoted to the leopards of tropical West Africa. This was one of nine dealing with the various regions into which Pocock considered the continent could in this connexion be conveniently divided.

In his final summary Pocock (1932) admits 17 races of *pardus* in Africa; and these he puts into five "principal environmental colour variations", briefly as follows:

1. "savannah" or "veldt" type. Yellowish-tawny leopards—including the reputed West African *reichenowi*.
2. desert type from areas of low rainfall and sparse vegetation. Stone-coloured, buffy-grey leopards.
3. mountain type occurring at high altitudes. Very dark tawny-brown or deep olivaceous-greyish leopards.
4. forest type of the West African tropical rain-forest area. Dusky leopards not so dark as the mountain type, but darker and noticeably less richly tinted than the scrub or bush leopards—represented by *leopardus*.
5. "dwarf" forms, possibly due to the effects of environment, the males failing to acquire their usual marked cranial characteristics.

In reviewing the evidence cited by Pocock and the conclusions to which he came as regards West Africa a few general points must first be made. The comparatively scanty material available to him in 1932 "consisting, with one exception, of a few skins without skulls, and a few skulls without skins" has now been considerably expanded to 25 skins, 6 of them accompanied by skulls; and 6 skulls without skins. In fact Pocock had even fewer truly West African specimens than he thought since he included under this head Gaboon, Spanish Guinea and parts of the Congo.

In reading Pocock's paper through one cannot but be struck by the obviously wide variation of both colour and pattern amongst the specimens from almost all of his various regions; and as he implies in his summary his subspeciation is on an ecological basis rather than on morphology or any precision of appearance. On page 578 he admits inability to make a determination in the absence of information as to whether Mamfe was forest or savannah. This being so, a great weakness of his paper lies in his lack of accurate knowledge of West African vegetation and hence the fallibility of some of the conclusions based on this and on other questionable matters of provenance brought out in the following paragraphs.

In dealing with the dark forest form *leopardus* Schreber Pocock gives the area of distribution as the "forested district of West Africa from Senegal to Spanish Guinea", the type locality being Senegal. Senegal is not, and has never in recent times been, in the high-forest zone. This is unfortunate if, as Pocock thought, *leopardus* should be accepted as the name of the forest race. However, in Schreber's original diagnosis no single type locality was given, only the general distribution from Senegal to the Cape of Good Hope. This Schreber adapted from Buffon who gave the distribution of the leopard as Senegal, Guinea and other southern regions. The only reason that Senegal is taken as the type locality is that J. A. Allen (1924) and Cabrera after him, thought that it should be so since Buffon referred more particularly to that district than to any other. This is scarcely so. Buffon, who never used *leopardus* or any other scientific name, having given the range as above only subsequently used such an expression as "the leopard of Senegal" for the sake of brevity; and, indeed, his last reference to it (9: 169) is in fact (in translation) "This leopard of Senegal or Guinea . . .". The choice of Senegal instead of Guinea as the type locality is arbitrary; it is both unfortunate and insupportable if *leopardus* is to represent the forest leopard.

Senegal, therefore, cannot logically be equated with the forested districts of "Guinea"—by which Pocock understood the coastal regions of West Africa from French and Portuguese Guinea in the north to Spanish Guinea near the equator. Another error into which Pocock fell was to regard the whole of Sierra Leone and the whole of the Gold Coast (*i.e.* Ghana) as lying within the forest zone and that broad references to these countries without specified localities on labels or in Rowland Ward's Records necessarily implied that the specimens must have come from the high-forest. This is not so; and, in fact, none of the 7 skins from Sierra Leone now in the British Museum is from this type of vegetation; and of the 6 Ghana specimens only 2 certainly and 1 doubtfully were forest animals. When, therefore, Pocock claims (1932: 575) that entries in Rowland Ward from these two territories demonstrate that forest leopards can attain a large size he is on very questionable ground.

Apart from vegetation the provenance of some of the specimens used by Pocock as the basis of his arguments is also open to some uncertainty. First of these is Winwood Reade's specimen from Senegal. Doubts regarding the true origin of some of this collector's material have been set forth earlier in this present work in connexion with *Herpestes ichneumon* and *Profelis aurata* (see p. 428); and, while no definite assertion can be made, it seems, in the light of the coincidence of three questionable specimens from three different genera, very possible if not probable that the specimen here under reference really came from the Gabun forest. Pocock's claim (1932 and 1936) that it, together with two other undeniable forest skins, "completely bear out Buffon's statement that the leopards of Senegal and Guinea are alike" cannot be unreservedly accepted. Secondly, Pocock's statement (1932: 577) that the Alexander-Gosling expedition collected in the Lake Chad district is misleading in its half-truth since these travellers covered a wide stretch of the continent from west to east, in differing vegetation zones, of which Lake Chad was only one small part. There is no evidence available to connect the specimen cited with any particular point in this range. Lastly, though the specimens are extralimital to this study, it may be pointed out that the sole authority for the provenance of the three Cette Cama (Gabun) skulls on which Pocock placed considerable stress was a London taxidermist not, in the early years of this century, a wholly reliable source. In the light of some of what follows below it is at least questionable that these very large skulls were in fact from forest-living animals.

Pocock is perhaps scarcely to be blamed for some of these errors and doubts, and they are brought to notice here not with any purpose of denigrating the work of this great and indefatigable mammalogist but only to obviate their unquestioned acceptance in any future review of *pardus*. Their occurrence is the more to be regretted in that, ignoring wrong deductions made on their basis, Pocock's conclusions seem, on the evidence of present British Museum material, to offer a reasonable foundation for the classification of West African leopards. To get at this it is best, particularly in the light of somewhat more abundant study material, to reverse Pocock's method and give primary consideration to the skulls rather than to the skins.

Ten of the twelve available skulls can be assigned without question either to the forest (6) or the Sudan woodland (4). The sex given on the labels would appear, from morphological evidence, in two cases to be wrong, and the present writer agrees entirely with Pocock's notes on the labels that they should be reversed. The results of measurement are shown in the table at the end of this section (p. 459). It will be seen that, sex for sex, the forest leopard is appreciably smaller than that of the Sudan zone. The doubt pertaining to the forest origin of Pocock's extremely large Gabun skulls, mentioned above, is now apparent.

The skins are altogether more difficult. No measurements exist for any of them; and there is a wide range of pattern and colour so that it would not be difficult to describe from them alone several distinct forms. However, starting on the basis of the skulls, part of the available material can be arranged in two corresponding groups, forest and Sudan woodland. Pocock's distinction between *leopardus* and *reichenowi* then becomes apparent; but it must be said straight away that though the difference is evident in comparison it is not so absolute that the inexperienced eye could unfailingly assign a single skin to its correct provenance. Spots are not of much, if any, value as a taxonomic character. They perhaps tend to be somewhat heavier, the rings broader and rather less broken in forest than in Sudan skins, but there is a good deal of variation and such distinctions do not always hold true. The size and disposition of the markings of skin No. 48.766, forest, fig. 60a, are not very different from those of No. 35.10.22.71, Sudan. There is, however, a tendency in forest animals to form quite distinct spinal lines of elongated and often solid spots which is far less, or scarcely, apparent in Sudan zone specimens.

Colour is a more reliable distinction although it is quite widely variable. In broad terms there is a general dullness of hue in the forest skins largely brought about by a hard to define but unmistakable greyness of the interstitial background colour. In contrast, the Sudan skins, variable as they are in absolute terms, all have a lively brightness and warmth of tone.

So far no account has been taken of specimens from other vegetation zones. There are in the British Museum 7 skins from the Guinea woodland, all the north-eastern part of Sierra Leone. Part of their interest lies in the fact that 6 of them are said to come from a single locality, Gberia Timbako, Koinadugu District, but as they are devoid of skulls they were probably purchased and their provenance as living animals therefore not completely certain. However, all 7 reputed Guinea zone skins partake much more of the Sudan colouring than of the forest, there being a complete absence of the latter's characteristic greyness. Specimen No. 60.176 from Gberia Timbako is not very different from the Sudan zone specimen No. 35.10.22.72 from the Sicili River (Ghana); but it is, however, very different both in its colouring and spots from its companion Gberia Timbako skin No. 60.174, which has a deeper rufous tone besides broader-ringed, blacker spots that more resemble those of one of the forest skins from Juaso (Ghana), No. 1938.7.25.1, fig. 60b, than any Sudan zone specimen.

Since neither skulls nor any body measurements of Guinea zone animals exist it is not possible to assess size; nor does any constant distinction of colour or maculation between Guinea and Sudan zone skins emerge from the existing material. It is conceivable that leopards born within the grassless closed-forest respect the sharp natural boundary that exists between it and the densely grassed contiguous Guinea zone and therefore remain within it; but that animals born in one or other of the grassed open-woodland zones see no barrier to roaming indiscriminantly from one indefinitely bounded type to another. Be that as it may, it is not considered in this work that the data at present available justify anything more than a broad division of West African material into two sections, closed-forest and open-country. This, in effect, is what Pocock (1932) did, assigning the two races to *leopardus* Schreber and *reichenowi* Cabrera respectively.

Both of these would at first sight seem to be justifiable names; but, as already pointed out, if *leopardus* is to represent the forest leopard, as it reasonably might, then the arbitrary choice of Senegal rather than "Guinea" as the type locality is most inappropriate. As for *reichenowi*, Pocock assumed (1932: 577) that Bornu, whence one of his two assigned specimens came, was "no doubt very similar to Yoko", the type locality, and that there was therefore no ecological objection to lumping the Nigerian and the Cameroun animals together. The vegetational assumption is, in fact, not valid since Bornu is in the dry Sudan zone and Yoko in the moister invasive Guinea woodland. Later, Dobroruka (1966a), having examined specimens from northern Cameroun, Mango mountains and Duma (Ubangi), including a topotypical skull, came to the conclusion that *reichenowi* was identical with the leopards of the upper Nile, that is, in his view, with the nominate race, *P. p. pardus*. No one, however, knows where *pardus* came from. Its type locality was given by Linnaeus (1758) as India but was fixed later (1911) by Thomas as Egypt, and subsequently (1924) designated by J. A. Allen as Algeria—thus establishing as representing the nominate race an animal whose characters, range of colour and maculation have never been clear and, since it is in all probability extinct, are never likely to be known. Pocock by implication rejected Allen's designation; for in his 1936 paper he gave the upper Nile as the type locality—that is, none of the hitherto postulated areas. Nevertheless, it was doubtless on the basis of this that Dobroruka equated *reichenowi* with *pardus*.

Pocock himself, indeed, had already half come to Dobroruka's conclusion, stating (1936: 924) that in his opinion *reichenowi* was only provisionally admissible since the range of the race in question probably extended to the Egyptian Sudan and the upper Nile and the animal was thus either *pardus* or else *chui* Heller, 1913—which in any case itself was likely to prove to be identical with *pardus*. Dobroruka (1966a), however, differed from Pocock in believing that the latter's description of the West African specimens which he assigned to *reichenowi* depicted a paler, yellower animal that was thus not of that race (or *pardus*) but required to be distinguished by a new name.

The present writer, having seen how much variation in ground-colour and in markings regularly occurs within a limited area, does not place much weight on assertions that leopards from given localities are truly characterized by specific shades of colour and thus recognisably, and consistently, differ from those of other localities by slight nuances—the more so where the evidence for such nuances rests upon written descriptions by different authors. Further, he is of the opinion, as already mentioned, that open-country leopards are in the course of their lives most likely wide-ranging, in respect of different woodland zones as well as of distance, resulting in considerable interchange and interbreeding. The case for splitting them up into a number of validly definable races is far from proven. In consequence it would be less confusing and just as near the at present ascertainable truth to regard the open-country leopards, at least those of the circum-Saharan regions here under discussion, as all being, in contradistinction to the duller-toned forest animals, of the nominate race *pardus*. This course is adopted in this present work. In this connexion it is of interest to point out that Dobroruka (1966b), investigating the leopards of South Africa, came to the conclusion from study of the usual taxonomic characters of colour, marking and size that three good subspecies could be distinguished; but that Hemmer (1967), was, however, as the result of subsequent statistical assessment of these characters unable "to justify splitting up the leopards of eastern, south-western and southern Africa in several subspecies".

There remain two specimens to be mentioned. The first is a skull, No. 49.604, labelled merely "West Africa". From its size and structure this would seem without doubt to be that of a forest female. More controversial are a skin and skull of Sanderson's, No. 48.768 from Bamumbo (Cameroun), which lies at an elevation of some 1000 metres in a region of high precipitation on the escarpment between Mamfe and Bamenda. The vegetation is essentially heavy rain forest but has been much destroyed and substituted by extensive stands of oil-palm and areas of invading grass. The skin has, rightly, the characteristic dullness of a forest animal; but the skull, that of a fully mature or even old male, is the biggest in the British Museum, far exceeding the forest series and somewhat larger than the Sudan woodland male. The specimen is therefore difficult to place. There is neither date nor any field note on the label, but Pocock (1936) states, presumably from information supplied by the collector, that it was shot on February 16th "in the palm belt at the junction of the forest country with the mountain grass". This does not necessarily mean that it was shot by Sanderson, who did, in fact, obtain a good number of specimens from local hunters. The skin would scarcely seem to have been prepared by, or under the eye of, so experienced a collector as Sanderson; and the bullet holes seem more consistent with those made by a Dane gun than a modern rifle. Lastly, the skull has none of the appearance of having been professionally collected and prepared, lacking its lower jaw and being smoked and dirty as from long suspension in a ju-ju house. It may, thus, not belong to the skin. Hunters in this border area could as easily obtain leopards from the adjacent very open Bamenda district as from the dense Mamfe forest and may well have sold as a reputed unit two separately and distantly derived specimens.

It should be added that in none of the British Museum skins from whatever locality does the length and texture of the pelage vary enough to be reckoned a usuable taxonomic character. Some seems a trifle less harsh than others, but this is probably as much a matter of preparation as of anything else.

Panthera pardus pardus (Linnaeus) West African Open-country Leopard

The skull measurements of this, the larger race, are shown below but there are no collectors' body measurements. A specimen from Lake Chad is given in Rowland Ward's Records as having a total overall length before skinning of 249 cm (8 ft 2 in). As understood in this present work this form may occur throughout West Africa except the forest belt. It is said to be rare in the Sahel zone of Mali, though it does occur there, more especially in the wooded islands (*toguérés*) of the flood plain of the middle Niger. It is common in the Sudan and Guinea woodlands both in West Africa and extralimitally. As regards the former, British Museum specimens exist from Wule District (Gambia); near Sefadu, Kono District, and 5 skins from near Gberia Timbako, Koinadugu District (Sierra Leone), 2 skins and skulls from Sicili River, Northern Territories (Ghana); 2 skins from Bornu, and a skull from Gorgoram, Yobe River (Nigeria).

The skins in this race are very variable but are all characterized by their bright, lively, warm coloration with no trace of interstitial greying as in the following race. However, the two pairs from Bornu and the Sicili River demonstrate how specimens can vary in a single locality. The different maculation of the first pair is illustrated in fig. 60c and d; their colour is also appreciably different, skin No. 1939.1648 being considerably redder than No. 7.12.12.2. The two Sicili River animals are also pretty distinct as regards both markings and colour, No. 33.7.14.1 having much smaller spots and a more general redder hue than No. 35.10.22.72, both ♀.

Panthera pardus leopardus (Schreber) West African Forest Leopard

This is the smaller of the two West African races, the skull sizes being shown in the table that follows. It is, once again, not possible to give any figures for body size since no field measurements exist and, as shown in Rowland Ward's Records (1928), a skin may stretch anything up to 380 mm in dressing, so that measurements from museum examples are valueless. This form may occur anywhere in the forest belt, even near centres of population, from Sierra Leone to Cameroun and beyond, specimens in the British Museum coming from near Monrovia (Liberia); Goaso, Juaso, Bessiadzi and Foso (Ghana); Ikotmbo, Oban and Ogoja Province (Nigeria); various localities around Mamfe (Cameroun). Kuhn (1965) records it from the following Liberian localities: Kpeaple, Freemantown, Grahnstown, Tappita, all in north central Liberia. Eisentraut (1963) mentions early records of leopards at various points around the foot of the Cameroun Mountain and up to 1500 metres; but he concluded that in recent times these predators have there become extraordinarily rare.

As stated above, both coloration and maculation are very variable; but the background colour between the spots has a dull, somewhat greyed appearance. The spots are often heavy; and there are broad oblong spots forming interrupted parallel lines down the spine.

Table 29: Numerical data for *Panthera pardus*

	p. pardus, ♂	*p. pardus,* ♀	*p. leopardus,* ♂	*p. leopardus,* ♀	Cameroun, Bamumbo
Vegetation	Woodland	Woodland	Forest	Forest	?
Number in mean	1	3	1	5	1
Condylobasal length	224	185	204	172	230
Basilar length	205	174	186	156	(210)
Palatilar length	102	86	99	81	105
Zygomatic breadth	154	126	147	118	163
Upper cheekteeth breadth	83·4	74·9	76·1	70·5	89·8
Nasals, length	68·5	60·7	71·0	57·1	82·3
Interorbital breadth	45·4	37·2	39·8	32·1	43·3
Postorbital constriction	41·0	41·6	36·3	40·1	39·4
Braincase breadth	75	71	75	68	80
Toothrow (c—m^1)	78	68	73	63	80
p^4 length	27·7	24·7	24·6	23·5	28·3
m^1 breadth	8·8	7·4	(6·5)	5·8	8·5
m_1 length	18·2	18·0	—	16·5	—
RATIOS (per cent)					
Zygom. br./condylob. l.	69	68	72	69	71
Braincase/condylob. l.	33	38	37	40	35
Braincase/zygom. br.	49	56	51	58	49
Palatilar l./condylob. l.	46	46	48	47	46
Interorb./postorb.	111	89	110	80	110
p^4/c—m^1	35·6	36·4	33·8	37·4	35·4

Subgenus **LEO** Brehm, 1829

Lions

The characteristics of this monospecific subgenus can be gathered from the account of the species which follows. The name *Leo* was originally used by Oken, 1816; but since that author's *Lehrbuch der Naturgeschichte* has been rejected by the International

Commission on Zoological Nomenclature it can fortunately without causing any confusion be better attributed to Brehm.

PANTHERA LEO (Linnaeus) Lion

Felis leo Linnaeus, 1758, *Systema Naturae*, 10th edition, 1: 41. Constantine, Algeria, as designated by J. A. Allen (1924): 222. *Leo* was the Latin name for a lion.

Felis leo, race 3, *senegalensis*, J. N. von Meyer, 1826, *Dissertatio inauguralis anatomico-medica de Genere Felium*: 6. Senegal, inferred from the given name. (Not *Felis senegalensis* Lesson, 1839, for a small-spotted serval).

Felis leo, ß. *senegalensis* J. B. Fischer, 1829, *Synopsis Mammalium*: 197. Senegal, inferred from the name, which was based on the "Lion du Sénégal" of Cuvier & Geoffroy, *Histoire Naturelle des Mammifères*, Part 9, 1819.

Leo gambianus Gray, 1843, *List of the Specimens of Mammalia in the . . . British Museum*: 40. West Africa, interior of Gambia. A *nomen nudum*.

Felis leo kamptzi Matschie, 1900, *Sber. Ges. naturf. Freunde Berl.*: 92–93, and Plate (skull). Yoko, upper River Sanaga (Cameroun). This was named after Major von Kamptz, Commandant of the German Imperial Troops in Cameroun, who made a collection of several mammals, of which this was one

Distribution and general. The lion is certainly among the best known of all animals, in popular imagination the King of Beasts—a title that has often been disputed by animal lovers from India who maintain that the tiger has far better claim to it since it is somewhat bigger, yet more powerful and certainly more courageous. The lion owes its fame to the proud bearing and impressive mane of the male animal; and its precedence in popular estimation over the tiger to having played a peculiarly significant role in western civilization for many hundreds of years during which the tiger was by comparison unknown. This role may have been very closely real in the Roman arenas but was mostly more remotely symbolic in a widely accepted folk tradition, the lion having become since the most ancient historic times, from biblical lands to northern Europe, a universally understood emblem of might, dread or endurance, as exemplified in poetic literature, statuary, heraldry or even quality marking. It remains so to this day. The reputed nobility of the lion has influenced also the collective noun coined to denote a congregation of them, a "pride" of lions—a term dating from the middle of the 15th century. Its modern common use, however, is a relatively recent cultural revival, "troop" having sufficed as the accepted description in both literature and speech until the 1920s. Lions are, in nature, often far more readily visible than almost any other of the wild cats, not uncommonly roaming or lying at ease in the open or only partly concealed; whereas the tiger, like the leopard, is inherently far more secretive and is seen only when it breaks cover.

In prehistoric, neolithic, times the lion was spread not only over the whole of Africa and much of Asia but over a good deal of Europe as well. Indeed, in early historic times it is possible that it still existed in Greece. It certainly then occurred around some of the shores of the Mediterranean, not only in north Africa but without doubt in Asia Minor and very probably in Syria and Palestine as well. Further, it must have been abundant since it was presumably from these conveniently neighbouring sources that, somewhat later, it was imported into Rome in exceedingly large numbers. The species continued to be plentiful in Africa and southern Asia until very recently; but within the last hundred years or so it has been extensively destroyed, a process which reached a peak in the first half of the present century, when "big-game hunting" became a fashionable pastime. This, together with the fact that the vital role of the lion and other carnivores in preserving a proper balance of nature was not appreciated and they were relentlessly destroyed as wholly undesirable "vermin", has brought about the present position where it has ceased to exist over vast stretches of its recent range and occurs only in much reduced numbers in the areas in which it still maintains a foothold. When one reads of the degree of destruction that went on unquestioned the marvel is that the species has not followed the dodo into extinction. Without here repeating well-known names, it is on record, sometimes from their own pens, that in pursuit of "sport" or under some seemingly more laudable-sounding pretext or another a good many hunters have individually killed or helped to kill scores of lions during the course of their lives—apart from the countless thousands of less prominent figures who, following their own personal satisfaction or gain, have achieved a lesser slaughter.

The result is today that the lion is extinct in Asia except for one small district in north-western India; and as far as Africa is concerned its range is very greatly reduced. From having flourished everywhere in the continent except the closed forest it is now to all intents and purposes confined to the tropics alone, and even there has become extinct in many areas and rare in others. The species was virtually exterminated from Egypt a couple of centuries ago; the last survivors were killed in Algeria and Tunisia in the early 1890s, and in Morocco in 1920. At the other end of the range the lion retreated from the Cape and Natal a very long time ago and exists now in only a few of the more northerly parts of the Republic, its southern limit today being roughly 20 to 25° S. except in nature reserves or as an occasional stray. Lions are now at their most plentiful in Tanzania and Kenya.

As for West Africa, there has been a very considerable recession, especially in recent times. It should perhaps first be made clear that the lion's most favoured vegetational types in West Africa are the Sahel and Sudan zones. However, the species is also to be found, less commonly, in the Subdesert and, during the dry season when the dense grass has been burnt and the country assumes a relatively open character, as a temporary visitor in the Guinea (or Invasive) woodlands, whither for a restricted period it follows the game. It never enters the true high-forest except possibly occasionally to lie up in its extreme fringes abutting the grasslands; but it may shelter during the day in the light forest cover fringing river banks. In East Africa lions have been recorded as ascending as high as 3500 metres into bamboo forest, but such elevations scarcely exist in West Africa apart from the Cameroun Mountain. Nevertheless, lions are known to occur at some 2000 metres or more in some of the Cameroun highlands. There are in West Africa no extensive open plains such as exist, and are frequented by lions, in the more easterly and southerly parts of the continent; nor are there vast herds of ungulates whose migrations in search of fresh grazing commonly, in those regions, determine the complementary occurrence of their predators. The lion in West Africa, in fact, leads, and always has led, a far more restricted existence than in East Africa, and one with considerably less abundant food resources.

Rock paintings show that in common with several other now extinct species the lion must once have dwelt in parts of what is now the Sahara (Lhote, 1951). It has been absent from this area for very many centuries but continued to exist on the edge of the desert in Aïr up to some 60 years ago. South of this it occurs over a fairly wide area, though nowhere abundantly and in rather scattered fashion. It is found along the course of the River Senegal and is probably, in this region of Africa, at its most plentiful around the great bend of the Niger, both north and south of the river. Thence it ranges across to Lake Chad and beyond, taking in the northernmost parts of Gambia, Guinea, Sierra Leone, Ivory Coast, Ghana, Togo, Dahomey, Nigeria and Cameroun.

Particular records for West Africa are few, and some are now so much out of date that they may not truly reflect present distribution. According to a letter in the British Museum from the late Sir Cecil Armitage, who was at the time Governor of Gambia as well as a keen sportsman, lions turned up in 1926 within 20 km of Bathurst; and later, in 1929, one was shot on the river bank at Basse near the extreme east of the territory. One of the few West African specimens in the British Museum had been shot at Tambana a few years earlier; and another near Bathurst. The situation today in Gambia is unrecorded, but doubtless wanderers from further east still from time to time enter the country. Monod (1940), writing of Portuguese Guinea, noted that at that date lions had become rare and existed permanently only in the neighbourhood of Corabal and Buba, where they were pretty common. From these places they sometimes visited Chitoli and occasionally roamed into other parts.

Stanley (in Goddard, 1925: 227) recorded that lions were nothing more than rare visitors to Sierra Leone at the height of the dry season from the neighbouring territory to the north. One was shot in 1924 at Yiraia, north of the Loma Mountains (about 9°26 N, 11°16 W), while it was devouring a giant pangolin; and there is an account of this together with a photograph of both animals in Stanley & Hodgson (no date but c.1930). T. S. Jones (personal communication) was informed by a member of the Veterinary Department that as recently as 1956 a lion had been seen in Sulima Chiefdom, where it had killed cattle. There seems to be no later record than this for Sierra Leone, nor is there any specimen in the British Museum from that country.

There is, however, a skin in the British Museum from Ghana (Tamale, Northern Territories in Doka woodland, received in 1946); and one from somewhat to the north of this, an unnamed locality in the Voltaic Republic, Sudan woodland, received in 1930. G. S. Cansdale, quoted in Guggisberg (1963) gives the impression of much wider occurrence and more permanent residence in Ghana than is the case in Sierra Leone. In this note he stated that lions were still found in many parts, as far south, indeed, as the Afram Plains. The Northern Territories were their main stronghold; but he had also heard them roaring in the north-west corner of Ashanti near the River Volta, where they were locally common. This lies in Guinea or Doka woodland; but whether the lions were there at all seasons of the year is not clear. Cansdale also said they occurred as well in thinly populated grass areas in the extreme south of western Togo. Lions also exist at the present time in the Parc National of West Dahomey (Howell, 1968).

In Nigeria the species has never in recent times been numerous and is now much more uncommon than it was even 40 years ago. Nevertheless, in spite of a fairly dense human population lions have continued to survive, though as somewhat of a rarity, in the drier vegetation zones, chiefly north of the Benue; but they have also for long existed west of the Niger, especially in the once remote and unpopulated district of Borgu. Since the creation of the Borgu Game Reserve there is, in fact, some sign of an increase in their numbers there. These were down to about 30 in 1962, but in 1968 they were estimated to be between 50 and 75, and with increasing and more stable food resources they are themselves becoming less inclined to wander (Howell, 1968). They may still exist a little further south, at least as seasonal visitors, in Old Oyo and Upper Ogun. For the rest, the species may be come across in limited numbers, and in pairs rather than in prides, throughout the open woodlands of northern Nigeria from Sokoto and Argungu to Bornu: but the lion being often somewhat of a wanderer, especially where game is scarce and sporadic as in much of this region, cannot always be definitely related to a given locality and often suddenly appears in unexpected areas from which it is normally considered absent. Some places in which it turns up may, in fact, be very unexpected indeed. A score of years or more ago one lay for some time only partly concealed in the grass opposite Yola police station watching all the comings and goings until it was eventually shot by a police officer. Another was killed not long ago by a lorry on the road between Potiskum and Jos; and A. J. Hopson, in a personal communication, records that as recently as 1968 two young lions were shot by Fulanis on the Bama ridge between Maiduguri and Bama, having killed two people. With the increase in prey species taking place in the Yankari Game Reserve (Bauchi Province) lions may there, as well as in Borgu, now be becoming more numerous and sedentary. Two skins from Nigeria exist in the British Museum, one without any locality, the other (Sanderson, 1940) from the Ogoja Province.

This last locality, which is contiguous with Cameroun, is nevertheless rather unusual. In Cameroun itself lions still occur in many parts. Over a long period of years at least one pride existed with little disturbance on the Mambila Plateau, 200 km north-east of Bamenda, but is now in some danger. From there an occasional straggler has reached Ndu and other places somewhat further south. But it is considerably further north of this that the lions of Cameroun and the neighbouring country of Chad become appreciably more common; that is, around Rei Bouba and other localities in the upper Benue area and along the Logone and Shari Rivers to Lake Chad and further north towards Wadai and east to Sudan. One of the reputed West African races was described in 1900 from a specimen from Yoko, which is in the Invasive woodland zone somewhat north of the River Sanaga, one of the southern boundaries of the area taken in this work as constituting West Africa. According to Guggisberg (1963) lions still exist in this locality, or existed till recently, 10 specimens having been killed there in 1953.

Description. The lion is far and away the largest of African carnivores, a fully grown animal weighing between 170 and 220 kg, that is to say some three or four times as much as a leopard. The males are appreciably bulkier than the females though not so greatly different as regards the usual body measurements. It has been argued that West African lions are smaller than those from East Africa, and it is possible that a far more abundant food supply and a less harassed, more stable, existence in the east may lead there to the attainment of better growth; but the amount of comparative material and field data available from West Africa is really far too slight to make any reasonably reliable deduction possible. As so often, in mammalogy as in other matters, there is a danger of seizing upon the exceptional as representative. In Rowland Ward's Records the largest specimen is East African and is given as measuring from nose to tail tip 332 cm; but the average is certainly very considerably less. The three largest West African animals, from Lake Chad, Northern Nigeria and Sierra Leone, in the same reference work range from 290 to 297 cm. The average adult come across in West Africa would, however, probably be more in the nature of 270 cm, of which roughly 180 cm would be head & body and 90 cm tail. Shoulder height might be of the order of 100 cm; the weight 190 kg.

Adult lions differ very markedly in appearance from juveniles in that the latter are heavily spotted all over whereas the former, save in exceptional cases, are self-coloured on back and flanks. The colour description of a lion's pelage is in general terms given as tawny, that is to say a pale to medium brownish hue such as is commonly brought about by the tanning of leather; but, in fact, the colour of lions has a fairly wide range between dull yellowish and medium reddish-brown, and may sometimes be considerably darkened by an abundance of black tipping to the individual hairs. These different shades of brown have been used to diagnose local races but may, indeed, commonly be found to exist within a single pride. It is not, therefore, possible to provide a general colour description of West African lions, and the matter will be gone into a little more fully in the taxonomic section which follows later. There is usually some intensification of colour along the spine. The colour of zoo-kept lions may change markedly.

The pelage is very short, rather harsh and close-lying. It is composed of relatively sparse, very fine underfur, 6 to 8 mm long, sometimes yellow-tipped; and of flattish-sectioned sub-bristles some 10 to 14 mm long, the petiole being comparatively short, about 4 mm, the blade quite long, 6 to 10 mm, and of whatever shade of yellowish-brown the coat may be except for a shorter or longer black tip. In the majority of cases the direction of the pelage is reversed on the back from about the hips to the shoulders or a little further, there being whorls at each end where the change of direction takes place. This is so in four of the West African specimens in the British Museum, but in the fifth, that from Gambia, there is no sign of this character.

In the lioness, where it is not obscured by the existence of a mane, the reverse of the hair is usually continued forward as a low, narrow crest along the back of the neck to the crown.

In the adult male lion there is an abundance of lengthy hair, termed the mane, around the sides of the face, over the top and sides of the head, neck, chest and between the shoulders. The ears are only partly or not at all concealed. In some reputed races, or at any rate individuals, the mane extends further along the back and in some cases along the underside of the body; and there may be tufts on the elbows. Apart from the extent of the area it covers, the mane varies a good deal in length, abundance and colour, this last ranging from black to bright gingery-yellow. All manes have at least a few black hairs amongst them and blackness comes about when that colour predominates over tawny. Maturity has a good deal to do with the existence or size of a mane, and reports of manelessness or of poorly developed specimens may be due to relative youthfulness. Reliable evidence of age rarely exists in these cases; for it is often judged at some distance in the field or, in study specimens, may be impossible to come by since, often enough, no skull accompanies the skin. However, Mazak (1964b) has studied the colour of manes in relation to age and finds that in their early stages they are always yellow or tawny, and only much later develop a dark colour, eventually black. This explains why a single pride may contain adult males with either black or tawny manes, as commonly observed. This author found blackness to have no connexion with true melanism but to be the result of age and individual idiosyncrasy; and it was not a racial characteristic. There is, indeed, little evidence that mane colour or size have any of the significance once accorded them by taxonomists. This is borne out, for instance, by both text and photographs in Guggisberg (1963: 47), clearly demonstrating that colour and abundance of growth differ widely in a single locality. There may be tendencies in a given area but certainly no constancy—the black-maned lions once held to predominate in South Africa, but now extinct, being a possible example (Mazak, 1964a). Nevertheless, the fact remains that despite the thousands of lions that have been killed there does not exist enough concrete evidence to lead to any certain conclusion.

Interpretations of what is characteristic of an area differ. In the relevant section, published in 1819, of Geoffroy & Cuvier's Histoire Naturelle des Mammifères, on which ten years later Meyer's *senegalensis* was based, the Senegal lion was said in the text to differ from the Barbary lion by its yellower, more brilliant coat and a mane that was neither so long nor so thick; but the accompanying Plate depicts a pretty abundant blackish mane, and blackish elbow tufts. Matschie (1900) reviewing the various forms gave the colour of the Senegal race as red-yellow, the mane poorly developed. Of the four male West African specimens in the British Museum two, from the distributional and environmental point of view, might be supposed to be Senegal lions, those from Gambia and Upper Volta. Neither has any sign of a mane or elbow tufts. Sir Cecil Armitage, who took a good deal of first-hand interest in these matters, stated in the British Museum letter referred to in the previous section (page 462) that the lions of Gambia were practically maneless; and certainly a young male from Gambia in the London Zoo in the 1930s evinced no sign of a mane. The Sierra Leone lion shown in the photograph facing page 144 of Stanley & Hodgson (n.d.) had a poor, rather short mane. The other two British Museum West African specimens, both from Nigeria, might be regarded as more probably belonging to Matschie's *kamptzi* from Cameroun. What is left of the manes of these is a very bright ginger colour, in places almost orange, with a few scattered black hairs; but a Nigerian lion from Lokoja, in the same kind of vegetation on the Niger near the confluence of the Benue, also on exhibition at the London Zoo in the 1930s, had a fairly well-developed mane certainly not bright ginger.

The mane, therefore, is of very variable appearance and no set description of colour or abundance is possible for West Africa. Another factor has not been mentioned. It is sometimes asserted that manes are apt to get worn out, or torn out, by constantly thrusting through dense undergrowth, and that the full potential of a lion may only become evident after some time in captivity. There is some possibility of truth in this as concerns lions which habitually live amongst dense thorn bushes; but it counts for little or nothing for the great majority that spend their lives in sparse open-woodlands.

The heads of both lion and lioness are basically of the same shape, masked, however, in the former by the mane. It is rather rounded and broad in general feline fashion but the massive muzzle not so shortened as in the most typical cats. The ears are of fair size, set well apart on the sides of the head, with a marginal bursa, the apical part very rounded, almost semicircular in outline. The front face of the pinna and the ear opening are well protected by dense, long, stiff hairs. On the posterior side there is an intense black patch occupying the middle part, a little variable in shape but in general with concave upper and lower margins resulting in a band that is broad at the ear rims and narrow waisted in the middle, leaving both basal and apical areas of the normal coat colour. The pinnae have considerable freedom of movement, able to stand erect, lie flat or by twisting to present the posterior black marks to view from the front as a threat.

The nose is broad and flat; the rhinarium very narrow, having no dorsal face whatsoever but continuing laterally backwards around the somewhat comma-shaped, posteriorly long, slit-like nostrils. From the rhinarium a bare vertical median stripe parts the heavy upper lips, which are white or whitish and plentifully furnished with strong vibrissae, the majority of them set in about three or four parallel rows. The lower lips and chin are also white or whitish; and there is a conspicuous pale line beneath each eye and, less obvious, often a smaller similar mark at the inner corner. The eyes themselves are fairly large with yellowish-amber irises and pupils that remain round on contraction. In the adult the eyes have for the most part, except at the approach to a kill, a rather tired or sombre look and are often held half closed. This is quite different from other African felines, say the alert, perky look of the serval or penetratingly fierce stare of the caracal. There are well-developed superciliary tufts of vibrissae. The legs are stout and extremely muscular, the paws massive and armed with very powerful retractile claws. The tail is, in its colour and close-lying short hair, exactly similar to the body. It is very flexible, about two-fifths to a half of the head & body in length, of circular section but markedly tapering from root to tip, the latter carrying a small tuft of long black hairs. Hidden amongst this last is an elongated patch of hard, calloused skin, sometimes popularly referred to as the "thorn".

Young lions are spotted all over, the spots being rather of the "rosette" form characteristic of leopards but far more obscure, of paler colour and more closely approximated than is general in that species. There is some tendency for them to be disposed in transverse lines. In all but extremely exceptional cases these markings disappear entirely from the back of the adult animal but may sometimes remain fairly clearly on the lower flanks. The belly, legs and feet may more frequently remain spotted throughout life. In colour, the underside, chest and insides of the limbs are whitish or at least very pale buff.

Skull (figs. 63 and 64). This is very similar in appearance to that of the leopard except that it is almost twice its size. It is yet more solidly built, with massive zygomatic arches and a large sagittal crest for the attachment of powerful muscles. This crest exists also in the female though it is there a little lower; and, apart from a slight disparity of size, there is not that clear difference of build between the sexes that exists in the leopard. But proper comparison in this respect is not so easy as it might be since a very high percentage of British Museum African specimens were not sexed by their collectors and relatively few authentic adult female skulls are available. Only a single West African skull, a male, exists.

The braincase, as in the leopard, is very narrow; and, in fact, appears to be in proportion even narrower. Both are much more slender than in the rest of the Felinae; in the only West African lion skull available the braincase measures some 34 per cent of the condylobasal length; in members of the genera *Felis* and *Acinonyx* it lies between 42 and 54 per cent. The skull profile is not so curved as in the leopard, falling away much more gradually both anteriorly and posteriorly from a slightly sunken frontal region between the postorbital processes. These latter are short, blunt and distantly separated from the large, sharp jugal processes leaving a widely open orbital ring. The rostrum is slightly longer than in the leopard. The upper branch of the premaxilla extends, very narrowly, for a short distance between the nasal and maxilla; the anterior nares are large and open. The palate is broad in comparison with the majority of Carnivora but not so broad in relation to the condylobasal length as in the other two feline genera. The postdental palate is much wider than long. The mesopterygoid fossa is wide and deep, the pterygoid processes basally large but distally slender, very long and hooked towards the rear. The bullae are not large in comparison with the overall skull size; but the flanking mastoids have very well-developed subpyramidal processes; and each paroccipital process comprises a broad flat portion that closely invests the posterior face of the bulla and a thick downwardly projecting finger. The lower jaw is massive, the rami deeply excavated posteriorly, the angular processes strong and incurved.

The incisors of both jaws form solidly compact transverse rows; the outer ones of the upper jaw much larger than the inner ones and subcaniniform in shape. The canines themselves are extremely large, about 60 mm tall. The cheekteeth are set in a straight row; p^1 is lacking; p^2 is much smaller than the rest and is little, if at all, larger than the inner incisors; p^3 has one cusp anterior and two posterior to the main triangular cusp; p^4, the carnassial, is very powerful, the blade trifid, but there is no cusp above the antero-internal root. The solitary upper molar, set transversely in the jaw, is small and with limited function, bearing against the posterior face of the lower carnassial. In the mandible the canines are very large but not quite so tall as those of the upper jaw. There are very long diastemas between them and the anterior premolars (p_3), and when the jaw closes a very large postcanine gap results. The two premolars are each trifid; the carnassial much smaller than that of the upper jaw.

Hollister (1918) found that the "skulls and teeth of females vary much more than do those of males. The range of variation in size of the teeth in lionesses from one locality is startling". Much the same applied to bullae. J. A. Allen (1924) stated that the upper carnassial is relatively shorter and broader in females than males and more variable in both size and form. He also found the upper canines to be extremely variable, and the vestigial upper molar the most variable of all.

It is perhaps worth recording here that in an earlier paper Hollister (1917) was emphatic that lions bred in captivity were useless for taxonomic purposes as, through the absence of normal muscular use called for in the wild, the skulls display very pronounced differences in development and consequent measurements and proportions.

Habits. The lion has been more written about, more photographed, more talked of than any other animal; and therefore a good deal is known about the species. The literature is indeed vast, some of it scientific, the greater part of it anecdotal, not all of it wholly reliable. The most complete, recent, survey of this much discussed animal from the earliest times to the present day is that of Guggisberg (1963) who has brought together a very detailed account from his own wide firsthand experience and an extremely lengthy reading list. The notes which follow are necessarily by comparison brief and therefore often of a general nature in a field where generalizations are risky. In the introduction at the beginning of this present work the reader was cautioned that all mammals are individuals with recognisable characters of their own; the lion is perhaps more of an individualist than any other. Each animal has clear personal idiosyncrasies; prides may differ from one another in their group behaviour; and in different parts of the continent whole populations may exhibit diverse preferences in feeding or peculiarities of hunting methods. What we know of the lion comes almost com-

FIG. 63. *Panthera leo*: skull, B.M. No. 21.7.23.1, ♂, [illegible]; lateral view

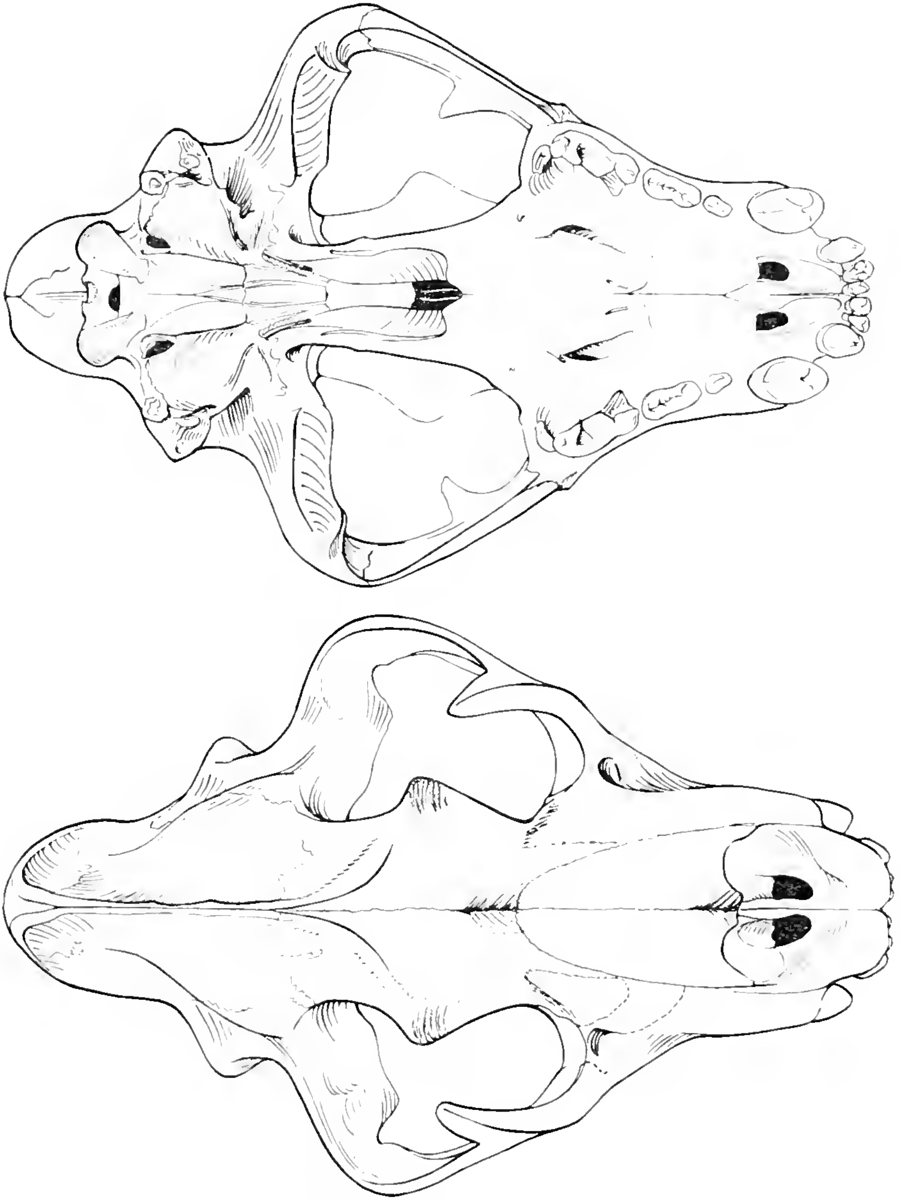


Fig. 64. *Panthera leo*: skull, B.M. No. 21.7.23.1, ♂, × $\frac{3}{8}$; palatal & dorsal views

pletely from observations made in eastern or southern Africa and may therefore be found to be not always equally true of West Africa. Some differences certainly exist. Howell (1968) writing of the lions of Borgu in western Nigeria characterizes them as "lethargic, unaggressive" and says that the local people do not fear them and allow them to reside permanently near the villages, and if necessary rouse them when they are sleeping to move them from the path. They even chase them from kills. Anyone acquainted with lions in East Africa would agree at once that this is certainly a marked difference in character; and, indeed, it would be foolish to assume that even in West Africa such docility was common. In dealing with habits and behaviour, therefore, one can only speak in generalities.

Lions are, for the greater part, nocturnally active; that is to say they most commonly do their hunting and killing by night; but this does not prevent their pursuing these activities in daylight if circumstances are suitable. Lions, indeed, may be commonly observed at any hour of the day unpurposefully on the move or cleaning themselves, or playing or climbing into the lower branches of trees, or reclining along them except in localities where they are under constant harassment, when they become secretive and entirely nocturnal. Otherwise, except when hunting, they take no particular pains to conceal themselves, even lying about in the open under the shade of a tree or at most half hidden in grass or other low vegetation. This does not mean that they are readily seen; for they generally match such cover extremely well, a lion's mane being often difficult to distinguish at any distance from a dry grass tussock.

Solitary lions exist, both male and female; but for the most part the species is distinctly social, living and hunting in "prides". The lion is, in fact, the only cat that regularly does so in companies of any size, the cheetah being limited mostly to pairs or rarely more than three. Since the pride is the basic unit in the life and behaviour of the lion it is as well to examine it in some detail. It may consist of four or five individuals but numbers of up to a dozen not uncommonly exist; and in parts of East Africa where game is plentiful prides of 30 or even more are known. Howell (1968) says that in western Nigeria prides of up to eight are to be seen. There is, of course, an optimum size for a pride; and this is dictated by the size of the prey most commonly available and the amount of scavenger competition. A solitary lion is at a disadvantage in two ways: the size of the prey that can be tackled single-handed, and the fact that when it leaves its kill in order to drink, as lions always must, there is no one to guard the carcass from jackals, hyaenas, vultures or other hungry raiders. Co-operation in a pride not only enables larger victims to be brought down and killed but ensures also a greater success rate as well as subsequent protection of the meal while some of its members absent themselves to drink, rest or defaecate. If large ungulates such as zebras are regularly available then a single kill can satisfy a fair number of lions and the pride can be numerous; but if, as in West Africa, such meaty prey-species are not available and recourse must most commonly be had to gazelle or kob then a single victim can satisfy only a smaller pride, or more than one kill must be made.

The pride is not, as often popularly supposed, made up of a single lion lording it over his harem of females. It may be all male, all female or a mixture of the two. All-male prides are the most unusual and are generally rather loose associations of 2, 3 or 4 lions which prefer to consort with one another but often break up, at least temporarily, to join other prides or lionesses looking for mates. The most stable pride is one that is wholly or basically an association of adult lionesses, some perhaps with families, some without. They assist one another not only in hunting but in protecting and caring for the young. Such prides may be joined for short periods by one or two males, especially if one or more of the lionesses comes into season. The purely female pride is thus turned into a mixed one; but such prides may also simply be the natural outcome of the male and female cubs of one or more mothers growing up and remaining together. On the whole, lionesses are far more static than lions, which are more given to deserting the family or pride and joining others. Estes (1967) cites the case of one male that simultaneously dominated two prides. Though one lion may be hierarchically dominant there may be more than one adult male in a pride. Amongst the females themselves one always assumes the dominant role. When one dispassionately analyses the lion organization it becomes apparent that though it is the magnificent bearing and impressive roar of the male that have captured popular imagination it is in fact the lioness that is the backbone of the society. The pride is essentially a feminine unit; and, as will be seen later, it is mostly the lionesses that initiate and lead the hunt—though after the kill they may have to stand back while the males satisfy themselves; and it is the females that bring up and almost unaided train the future generations, which, later, often keep in touch with their mothers for several years. Apart from short bursts of intense activity when capturing and killing prey all lions are by nature rather indolent, displaying nothing of the inquisitive fussiness of the mongooses, the ceaseless playfulness of the otters, the vigorous hunting of the dogs, the earnest journeyings of the ratel or civet, or even much of purposeful prowling of the leopard. For the most part they prefer to lie about, doze or watch the world go by; and in this the lion itself excels the lioness.

In the normal course of events, that is to say with nocturnal, not daylight, hunting in view, the pride rouses itself from its lethargy in the late afternoon, the members walking round greeting one another by head rubbing (Estes, 1967). The cubs, and in a more restrained fashion the lionesses, but not the mature males, engage in good-humoured play, chasing one another, lying in ambush, springing out and tumbling one another over. Eventually, as the day draws to its close, the lionesses sit up and begin to stare at neighbouring herds of game with intensity as if weighing up the possibilities of a kill. They may sometimes climb into low trees to secure a better view. Eyesight, thus, plays a prominent part in the business of hunting, and the lion's eyes are, in fact, exceptionally large; but the sense of smell, though not so acute as in the canids, is also highly important and the wind is often tested with the nostrils for any message it may carry. It is the dominant lioness that takes the lead, decides if and when to move off and in what direction.

In popular imagination the lion always obtains its meal in one way: it stalks its prey and with a mighty roar leaps upon its back, clawing and biting the victim to death. Such a picture is only partly true. Lions, being lazy, will readily scavenge the kills of others if they get the chance, driving competitors away by their superior strength. Indeed, reversing the generally held notion, they not uncommonly let spotted hyaenas do the killing and then come in and rob them. To this end they are great observers of vultures in the sky—though if they have to travel any distance there may be little left of a carcass revealed in this way by the time they reach the site. Or, in the course of their wanderings they may come across a welcome meal by accident, a deserted fawn in the grass, a resting oribi taken by surprise, or a bustard suddenly flushed—to be immediately struck down with a sideways swipe of the paw. At times, instead of the usual hunt a warthog or aardvark may actually be dug out of its burrow. This is unusual for a felid; and it may entail considerable effort, Schaller (1972a) recording a case in which about 3 metres of tunnel were thus laid open. The same author twice saw a lioness pull a swimming gazelle from a river.

But the most usual forage certainly does entail stalking, though the climax to this, that is to say the kill, may be achieved in two different ways: a very close approach succeeded by a sudden rush; or a more distant approach followed by patient waiting in ambush for the prey itself to come near enough to be successfully attacked. Taking the prey almost completely unawares is an essential element of the lion's technique since the species is normally incapable of running far or for very long as fast as most ungulates can go once they have got into their stride. Hence the surprise spring is the lion's chief aim; or, as second best if it cannot get itself close enough for this, a very short run of not more than 50 to 100 metres at high speed—about 60 km/h—before the culminating leap. During such a run the body is held low, the tail stiffly erect. If the attack does not succeed, the lion never, or rarely, makes a second attempt since by that time an antelope would be well on its way to escape. However, Guggisberg (1963: 108) records an unusual chase which he witnessed covering about 500 metres.

The stalk, therefore, is vital. It is carried out in complete silence except possibly for an occasional low "*huh*" of suppressed tension, accompanied by a nervous flick of the tail, especially as the approach becomes nearer and the excitement mounts. The head and body are held low to the ground and movement is slow and gradual. The utmost use is made of the slightest cover; for, despite its bulk the lion is, when it wishes, a past-master at the art of merging into its background. It crouches motionless until it sees its chance of advancing further. With eyes never lifted from its prospective victim it waits until its prey's head is down in the grass, or until in the course of grazing the animal turns away and is badly placed to detect any movement as its attacker proceeds to its next cover. Should the prey itself get behind cover the stalking lion may take full advantage of this and, in no danger of being observed, carry out its next advance at a full trot. A stalk, therefore, may be a fairly continuous action if the cover is favourable and the prey not very alert; or it may resolve itself into a long-drawn-out affair punctuated by lengthy pauses whilst the lion with infinite patience motionless awaits its opportunities to advance. Approach to the prey is rarely made from the front since the risk of being observed, even with a cautious use of cover, is too great; but Schaller (1972a) did once see a lioness run directly towards some gazelles and capture one, but this direct onslaught was largely obscured by the lie of the land. In considering its attack the lion must, however, take the wind into account and with this factor in mind manoeuvre itself only so much to the rear of its intended prey as it can safely do without being in danger of alarming them by its scent. However, lions, like dogs, sometimes roll on their backs in dung or other odoriferous matter on the ground, and the only satisfactory explanation of such a habit would seem to be the instinct to disguise their own smell and thus render approach to their prey easier.

Lone lions must, of course, hunt for themselves; but where a pride is concerned it is usually believed that hunting is a co-operative affair. Nevertheless, this is not a matter upon which it is easy to be completely certain or about which there is unquestioned agreement. Where it appears that co-operation has taken place has there really been a common and well-understood plan of attack by several lions or has one, possibly more active and dominant, made a kill, the others watching and ready to take advantage of this animal's superior skill and energy? In a field study of the lion Estes (1967: 27) never witnessed co-operative hunting, though he agreed that it might occur and thought that perhaps the black patch on the back of the ears might assist visual contact between the members of a hunting party. Kruuk & Turner (1967) considered it at least doubtful that lions co-operate in hunting and thought it probable that each lion went its own way but took advantage of any situation arising from the action of its companions. A group might all stalk at the same time, keeping some distance apart; but this is not the same as a deliberately concerted plan of attack. There are, however, a good many accounts of hunts in which these animals, in Guggisberg's words (1963: 109) "show a high degree of co-operation and act with amazing strategy". This co-operation usually takes the form of stealthy approach by a group in open formation to a herd of grazing ungulates which are, at the correct moment deliberately alarmed from a given quarter by some of the aggressors and driven into the jaws of one or more strategically placed, concealed members of the pride who, as the fleeing animals pass, spring out of ambush upon an unsuspecting prey and effect an easy kill or kills. The rest of the pride then close in at a trot to enjoy a meal. Some accounts add the giving of a vocal signal when the whole ambush has been set up and all participants are in position.

Such a sequence of events may be deliberate. On the other hand, if the members of a large pride are sufficiently spread out on the hunt, slinking along under cover, each acting primarily for itself, it is virtually certain that at some point the prey will take alarm and there is a very good chance that the ensuing frightened stampede will inevitably pass within striking distance of some of the widely dispersed lions. Appearances are not always what they seem, and it is sometimes difficult to arrive at a correct interpretation of animal behaviour. Nevertheless, Schaller (1972a) is in no doubt that co-operation takes place and, in fact, brings 30 per cent success in the kill as contrasted with only 17 to 19 per cent for single stalking. Indeed, where really large or powerful prey is tackled, as it sometimes is, concerted approach and kill by two or more lions is generally essential.

One thing, however, seems certain; that in the vast majority of cases the lionesses take the most active part in hunting and killing. In fact, Schaller (1972a) records that in 71 hunts observed by him a male took the initiative in only two cases. This may be because it is tacitly recognised as falling to the female's duty to feed first its young and then later the adolescent or grown male; or that she naturally has more skill; or, being less cumbersome, is more agile and energetic; or, the common explanation, that the males are plainly lazy. Male prides must, of course, kill for themselves; but where a pride consists of both sexes the males, or at least those that are fully adult, follow the females well to the rear of a hunt, only running up when the kill has been made, often securing a major part of it. This in Schaller's view (1972a) has its advantages for the pride; for not only are the lionesses less conspicuous in the hunt but, in addition, large males in the rear may well discourage spotted hyaenas from making attempts to snatch the young while the attention of the females is concentrated elsewhere.

The aim of the lion in the majority of stalks is to get rather closer, if possible, to its intended prey than about 100 metres so that the ensuing rush from cover takes too brief a time for the victim to realize its danger and accelerate to its top speed. At 60 km an hour a lion would cover 100 metres in 6 seconds. It prefers, of course, to get so close that a single standing spring is sufficient to carry it onto the victim's back. In places, however, the terrain is so open that really close approach is not possible and the only hope of success lies in quietly waiting in ambush until grazing brings the herd within attacking distance. A remarkable degree of patience is sometimes called for—and exercised, as both Estes (1967) and Schaller (1972a) testify, the latter recording that a lion may wait as long as 9 hours. This, of course, can be very considerably shortened if the lion is not solitary and if, as asserted by many, concerted hunting takes place and the prey is deliberately driven into a tacitly understood ambush.

This raises the interesting matter of the reaction of prey to predators. Many observers have noted how quite unconcerned a herd of antelopes can be in the presence of potentially dangerous carnivores; and this applies as much to lions as to others. Antelopes instinctively know when lions are well-fed and not interested in them, or when they mean business. In the first case, while keeping a wary eye on them, they will go on grazing even though the lions may be only 100 metres away; in the second case they take alarm as soon as there is any movement and further lengthen the distance, though not a great deal, between themselves and their possible attackers—only far enough, indeed, to be able to keep the lions still in view (Krumbiegel, 1953). This is on the principle that what can be seen can be avoided; it is the surprise attack of the hidden foe that is to be feared. It has many times been asserted that lions roar to frighten antelopes and stampede them towards an ambush. Careful observation indicates that this is not true. Lions do not roar as a preface to a kill but afterwards, mostly as a means of announcing territory or of communication within the species itself. Estes (1967) found that game took no notice at all of lions roaring and played tape recordings 40 metres away from a herd of antelopes without exciting the least alarm.

Lions are widely regarded as feeding almost exclusively on antelopes or zebras; but though in certain parts of Africa this kind of prey may be the commonest they do, in fact, indulge in a very much wider range of diet, from the very large to the unexpectedly small. It is remarkable, too, that preferences clearly vary with locality, if not with individual prides. Goodwin (1953), writing of the Serengeti (Tanzania) reckoned that zebra was the favourite kill; Estes (1967) found that in the Ngorongoro crater, not far away, adult wildebeest came first with zebra second, the two between them accounting for over 90 per cent of the kills. On the other hand, Mitchell *et al.* (1965) show that in the Kafue National Park (Zambia) the lion's favourite prey was easily buffalo, 130 of them being taken as compared with 67 hartebeest, 30 zebra and 25 wildebeest. Choice must, of course, depend to some extent upon availability and in West Africa is very much more limited. Howell (1968) thinks that in western Nigeria Buffon's kob forms the main source of food; but further north in the region, in the drier zones, gazelle most likely play a more important role; and probably the ubiquitous warthog forms one of the commonest meals throughout the area. Other ungulate species which must with greater or lesser frequency fall prey to lions in West Africa are hartebeest, both western and Senegal, defassa waterbuck, reedbuck, bushbuck, oribi, duiker, buffalo and roan. The young of the larger species, Lord Derby's eland, giraffes, now rare, and hippo may also be taken as opportunity offers; but lions are very wary of attacking the adults of these, and usually find it too dangerous to attempt baby elephants. Nevertheless, anything is possible; and lions incontrovertibly sometimes co-operate in the final bringing to earth and killing of large prey that proves too strong for a single attacker. Vivid accounts have been given of fearful tussles between two or more lions and large victims, sometimes lasting a couple of hours. Schaller (1972a) described how five lions acted together in capturing, bringing down, turning over and killing a buffalo, though this was not so much a struggle as the co-operative finishing off of an already exhausted animal.

The species is not above stealing its meals from other animals, and one of the most unexpected surprises revealed by modern field research is how frequently lions feed from the kills of hyaenas, not, as usually believed, the other way round (Kruuk, various papers). The inter-relationship of the two species in the matter of killing and feeding is not always as simple and straightforward as it might from this appear—see page 368. Lions take a variety of foods besides the flesh of the ungulates; but these foods are scarcely deliberately hunted as antelopes are but are, save in exceptional cases, come across by accident. Whether a lion is interested in these smaller items depends on its degree of hunger, its lack of success in pursuit of better victims, its state of health and consequent ability or inability through sickness or age to deal with larger prey. Aardvarks, giant pangolins and crested porcupines are often taken, the last sometimes, as evidenced by residual quills, the cause of painful and incapacitating wounds in body or paws. Occasionally a grass monkey may fall as chance prey to a lion, but these animals are normally too wary and agile to be caught. Much smaller things are known to be taken from time to time: hares, ground squirrels, fat gerbils and other rodents; lizards, tortoises, pythons and lesser snakes; and even insects such as locusts or termites when they swarm. Terrestrial birds are often welcome, though the only one that forms a really satisfying meal, the ostrich, is now too rare to be of much account. And lions, like leopards, sometimes fish, capturing catfish, or others, from lakes or rivers with a sweep of the paw. Evidence of fruit eating is not very clear; but it has been said that they sometimes pick up fallen plums and berries and will eat groundnuts or even rotten wood; and that, like dogs, they eat grass to regulate their bowels. Lions are, indeed, not so exclusively noble in their choice of food as is often supposed; venison may be their common diet, but they sometimes take it when it is exceedingly rotten; they are not above cannibalism should one of the pride be killed; and, if pushed for a meal, will eat plain garbage from a village refuse heap.

Man-eating is a well-established fact. It is usually, though not invariably, carried out by old or sick lions. The reason for this is simple. Man, though equipped with a superior brain, is in comparison with the rest of the animal kingdom very inadequately provided in the matter of speed, strength, climbing capacity, sensitivity to smell and hearing, and other qualities vital to survival in the wild and is thus, unless he makes full use of his mental superiority, exceptionally poorly furnished to meet the challenge of cunning and determined carnivores lusting after his flesh. He is, in fact, when unarmed a singularly easy kill, well within the capacity of a sick or ageing lion. Moreover, lions are by nature indolent; and should by chance even healthy specimens discover how almost effortless a man kill is, they may well elect to continue exclusively with the same easily-obtained diet. Man-eaters have, indeed, been known to carry on their destruction week after week, causing the death of dozens of human-beings; and there have been several cases where villages or districts have had to be abandoned in the face of a persistent and relentless killer. Development projects opening up hitherto unpopulated areas have sometimes been brought to the verge of failure.

Next easiest to man himself comes domestic stock, which, often designedly kept in confinement, is thus unable to escape and is, in any case, ill-acquainted with the struggle for existence in the outside world. In West Africa the cattle, sheep and goats of nomadic herdsmen are particularly vulnerable being, in this case, quite unprotected by any fencing; but though from time to time losses occur (Howell, 1968) the lion population is in most areas so limited that predation does not constitute the constant and serious threat that it does in other parts of the continent. Even where dense and high fences of thorn trees have been built around more permanent farmsteads lions have commonly been known to leap or scramble over them and find their way out again burdened with a heavy carcass.

To sum up, idiosyncratic choice may possibly enter slightly into the question, but what lions live on, in fact, depends primarily on availability, and secondly on their own degree of skill. The former is basically determined by many ecological factors and may vary with the seasons; the latter depends on age, experience, inherent ability and the state of health. As Schaller (1972a) has pointed out the prey lies most commonly in the middle range of weight, small animals being rarely worth the effort, while really large species may well be too strong to tackle successfully. The latter difficulty may on occasions, but rarely, be overcome by co-operation in attack. There are numerous well-authenticated accounts of two or more lions entering into very prolonged struggles with adult elephants or, more commonly, hippos; but even then they may not succeed. Goodwin (1953) mentions the case of three lions attacking a hippo but being compelled to let go when their intended victim dragged them into the water. Kruuk & Turner (1967) thought that lone lionesses tended to kill smaller game than lone lions.

The methods by which lions actually bring about the death of their victims necessarily vary with circumstances; and there is, moreover, some evidence that there may be different fashions in different areas depending partly on the type of prey most commonly to be tackled in a district, and possibly partly on a continuing local tradition handed down through the instructional influence of pride mothers. Small prey, of the nature of the slower-moving mammals or ground-haunting birds, are struck and stunned or perhaps killed outright with a single blow of the paw followed if necessary with a quick bite. Swift-running ungulates have to be dealt with in quite another way; and even here it is obvious that there must be differences since an antelope of the size of a reedbuck or oribi must collapse at once under the sheer weight of its attacker whereas an animal of the size and strength of a hartebeest or waterbuck is not so immediately affected by bulk alone. The essential first move in a kill is to make effective contact with the victim, and this the lion brings about by a powerful leap, either standing from ambush or as the climax of a short approach run. This, of course, is quite different from the cheetah's method (see page 502). In dealing with the larger ungulates the lion generally aims to land not squarely on its victim's back but a little sideways upon the shoulder and flank, the hind-claws deeply embedded in the latter, one fore paw clutching the shoulder or neck on the far side of the body, the second one the chest or neck or, often, seizing the muzzle and twisting the head round. In the case of a running chase this may cause the prey to stumble and fall, and with the speed at which the crash takes place, the angle of the head and the extremely heavy weight on the antelope's back may well result in the latter breaking its neck. In the case of a standing leap on to a more or less stationary prey, or if, as the result of these tactics, there is no immediate collapse, the lion sinks its teeth into the neck vertebrae and spinal cord. Once the prey has come to the ground the lion, instead of the neck bite, seizes the throat of its victim and brings about death by suffocation in the manner of a cheetah.

Such is the standard pattern of effecting a kill; but there are, as always, exceptional happenings. Without becoming anecdotal it is not possible to detail these but the following briefly summarizes some of the commoner or more interesting observations that have been made. With medium-sized prey which draws sufficiently near to an ambush lions sometimes do not trouble, or find it necessary, to spring, merely rising onto their hind legs, seizing the animal with the forepaws and clawing it to the ground or giving it a bite in the cervical vetebrae. Hamstringing, that is to say severing the vital tendon of the hindleg, is a well-authenticated method of incapacitating such large and powerful prey as a fully-grown buffalo or eland, or even immature elephants. This may exceptionally be effected by a spring from ambush of a single lion but more usually calls for the co-operation of two or more attackers, some to occupy the head end of the prospective victim whilst another fastens its teeth into the vital place above the hock with a severing bite.

Possibly the most interesting variant in killing is recorded by Eloff (1964). This is seemingly employed only by the lions of the Kalahari (Botswana) but is worth a glance here with a view to stimulating careful observation in West Africa. In this subdesertic region of southern Africa the lions leap not upon the fore but upon the hind quarters and, as dissection has shown, by a combination of their own oppressive weight and an upward jerk of the victim's haunches break its back at its weakest point, that is between the last lumbar and first sacral vertebrae, snapping the spinal cord. Death is finally brought about in the usual fashion by a bite in the throat. This method is chiefly used with gemsbok, but horses, donkeys, cattle, blue wildebeest and eland have been observed killed in a similar way.

Real co-operation in killing, if not in hunting, certainly often takes place. The incident observed by Schaller (1972a) and mentioned earlier (page 475) may be cited as an example. In this, five lions worked together in bringing about the death of a bull buffalo that had already been badly mauled by another pride and was in no condition to put up any resistance. Nevertheless, the moves used by the lions formed a deliberate co-operative sequence. The first grabbed the victim by the rump; a second placed a paw over the back and bit the shoulder, bringing the buffalo to its knees. Two lions then pulled him onto his side, and, by manipulating a leg, turned him fully onto his back; a third bit the victim in the throat, whilst the fourth held the nose and mouth closed. The fifth lion did nothing very much. The whole affair took about 25 minutes; death by suffocation resulting in about 10 minutes.

Kills are sometimes multiple, a pride frequently killing more than one of the lesser antelopes at a time. Kruuk & Turner (1967) mention a lioness which killed four gazelles in one morning, two of them at a single rush. Achievement of a kill is by no means always so easy and there are accounts of prolonged struggles with powerful prey which may last as long as an hour or two during which the victim is lacerated by tooth and claw all over its body before finally succumbing, exhausted though not actually successfully bitten in a lethal spot. But an attack may go awry much earlier than this and never achieve a kill. If an immediate kill is not made it may, indeed, result in the death of the assailant from a forceful kick in the skull or the penetration of the body by a powerful sweep of a horn. Even porcupine quills have been known to be responsible for the death of a lion. At best, lions are far from being infallible killers. It has already been pointed out above how Schaller (1972a) reckoned that the success of stalks might be as low as 17 to 19 per cent for a single lion, increased to only 30 per cent by co-operation. The success rate for a single lion running at its prey he found to be as little as only 8 per cent. From the prey's point of view there is obviously more safety in standing clear of cover than grazing on the edge of the herd where an approach by an aggressor is far more likely to meet with success.

After a successful kill the lion or lions may be content to make a meal at the site in full view in the open or may drag the carcass to the protection of the light cover of a tangle of shrubs or of tall grass. This in the case of large and heavy prey may call for the exercise of tremendous muscular power. The first step in feeding may be to lick up any blood that is available; the belly is then ripped open, the intestines clawed out and sometimes, but by no means always, buried or at least covered by having earth scraped over them. Sometimes they are eaten; but always the tit-bits first consumed seem to be the liver, kidneys, spleen, lungs and heart. These disposed of, a start is made on the haunch, flank or breast. If there are any soft bones, such as ribs, they and the skin are eaten together with the flesh; but strong leg bones and the like are left. Behaviour to others during feeding varies very much since all lions possess different temperaments. Like other animals they may utter protective snarls while feeding and strike out at other lions which they may consider to threaten their own particular portion of the meal, or at hyaenas or jackals if these are foolhardy enough to attempt a theft. But while a number of lions or lionesses may feed together off a corpse—Goodwin (1953) observed six males to share one without quarrelling—it has been noticed that the females, although they have done the killing, may have to wait until the pride male has satisfied himself (Estes, 1967). The attitude adopted towards the young seems to vary considerably; but it has been said that lions are more tolerant towards them than are the lionesses, which may drive off hungry cubs and keep them waiting (Schaller, 1972a).

Lions, provided there is abundance, tend to gorge themselves at a meal until they are almost immobilized; their bellies hang low and heavily swing from side to side as their owners walk. At such times neighbouring antelopes become fully aware that they themselves then stand in no danger whatsoever. If the kill has been a small one it may be entirely consumed at a single sitting by the lion or pride responsible; but if it is larger and not fully disposed of the remains are often carefully guarded and used for a second, or even a third, meal. This is more easily achieved when a pride is concerned and turns can be taken to sleep, drink or defaecate; but even a single lion may stand guard over its kill for a long time. There are many thieves ready to pounce upon a deserted corpse, other felines, hyaenas, jackals and vultures. But a guard, or at least a successful guard, is not always kept. A single lion, having satisfied his immediate wants, has no recourse but to stand guard itself; and this is not always continuously possible for it must desert the carcass at least temporarily to drink or to defaecate. Further, a single lion may be driven off by a determined pack of hungry hyaenas, especially when he himself is well-fed and consequently lethargic and less aggressive. The problem of the lone animal may sometimes be increased by its own action; as already mentioned, Kruuk & Turner (1967) observed a solitary lioness to kill four gazelles in one morning, two of them at a single rush; but she ate only one. These same authors state that lions may stay for days with a kill, keeping hyaenas at bay and utilizing it to its utmost. The lone lion's problem is somewhat reduced by the fact of pretty rapid digestion and the ability, therefore, to make a second meal after no great interval.

Water is a very essential accompaniment to the lion's meal, and always immediately after feeding, or sometimes even in the middle of a long and heavy feast, these animals visit a stream or pool and drink deeply. This, when a pride is concerned, they do singly, not all together, so that there is always someone to guard the remains of the kill against marauders. Lions often drink at other times too, perhaps in the evening before setting out to hunt, or, more regularly, at the end of the night before retiring to rest during the day, irrespective of whether a meal has recently been taken or not.

After feeding, lions clean themselves up from blood left on the fur by licking, cat fashion. One lioness may do this to another lioness's face where it is more difficult for the animal's own tongue to reach; but with a lion the encircling mane makes attempts at cleaning up more difficult. Some cleaning of the face and coat is also carried out by rubbing with paws or on the ground, or rolling on the back.

How destructive are lions; how often do they feed; and how much do they eat? These are all questions which have only recently begun to be seriously studied; and the answers are still not very clear. It has already been pointed out above that lions can scarcely be regarded as highly efficient hunters in view of the fact that their success rate, even acting in consort as a pride, was found by Schaller (1972a) to be no greater than 30 per cent. They are, indeed, at least in East Africa, dependent to a very great extent on the energy and skill of other predators, notably the spotted hyaena, as Kruuk and others have revealed (see page 475). The situation is far from straightforward: lions may steal their meals from hyaenas, but the latter may perhaps sometimes make use of the lions to effect a kill (Estes, 1967). Careful scientific observation is only just beginning to replace hearsay and tradition, and we are merely on the fringe of appreciating the complexities of predation in Africa. One of the most unexpected discoveries is the extent of the reversal of the long-held belief of the roles of the lion and spotted hyaena as noble killer and despicable sneak-thief: Schaller (1972b) found that of 63 carcases on which lions were observed feeding no less than 81 per cent had been killed by hyaenas. This was for the Ngorongoro Crater (Tanzania); it is by no means certain that a comparable situation applies in western Africa, where the conditions of vegetation, abundance of animal life in general, and the concentration of ungulate herds in particular are almost everywhere in that region vastly removed from those existing in the east.

These are questions demanding local research; as, too, with Schaller's findings (1972c) on the differing effects of predation in general on the limitation of species: namely, that in Ngorongoro it was of no consequence for buffalo, nor an important factor for wildebeest, but has considerable effect on zebra and gazelle populations. These are matters which, with the greater interest now taken in the preservation of wild life, including increasing populations of lions, call for closer investigation and understanding in West Africa. It has been pointed out earlier in this work that predators are very quick to perceive any weakness in prospective prey, due to sickness or injury, and often select such subjects for their victims as easier to secure than animals in full vigour. Thus, while lions and other predators cause some destruction amongst the ungulates they not only preserve a reasonable balance of nature in a given locality and help to prevent overgrazing but, in fact, as Schaller (1972c) points out may very well actually benefit the prey species by weeding out the sick, old and generally less capable indviduals, keeping the herds healthy and alert.

To get down to figures, several estimates of how much lions eat in the course of a day or of a year have been made but vary widely; but some sort of an average can be arrived at as at least a better guide than a pure guess. The smallness of the amount of annual destruction attributable to a lion will probably come as something of a surprise to those who have given little thought to the matter. Figures derived from animals kept in captivity are no very good guide since such conditions call for the use of relatively little energy. In these circumstances they may consume something in the nature of 4 to 6 kg of meat a day. In the wild, however, a lion may need 6 per cent of its own weight a day (Krumbiegel, 1953), that is to say for a large lion something like 10 to 12 kg. But the matter is not arranged quite like this, for wild lions more often than not feed somewhat irregularly, gorging themselves for one, two or three days, then going for as long without killing or eating. At such a feast a healthy fullgrown lion may get through as much as 20 to 30 kg—and then not very long after come back for more. Perhaps a better way of looking at the question is to estimate how much destruction a lion may cause amongst the ungulates in a year. No exact enumerations over long periods have been possible; but a number of authors from observations made in eastern and southern Africa have given fairly closely reasoned estimates based on the short-term behaviour of a pride. These in sum boil down to the likelihood that a single lion is responsible for the death of something between a dozen and a score of prey animals in a year. This, of course, is in a way fairly meaningless since the victims vary considerably in bulk from, say, a large bull buffalo or eland to a gazelle; but it is intended to represent animals of average size from the mixture of prey upon which lions commonly feed. Surprisingly low as it is it would be still smaller were only large prey such as wildebeest or zebra continuously concerned. On the other hand this mean figure for animals destroyed annually must almost certainly be somewhat higher for West Africa since large prey species are there relatively uncommon, and much greater dependence must rest upon the smaller sorts of antelope, warthog, and probably a good deal of much lesser fry. Solitary lions, because of the difficulty with which they are faced in guarding their kills, almost certainly feed less efficiently than a pride and are forced into killing at a higher rate. But what they themselves do not consume of their kills goes to satisfy other predators, so that in sum the total of destruction of prey species works out at much the same. It is said that man-eating alters a lion's whole attitude towards guarding its kills, and that it never returns to the remains of a human corpse, or for that matter to any other once it has taken up this habit (Goodwin, 1953).

Lions are large and powerful enough not to fear attack in the ordinary course of events from any single animal other than man. Nevertheless, they do on occasion find themselves faced with dangerous opponents and are sometimes killed by them. Their commonest enemies in the competition for food are spotted hyaenas, though in this struggle the lion stands in no actual danger of its life. The conflict is one which turns in favour of one side or the other according to circumstances. It has already been mentioned above that a determined and angry pack of hyaenas may scare a lioness off her kill—or sometimes more than one lioness; but Estes (1967) once witnessed how a fully-grown male lion could restore the situation and drive the hyaenas from their stolen meal and allow the cowed lionesses to return—and, indeed, even permit them to eat their fill before he himself fed. Yet the conflict may start earlier than this especially where large prey species are concerned. Spotted hyaenas may closely trail a hunting lioness, carefully following her at a distance as she, her attention concentrated on her prospective victim, stalks her prey unaware of their interest in her. Should her ultimate attack prove immediately successful in bringing her prey crashing to the ground the hyaenas rush in and, if she is really solitary, drive her from her kill; but if she leaps upon the prey's flank, grasping its head, and the victim does not fall at once but is strong enough to continue galloping over some distance the hyaenas may close in, tearing at its hindquarters until the lioness becomes so disconcerted at this unlooked-for turn of events that she lets go and jumps clear (Estes, 1967). The prospective victim would then be followed by the hyaenas to which, partially disabled and exhausted as it must surely be, it falls an easy victim. Thus hyaenas may at times make use of the superior strength of the lion; but the reverse side of the picture, detailed earlier herein, must not be forgotten, where the lion, apparently far more frequently, makes use of the energy and hunting skill of hyaenas.

Apart from the ever-present competition of hyaenas, lions may in their search for food find themselves in difficulties from other sources. If attack on some of their more powerful prey—the larger antelopes, buffalo or zebra—is not executed with sufficient surprise or skill, as may happen with young and relatively inexperienced lions, the aggressor may find itself impaled by a horn or badly injured or even with its skull fatally fractured by a powerful kick. Baby elephants have been attacked by lions, sometimes successfully, but sometimes with dire results for the attackers from an infuriated cow coming to her offspring's defence. Estes (1967) records a case of a lioness that made an attempt upon a rhino calf and was killed by the mother. Less spectacular than such battles but no less fatal for the lion is when a young animal not yet in its full strength drinking at a stream is seized in the muzzle by a crocodile, dragged into the water and drowned. Such reptilian attacks do not always succeed.

As regards its attitude towards other animals not strictly in the prey class, a lion may on occasion attack other large carnivores. This as a rule is in response to some real or imagined threat, possibly to its cubs; but need not always be so. Guggisberg (1963) relates how a family of ten lions came across an old sleeping cheetah and killed him. Edmond-Blanc (1957) cites the case of a lioness, probably in defence of her newly-born young, attacking a fully-grown leopard; and others have noted much the same sort of thing. Their attitude towards their own kind is mostly remarkably tolerant, but from time to time lions and lionesses have been known to kill each other, mostly in cases of trespass (Guggisberg, 1963; Schenkel, 1966).

This raises the question of territory. Despite the amount of observation that has been devoted to lions nothing very definite has so far emerged on this matter in any part of Africa. The fact is that, apart from the difficulty of checking such ill-defined boundaries as may be involved and of estimating large areas, the matter is not entirely straightforward in this species, where factors of sex and varying social habits play important parts. Guggisberg (1963: 148) expressed the view that there is a fundamental difference between the territories of female and male lions; and this is so since lionesses are appreciably more sedentary than lions, which are often frankly nomadic, ranging over relatively large areas. But there are other complexities. There is, for example, the difference in requirement between a single lion, a single lioness, a lioness with cubs, a pride of lionesses, a mixed pride, large or small. There is also the very basic factor of the density of prey species in a given area; quite obviously where, in parts of East Africa, there are abundant herds of game there is no need for lions to concern themselves with large areas such as would have to be hunted over in, say, much of West Africa where prey may be reckoned in scores rather than in hundreds or even thousands. It is clear that estimates of territorial size made in Tanzania can have little application to the region covered by this present work. Further, where the density of lion population is itself high there is a need for the limitation of hunting territory and the fairly strict observance of boundaries; in West Africa, where by comparison lions are few and far between, a pride may seek for food quite undeterred over very wide and possibly undefined areas. Such a situation may change in the course of years as both game and predators become more abundant and concentrated in the restricted areas of national parks.

However, for what they are worth as some rough indication of the sort of position found to exist in other parts of the continent, these figures may be quoted: Krumbiegel (1953) recorded that in the Kruger National Park (South Africa) a lion needed about 15 sq km of territory; Schenkel (1966) estimated the home range in Nairobi National Park as being from 25 to 50 sq km; and Schaller (1972a), for Ngorongoro, Tanzania, found that a pride of lionesses might have a territory of anything between 20 and 400 sq km, and that nomads might roam over as much as 4000 sq km. As this last author points out, one of the great benefits of a fixed and not too large territory is the acquisition by all members of the pride of an intimate knowledge of its topography, and this gives advantage in hunting not only in knowing the favoured grazing grounds, drinking points and probable movement of herds but also in becoming closely acquainted with every scrap of cover, major or minor, which the lie of the land and vegetation offer.

Where territories exist their boundaries must be demarcated and guarded. Scent-marking by urination is the method used by lions. Schenkel (1966) noticed that this was effected in two ways; by squirting urine upwards into the branches of bushes where it would remain evident at head height, emphatically registering ownership at that particular point of the boundary; or by squirting it downwards onto the ground and trampling in it so that the paws subsequently leave a trail of ownership along the path taken. A less permanent but more impressive way of declaring occupancy is for the pride leaders to stand on some slight eminence and roar; and this, indeed, is probably the main purpose of the lion's famous deep-throated, far-reaching roar—not to announce that the animal is on the hunt or to frighten game, as often said; for this, by alerting its prey would, in fact, deprive the lion of the most essential element of its attack, surprise.

Territories are not always strictly respected, and may sometimes even overlap (Schaller, 1972a); but intruders are frightened off if possible by aggressive behaviour, though as a last resort recourse may be had to fighting and possibly killing. Awareness of rightful possession gives to the owner a feeling of confidence often obviously exhibited in its bearing; and the reverse is true of intruders, which are apt to behave in a guilty, morally inferior manner which as often as not renders their expulsion without actually fighting easy; or, should it come to combat, victory over them more readily achieved. In this connexion Schenkel (1966) observed that while lions may not avoid territories belonging to other prides, if they do trespass they become wary to an unwonted degree. He once observed two lionesses and a half-grown male to make a kill within the territory of another pride; but they made no attempt to start eating until they had carefully scrutinized the surroundings to make sure that the real owners were not about in the neighbourhood. When lions acquire the wandering habit, mostly males, they often travel very far indeed, though, in fact, little positive research has been done into this. But they appear to be received into other prides mostly without much question; and it would seem that this must depend upon there being females in season ready to welcome them as mates. There are also, though much more rarely, nomadic females; but these make poor mothers.

It has been said above that the main purpose of the lion's roar is to assert ownership of a territory; but there is, in fact, some disagreement over the use of this the best known of the lion's vocalizations. Goodwin (1953), for example, wrote that deep guttural roaring starts at sunset and continues up to the kill; others have told of roaring continuing throughout the night; and some of its being used after a kill as a paean of triumph—or more probably to announce success to the rest of the pride and gather them to the meal. While roaring may well be carried out in the early evening to warn other lions away from a hunting territory its use as a preliminary to the hunt itself seems improbable since it would serve to alert all game within a considerable distance. The roar, which is performed with the head lowered so that the sound is deflected upwards off the ground, may in fact carry a mile or even two according to weather conditions and topography. Other vocalizations are a grunt uttered when charging; and a similar sort of repeated grunt in five or six stages of crescendo under the influence of mild excitement, sometimes ending in a sigh due to the eventual intake of breath. In defence of itself, its young or its food the lion utters deep warning growls which, if they prove ineffective, may be increased to a semi-roar. The teeth are bared, the lips being drawn back, and the ears laid flat and turned so that, in the female, the black marks on their backs are exposed. In a previous section it has been explained that lions are enabled to roar loudly because of the specialized elastic bone structure in the throat permitting a 50 per cent expansion of the vocal chords. This structure inhibits the rapidly vibrating purr of the smaller cats, though a throaty rumbling can be achieved. In areas in which they sense themselves in considerable danger from persistent hunting by human beings—as for example in the case of man-eaters—lions cease to draw attention to themselves by roaring.

When the lion goes about affairs of an unimportant nature it does so at an easy, sedate walk; when in more of a hurry it breaks into a relatively rapid trot, which it can if necessary maintain over some distance. Both the easy walk and the business-like trot may, as well as the slow, painstaking slink, be used in approaching prospective prey; the trot being employed mostly in the early stages when at a distance, but also, more rarely, at closer quarters when the cover is so favourable that the intended victim is in no position to detect rapid movement. The lion's most purposeful gait is the gallop. This is carried out in the usual feline fashion of both fore and hindfeet used approximately as pairs, alternating in their contact with the ground. It may reach a speed of some 55 to 60 km an hour but normally cannot be maintained for much more than about 100 metres, that is to say for 6 or 7 seconds. As the speed of most of its quarry is of the order of 65 km an hour the necessity of surprise and of accelerating to maximum speed before the prey has had time to react to attack is obvious.

The final approach to the victim is a spring, a movement calling for the lion's extreme muscular power, executed with the claws extended, as with an athlete's nailed shoes, leaving their marks obviously in the soil at the point of take off. This, of course, is a running jump; as a standing jump it is said that this species can cover 12 metres in length and reach a vertical landing place nearly 4 metres high (Guggisberg, 1963). There is good evidence that in cases of necessity, such as withdrawing with killed prey from a fenced enclosure, a lion can leap a couple of metres, possibly in two stages, carrying a corpse weighing perhaps 300 kg, the body, at least sometimes, supported across its back.

The spoor of a lion is, of course, larger than that of any other African carnivore but, strangely in view of the great discrepancy in body size, not as much bigger than that of a leopard as might be expected. The feet are, indeed, short, broad, compact and difficult to spread; and in the forefeet the webs reach almost to the distal ends of the digital pads, but in the hindfeet are less extensive. The spoor of the sexes can be told apart because in lionesses the fore and hindfeet are subequal in size, whereas in the males the forefeet are bigger than the hind. In a large lion the mark left by a forepaw may measure some 120 mm across and about 110 from front to rear; hindpaws and females are about 10 mm less. The middle subdigital pads show in the footprint as long narrow ovals, 45 × 20 mm, the two outside ones shorter and broader, 35 × 25 mm; the central pad is roughly triangular with very blunt rounded corners, and a hind-margin that is often concave. It measures in the male roughly 80 × 60 mm. In soft ground the print left by the spreading foot of a spotted hyaena measures not a great deal less but differs markedly in exhibiting long claw marks, absent from the lion except at the point of take off for a leap.

Lion cubs are tolerably good climbers, starting at a fairly early age on trees with sloping trunks in the shade of which their parents may be resting. While it is a common thing for adult lionesses to climb to, and lie along, the lower branches of small trees it is often held that they never climb higher, being unwilling, possibly, to trust their heavy weight to the smaller upper branches. However, in this as in other matters of behaviour lions differ individually; and while some, doubtless, make no attempt to climb, others have been seen relatively high up, as much as 10 metres above ground. This may be sometimes apparently only to survey the countryside for game, cheetah fashion; but cases are recorded where a lion has climbed high in order to rob a leopard's larder, Schaller (1972b) having witnessed no less than three such instances. Lions not infrequently stand upright on their hindlegs at the base of a tree, stretching their forelegs up the bole, scratching at the bark in the action commonly known as "sharpening its claws"—though this seems more likely to blunt the fine points than the reverse. Lions are also competent swimmers, taking readily to water if necessary and crossing rivers 30 metres wide without difficulty.

Lions may occasionally be monogamous but are much more commonly polygamous. A lion may remain faithful to a lioness, or to the lionesses of a pride, for some years; others are given to wandering far afield seeking new mates, or possibly to establish themselves for the first time as eligible partners. Visiting lions may sometimes become involved in scuffles, which occasionally may develop into something more serious resulting in the death of one of the contestants; but within the pride there is little or no interference by the others with the mating of the dominant male. Despite various general claims to the contrary, no favoured period of the year for mating has been clearly established. Lionesses can come into season about every three months, or somewhat less, and remain on heat for some four days, the last of which appears to be the critical one for conception. During this time they emit a powerful odour and announce their readiness for coupling far and wide by spraying their urine over shrubs, grass tufts and the like. Such advertisement may not be of much moment within a mixed pride but is important in prides consisting of females alone or accompanied only by their last litters. Apart from any preliminary dispute there may be for her possession there is little display or noise; the chosen male follows his prospective partner about closely for some time, nose to tail, and occasionally licks her. Eventually she lies down on her belly in the crouching position, the lion straddles her with his forelegs and effects penetration from behind. This may take place in a secluded spot or in full view of the pride; and it may happen by day or by night. The act is repeated three or four times in fairly rapid succession at intervals of from 10 to 20 minutes. According to Dathe (1947) the lion bites the lioness in the back of the neck only at the moment of ejaculation. He utters occasional growls.

The period of gestation is generally between 105 and 108 days, but as long as 112 days has been recorded. This discrepancy might be accounted for by the observation having possibly been reckoned from a mating on the first day of a lioness's four-day season whereas fertilization takes place only on the last day. As her time approaches the prospective mother seeks out a secluded spot a little removed from her pride amongst dense undergrowth or rocks should these be available. Here she gives birth usually to between 2 and 5 cubs, 3 being perhaps the commonest number. According to Krumbiegel (1952) as many as 9 in a litter have been known. Mitchell *et al.* (1965) found the sex ratio to be 1 male to 1·73 females.

Schenkel (1966) furnishes details of the early days and development of wild litters in Nairobi National Park; and Hopkins (1968) a seemingly unique account for West Africa of hand-raising orphaned cubs in Nigeria. There are numerous other less detailed field observations from East and South Africa; and records of birth and development in zoos, though the latter may not, of course, necessarily be typical of what takes place amongst wild populations. The cubs may apparently be born either with their eyes closed or with them open (Guggisberg, 1963); but as information regarding this obviously emanates almost entirely from zoos the latter condition may possibly be the outcome of unnatural circumstances. According to Goodwin (1953) in the Serengeti the eyes are closed at birth and do not open until the 6th to 9th day. When they do open they are blue and cloudy and obviously not fully functional for some time. The length of the new-born cub is of the order of 300 mm; its weight between 1·0 and 1·75 kg. The head is rounded, the ears small, the tail relatively shorter than in the adult, the coat soft and usually heavily dark-spotted; but cases are known where the spots have been almost completely lacking.

Hopkins (1968) furnishes details of early development as exhibited by a wild West African lion cub hand-reared in Nigeria. In this animal eruption of teeth took place in the mandible a few days before the corresponding ones in the upper jaw. At 3 weeks 4 incisors were visible top and bottom. At this age, too, the cub started to drink water and was steady on its legs but could not walk far, though at 6 weeks it could run. The lower canines appeared in the 4th week; and at about the same time the eyes started to lose their blue hazy look and become brown with a black pupil, the whole process of clearing taking about a couple of weeks. The voice at this stage was a staccato mew. At 8 weeks the first, lower, premolar developed and the cub evinced an interest in solid food; at 12 weeks it tore at chunks of meat, though the carnassials did not, in fact, appear until the 15th week. The black end to the tail also developed rapidly at this time; but a photo demonstrates that there is nothing of the adult contrast between long tuft and close-haired shaft but that the whole structure is still woolly throughout. According to Hopkins the growth curve was fairly regular up to a weight of 18 kg at 19 weeks. At the age of 4 months the cub could run fast and leap.

So much for physical development in circumstances of careful hand-rearing; some data regarding social and behavioural advancement in the wild can be assembled from the observations of various authors. A few days after giving birth the mother, unless she is a lone female, rejoins her pride for a period or periods every day; but the cubs remain deeply hidden and the other lions make no attempt to go near them. She is, of course, compelled to leave them from the necessity of feeding herself, which she may do by taking part in pride activities or, if she is solitary, hunting for herself. Such periods of absence are times of danger for the helpless cubs; for no matter how well hidden they may be their scent may give them away to other marauding carnivores, perhaps especially hyaenas. This period during which the cubs are daily, or nightly, at high risk through the enforced absences of their mother may last for some weeks. It may be added here that while most lionesses are excellent mothers there are unquestionably some that are very bad and deliberately desert their young.

At the end of three or four weeks, when the infant lions have grown sufficiently strong to be able to get about, the mother on returning from her excursions to the hiding place summons her cubs with a gentle roar, and they hasten to welcome her, scrambling out of the nest uttering high-pitched answering squeaks, and when they reach her rubbing their heads against her muzzle and legs in a greeting ceremony (Schenkel, 1966). She in her turn licks them and, in the early days, permits them to suck, sometimes lying actually on her back to allow them to do this; but at a later stage of advancement she may present them with some small animal she has brought. They then play together in the open, the cubs amongst themselves with mock-fighting, tumbling each other over or wrestling; or with their mother by clambering over her or playing with her tail, which she flicks from side to side, while she responds with soft taps of her paws or pokes with her nose. When the young are feeding from the breast they mould it with their paws in a manner commonly seen in domestic cats and dogs.

According to Schenkel the cubs are introduced to the pride when they are about 10 weeks old, and they are then treated by the other lions with tolerance and apparent affection—though response to their playful advances may be colder on the part of adult lions than by the lionesses and younger members. Thenceforward, during their mother's absence they may be guarded for some of the time by other females; and such care may extend also to suckling them by such as are in milk. Indeed, cubs from two or more different litters, and perhaps of quite different ages, may feed side by side off a single lioness. The amount of communal care is, indeed, remarkable and at this stage is almost completely devoid of jealous squabbling. However, the mother always returns her cubs to their own hide-out, the original birth place being, according to Schenkel (1966) retained as this for some two or three months, the location of the retreat thereafter being changed every four to six days. This last has the advantage not only of putting possible predators off the track but, probably more importantly, also of gradually widening the young lions' knowledge of the topography of their pride's territory. Two or three weeks after their introduction to the pride, when they have become well acquainted with the others as well as stronger from rough-and-tumble play with young adults, they accompany their elders on hunting expeditions and thus, from the early age of about three months, start to observe essential techniques and acquire a wider knowledge still of the terrain. At a kill they are almost always allowed to be amongst the first to feed; but the adoption of a meat diet does not mean the cessation of breast feeding, and it is no unusual thing for young lions to make a heavy meal at a kill and then persuade their mother to give suck. Weaning starts at about 6 months; but cubs commonly go on attempting to suck up to perhaps 10 months, though the milk may have dried up some time before this. Play at this stage, in conjunction with the other members of the pride, becomes more purposeful, losing its mere kittenish abandon for actions essential to success in later life: crouching both to hide and to spring, sudden pounces upon the back, aimed sweeps of the forepaws, and biting in the neck.

Development is, of course, continuous; but from about the 10th month important changes are observable. At this time the juvenile pattern of spots, save in very exceptional cases, has largely vanished from the back and flanks; and when the cubs are a year old the milk dentition is replaced and the whole body begins to throw off its childish look and take on the undoubted appearance of a young adult. Up to this period, although there has been some freedom to come and go amongst the pride and to take part in its activities, this has nevertheless for the most part been very much under the eye and protection of the mother. From now on, though she still takes them with her and tries to inculcate upon them the correct techniques of hunting and killing, they gain ever more and more self-confidence in this and other matters, becoming fully independent individuals at about 18 months. The lioness may then remate, or she may have already done so and be more concerned about the birth of a new litter than with her existing one. Two litters in one year have been recorded. However this may be, at the same time as the youngsters gain independence the attitude of the pride changes towards them; and from being favoured members of the society they now receive no further special treatment but have to learn their place and show due respect to their elders. These, instead of allowing them privileged access to a kill, may as often as not drive them away, compelling them to take a low place in the feeding order, and even at times to go hungry. It is without question a very trying period for adolescent lions; one, indeed, which has sometimes fatal results. There is the danger of loss of strength and vitality through under-nourishment at a time of still very active growth and large appetites; and of injury arising from lack of expertise in hunting, as well as from the fierce repulsion by senior members of the pride themselves. One observer has drawn attention to the number of young one-eyed lions probably the result of angry swipes by impatient adults at this stage.

The difficulty of establishing themselves fully into the pride is often the reason for young lions leaving it and striking out on their own; but their relative inexperience in hunting, apart from risk, may bring such low success that they face feeding difficulties as great as those they have left behind. It is not until they are about five or even six years old that lions attain their prime, though sexual maturity may be reached at four. In the males the mane, which may show its first signs of growth at about 18 months, attains a fair size at 3 years but goes on increasing in luxuriance for twice this time. Thereafter it may darken in colour from the increase in the number of black hairs in it until at length these may dominate—though of this eventual blackening nothing is recorded for West Africa. The sex link of this structure is nicely illustrated by the fact that a castrated lion lost its mane. In captivity lions have been known to live for almost 30 years, though this is an exceptional figure. Of their life-span in the wild nothing is known but almost certainly never reaches anything like that under sheltered conditions.

At one time, not so very long ago, the successful breeding of lions in zoos was regarded as something unusual and a matter for congratulation. In recent years, however, with a better understanding of basic requirements it has been found that they are capable of breeding very freely in captivity; so much so, in fact, that their potentiality in this respect has sometimes become a source of embarrassment. Litters may be of large size, 5, 7, 9; and the care with which the cubs are treated and sheltered from harm ensures a survival rate far in excess of what must prevail in nature. There is no doubt that under natural conditions there is, despite the watchfulness of the majority of mothers, a tolerably high rate of mortality from predators, accident and disease in cubs and young adolescents up to the age of two years or more. There may, indeed, be as little as a 50–50 average chance of survival to becoming a parent; but the death-rate is doubtless higher as regards large litters than where there are only one or two cubs. The weights of 7 cubs born at Arnhem Zoo in 1964 at the end of 6 weeks were: 2 males 5·5 to 6·3 kg; 5 females 3·5 to 4·8 kg (van Hoof, 1965). In zoos, crosses of lions with other big cats have sometimes been successfully made. Pocock (1908a) records a lion-leopard-jaguar cross; and one between a leopard and a lioness, resulting in two cubs, took place in Japan in 1959. No such thing as this is ever likely in nature.

Taxonomy. The generic status of the lion has already been gone into earlier in this work (page 437 *et seq.*), and it remains here to consider the question of specific and subspecific division. It was at one time believed that Asiatic and African lions represented different species; and at times it has been held that within Africa itself differences were such as to merit yet further distinction at this level. Such opinions are no longer current, and it is generally appreciated that throughout the major duration of their history there has been little practical isolation of the Asian from the African lions (Mazak, 1964b); and that variations of colour or size have certainly neither the degree nor constancy necessary to warrant differentiation at specific level.

The position at subspecific level is rather more in dispute. G. M. Allen (1939) accepted 10 African races; but it is now recognised that the grounds on which at least some of these were founded are very shaky. The characters used in diagnosis have been colour of both body and mane, together with size, particularly of skull and teeth; and most modern authors and field observers are emphatic that all these are highly inconstant. Pocock (1945) writing of the few remaining Asiatic lions, now limited to north-west India, observed that the variation "within the confined limits of the Gir forest covers that of the lions of the whole of Central Africa which have been assigned to several subspecies largely on differences of colour". As regards morphology, J. A. Allen (1924) found the teeth of African lions extremely variable in size and form in both sexes, there being a variation in length and breadth of from 11 to 15·7 per cent. "These statistics indicate that cranial and dental characters are not so stable a basis for the discrimination of regional forms as has been often assumed . . .".

There is abundant other testimony to the high variability of lions in single localities; and the present author is not convinced that it is possible to draw useful taxonomic distinctions between the lions of different areas. Roberts (1951) thought that because of the lion's habit of wandering local forms do not become stabilized; but if large areas were taken into consideration recognisable differences do exist. Unless the provenance is known it seems virtually impossible to assign a specimen certainly to any particular race. Nevertheless, it can be argued that mean differences exist and have their taxonomic value. In spite of his findings quoted above regarding the inconstancy of commonly used morphological characters J. A. Allen (1924) aimed to differentiate the lions of different localities by their mean measurements. To the present writer this does not appear very convincing; but it is fair to add, however, that Allen took a widely different view and, writing of the four geographic races he sought to establish, asserted that the two extremes of them were "not only widely separated geographically and environmentally, but appreciably in size and so strikingly in coloration that if one had to deal with them separately, or without the connecting intermediates, it might seem reasonable to consider them as specifically separable".

Be that as it may, the amount of material available from West Africa is so limited and so poor that it is impossible to draw from it reasonable conclusions as to the existence of valid races. Of the two that are commonly held to occur in the region covered by this present work the following may be said. Exactly what *senegalensis* is and whether there is any valid difference between it and what Linnaeus described as *leo* it is not really possible to determine; and, apart from reputed colour distinction—notoriously inconstant, and in this case founded on a single skin—Matschie's diagnosis of *kamptzi* depends on the comparison of complex and rather artificial ratios in cranial and dental measurements that have no real taxonomic worth. The five West African study specimens available in the British Museum exhibit a fairly wide range of colour, the one constant factor being the bright orangey colour in the manes of two of them. Jeannin (1936) with wide field experience found himself unable to distinguish races and asserted that he had come across lions in Cameroun that corresponded to the four reputed subspecies *senegalensis*, *kamptzi*, *somaliensis* and *massaica*. Obviously the position is such that, at any rate in the opinion of the present author, any attempt to distinguish West African lions more finely than as *Felis leo* and relate them to reputed subspecies would be to claim an accuracy and a knowledge not warranted by the existing study material and unrealistic racial diagnoses.

However, it may be of interest to record here the appearance of the specimens which at present exist in the British Museum.

B.M. No. 21.10.7.1, ♂. Tambana (Gambia). Sudan or Guinea woodland. This is basically of a brownish hue but is considerably darkened by heavy speckling with black-tipped hairs. There is no mane or elbow tufts; and no reversal of fur on the back. The skin is in poor condition with large gunshot wounds and slit-like scars. This has no study skull; the measurements which are given below are those of a young adult from Tambana (Gambia).

B.M. No. 30.4.7.1, ♂. Upper Volta. Sudan woodland. This is very greyish-sandy—a much greyer skin than any of the others. There is no sign of a mane, and no elbow tufts; the dorsal fur is reversed.

B.M. No. 46.387, ♂. Tamale (Ghana). Doka woodland. This has a greyish-sandy colour. There is a not very abundant mane of a bright orangey-ginger colour; no elbow tufts; dorsal hair reversed.

B.M. No. 48.762, ♂. Ogoja Province (eastern Nigeria). ? Guinea woodland. This agrees fairly well in pelage and mane colour with the previous (Ghana) specimen, but only a mere remnant of the mane, on the side of the face, exists. There are no elbow tufts; the whole specimen in very poor condition.

B.M. No. 71.1754, ♀. Nigeria. Vegetation unknown. This is of a sandy colour, a shade paler, having slightly less reddish tinge than the two previous specimens (Ghana and Ogoja); perhaps faded since, though in fair condition, it is mounted as a rug. Skull in the mount.

Table 30: Numerical data for *Panthera leo*

	Gambia, ♂ No. 21.7.23.1
Vegetation	? Sudan
Number in mean	1
Condylobasal length	310
Basilar length	284
Palatilar length	148
Zygomatic breadth	229
Upper cheekteeth breadth	128
Nasals, length	94
Interorbital breadth	69·5
Postorbital constriction	60·1
Braincase breadth	106
Toothrow (c—m^1)	115
p^4 length	37·7
m^1 breadth	12·2
m_1 length	27·3
RATIOS (per cent)	
Zygom. br./condylob. l.	74
Braincase/condylob. l.	34
Braincase/zygom. br.	46
Palatilar l./condylob. l.	48
Interorb./postorb.	115
p^4/c—m^1	32·8

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, *Naturliches System der Amphibien, etc.*: 30. Type species *Felis jubata* Schreber. This name is from the Greek *cyon, cynos* 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, cynos* 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 Hilzheimer (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. Hilzheimer, 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 *fide* 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 soemmeringii 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 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. 65. *Acinonyx jubatus*: skull, B.M. No. 32.12.27.1, ♂, × $\frac{4}{5}$; lateral view

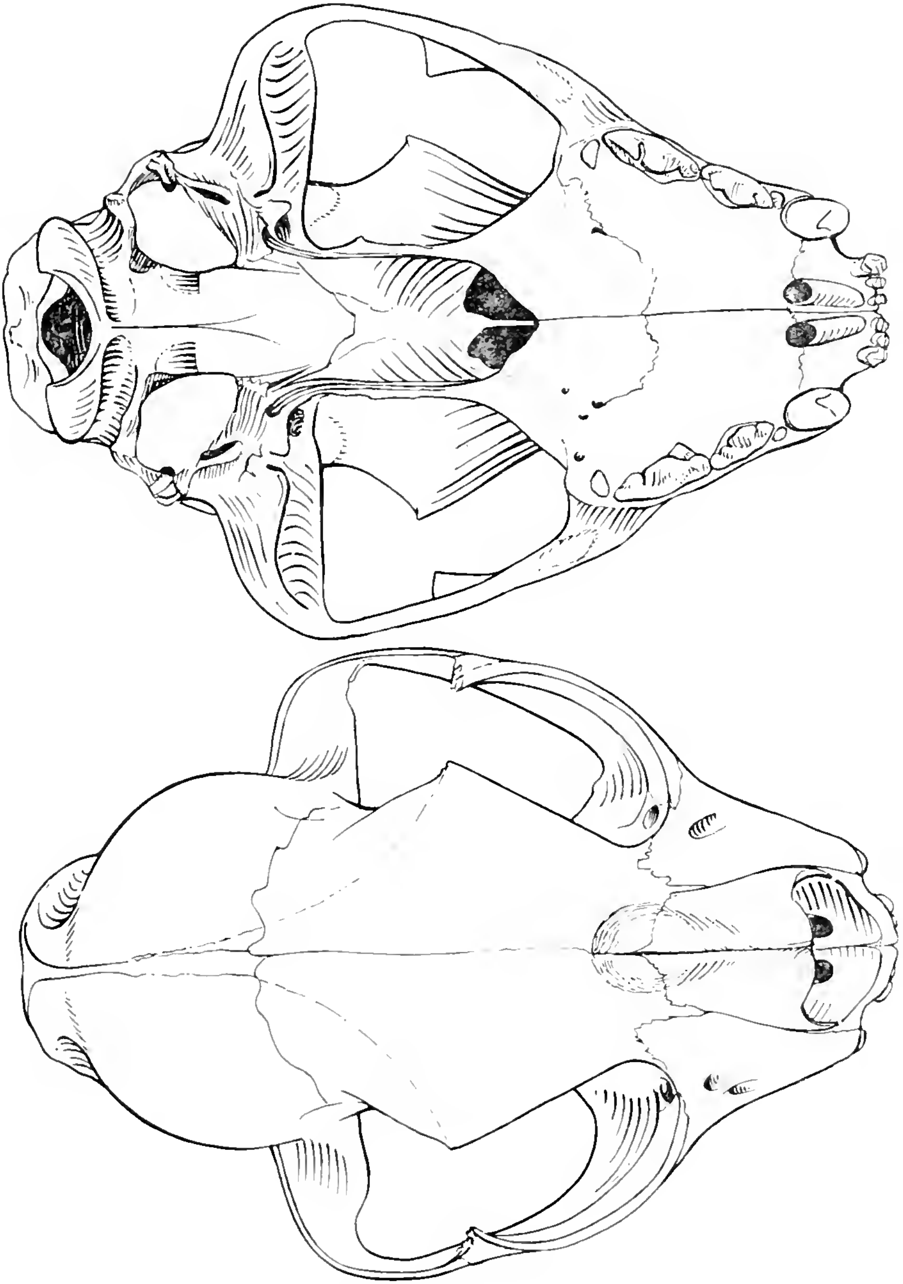


Fig. 66. *Acinonyx jubatus*: skull, B.M. No. 32.12.27.1, ♀, × $\frac{4}{5}$; palatal & dorsal views

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 *Lycaon*, 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 severence 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 overtoppling 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 conflictions—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 8½ kg at 5½ 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 3½ 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 Fitzinger'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	Lake Chad	Uganda
Vegetation	Sudan	Sahel	?Sudan
Number in mean	1	1	1
Condylobasal 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.

GLOSSARY OF TERMS

alveolus	Tooth socket.
anterior	To the front; foremost; furthest from the tail.
antitragus	A lobe, sometimes emarginate, near the base of the outer margin of the ear pinna.
auditory bulla	See bulla.
auditory meatus	The external orifice of the ear; the earhole.
basal length	The distance from the most anterior margin of the foramen magnum to the anterior limit of the premaxilla (i.e. exterior to the incisors).
basilar length	The distance from the most anterior part of the foramen magnum to the anterior margin of the palate (i.e. interior to the incisors).
bifid	Divided into two parts by a notch.
biotope	Habitat.
braincase	Strictly, that part of the skull actually housing the brain; the cranium; in contradistinction to the rostrum it is that portion of the skull lying posterior to the anterior line of the orbits.
braincase breadth	The greatest transverse measurement across the braincase taken usually just above the squamosal processes.
bristle-hair	Usually the main constituent of the outer fur; see page 12.
buccal	On the cheek side of the teeth.
bulla	One of the paired subglobular bones seen on the underside of the skull housing middle and inner ear structures.
bursa, aural	A small pocket situated on the external rim of the ear pinna.
canine	The tooth immediately posterior to the premaxilla; in the Carnivores almost always the tallest in the jaw, pointed and recurved; the "dog-tooth".
carnassial	One of the blade-like sectorial teeth in the Carnivores; see page 17.
caudal	Pertaining to the tail.
cheekteeth	The premolars and molars together; see page 16.
cheekteeth, greatest breadth	Measured across the outside of the teeth of the upper jaw, usually, but not necessarily, the posterior angle of the carnassials, p^4–p^4.
cingulum	A prominent girdle around the base of the crown of a tooth just above the alveolus.
circumanal	Around the anal orifice; see page 11.
cline	A gradual and sequential change of character without significant break such as would justify division into separate species.
condyle	A rounded process on a bone serving as an articulation with another bone.
condylobasal length	The distance from the most posterior face of the occipital condyles to the most anterior face of the premaxillae.
cranium	Braincase; laxly, the whole upper portion of the skull without the lower jaw.
cusp	A point or elevation, often subconical, on the crown of a tooth.
deciduous	Used of teeth; falling out naturally at some period of life, not in response to old age or disease.

dental formula	A method of expressing in succinct form the number of each category of tooth characteristic of a given genus or species. It is in pseudo-fractional form, citing the teeth in correct order from incisors to molars for one side only of the mouth, the upper and lower jaws respectively above and below a horizontal line, the total shown being, however, that for the entire mouth and thus twice the sum of the given figures. The number of incisors (3) and canines (1) being constant throughout the Carnivores the formula is often reduced to that of the premolars and molars alone; see page 16.
diastema	A gap between two teeth.
digit	Finger or toe.
distal	Further from the medial axis or point of attachment or origin.
dorsal	On or pertaining to the back.
emarginate	Having a notch or indentation in the margin.
epihyal	The upper part of the hyoid arch.
foramen (plur. foramina)	A (usually) small aperture in a bone or between bones, circular or elliptical in shape, for the passage of a nerve, muscle or blood vessel.
foramen magnum	The large opening at the posterior end of the skull through which the spinal cord passes.
frontal	One of the paired bones lying between the nasals and the parietals and forming with them the roof of the skull.
genal	Pertaining to the cheek.
glenoid fossa	The long subcylindrical cavity on the underside of the skull which receives the mandibular condyle to form the hinge connecting the lower to the upper jaw.
glossal	Pertaining to the tongue; situated on the tongue side of the teeth.
habitat	The kind of place, vegetationally speaking, which an animal normally inhabits.
hallux	The 1st digit of the hind limb.
hyoid chain, hyoidean apparatus	A U-shaped series of bones between the root of the tongue and the larynx; see page 377.
incisor	One of the category of teeth set most anteriorly in the skull and nearest to its medial axis, in the upper jaw arising from the premaxillae.
infra-orbital	Situated below the orbit or eye-socket.
inner	Nearer the medial axis.
interdigital	Situated between the toes.
interorbital breadth	The least distance between the upper rims of the orbits measured across the top of the skull.
interramal	Situated between the two branches of the lower jaw.
jugal	The middle bone of the zygomatic arch joining that arising from the maxilla to that from the squamosal.
jugal process	A pointed projection of bone on the upper side of the jugal, forming the lower part of the orbital ring.
lambdoidal crest	An alternative name for the supra-occipital crest.
lateral	Situated to the side of the main axis.
longitudinal	Lengthwise; running in a head to tail direction.

mandible	The lower jaw.
mastoid process	A process of bone immediately posterior to the ear.
maxilla	That bone of the upper jaw which bears the canines and cheekteeth and forms the major part of the palate.
meatus	A tubular passage or, more restrictedly, its opening.
mesopterygoid fossa	On the ventral face of the cranium posterior to the palate, the channel, usually broad and deep, between the fine pterygoid bones, i.e. the posterior part of the nasal passage.
medial	Situated in the middle or along the middle axis.
milk dentition	The teeth, usually simple in form and erupting soon after birth, which precede and are replaced by the permanent teeth characteristic of the mature animal.
molar	One of the most posterior category of teeth, not preceded by any corresponding milk-teeth.
morphology	The branch of zoology that deals with the form and structure of animals.
muzzle	That part of the face that lies anterior to the eyes.
mystacial	Resembling a moustache.
nares	The nasal passages; or their openings, as in anterior nares, posterior nares.
nasal length	The distance from the most posterior point of junction of the two nasal bones to the most anterior tip of one or the other of them (not the medial line, as in some works).
nomenclature	The scientific naming of animals.
nuchal	Pertaining to the back of the neck.
occipital condyle	One of the pair of smooth processes of the exoccipital bone at the posterior end of the skull lateral to the foramen magnum serving to hinge the head to the neck.
occipital crest	A process, often flange-like, of the supra-occipital bone which forms the upper posterior portion of the cranium.
occlusal surface	The surface of a tooth which closes against the corresponding tooth in the opposing jaw.
oestrus	The state of being on heat, or in season, of a female.
orbit	The eye socket; or, more especially, the bony ring or partial ring surrounding it.
outer	More distant from the central axis.
palatal length	The distance from the most anterior point of the posterior margin of the bony palate to the foremost edge of the premaxilla.
palatilar length	The distance from the most anterior point of the posterior margin of the bony palate to the posterior alveolar rim of the incisors.
paratype	A specimen forming part of the original material used and mentioned by an author as the basis of description of a new species or subspecies and from which he has selected and designated a holotype.
paroccipital process	An outgrowth of the occipital bone extending in a downward direction, sometimes finger-like but sometimes spreading over the posterior surface of the auditory bulla.
pectoral	Pertaining to the chest.
pelage	A general term for the fur of an animal.

perineal	Pertaining to the region between the anus and the scrotum or vulva.
petiole	Herein used to denote the slender stalk of a sub-bristle-hair; see page 16.
phylogeny	The evolutionary history of an animal.
pinna	The external ear flap or conch.
postcanine gap	A space unobstructed by teeth posterior to the canines, evident when the jaws are closed; see page 18.
postdental palate	A medial extension of the main palate backwards and lying posterior to the molars.
posterior	To the back of; hindmost; furthest from the head.
postorbital constriction	The shortest distance across the top of the skull posterior to the postorbital processes.
postorbital process	An outgrowth from the frontal bone, in the carnivores usually fairly long, forming the upper rim of the orbit.
pregenital	Anterior to the genital organs.
premaxilla	One of the pair of bones forming the extreme anterior part of the palate and rostrum below and at the sides of the nares, and from which the upper incisors arise.
premolar	One of the teeth lying between the canine and the molars and in the adult state always preceded by a milk tooth.
prescrotal	Situated in front of the scrotum.
process	A natural outgrowth from a bone or other structure.
proximal	Closer to the medial axis or point of attachment or origin.
pterygoids	The paired, vertical, thin, wing-like bones on the ventral face of the cranium to the rear of the palate, forming the lateral walls of the posterior part of the nasal passage.
ramus	One of the two branches of the mandible.
rostrum	The, usually tapering, portion of the skull lying anterior to the orbits.
sagittal crest	A longitudinal ridge of bone situated on the medial axis of the cranium, sometimes lacking, sometimes well developed into an erect plate.
sectorial	Adapted to cutting.
septum	A partition separating two cavities.
sinuous	Having a number of curves: wavy.
sub-	In combination with shapes or terms (as subequal, subcylindrical), approximately, roughly, almost.
sub-bristle-hair	Shortened to sub-bristle, one of the components of the top fur of mammals; see page 12.
submental	Beneath the chin.
subocular	Beneath the eye.
superciliary	Situated over the eye.
supra-anal	Situated above the anus.
supra-occipital crest	A more correct term for the occipital crest.
suspensorium	One of the bones of the hyoid chain.
taxonomy	The systematic arrangement of the animal (or plant) world in a natural order of evolutionary relationship. It is necessarily closely associated with nomenclature, which is thus, for convenience but

	somewhat laxly, included under the side-headings in this present work.
terete	Having a cylindrical or slightly tapering form.
toothrow	The complete series of teeth on one side of the jaw from incisors to molars; sometimes for the purposes of convenient measurement limited to the distance from the anterior rim of the canine alveolus to the posterior face of the last molar.
total length	The greatest length of a skull from its most posterior point to the front edge of the most forward bone or tooth.
tragus	A cartilaginous process sometimes found near the base of the inner margin of the ear pinna.
transverse	In a direction across the body from side to side.
trifid	Divided into three parts by two notches.
trilobed	Having three lobes; trifid.
tympanic bulla	See bulla.
type	The specimen used in the original description as the basis of naming a new species or subspecies. More properly referred to as the holotype.
type locality	The exact place from which an original type specimen came.
ventral	Pertaining to or on the abdominal side; on the under as opposed to the upper or top side of a structure or animal.
vibrissa	A stout, stiff and generally very long, tactile bristle growing singly or in small clusters, mostly in a few constant and well-recognised sites on the body; see page 11.
zygoma (plur. zygomata)	The arched bone supporting the cheek on each side of the skull, comprising processes from the maxilla and the squamosal connected by the jugal bone.
zygomatic arch	The zygoma.
zygomatic breadth	The greatest width across the bones forming the zygomatic arches measured at right-angles to the main longitudinal axis of the skull.

NOTE ON THE AREA TAKEN AS WEST AFRICA

This and cognate matters were dealt with at greater length in Rosevear (1965), where reasons for the choice of boundaries were given. Briefly, the West African region is taken as bounded on the west by the coast line but including the island of Fernando Póo; and on the north by the 18th parallel of latitude. The southern and eastern boundaries are taken as the River Sanaga (Cameroun) from the sea to its source and thence the watersheds dividing the Congo and Nile systems from those rivers that run either into Lake Chad or into the Atlantic Ocean north of the 4th parallel. The area thus enclosed is indicated on the accompanying map, page 521.

The southern boundary, which seems at least in some measure to be a natural one, cuts across existing political units, the names of which can, thus, not be usefully employed; the term "upper Cameroun" is used, therefore, to indicate the part of that country which lies inside West Africa as defined above. "Extralimital" means outside the region dealt with in this work.

The name Congo, in reference to extralimital distributions and other matters relevant to this work, is used rather laxly to indicate the basin of the river, especially to its north, rather than the river itself or any political unit.

NOTE ON VEGETATION

The West African vegetation was dealt with fairly fully, together with photographs of the different types and maps of the zones, in Rosevear (1953); and in a shortened version without illustrations but with a map in Rosevear (1965). The vegetation of the continent of Africa south of the Tropic of Cancer, using a somewhat different terminology but accompanied by a large coloured map, has been succinctly treated, in both French and English, in Keay *et al.* (1959).

The system of classification used in this present volume has been accepted and commonly employed in biological works of varying kinds for half a century or more. It is admittedly of a broad nature, taking little or no note of sub-associations of vegetation within the main categories; but it has nevertheless served, and continues to serve, a useful purpose and will seemingly do so until far more detailed ecological studies of both plant and animal life have been achieved.

The terminology used in this present work, as in the others of this series of monographs on West African mammals, differs from that commonly employed only in the substitution of "woodland" for "savannah". The reason for this change is that it seems to the author that it is important to bring constantly before the naturalist that trees do, indeed, play an extremely important role in these zones, providing for many mammals sources of food, shade, shelter and refuge in alarm. It seems likely, at least to the present writer, that a good proportion of the open-country mammals, whether giraffes, polecats, squirrels or tree mice, are more actively aware of the arboreal than of the graminaceous constituents of these zones. The French term "savanne boisée" contains an essential conception of this class of vegetation that should always be present in the mind of the field zoologist. Moreover, in dealing with West African animals it is important to emphasize the vast difference of appearance and ecology between these zones and the extensive areas of open plains which cover much of East Africa, where the tree species, though possibly basically the same, are so incomparably more scattered as to offer little hindrance to vision over long distances.

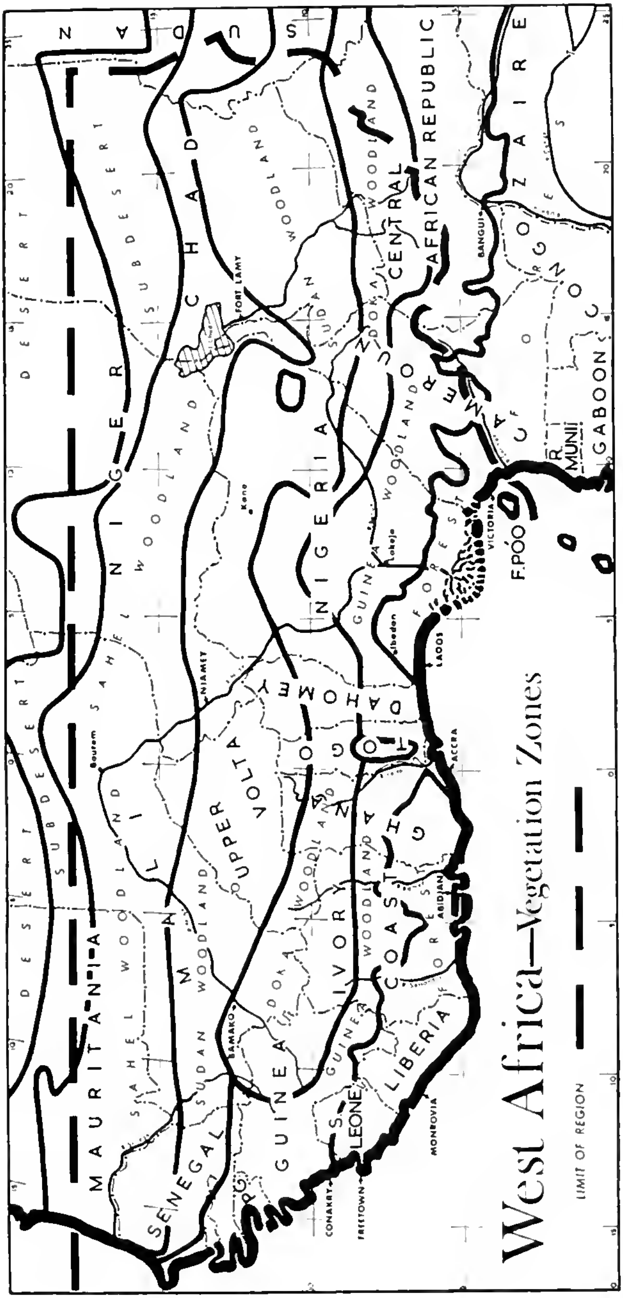
It is scarcely possible to define the various zones succinctly and at the same time clearly; and it is even less feasible to indicate their limits. However, the latter can be gathered in a broad way from the accompanying small-scale map, page 521. In using this two things must be borne in mind: the boundary lines are throughout much of their length nothing more precise than the mere joining of distantly separated though fairly accurately known points of change; and, secondly, the division between zones is, in fact, rarely clear-cut, there being, often, a belt in which the definitive species are to a greater or less extent mixed. The differing belts of vegetation are mostly the outcome of various climatic factors of which the chief are rainfall, atmospheric humidity especially at the peak of the dry season, and the number of months that this season itself lasts. In succession from the coast inland to the Sahara, that is in conditions of ever-increasing aridity, the chief zones are as follows:

High forest. Typically consisting of trees in different strata from very tall to low, the crowns of which form a complete canopy blocking out the sky (hence the alternative term "closed forest"). Grasses absent. Vast areas of the zone have, however, been destroyed for farming and other purposes, completely altering its character and opening up the ground to light; grasses gain admission on a temporary basis until they are shaded out by the gradual regrowth of tangled shrubs and eventually the forest; but on areas such as broad roadsides that are constantly kept open grasses find a permanent home. There are therefore a number of very distinct habitats within the high forest zone. "Rain forest" is another commonly used alternative term. It must be added that "forest" as often used in East Africa in the context of animal habitats is, except in Uganda, a very different matter and would generally be regarded in West Africa as little more than rather dense woodland.

Invasive woodland. This is immediately contiguous to the high forest and is, in fact, on climatically potentially forest land; but constant severe clearing of the original forest for farming has in the past admitted abundant grass through which the fires from the adjacent Guinea woodland have swept annually, eventually destroying all regeneration of forest-zone, fire-tender species. Only the fire-resistant trees of the Guinea zone could in these circumstances obtain a foothold; and the Guinea woodland, therefore, has almost completely invaded the area except for a few relic patches of forest which for religious or other reasons were unfarmed and have been preserved in their original state, fire being unable to sweep through them owing to their intrinsically damp nature and the characteristic absence of grass. The zone is thus to the eye indistinguishable from the contiguous Guinea woodland except by the occasional presence of forest patches unassociated with water courses. The name "derived savannah" is commonly applied to this region, a meaningless term since the present vegetation is derived from nothing but is of a type invading an area to which it climatically has no claim and is thus more logically invasive savannah or, in this work, woodland.

Guinea woodland. This is characterized by a dense, continuous ground cover of tall, coarse grasses, 2 to 3 metres high, amongst which stand thick-barked, fire-resistant trees mostly of small to moderate size and of twisted shape, their crowns rarely touching to form a canopy. A few tree species of larger size also exist and sometimes stand in close clumps. In most years the grass is deliberately burnt in the dry season (November to March) and springs again in lush green form from its tufts. This, in conjunction with the freedom of movement then possible, attracts animals normally absent during the rains. High forest penetrates, sometimes deeply, into the zone along water courses, so that it is possible for species appropriate to that vegetation to occur in what from the map appears to be Guinea woodland. Because of its more fertile nature much of this "fringing forest" has now been destroyed for farming; but elsewhere in the zone the effects of cultivation are neither so marked nor so permanent as in the forest.

Doka woodland. This is of very similar appearance to the Guinea woodland except for its slightly less abundant grasses and its dominance by the tree known in Hausa as *doka* (*Isoberlinia*).



West Africa—Vegetation Zones

Sudan woodland. Although the overall appearance of this important zone has a unifying "atmosphere" which distinguishes it pretty clearly from the Doka on the one side and the Sahel on the other the vegetation is, in fact, very variable and is made up of a mosaic of communities each determined by geology or soil moisture. Succinct description is, therefore, even more difficult than in the case of the other zones. Broadly the Sudan may be distinguished from the Doka by the virtual absence of that tree and by the markedly greater number of thorny species. These are mostly different kinds of *Acacia*; but the zone nevertheless differs from the Sahel by the relative uncommonness in it of *Acacia raddiana*. The grass cover is of lower height and sparser than in the preceding zones, so that vision is less obstructed, passage easier, and the annual fires less intense and damaging.

Sahel woodland. The tree cover here is much more limited both as regards variety and numbers. The zone is, indeed, dominated by a single species of *Acacia*, the flat-topped *A. raddiana*, which covers considerable areas, the individual trees, however, standing at some distance from each other. There are stretches from which *Acacias* are lacking, fairly thickly covered with the grotesquely shaped shrub *Commiphora*. Throughout two-thirds of the year, from about mid-October to mid-June, there is little or no rainfall.

Subdesert. Here the rainfall is too slight and the atmospheric humidity too low to support any tree growth. There are a few low scattered shrubs and, during the very brief rains, a sparse growth of tufted grass and annual herbs, often growing from bulbous roots which constitute a welcome source of food to many mammals. There are sand-dunes, some stable, which provide subterranean shelter.

Desert. This does not exist within the limits taken for West Africa in this present work. It is characterized by the complete absence of vegetation except in a relatively few favoured locations such as oases or above underground water-courses.

Besides these main zones, which each cover very large areas and extend across the continent from west to east, there are a number of minor types of vegetation which owe their existence to local factors of rainfall, soil, topography or altitude. The commonest of these are:

Mangrove. This occurs in coastal and sub-coastal areas subject to flooding by brackish water diurnally. To all intents and purposes these swamps are made up of two arboreal species, the red mangrove (*Rhizophora*) and the white mangrove (*Avicennia*). The former exhibits two clearly recognisable types of growth: the tall primary growth on very soft, newly deposited silt—a biotope offering no refuge to any but purely arboreal or purely aquatic mammals; and the low, tangled secondary growth on firm, peaty, root-riddled soil, flooded only at the highest tides, and of annually lessening submergence. These latter areas are thus increasingly open to and invaded by terrestial mammals.

Fresh-water swamp. This is high forest, within the main zone and often just inland of the tidal mangrove swamps; but it comprises species that can withstand annual seasonal flooding by fresh water from the overflow of rivers during the rains. There are also more restricted areas of permanently inundated fresh-water swamp fed by small inland streams and occupied almost solely by the *Raphia* palm.

Coastal scrub. Although contiguous to the seaboard and thus apparently well within the region of high precipitation and humidity which fosters the tropical rain forest, the vegetation of these relatively small areas is almost Subdesert-like in its sparseness, consisting largely of low, tufted grass and scattered shrubs, the latter often seemingly connected with old termitaria. The underlying causes are various—past destruction, lowered rainfall due to the direction of the coastline, and soil factors. It is not to be confused with strand vegetation, which consists of psammophilous grasses and creeping herbs growing along sandy shores.

Mountain forest. This, which lies between about 1000 and 2000 metres and is pretty constantly enveloped in cloud, partakes of all the characters of normal lowland high forest except that with increasing altitude the trees become progressively smaller and are, throughout, draped with mosses and lichens.

Montane grassland. True Montane grassland lies at 2000 metres or higher and consists of more or less continuous short grasses and herbs, with a complete absence of woody growths. The mistake is not infrequently made of confusing highly degraded "savannah" lying at moderate altitudes with this.

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NOTES:

1. English or other vernacular names are printed in CAPITALS.
2. No distinction is drawn between currently accepted names and synonyms; generic names are spelt with a Capital.
3. Subspecies are referred to the recognised genus not to the species.
4. Page references are in Arabic figures (9); major references are bold (**9**).
5. References to Figure numbers are in italics (*9*).
6. References to Colour Plates are in Roman style numerals (IX).

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