Notes on the Sand Cat, *Felis margarita* Loche, 1858

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Receipt of Ms. 4. 9. 1975

The Sand Cat *(Felis margarita* Loche, 1858) has remained one of the least known species of Felidae since its description over a century ago. Only a very few specimens are available for study in collections, and so little had been written about the species by the early years of this century that when Ognev (1926) studied the first examples from Turkestan he was convinced that he had found not only a new species, but a new genus, giving it the name *Eremailurus thinobius.* A few years later Heptner and Dementiev, seeking comparative material, could trace but a single specimen, in the Paris Museum; this however was sufficient to demonstrate that Ognev had merely rediscovered Loche's species in a considerable northeasterly extension of its range, although the paucity of material did not permit them to say for certain whether the Turkestan and Saharan forms were absolutely identical, or whether two separate subspecies could be maintained (Heptner and Dementiev 1936).

Pocock (1938a, b) recorded the accession to the British Museum of two specimens of the same species; as both of them differend from Loche's type description, and from each other, and were from widely separated localities in the Sahara, he did not hesitate to make each of them the type of a new subspecies: *F. margarita meinertzhageni* and *F. m. airensis.* These, together with *F. m. thinobia,* he maintained in his uncompleted catalogue of 1951. Even by this date, it appeared as if the range of the species was markedly discontinuous.

Not long afterwards however, a living specimen from the Arabian peninsula arrived in the London zoo, partially closing the gap between the Saharan and Turkestan portions of the range (Hayman 1952; Haltenorth 1953a). In his textbook on the genus *Felis,* Haltenorth (1953b) allocated the Arabian cat to *F. margarita* but retained *F. thinobia* as a separate species: according to his view, the two desert species together with the South African *F. nigripes* and the Chinese *F. bieti* had been derived independantly, converging through similar adaptions, from the widespread *F. silvestris.* As will be shown below, it would no longer be possible to hold to this view: not only are *margarita* and *thinobia* closer than could be accounted for by convergence, but they show certain similarities to the distinctive species *F. chaus;* moreover the distributional gap is closing as more and more records accumulate. Indeed, in her survey and reinterpretation of coat patterns in the Felidae, Weigel (1960) was already in a position to report the discovery of *F. margarita* in the Iranian desert near Teheran: a record which has not been duplicated since that date, although there is no reason to cast doubt upon it.

Harrison (1968) gave detailed descriptions of the Arabian skins known to date, while Heptner (1970) and Heptner and Sludskij (1972) reviewed the knowledge of the Turkestan race, of which a fairly respectable total of specimens had meantime accumulated. Lay et al. (1970) reported the discovery of the species in the Nushki desert, Pakistan; Walter Scheffel of Maintal, Germany, acquired living specimens from this region and from these, together with the remains of animals which had died in the initial stages of the setting up of the breeding group, Hemmer (1974a, b) was able to characterise the Pakistan Sand Cat as a new subspecies, *F. m. Scheffeli.*

Z. Säugetierkunde 41 (1976) 286—303

ISSN 0044—3468/ASTM-Coden ZSAEA 7

Finally Schauenberg (1974) has reviewed aspects of the species' morphology, taxonomy and ecology.

It is the purpose of the present paper to review that taxonomy of *Felis margarita*, at the same time laying down standards with regard to its variation by age, sex and individual. We describe the Arabian Sand Cat as a new subspecies, and attempt to elucidate the relationships of the four recognisable races to each other and to a standard of specialisation. For this latter purpose it is necessary first of all to discuss the systematic position of the species within the Felidae and the genus *Felis*.

Relationships of *Felis margarita*

Four rather different views have been put forward in the literature concerning the relationship of the Sand Cat to other felids. According to Heptner and his associates the species is closely related to the Manul or Pallas' Cat and should be placed alongside the latter in the subgenus or genus *Otocolobus;* this is the only schema which dissociates it from the nominate subgenus or genus, *Felis*. Haltenorth has proposed that there is not one species but two, independently derived from local variants of *Felis silvestris*. Schauenberg acknowledges the unity of the species, but again places it closest to *F. silvestris*. Finally Hemmer notes similarities to *F. chaus*, and proposes to regard *F. margarita* as a species standing between the latter and *F. silvestris*. We will discuss each of these views in turn.

1. Heptner and Dementiev (1936) noted similarities in the form of the skull between *F. margarita* and *Otocolobus manul*, which they proposed to formalise by allocating *Otocolobus to Felis* as a subgenus including both species. Heptner (1970) reiterated this view, and it was defended by Heptner and Sludskij (1972). The latter publication is very explicit as to the degree of the affinity between *margarita* and *manul*, in that the composite subgenus *Otocolobus* is maintained in the face of a revocation of the generic taxon *Prionailurus*, traditionally (Weigel 1960) thought of as one of the most distinct of the genera of smaller cats.

Pocock (1951) offered a brief criticism of this view of the species' affinities (p. 179); Haltenorth (1953b) and Weigel (1961) both refused to accept it; and Schauenberg (1974) has most recently gone into some detail in a refutation of it, drawing attention to recent information on the karyotype (Jotterand 1971) and the shape of the pupil in addition to long-known features of skin, skull and dentition. Such similarities as are supposed to exist do not in any case extend very far, and evaporate completely when living specimens are observed side by side, as in Scheffel's private collection.

2. Pocock (1938a) kept *thinobia* separate from *margarita;* in 1951 he united them on Heptner and Dementiev's evidence, but remarked that the apparent gap in distribution might still be best explained by postulating that they had evolved convergently from local representatives of *F. lybica* (now itself regarded as conspecific with *F. silvestris*). It was left to Haltenorth (1953b) to seriously adopt and defend this theory, citing chiefly the *caudata*-like spotted pattern of young *thinobia* as evidence of the latter's affinity with Central Asian races of *F. silvestris*. As Hemmer (1974a) has shown, however, the degree to which the flank stripes may be broken into spots, or indeed expressed at all, is rather variable within and between both *margarita* and *thinobia*, adult and young, so the supposed resemblances between a given Sand Cat and its neighbouring Wild-Cat races fall away. Moreover the need to postulate such a convergence has now fallen away with the virtual closure of the geographical gap between the two races.

3. Hemmer (1974a) points out resemblances between *F. margarita* and *F. chaus*

namely the yapping courtship call (Partnerruf), the similarity of the skin markings (ex Weigel 1961), and the large size of the teeth. As these characters, as well as the exact nature of the relationship between the two, need further discussion, we will return to this theory below.

4. Schauenberg (1974) doubts the validity of the relationship postulated by Hemmer; he notes the dissimilarity between the broad skull of *F. margarita* and the elongated narrow one of *F. chaus*, and states that there are "great analogies" between the raucous call of the Sand Cat, resembling the bark of a small dog, and that of a desert race of *F. lybica;* moreover, "it would be imprudent to attempt to establish such a classification on ethological observations and to base systematic conclusions on superficial studies". For Schauenberg, the skull of *F. margarita* closely approximates those of *F. lybica, F. ornata, F. silvestris* and *F. nigripes,* all of which he regards as valid species; and this is the most likely guide to its systematic position.

As indicated above, we do not consider that theories (1) and (2) are appropriate any longer in the light of modern information. In particular Haltenorth's theory was proposed explicitly to account for a supposed distributional gap, which is now known to be illusory. We will therefore confine ourselves to a consideration of theories (3) and (4). In so doing it is necessary to distinguish clearly between what have been commonly referred to as "habitus" and "heritage" characters. The former are those which are strictly related to presentday ecological conditions, and so are not relevant as such to an elucidation of phyletic/systematic affinities. The latter are not so related; presumably they reflect the adaptions of ancestral forms in some way, so that modern taxa showing similarities which are unrelated to their ecological status can be supposed to be descended from a common ancestor with those characters.

That is not to say, of course, that "habitus" characters are meaningless in systematic terms. These are, of course, the features which distinguish the members of a living sister-group and their degree of development is a useful indicator of differential specialisation. This point will be returned to below, when considering the subspecies of *Felis margarita.*

The living species of the genus *Felis* (and here we exclude the poorly known *Felis bieti)* can be arranged according to environment in the following series:
desert — desert/steppe — savannah/bushland/woodland — wet bushland
margarita — *nigripes* — *silvestris* cf. *lybica* — *silvestris* cf. *silvestris* — *chaus.*

We suggest that all characters following this sequence may be regarded as „habitus“ characters as follows:

a. Skull breadth. As zygomatic breadth is nearly isometrically related to skull length (see below under Intraspecific variation), it is justifiable to calculate a simple index, $\frac{\text{zygomatic breadth} \times 100}{\text{greatest length}}$ · Using figures given by Haltenorth (1953b), Pocock (1939) and Heptner (1970), we obtain the following results for this index:

species	mean	standard deviation	(n)	
Felis chaus	65.9	2.1	(33)	
Felis silvestris silvestris gp.	70.7	2.4	(105)	70.4 (281)
„ „ *lybica* gp.	70.0	2.3	(134)	
„ „ *ornata* gp.	70.9	2.5	(42)	
Felis nigripes	73.6	2.3	(6)	
Felis margarita thinobia	75.9	—	(29)	

Clearly, this is a "habitus" character following an exact ecological series, and so should be used with caution for elucidation of interspecific relations, contra Schauenberg (1974).

b. Bulla length. This measurement shows a negative allometric relation to skull (basal) length; the allometric exponent is around 0.8; in *F. m. scheffeli* the correlation coefficient is 0.98, and the allometric exponent has a value of 0.83 ± 0.07. Therefore we cannot take a simple index, but must use the integration constant b of the allometric equation, $\log y = \log b + a \log x$. For comparability, the allometric exponent was taken as 0.83 for all species, and the value of b calculated from it (from measurements taken by H.H.):

species	mean	standard deviation	(n)
Felis chaus	0.51	0.02	(2)
Felis silvestris silvestris gp.	0.53	0.02	(7)
„ „ *lybica* gp.	0.57	0.02	(13)
Felis nigripes	0.60	0.01	(2)
Felis margarita scheffeli	0.69	0.01	(7)

These values additionally correlate highly with zygomatic breadth index (allometric exponent, double logarithmic system, 2.0), giving an even better indication of habitat specialisation.

c. The mat of dense hair on the paws. The existence of a mat of hairs thick enough to cover the soles is a much cited diagnostic feature of *F. margarita* (illustrated in Hemmer 1974a). An index, $\frac{\text{hair length on soles} \times 100}{\text{hair length on the back}}$, was calculated as it appears that the relation is isometric. The values are as follows:

Felis chaus	13	(3)
Felis silvestris (all types)	30	(32)
Felis margarita scheffeli	58	(6)

Descriptions of *F. nigripes* suggest a position on this scale between *F. silvestris* and *F. margarita.*

In such features, therefore, the position of *Felis margarita* as the most specialised arid-country species is highlighted; intermediate "habitus" standing of *F. silvestris* is indicated, and the "wet-country" adaptations of *F. chaus.* It is against such background that "heritage" characters must be sought for phylogenetic indicators.

Weigel (1961) showed that in features of the skin pattern *F. margarita* has closer resemblance to *F. chaus* than to *F. silvestris* (this referred to form, not degree, of pattern expression). Here is a resemblance which does not follow ecological, "habitus" relationships. The relatively large teeth and the nature of the vocalisations are other such resemblances. Concerning Schauenberg's strictures about the use of ethological characters, it can only be objected that their value for systematics has been demonstrated innumerable times, especially by ornithologists, and is subject to the same constraints as in the case of morphological characters. The calls — especially the male's courtship vocalisation — of *F. margarita* and *F. chaus* differ in their marked shortness from those of all *F. silvestris* specimens studied by H. H., including a desertic race *F. s. griselda.*

Some further hint of the phyletic affinities of *F. margarita* may be derived from a comparison with the mandible of *Felis lunensis* from the Villafranchian of

Olivola, Italy, described by KURTÉN (1965). This species, considered ancestral to *F. silvestris* by KURTÉN, differs from the latter in the absence of a hypoconid from P_3; in which it resembles *F. margarita.* On the other hand, the well-developed hypoconid of *F. chaus* suggests the likelihood of convergent evolution in one or other case. *F. lunensis* lacks the relatively high-crowned P_3 common to *F. margarita* and *F. chaus* (including the fossil Javanese form of the latter).

Therefore, the Sand Cat stands somewhat between the Jungle Cat *(F. chaus)* and the Wild-Cat *(F. silvestris)* in many respects; in a few characters, namely those indicative of arid-country specialisation, it stands quite out on its own.

Skin of *Felis margarita*

We have at our disposal a good series of skins and living specimens of *F. m. scheffeli,* enabling us to draw up age/sex and seasonal parameters as follows:

The hairs on the back are tawny at the base, extending some way up the shaft; there is then a fairly dark segment, followed by a pale straw-coloured band, and a black tip of varying length. From dorsum to venter the flank hairs become progressively bleached, the dark midshaft section disappearing first, then the black tip, so that a typical hair of the lower flanks is pale fawn throughout. From flanks to venter is a rather rapid transition to white. On the neck both transitions — dorsum to sides, and sides to underside — are sharper than on the body. In summer the fur is relatively short, mostly 27—35 mm on the loins but with long guard-hairs of 39—46 mm; there are indications, varying in intensity, of transverse stripes along the flanks, invariably broken into elongated spots, and in one skin (SMF 38326) clear suggestions of dark longitudinal dorsal streaks. In winter, the fur is longer, 37—40 mm on the loins with long guard-hairs of 45—48 mm, with an "unbrushed carpet" look; the pattern is less obvious, exept in some cases for the dorsal lines which can be discerned. A flat skin gives the general impression of being grey with a buffy cast, much darker along the dorsal midline, and with a buff margin to the whole skin, especially clear along the neck.

Ears are more tawny at the base, with a black tip and a grizzled midzone where the black begins to come in; one specimen has white patches towards the base. Thick white hair clothes the inner surface of the ears.

The limbs are buffy outside, brighter than the body; hindlimbs paler than forelimbs; the whole inner surface of the hindlimb, from the groin, is whitish, whereas there is just a little on the inside of the forelimbs. There is always a black stripe encircling the upper segment of the forelimb above the elbow, more marked across the white surface than the buffy; this is the most sharply marked, and generally the darkest, element in the colour pattern. One specimen (SMF 40531) has two such bands which run together on the inner surface at the stifle. There may or may not be clear traces of broken stripes elsewhere on the limbs; all skins however show a row of brown spots from groin to hock along the buff/white border.

Paws have dark brown fur on the pads covering them; on the forefeet a black patch occurs on the ventro-medial surface of the 5th digit, grading at the edges into the buffy area, and extending up the heel to the dew-claw. This may however be difficult to trace and appears to fade with age.

The tail has a black tip, a light buffy band in front of that, and an alternation of buff and black bands in front of that, fading fairly rapidly and not extending more than one-third of the way towards the base. (The number of bands is racially variable: in *scheffeli* there are typically two black bands in front of the black tip, and some 4—5 brown ones in front of them are recognisable in adults). The tail, basally buff like the flanks, pales distally until the zone of the black bands is reached. The hairs along the dorsal midline are elongated, dark for most of their length but with a buff band just below the black tip. The dark bands are caused partly by an extension of the darker zones of the individual hairs, and partly by the way the hairs lie, overlapping each other.

On the face the zone of the mystacial vibrissae is white; a white ring encircles each eye, except medially where it is interrupted by a welldefined tawny stripe running down either side of the nose; above and below this stripe, on the medial side of each eye, is a large white patch. The upper side of the nose is light buffy or white. In some specimens there is a dark buff line running from the lateral eye corner towards the ear, dividing the buffy upper from the white lower portion of the cheek-ruff. The rest of the head — except the crown, which is coloured like the dorsum — is a bright buff. The white zones on the face are more conspicuous in winter coat.

Seasonal variation therefore consists largely in the greater visibility of the transverse broken-stripe pattern in summer, and probably the lesser amount of grey overlay on the dorsum and the smaller amount of white on the face. Individual variation follows much the same lines, and it is possible to find some skins that cannot be assigned to a given season by pattern alone. Two capture groups of Pakistan Sand Cats differ in the expression of the pattern: in the Scheffel group the pattern in most individuals is nearly obliterated, while in a group in the Brookfield zoo, Chicago, it is well-expressed. Each group descended from just a few individuals, and observation of one or the other alone would give a false idea of a rather narrow range of individual variation, if it be not born in mind that the now numerous members especially of the Brookfield line are genetically related.

Individual variation, therefore, is fairly well-marked, equivalent to that within a given population of *Felis silvestris* which is to say, along standard lines and not sufficient to obscure subspecific differences. Sexual variation in colour was not found.

The kittens of this form are all rather similar, whatever the pattern that they are destined to acquire as adults. They are more greeny-grey than the adults, with prominently banded hairs even on the face, and rather well-marked with broken stripes on the flanks and limbs, and a dark ochraceous streak down the back. The cheek-stripe and paw fur are also as dark as in the most boldly marked adults; on the other hand the white is less marked, both on the underparts and the face. More than eight tail bands are recognisable.

Skull of *Felis margarita*

Once again we use the Pakistan race, *F. m. scheffeli,* as a standard because of the relatively goods series, standardised by age and sex, available to us. Schauenberg (1974) has already indicated seven characters whereby this species may be distinguished from other members of the genus, so we will not dwell on this aspect here.

Available material indicates a considerable difference in overall size between males and females. In the Senckenberg (Frankfurt) series of three adult males and four adult females, the smallest male skull has a Greatest Length of 93 mm, the largest female, 84 mm; Basal and Condylobasal length show equally striking dimorphism. However Lay et al. (1972) quote skull lengths for two Pakistan Sand Cats (sex unstated) of 86.8 and 84.8 mm; if these are adult they are more likely to be female, but they do close the gap slightly. Schauenberg (1974) mentions five male skulls that he has studied, all from Nushki whence the Scheffel specimens came, but his total range is 83 to 90.5 for both sexes. This rather odd discrepancy could be explained by reference to the effect of different conditions of captivity, but as the Scheffel specimens, at least, were received as adults, and Schauenberg specifically states that the majority of imports from Pakistan survived for less than a year (implying that the skulls studied by him were from individuals that did not survive long in captivity), this suggestions is unsatisfactory as a general explanation. The two further explanations which occur to us are 1. that Schauenberg's specimens are not in fact adult, and 2. that there are local demes around Nushki.

The latter hypothesis is at present an imponderable; the former is quite possible, seeing that it sometimes requires a most minute examination of suture closure (especially the basilar suture) and dental eruption and wear to determine maturity. As an example, BM. 67.1429 — a skull of *F. m. margarita* — is certainly not fully grown but this fact would not be apparent on brief inspection; Schauenberg has evidently used it without demur in his series, nor can he be blamed for doing so except under the most stringent aging criteria.

Under these circumstances, therefore, we have decided to use only the Scheffel series for our comparisons, laying aside Schauenberg's series for the moment and treating the measurements of Lay et al. with caution.

The main skull breadth measurements (Zygomatic breadth, Bicanine breadth etc.) are nearly isometrically related to skull length and thus also show strong sexual size differences with no overlaps among confirmed adults. But Postorbital breadth is virtually identical in the two, and indeed in the skull of a kitten (SMF 44749), being a measurement which shows virtually no change in either age or sex, not significantly correlated with Greatest Length (r = 0.29), and with a regression line hardly deviating from horizontal (Hemmer 1974b: 31).

Table 2 lists the correlation coefficients and allometric exponents for various skull measurements with Greatest Length. Correlation coefficients are generally higher for *scheffeli,* being based on seven specimens from a single locality, than for *margarita,* based on six specimens from widely separated localities; none the less the *margarita* values are of interest for comparison, and of considerable significance for intraspecific comparisons (see below).

The length of the upper carnassial shows a very slight average difference (11.0 mm in males, 10.1 in females) which is well below the level of the overall skull length and breadth measurements, in which the female average is consistently 85 % the value of the male. The measurements of the occiput deviate in the opposite direction, in that its height in the female is only 77 % of that of the male, whereas the breadth is the normal 85 %. This reflects the greater tendency towards nuchal crest development in the male. The bulla shows smaller sexual dimorphism. The average for bulla length in the female is 87 % that of the male; for bulla breadth, the figure is actually larger, due to the low value of 11.5 mm in the male skull Senck.38333. This latter may not be fully-grown: it shows a widely open basilar suture, although all teeth are fully occluded. Therefore, the evidence that bulla size is not much different in both sexes is incomplete.

To sum up, the two sexes of the Pakistani Sand Cat are very different in size of skull — females being 85 % the size of males — but similary proportioned, except that the occiput is higher in the male, and the size of the carnassial and of the bulla is less reduced in the female.

Table 1

Skull measurements of *Felis margarita*

BM — British Museum (Nat. Hist.), London; Harr. — Harrison Zoological Museum, Sevenoaks; MNHP — Muséum National d'Histoire Naturelle, Paris; SMF — Senckenberg-Museum, Frankfurt/M.

	1 Occipital	2	3 Bulla	4	5	6	7	8	9	10	11	12	13
	ht.	br.	l.	br.	Carnassial l.	Zyg. br.	Postorb. br.	Bicanine br.	Infra-orb. br.	Inter-orb. br.	Condylobasal l.[1]	Basal l.[1]	Greatest l.
Males													
thinobia (from Heptner 1970)													
min.	—	—	23.1	14.9	10.6	65.0	—	—	—	—	84.2	—	90.4
max.	—	—	27.0	17.2	12.0	78.5	—	—	—	—	96.6	—	103.3
mean	—	—	25.2	16.4	11.4	73.0	—	—	—	—	89.0	—	95.4
			(both sexes)										
margarita													
BM 34.8.2.8	12	24	25	16	10.5	70	33	24	25.5	19	83.5	77	91
MNHP 1962.2933	12	25	25	16	10	66	34	22	23	17	81	75	89
BM 67.1429 juv.	13	24	24	14.5	10	64	32	21	23	16	79	73	87
harrisoni													
BM 59.634	14	27	25.5	16	10.5	74	31	25	26	19	83	78	89.5
Harr. 2.4747	14	25.5	25.5	16	10.5	71.6	33	24	25	19.5	81	76	90.5
Harr. 3.5868 YA	13	26	25	15.5	10.5	66	35	23	24	18	80	73	86
scheffeli													
SMF 38556	13	26	27.5	16	11.0	75.5	34.5	24	26	19.5	87	81	95.9
SMF 38557	14	25	27.5	16	10.8	71.7	33.1	23	25	19.5	88	81	96.7
SMF 38333	14	25	27.1	11.5	11.2	70.0	34.8	22	25	18.8	86	81	94.6

Table 1 (continued)

	1	2	3	4	5	6	7	8	9	10	11	12	13
	Occipital		Bulla		Carnassial l.	Zyg. br.	Postorb. br.	Bicanine br.	Infra-orb. br.	Inter-orb. br.	Condylobasal l.[1]	Basal l.[1]	Greatest l.
	ht.	br.	l.	br.									
Females													
thinobia (from HEPTNER 1970)													
min.	—	—	23.1	14.9	11.0	60.9	—	—	—	—	76.4	—	82.0
max.	—	—	27.0	17.2	11.3	76,1	—	—	—	—	92.0	—	98.7
mean	—	—	25.2	16.4	11.1	68.0	—	—	—	—	83.9	—	89.6
			(both sexes)										
margarita													
BM 39.1673	12	18	23.5	15	9.5	61	32	19	21	15	75	70	81
MNHP 1930.83	—	—	23	14	10.2	59	33	20	22	16	71	65	ca. 82
MNHP 1973.290	12	22	22.5	14	9	61	31.5	19	21.5	15	72	66	79
harrisoni													
SCHAUENBERG: age?	—	—	—	—	—	—	—	—	—	—	—	—	76.5
scheffeli													
SMF 40531	11	22	23.6	15	10.0	63.3	32.4	20	23	17.0	75	70	80.5
SMF 44815	10	21	24.0	15	10.4	61.6	34.8	20	23	16.9	77	71	83.4
SMF 38326	11	22	24.2	15	9.9	59.8	33.3	20	23	17.3	75	70	81.7
SMF 44750	10.5	21	23.6	14.5	10.0	60.9	33.8	20	23	16.1	73	68	80.1
Infant *scheffeli*													
SMF 44749	10	ca. 20	19.5	12.5	—	30.5	33	20	22	13	67	61	76

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[1] Condylobasal length and basal length not taken from prosthion to basion, but from orale to basion (by C. P. G.).

Table 2

Correlation coefficients and allometric exponents

double log system

allometry	subspecies	n	r	all. exp. (a) (regr. line)
Great.L./Zyg.Br.	*margarita*	6	0.90*	0.99 ± 0.22
Great.L./Zyg.Br.	*scheffeli*	7	0.95**	1.05 ± 0.15
Great.L./Bican.Br.	*margarita*	6	0.96**	1.54 ± 0.22
Great.L./Bican.Br.	*scheffeli*	7	0.96**	0.89 ± 0.11
Great.L./Infraorb.Br.	*margarita*	6	0.90*	1.09 ± 0.24
Great.L./Infraorb.Br.	*scheffeli*	7	0.96**	0.61 ± 0.08
Great.L./Int.Orb.Br.	*margarita*	6	0.89*	1.40 ± 0.32
Great.L./Int.Orb.Br.	*scheffeli*	7	0.94**	0.94 ± 0.14
Great.L./Postorb.Br.	*margarita*	6	0.66—	—
Great.L./Postorb.Br.	*scheffeli*	7	0.29—	—
Great.L./Occ.Br.	*margarita*	5	0.72—	—
Great.L./Occ.Br.	*scheffeli*	7	0.94**	1.01 ± 0.15
Great.L./Occ.Ht.	*margarita*	5	0.18—	—
Great.L./Occ.Ht.	*scheffeli*	7	0.89**	1.49 ± 0.30
Great.L./Bulla L.	*margarita*	6	0.95**	0.73 ± 0.11
Great.L./Bulla L.	*scheffeli*	7	0.93**	0.65 ± 0.11
Great.L./P^4-L.	*margarita*	6	0.80—	—
Great.L./P^4-L.	*scheffeli*	7	0.34—	—

** $p \leqq 0.01$; * $p \leqq 0.05$; not significant, $p > 0.05$.

The pattern of subspecific variation

Four discrete geographic groupings are known in this species: Sahara, Arabia, Pakistan, and Soviet Central Asia (Turkestan). The specimen mentioned above from Teheran may prove to represent a fifth, or this latter may turn out to be continuous with the Pakistani or Soviet one, or both. Most of the Saharan records are located within erg areas, some being specifically stated to have taken from the dunes; as such areas are themselves discrete, there may turn out to be quite a number of isolated populations. For our purposes, however, it will suffice to sort the specimens into the above four groups, this being all that the paucity of material will permit; that the differences do seem to run along these lines, seems to indicate that any differences within, say, the Sahara are minor or non-existent.

A word of caution is in order here, particularly concerning the Saharan Sand Cat localities (see Revision of subspecies). It is remarkable that there appears to be no authenticated record — certainly, no specimen — from east of longitude 9° E. In spite of intensive collecting in both Libya and Egypt by American expeditions, no specimen of *F. margarita* has turned up in either country, except for the record (HEMMER 1974a) from Sinai. The specimens from the localities 'Haidra' and 'Metameur' in eastern Algeria and in Tunisia quoted by SCHAUENBERG (1974) from LATASTE, which are now in the British Museum, are not *F. margarita,* but *F. silvestris* (*lybica* gp.) (POCOCK 1951). There is thus a possibility that one of the apparent distributional gaps may be real; it is a little ironic that this should be in effect a gap within the species *F. margarita* as recognised by HALTENORTH (1953b), not the one between *thinobia* and *margarita!* As to the suggested location in erg districts, HEIM DE BALSAC (1936) considers that the species is not restricted to such areas, while HEPTNER (1970) states that it is confined to sandy grounds but *not* necessarily within ergs. SCHAUENBERG (1974) goes into some detail about this matter, quoting a correspondant to the effect that the animal is found on compact ground between sand dunes. This is not necessarily in conflict with the habitat note on the label of the type of *airensis* ("sand dunes west of Air"), or that Paris Museum 1973.290 was taken at an oasis. The overall picture is one of a species adapted to an ecotone, digging its burrows in firm ground and hunting (diet consisting in the USSR largely of psammophile rodents according to sources quoted by LAY et al. and by SCHAUENBERG) in the dunes (ergs or barkhans).

The four subspecies recognised by us seem, whatever the correlation with major erg distribution, to be separated by large geographic barriers: the Saharan and Arabian races by the Nile, and perhaps by a large tract of the eastern Sahara itself; the Arabian and Turkestan races by the Tigris-Euphrates valley; and the Turkestan and Pakistan races by the mountains of Afghanistan.

HEPTNER (1970) found that *F. m. thinobia*, the Soviet race, is larger than the Saharan *F. m. margarita* and has a more reduced dark pattern, although there is variation in this respect. HEMMER (1974a, b) compared *F. m. scheffeli* of Pakistan with *thinobia*, which it mainly resembled, and found that it differed mainly in its relatively larger bullae and increased number of tail-rings. According to the specimens available to him, it would seem that the unnamed Arabian race would have a broad skull (as in *scheffeli*), but would be small like the Saharan from.

a. Skin

Although, as pointed out in describing *scheffeli* above, there is great variation in the degree of expression of the striping and spotting pattern, it seems fairly clear that Saharan and Arabian animals show a clear pattern very frequently (clearer in summer than in winter), none in fact showing an obliterated condition as is common in *scheffeli* and *thinobia* – not even in winter. The general tone of the colouration is brighter also: but this may go along with the well-expressed type of colour pattern, as the Brookfield specimens of *scheffeli* are bright in colour as well as well-marked.

Saharan skins in summer are pale to bright sandy-yellow with less grey-black overlay on the back than Pakistani skins; the flank-bands, though merely a dark ochery tone, are quite well visible, as are 4–5 dark stripes on the thigh; the upper arm stripes are very thick and black and there are always two distinct bands on the front surface. The paws tend to whitish; the ear-back has a considerable black tip; the face has much white on it, and the dark cheek-stripe and the "cheetah-stripe" along either side of the nose are well-marked. The underside, white as in *scheffeli*, is broken on the throat by a buff collar. In winter, the tone is greyer, with a much darker dorsal overlay; the impression is that the fading of the flank markings is not as complete as in *scheffeli*, but the greater extension of white zones is quite similar. In all coats, the number of recognisable tail-rings is less than in *scheffeli*, ranging in six specimens from 2 to 6 in number.

POCOCK (1951) drew attention to the difference between the type skins of his races *meinertzhageni* and *airensis*. The former is from El Golea, 30.35 N, the latter from In-Abbangarit, 17.54 N; both taken in early February, they differ conspicuously in the much shorter coat, paler colour, less blackened dorsum and clearer flank-pattern of the latter – the former having the most reduced flank-pattern of all Saharan specimens. A skin (BM. 67.1429) from Touaret, quite near In-Abbangarit, taken on August 30th., is quite like the type of *airensis* but even more extreme, supporting POCOCK's contention that there may indeed be some difference between specimens from the northern and southern Sahara. Among the skins in the Paris

Museum, none resembles *meinertzhageni*, although some are from northern Algeria (Laghouat, Beni Abbes) – admittedly, taken in summer between March and midsummer (including a colour photograph taken by F. Petter of a captive specimen, kindly shown to C. P. G.); a skin from Adrar mountains, Rio de Oro, from a specimen held in captivity in its country of origin and dying in late October, is equally unlike *meinertzhageni*. As far as degree of marking goes, and paleness of hue, there is no consistent difference between northern and southern skins, except that a skin from „Soudan" (i. e. Mali) is somewhat better marked than the others – more so than *airensis*.

We conclude that there is no difference between northern and southern specimens in summer, although there is a slight suggestion of such a difference in winter coat.

Five skins from Arabia are available for study; two in the British Museum, three in the Harrison Zoological Museum, Sevenoaks, Kent. Two were taken in winter, two in summer, the remaining skin by its appearance is probably a winter skin. The summer skins are very pale greybuff, less bright than in most Saharan skins; the flank pattern is quite clear, but never as well-expressed as the most extreme Saharan ones; the leg-stripes, too, are rather less prominent, but the upper arm bands are similar to those from the Sahara. On the underside, the buff collar is present but poorly marked; if anything, however, the whiteness of the underside is brighter than in Saharan skins, while the feet are white, making a rapid transition from the sandy tone of the shanks rather than being buffy-toned, grading into the flank colour as in Saharan skins. Winter skins are also pale, and have correspondingly less marked flank-stripes. In both seasons, there is a less extensive and diffuse darkening on the dorsum, a smaller dark grey (rather than black) patch on the ear-tip, and a much whiter tone to the paws than in the Saharan Sand Cat: these differences are clear enough in spite of the wide individual variation in the latter. The number of tail-rings, which Hemmer (1974 b) found to distinguish *scheffeli* from *thinobia*, was examined in Arabian skins but because of mutilation in two out of the five the results were unsatisfactory; the range, from 5 to 7 (or 9) visible rings, is above that for the Saharan form but overlaps it. The existence of a real difference may be seen better by comparing the mean interval between the rings existing in adult specimens and the tail length. This is much larger in Saharan and Turkestan cats then in Arabian and Pakistani ones.

A description of the Turkestan race depends largely on the descriptions of Heptner (1970) and Heptner and Sludskij (1972), although one of us (H. H.) has been able to study three skins from the Kyzylkum in the Academy of Sciences of Kazakhstan, Alma-Ata. The pattern is almost unrecognisable in these skins; it would seem that a well-patterned morph does occur, but is very rare; the number of tail rings recognisable in adults is reduced, often only 2 or 3, but up to 6 in kittens; and, as in other races, the colour is yellower in summer, greyer in winter, and the pattern is better expressed in the young.

This survey shows that the four geographic groups are distinguishable from each other externally. Western animals tend to be brighter in colour and better marked than those from eastern areas, with a buffy collar on the throat; the Arabian race is intermediate in these respects. The paws are lighter coloured in western animals, but in this case the Arabian form is more extreme than the Saharan. The number of tail-rings is higher in both Pakistani and Arabian forms than in either Turkestan or Saharan ones. The colour differences are thus not entirely clinal, probably because the range is disjunct rather than continuous, and the cline itself is stepped not smooth.

b. Skull

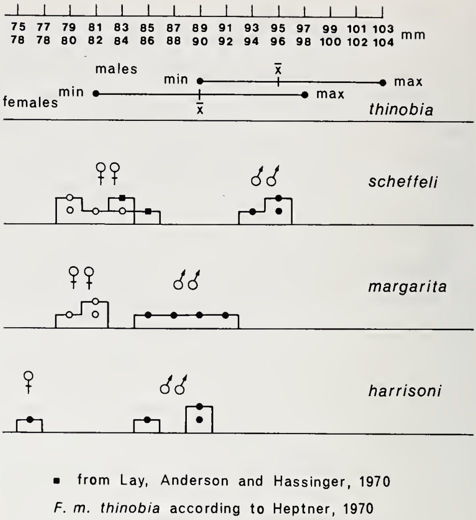
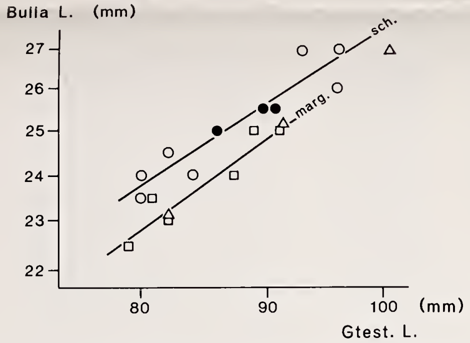


Fig. 1. Frequency distribution of greatest skull length in *Felis margarita.*

Previous authors have distinguished the larger Turkestan type from a smaller one of the other regions (Sahara, Arabia, Pakistan) (Hemmer 1974 b; Schauenberg 1974). It would now appear that matters are a little more complicated than this. Fig. 1 shows that in *thinobia* both sexes are large, in *scheffeli* (personally examined skulls only! — see above) males are large, females small, in *margarita* both sexes are small, while in the Arabian race males are small, and a single female skull (measurement given by Schauenberg 1974: age?) is quite diminutive. The male of *scheffeli* is similar in size to the male of *thinobia;* the female, to the female of *margarita.* This can be expressed by taking the mean female skull length as a proportion of the mean male: in *scheffeli* it is 85 %, in *thinobia* and *margarita* it is 94 and 91 respectively; in the Arabian form (only one female!) 85. Compared to *scheffeli* the measurements of *thinobia* given by Heptner (1970) do show a few differences apart from the degree of sexual dimorphism. In both sexes the carnassial seems to be larger: absolutely so in the female, relatively so in the male. Bulla length and breadth are not given by sex, but Hemmer (1974 b) has already shown that the individual measurements available indicate larger bullae for *scheffeli* (see also Fig. 2).

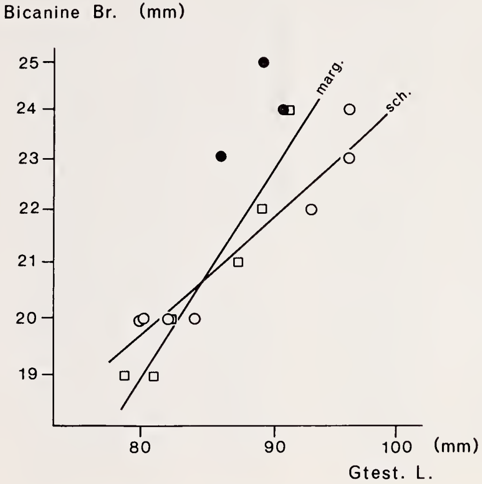
Male Saharan skulls differ considerably from one another, showing several features of evident allometry: the smaller the general skull size, the relatively smaller are the breadth measurements especially Bicanine and Interorbital breadth (Table 1; Fig. 3, 4). By contrast these allometric exponents are somewhat less than 1.00 in *scheffeli.*

Compared to *margarita* males, the Arabian skulls (males only, Fig. 5 a) differ proportionally, with more developed occiput and bullae, and rather broader zygomata, contrasting with the slightly smaller length measurements. Compared to *scheffeli* (Fig. 5 b) much the same differences are apparent, but except for the overall size difference they are less. To this extent therefore the Arabian Sand Cat may be looked on as a scaled-down version of *scheffeli;* the latter however lacks the former's expanded occiput and zygomata, but the bullae are just as enlarged compared to skull length. Both forms have rather large carnassials.

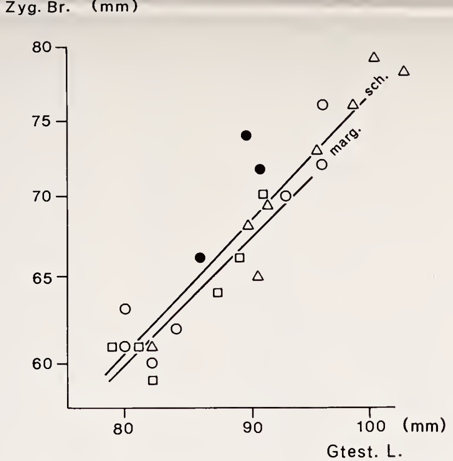


△ = *thinobia:* mean, min, max after Heptner 1970

Fig. 2. Double log scatter diagram bulla length/ greatest length. (Statistical data see table 2)



□ = *margarita*, ● = *harrisoni*, ○ = *scheffeli*



□ = *margarita*, ● = *harrisoni*, ○ = *scheffeli*, △ = *thinobia*

(measurements / mean, max, min / after Heptner 1970)

Fig. 4. Double log scatter diagram zygomatic breadth/greatest length. (Statistical data see table 2)

Fig. 3 (left). Double sog scatter diagram bicanine breadth/greatest length. (Statistical data see table 2)

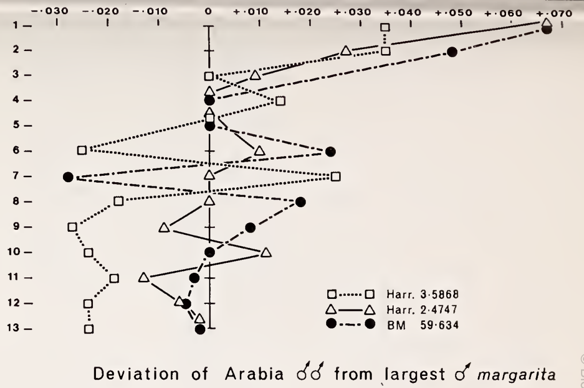


Fig. 5a

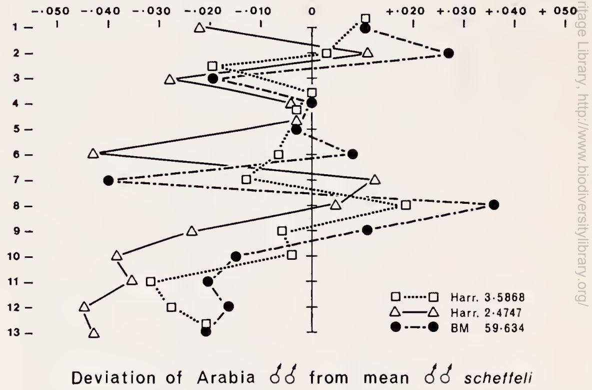


Fig. 5b

Fig. 5 (a and b). Log ratio diagrams: skull measurements as given in table 3

Revision of subspecies

Although material is rather limited, the available specimens do show a certain amount of geographical consistency in their external characters, and may be assigned to four subspecies as follows:

1. *Felis margarita margarita* Loche, 1858

1858 *Felis margarita* Loche, Rev. Mag. Zool. 10: 49. Negonca, north of Ouargla. (Variously mis-transcribed as *marginata, margaritae, margueritei, marguerittei:* Pocock 1951: 139 to 140).
1938 *Felis margarita meinertzhageni* Pocock, Proc. Zool. Soc. Lond. 43. Golea.
1938 *Felis margarita airensis* Pocock, Ann. Mag. N. H. (11) 1: 472. In-Abbangarit, west of Air.

Localities

Morocco

Beni-Ounif de Figuig (i. e. Revoil Beni Ounif), 32.03 N, 01.14 W (Heim de Balsac 1936, 1948).

Algeria

Tindouf region, 27.42 N, 08.10 W (Schauenberg 1974).
Beni Abbès, 30.11 N, 02.14 W (Schauenberg 1974; Petter pers. comm.).
Mazzer, Beni Abbès, 30.19 N, 02.16 E (MNHP 1955.87, skin only).
Hassi-In-Meguis, Tassili de l'Ahmet, 175 km NE of Ouallène, ca. 24.40 N, 02.30 E (Schauenberg 1974).
El Golea, 30.35 N, 02.51 E (BM 34.8.2.8, skin and skull, male, type of *meinertzhageni* Pocock; MNHP 1962.2933, skull, male).
Laghouat, 33.49 N, 02.55 E (MNHP 1930.83, skin and skull, female).
Negonça, N. of Ouargla, ca. 32.00 N, 05.16 E (Loche 1858, type of *margarita*).
Issebilen, 80 km E of Fort Polignac, 26.29 N, 08.01 E (Lavauden 1926).

Rio de Oro

Adrar Souttouf Mts., Armumuit oasis, 21.42 N, 15.36 W (MNHP 1973.290, skin and skull, female).

Mali

"Soudan" (coll. Lieut. Talat) (MNHP 1886.1186, skin, sex unknown).

Niger

In-Abbangarit, 800—1000 ft., san dunes west of Air, 17.54 N, 06.03 E (BM 39.1673, skin and skull, female, type of *airensis* Pocock).

Touaret, 500 m, 20.17 N, 07.08 E (BM 67.1429, skin and skull, juv. male).

Diagnosis: size small in both sexes, skull relatively narrow with relatively small bullae, small carnassials, low narrow occiput; high values of allometric exponents for breadth measurements/greatest length. Colour relatively bright; well marked, with buffy-white paws, buffy collar on throat, 2—6 tail rings.

2. *Felis margarita thinobia* (Ognev, 1926)

1927 *Eremaelurus thinobius* Ognev. Ann. Mus. Zool. Acad. St. Petersb., 27:356. Repetek, Turkmenia.

Localities: in Heptner (1970), Heptner and Sludskij (1972), Schauenberg (1974). Distribution extends over Karakum, Kyzylkum and Pattakum.

Diagnosis: size large in both sexes; skull relatively broad with low narrow occiput and relatively small bullae, but large carnassials. Allometric exponents for breadth measurements vs. greatest length apparently intermediate between *margarita* and*scheffeli*. Colour darker, greyer than *margarita*, with reduced markings; tail-rings 2—3 up to 6 in kittens.

Remarks: in the absence of original measurements, except for a few from Ognev (1935), this race cannot be fully compared to others in its skull characters.

3. *Felis margarita scheffeli* Hemmer, 1974

1974 *Felis margarita scheffeli* Hemmer, Zschr. Kölner Zoo, 17:14 (Feb. 1974); Senckenb. Biol. 55:29 (July 1974).

Localities: Nushki, Pakistan.

Diagnosis: males large in size, females small (on our data); skull broad with very large bullae but carnassials not as large as *thinobia*, and occiput not expanded. Relatively low values for allometric breadth/length exponents. Colour usually resembling previous race, but occurrence of more strongly marked individuals seems more frequent; more than 8 tail rings at least in kittens.

Remarks: compared to *margarita* this race (Table 1, Figs. 2, 3, 4, 5 b) has a relatively larger bulla, average greater breadths in facial region of skull, but lower values of allometric exponents of these measurements vs. greatest length.

4. *Felis margarita harrisoni* ssp. n.

Type locality: northern edge of Umm as Samin, Oman, 21.55 N, 55.50 E.

Holotype: Harrison Zoological Museum no. 2.4747, skin and skull, adult male, collected 2. 7. 67. To be transferred to British Museum (Natural History).

Paratype: BM. 59.634, adult male skin and skull; from an animal captured at about 6 months old, lived in London zoo from 25. 4. 52 to 19. 10. 59; from Beihan, western Aden Protectorate (now South Yemen), 150 mi. north of Aden, within a few miles of (North) Yemen frontier. Living animal figured by Haltenorth (1953 a) and Harrison (1968), skin and skull figured by Harrison (1968).

Origin of name: in honour of David L. Harrison, M. A., M. B., B. Ch., Ph. D., F. L. S., F. Z. S.; Curator of Mammals, Harrison Zoological Museum, Sevenoaks, Kent, England; author of three-volume monograph, The Mammals of Arabia.

Localities: Umm as Samim (type); Beihan (paratype); east part of Rub al Khali, Ramlat al Ghafa, 21.00 N, 55.00 E (BM. 48.414, skin only); Qatar, near Abu Dhabi frontier (Harrison Museum 3.5868, skin and skull, young adult); 20 km southwest of 'Ibri (40 km west of Wadi Alayn on Sunainah track), Oman (Harrison Museum 1.4519, skin only). A few additional records in Schauenberg (1974). Assigned to this race provisionally, a living specimen from the Sinai desert, in Zoological Institute of Tel Aviv University: photos seen by H. H.

Diagnosis: males small, female (one skull only, recorded by Schauenberg 1974) diminutive; skull broad with large bullae, high broad occiput, large carnassials. Colour more as nominate race with bright hue, well-expressed pattern etc., but even more sharply marked: less extensive and diffuse darkening on dorsal surface, clean white paws with relatively sharp transition to buff of legs; 5 to 7 tail rings in adults; but ear patch smaller, less dark.

Remarks: even given the high values for the allometric exponents in *margarita, harrisoni* is none the less extremely broad. The bulla is much larger. Compared to *scheffeli* also, *harrisoni* is broader, especially as regards becanine breadth and occipital breadth. A calculation of indices shows:
Bicanine br./Gtest. l. — *scheffeli* 24.4 ± 0.6; *harrisoni* 27.1 ± 0.8; $t = 6.07$, $p < 0.01$.
Occip. br./Gtest l. — *scheffeli* 26.5 ± 0.8; *harrisoni* 29.5 ± 1.2; $t = 4.70$, $p < 0.01$
(Index in *margarita* = 26.4 ± 2.4).

Relationship between subspecies

Skull length-breadth indices (bizygomatic breadth) of the four are as follows:

F. m. margarita	74.9 ± 2.0	(6)	
F. m. thinobia	75.9	(29)	(from means given by Heptner 1970)
F. m. scheffeli	75.9 ± 2.3	(7)	
F. m. harrisoni	79.5 ± 3.0	(3)	

In comparison with *harrisoni*, Student's t for *margarita* = 2.77 ($p < 0.05$), for *scheffeli* = 2.03 (p just > 0.05). Clearly, in the habitat series (above, under "Relationships of *Felis margarita*") where increasing skull breadth correlates with increasing habitat aridity, *harrisoni* ranks as the most highly specialised race of this species. The hypertrophied bulla is another indicator of specialisation, and so probably is the large carnassial. *F. m. scheffeli* is intermediate (breadth and carnassials as *margarita*, bulla as *harrisoni*), and *F. m. thinobia* rather less so (carnassials only enlarged). As far as the skin pattern goes, the two eastern races are more specialised, with greater reduction of the pattern and paler colouration; but again between the two western races *harrisoni* is on the whole more desert-adapted with the greater amount of white on the extremities.

Probably the ancestral form of the species most closely resembled *F. m. margarita;* from this a radiation of more specialised forms arose, with *thinobia* and *scheffeli* acquiring a more intensely eremial pattern of skin and *harrisoni* of skull.

Acknowledgements

We gratefully acknowledge the assistance of D. Kock (Frankfurt), J. E. Hill (London), F. Petter (Paris) and D. L. Harrison (Sevenoaks) in studying the specimens under their charge; W. Scheffel's (Maintal) kindness and cooperation in permitting us to study his living Sand Cats is much appreciated. Mrs. Joan Goodrum drew the figures.

Summary

The Sand Cat, *Felis margarita,* is a highly desert-adapted species, phylogenetically related in all probability to *Felis chaus* on the one side and *Felis silvestris* on the other. Its age, sex, seasonal and individual variations are described, and on this basis comparisons are made between the four geographical variants which are all recognised as subspecies (one of them newly described).

Zusammenfassung

Bemerkungen über die Sandkatze, Felis margarita Loche, 1858

Die Sandkatze, *Felis margarita,* ist eine in hohem Maße an das Wüstenleben angepaßte Art, die verwandtschaftlich aller Wahrscheinlichkeit nach zwischen der Rohrkatze, *Felis chaus,* und der Wildkatze, *Felis silvestris,* steht. Ihre Variabiltät wird im Hinblick auf jahreszeitliche und Altersveränderungen, auf den Sexualdimorphismus und auf individuelle Verschiedenheiten studiert. Eine auf dieser Basis durchgeführte vergleichende Betrachtung der vier geographischen Formen erlaubt, diesen jeweils den Rang von Unterarten zuzuerkennen, von denen eine neu beschrieben wird.

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Zeitschrift/Journal: Mammalian Biology (früher Zeitschrift für Säugetierkunde)

Jahr/Year: 1975

Band/Volume: 41

Autor(en)/Author(s): Groves Colin P., Grubb Peter, Hemmer Helmut

Artikel/Article: Notes on the Sand Cat, Felis margarita Loche, 1858 286-303