

Systematics of African *Nycteris* (Mammalia: Chiroptera) Part II. The *Nycteris hispida* group

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Abstract. In this paper the systematics of the African *Nycteris hispida* species group is discussed. Using multivariate statistical techniques, three species can be distinguished in this group: one extremely large *Nycteris grandis* Peters, 1865, and two smaller species: *Nycteris hispida* (Schreber, 1774) and *Nycteris aurita* (K. Andersen, 1912). It is shown why both latter species are generally lumped together, since they are very alike when external measurements are compared univariably. None of the three species shows sufficient geographical differences to permit subspecific division. Besides biometrical data, the distribution of the three species is discussed and a review of all publications concerning the various forms is presented. Additionally the sexual dimorphism in the different species was examined, indicating that one must be very careful in attributing sexual dimorphism if the specimens originate from a large geographic area.

Key words. Chiroptera, *Nycteris*, taxonomy, zoogeography, Africa, multivariate statistics.

Introduction

In 1912 Andersen subdivided the genus *Nycteris* Geoffroy & Cuvier, 1795 — then known as *Petalia* — into four separate species groups, according to a number of morphological characters. Two of the African groups — the *N. arge* group and the *N. macrotis* group — were already subject of a previous paper (Van Cakenberghe & De Vree 1985), while the last group — the *N. thebaica* group — will be discussed in a forthcoming paper. The presently discussed group — the *N. hispida* group — was characterised in having tricuspid upper incisors, a small second lower premolar and a small tragus, which has an equal width over its entire length as is shown in figure 1.

In this group, two species are generally accepted: the small *N. hispida* (Schreber, 1774) and the gigantic *N. grandis* Peters, 1865. A third form — *aurita* — described by Andersen in 1912 is considered by most authors to be a synonym or at most a subspecies of *N. hispida*, although some (e. g. Koopman 1975) believe it might be more.

Since the description of both former species, a fair number of forms has been described by various authors, which subsequently were considered to be either synonyms or subspecies. In this paper, the status of these forms will be discussed.

Material and Methods

A total of 1449 specimens, belonging to the various forms of the *N. hispida* group, were examined during this study. The material was obtained from the following collections, the curators of which we would like to thank:

British Museum (Natural History), London, G. B. (BM): J. E. Hill; California Academy of

Sciences, San Francisco, U. S. A. (CAS): J. Schonewald & L. F. Baptista; Carnegie Museum, Pittsburgh, U. S. A. (CM): S. B. McLaren & D. A. Schlitter; Koninklijk Belgisch Instituut voor Natuurwetenschappen, Brussels, Belgium (KBIN): X. Misonne; Kaffrarian Museum, King William's Town, Republic of South Africa (KM): P. Swanepoel; Koninklijk Museum voor Midden-Afrika, Tervuren, Belgium (KMMA): D. Meirte; University of Kansas Museum of Natural History, Lawrence, U. S. A. (KU): S. M. Kortlucke & R. Hoffmann; Muséum National d'Histoire Naturelle, Paris, France (MNHN): F. Petter & M. Tranier; Museo Civico di Storia Naturale "Giacomo Doria", Genova, Italy (MSNG): G. Arbocco; Museo Zoologico de "la Specola", Firenze, Italy (MZUF): M. L. Azzaroli; Naturhistorisches Museum, Bern, Switzerland (NMBE): P. Lüps; Naturhistorisches Museum, Wien, Austria (NMW): F. Spitzenberger & K. Bauer; Nationaal Naturhistorisch Museum (formerly Rijksmuseum van Natuurlijke Historie), Leiden, The Netherlands (RMNH): C. Smeenk; Royal Ontario Museum, Toronto, Canada (ROM): R. L. Peterson & J. Eger; Senckenberg Museum, Frankfurt-am-Main, Germany (SMF): D. Kock; Staatliches Museum für Naturkunde, Dresden, Germany (SMND): S. Eck; Staatliches Museum für Naturkunde, Stuttgart, Germany (SMNS): F. Dieterlen; Transvaal Museum, Pretoria, Republic of South Africa (TM): D. A. Wolhuter & I. L. Rautenbach; United States National Museum, Washington, U. S. A. (USNM): M. D. Carleton & C. B. Robbins; Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn, Germany (ZFMK): R. Hutterer; Zoologisches Institut und Museum, Hamburg, Germany (ZMH): H. Schliemann; Zoologisk Museum Universitet København, Denmark (ZMUC): H. J. Baagøe; Zoologisches Museum der Universität Zürich, Switzerland (ZMZ): C. Claude.

Material from the BM, RMNH, SMF, USNM, and ZFMK as well as part of the material from the MNHN was examined on the spot. Special thanks are due to the curators of these museums for their kind hospitality.

As far as possible, 11 cranial and 9 external variables were measured during this study: 1: Gl_s = Greatest length of the skull, 2: Cbl = Condylbasal length, 3: Sw = Width of the shield, 4: Zyg = Zygomatic width, 5: Mast = Mastoid width, 6: Brain = Width of the Braincase, 7: c-m³ = Length of the upper tooththrow, 8: c-c = Width across the upper canines, 9: m³-m³ = Width across the upper third molars, 10: Mand = Mandibular length, 11: c-m₂ = Length of the lower tooththrow, 12: Fa: Forearm length, 13: Meta 3 = Length of the metacarpus of the third finger, 14: 3 ph 1 = Length of the first phalange of the third finger, 15: 3 ph 2 = Length of the second phalange of the third finger, 16: Meta 4 = Length of the metacarpus of the fourth finger, 17: Meta 5 = Length of the metacarpus of the fifth finger, 18: 5 ph 1 = Length of the first phalange of the fifth finger, 19: 5 ph 2 = Length of the second phalange of the fifth finger, 20: Tib = Tibial length.

For more details on the measurements and statistical techniques, see Van Cakenberghe & De Vree (1985, 1993).

Results

Since the two generally accepted species represent two clearly distinguishable size groups, most analyses are performed on specimens from one of these size groups.

Figure 2 shows the results of a first canonical analysis on the tooth measurements of 66 specimens from *N. grandis*, which represents the large size group. In this species, some authors (e. g. Kock 1981 a) distinguish two subspecies, of which one — *marica* — occurs in East and southern Africa. Included in this analysis are seven groups, each from a different country. The number of specimens for each group is given between brackets: 1 = Ghana (15), 2 = Ivory Coast (5), 3 = Cameroon (18), 4 = Liberia (3), 5 = Tanzania (6, including the holotype of *marica* "T1"), 6 = Togo (4) and 7 = Zaire (15). Variables 8 ("v8" = c-c) and 10 ("v10" = Mand) are the best separating variates, which result in the separation between Zaire and five of the remaining countries. The large overlap between the animals from Tanzania and the five

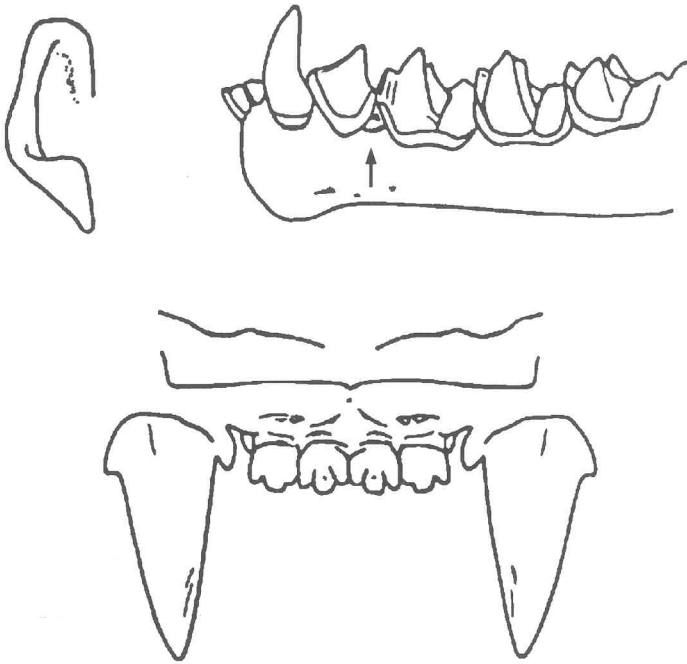


Fig. 1: Morphological characters of the members of the *N. hispida* group.

remaining countries (Ghana, Ivory Coast, Cameroon, Liberia and Togo) indicates, that if a subspecific difference should occur, it cannot be found between West and East Africa. The large overlap between Cameroon and all other groups, furthermore indicates that the differences with Central Africa are also small. Similar results are obtained from analyses on all the skull and the external measurements. Therefore, one can conclude that there is no justification for subdivision into subspecies.

In the small size group, the situation is more complicated. As a result of the vast distribution area, many different forms were described, of which the East African *aurita* is discussed more thoroughly.

A first principal components analysis on the tooth measurements of 46 specimens from East Africa is represented by figure 3. For this analysis, 24 specimens from Kenya ("1", including the holotype of *aurita* "T1"), 12 specimens from Tanzania ("2") and 10 specimens from Uganda ("3") were used. All five original variables are correlated positively with the first principal component (P. C.₁ — from 0.82 for c-c to 0.95 for Mand), indicating that the first P. C. is a good indicator for the size of the animals. From the graph one can see that the material from Tanzania ("2") can easily be divided into two groups. In the Kenyan material ("1"), where the separation is less clear, the specimens on the extreme left represent animals from Kilifi and Tana river, which are also found in the cluster on the right, indicating sympatric occurrence of two different forms. On the other hand, the specimens from Uganda are very

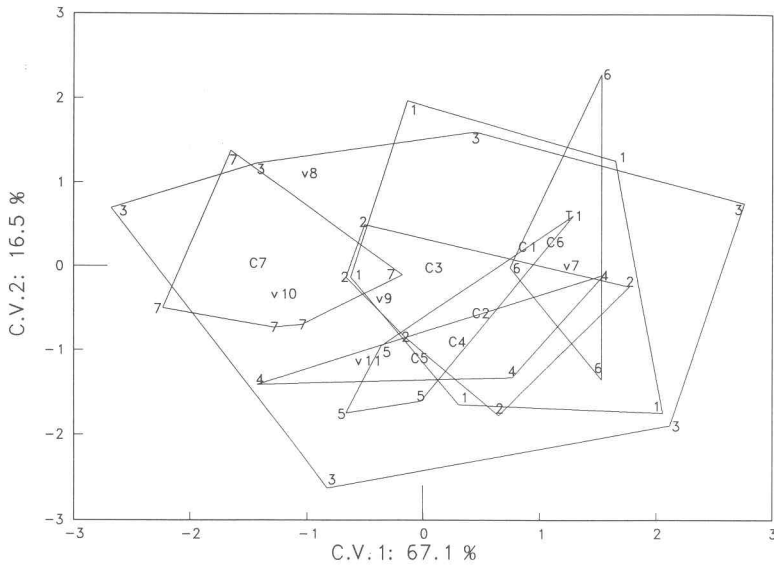


Fig. 2: Canonical analysis on the tooth measurements of 66 specimens belonging to *N. grandis*, subdivided by country. 1 = Ghana, 2 = Ivory Coast, 3 = Cameroon, 4 = Liberia, 5 = Tanzania, 6 = Togo, 7 = Zaire. T₁ = holotype of *marica*.

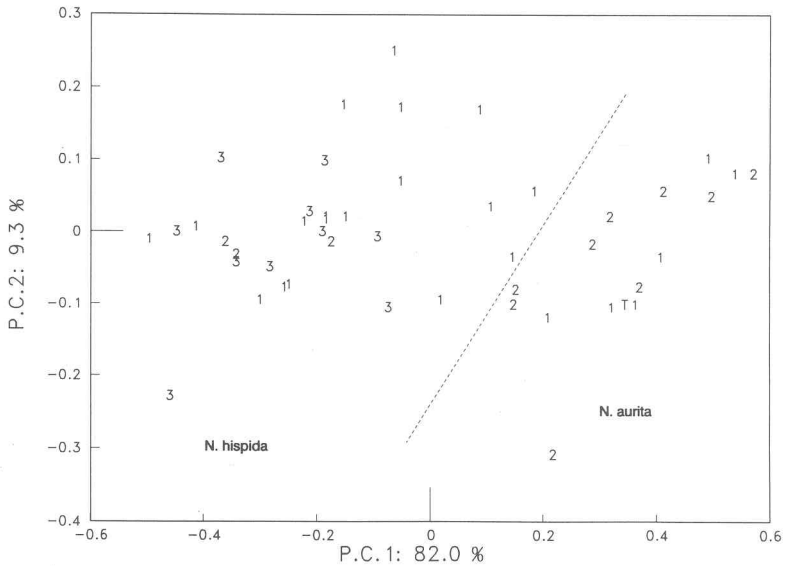


Fig. 3: Principal components analysis on the tooth measurements of 46 specimens from Kenya ("1"), Tanzania ("2") and Uganda ("3"), belonging to the small size group of the *N. hispida* group. T₁ = holotype of *aurita*.

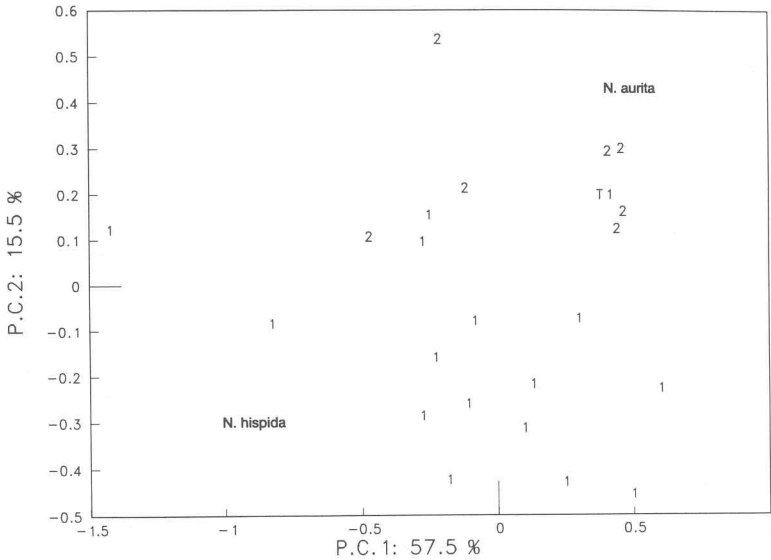


Fig. 4: Principal components analysis on the external measurements of 23 specimens from East Africa, belonging to the *N. hispida* group: "1" = *hispida*, "2" = *aurita*, T₁ = holotype of *aurita*.

uniform, but only occur on the left of the graph. The dashed line, therefore separates two different forms in East Africa, distinguished by this analysis: *hispida* from Uganda, Tanzania and Kenya and *aurita* occurring in Tanzania and Kenya, in the latter country even sympatrically. The holotype of *aurita* ("T₁") enables the identification of the right hand cluster.

A second principal components analysis (figure 4) is performed on external measurements of all available East African specimens. In this figure, the symbols represent *hispida* ("1") and *aurita* ("2", including the holotype "T₁") as they resulted from the previous principal components analysis. All external measurements are correlated positively with P. C.1, with values varying from 0.44 for 5 ph 2 to 0.94 for Meta 5, again indicating that size is represented by the X axis. Fa, Meta 5, 5 ph 1 and Tib correlate positively with P. C.2.

In contrast to the previous analysis, this graph shows the separation between both forms is not along P. C.1, but more or less along P. C.2. Both groups are indeed significantly distinct in their scores on the second axis: $F = 24.937$ with 1 and 21 df., ****. The analysis shows that for the external measurements, absolute size is not critical, rather the proportions of the different measurements determine whether a specimen belongs to *hispida* or to *aurita*. This explains why most authors have difficulties in separating *aurita* from *hispida*, since they usually use external measurements.

Analyses on specimens from Northeast Africa (i. e. Sudan, Ethiopia and Somalia), an area which closely allies with East Africa, also reveal the presence of two forms in both latter countries.

As a result of the sympatric occurrence of both forms in Kenya, both need to be considered as species.

A subsequent multivariate analysis is performed on the tooth measurements of 754 specimens belonging to the small size group. For this canonical analysis, illustrated by figure 5, the specimens are subdivided into seven groups representing various African regions. Between brackets, the number of specimens in each group is indicated: 1 = *N. aurita* from East Africa (14, including the holotype, "T1"), 2 = *N. hispida* from East Africa (32), 3 = *N. aurita* from Northeast Africa (4), 4 = *N. hispida* from northeast Africa (65), 5 = *N. hispida* from West Africa (534), 6 = *N. hispida* from Central Africa (97, including a paratype of *pallida*, "T2") and 7 = *N. hispida* from southern Africa (8). This analysis indicates the importance of $c-m_3$ ("v11") as the best separating variable. All variables are correlated positively with the first canonical variate (C. V.₁), with values between 0.41 for $c-c$ and 0.96 for $c-m_3$. This graph shows that *N. aurita* can easily be separated from *N. hispida*. The holotype of *N. aurita* and the paratype of *N. pallida* fall into the *N. aurita* and *N. hispida* clusters, respectively. Moreover, all the regional groups of *N. hispida* are very similar. Consequently, it is believed that *N. hispida* cannot be separated into recognizable subspecies.

Further substantiation of the existence of two distinct species in that area resulted from a discriminant analysis on the tooth measurements of 19 specimens belonging to *N. aurita* and 778 specimens belonging to *N. hispida*. For all five variables, the discriminant function is as follows:

$$X = 7.126 * c-m^3 - 2.044 * c-c - 1.754 * m^3-m^3 + 5.523 * Mand + 12.698 * c-m_3.$$

The chance for misclassification equals 1.28 % for a Mahalanobis distance of 19.915 with a Hotelling T² of 369.370 and an F-value of 73.502 for 5 and 791 df., ****. Stepwise selection of the variables, revealed the length of the lower tooth row being the best separating variable. The discriminative value for the total subset equals 164.245; for which no specimens of *N. aurita* are misclassified, and 9 specimens of *N. hispida* might be misclassified. When moving this value slightly (e. g. 167.5), only one specimen belonging to *N. aurita* would be misclassified, namely ZFMK 60.258 from Lembeni, Tanzania. However, a reexamination of this specimen proved that it clearly belongs to this species.

The univariate difference between *N. aurita* and *N. hispida* is less clear as is illustrated by table 1. For all variables, *N. hispida* shows a larger range than *N. aurita*, although *N. aurita* always scores very high in the range of *N. hispida* (see also tables 3 and 5). Table 1 shows that all skull measurements, the forearm length, the tibia length and 3 ph 2 are significantly distinct, whereas none of the remaining external measurements are significantly distinct. This also explains why these species were not clearly separated by multivariate analyses on the external measurements. However, it also confirms that *N. aurita* clearly differs from *N. hispida* in its cranial measurements.

It was not possible to study the univariate sexual dimorphism of *N. aurita* in detail, because of the lack of specimens. For *N. grandis*, a total of 45 males and 36 females was examined on sexual dimorphism. None of the variables examined showed any significant differences between both sexes.

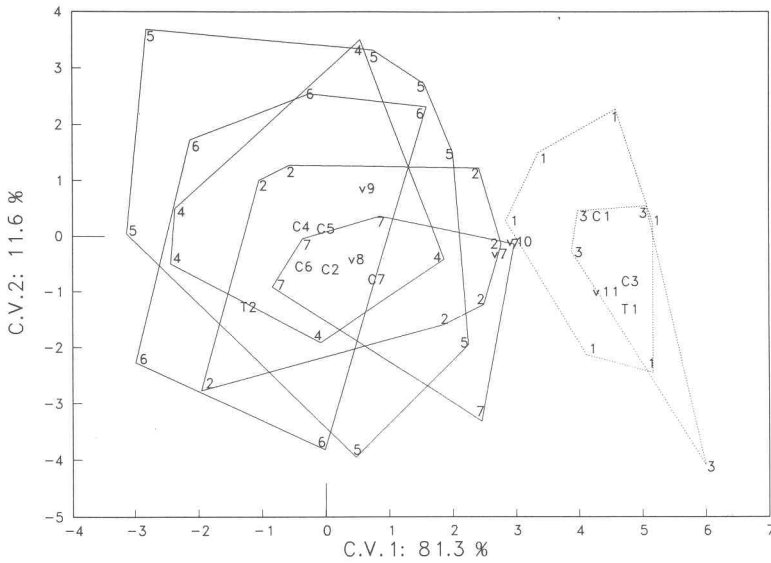


Fig. 5: Canonical analysis on the tooth measurements of 754 specimens belonging to the small size group of the *N. hispidus* group, divided by region. *N. aurita* = 1 = East Africa, 3 = Northeast Africa; *N. hispidus* = 2 = East Africa, 4 = Northeast Africa, 5 = West Africa, 6 = Central Africa, 7 = Southern Africa. T₁ = holotype of *aurita*; T₂ = paratype of *pallida*.

Table 1: Univariate differences between *N. aurita* and *N. hispidus* (Significance levels: ns: $\alpha > 0.05$; *: $0.05 > \alpha > 0.025$; **: $0.025 > \alpha > 0.01$; ***: $0.01 > \alpha > 0.005$; ****: $0.005 > \alpha$).

Var	<i>aurita</i>	ⁿ <i>hispidus</i>	F value	df	sign
Gls	13	599	167.223	610	****
Cbl	13	566	175.471	577	****
Sw	13	608	26.201	619	****
Zyg	13	576	56.141	587	****
Mast	13	590	46.014	601	****
Brain	14	631	16.588	643	****
c-m ³	21	667	196.674	686	****
c-c	19	637	67.898	654	****
m ³ -m ³	19	658	64.774	675	****
Mand	21	647	293.943	666	****
c-m ₃	21	659	293.213	678	****
Fa	24	488	62.513	510	****
Meta 3	20	219	4.632	237	ns
3 ph 1	20	219	1.730	237	ns
3 ph 2	20	215	10.746	233	***
Meta 4	20	215	0.166	233	ns
Meta 5	20	214	4.188	232	ns
5 ph 1	20	217	3.340	235	ns
5 ph 2	20	215	3.824	232	ns
Tib	20	224	51.461	242	****

The sexual dimorphism in *N. hispida* was examined by means of 427 males and 394 females from West Africa. Table 2 unexpectedly indicates that both sexes are significantly distinct, if examined for the entire region. To exclude geographical differences, a number of analyses are performed using separate countries, and if possible, separate localities. Because in most groups only the skull measurements could be compared, only these are included in the analyses.

In Senegal (SEN), variables 4 and 10 (Zyg and Mand) and Fa ($F = 8.059$ with 1 and 26 df., ***) are found to display significant differences. In Ivory Coast (IVC), only Fa ($F = 7.155$ with 1 and 13 df., **) is significantly distinct, while none of the cranial measurements shows significant differences. Specimens from Kong, Ivory Coast (6 males and 10 females) are distinct for variables 4 and 6 (Zyg and Brain). In all other West African countries *N. hispida* shows a more elaborate sexual dimorphism. Table 2 gives a summary of the results of a series of F-tests: the stars indicate significant distinction.

For West Africa, one can conclude that *N. hispida* shows a very extensive sexual dimorphism, more elaborate than that of any other species examined.

For the 40 males and 37 females from East Africa, significant distinction is only found for Fa, Meta 3, Meta 4 and Meta 5. The material from Tanzania could only be examined on the skull measurements and the forearm length, which were not significantly distinct. The material from Kenya is significantly distinct for c-m³, Fa, Meta 3, Meta 4 and 5 ph 1.

In Northeast Africa, significant distinction is found for Cbl, c-m³, m³-m³, Mand, Fa, Meta 3, 3 ph 1, Meta 4, Meta 5, 5 ph 1 and 5 ph 2, whereas for Central Africa only Sw and the external measurements, with the exception of the tibia length, are significantly distinct. This reflects clearly the situation for Zaire. The very few

Table 2: Summary of the univariable sexual dimorphism in cranial measurements of *N. hispida* from West Africa. The numbers represent skull measurements 1 thru 11.

	1	2	3	4	5	6	7	8	9	10	11
W-Africa	****	****	****	****	***	****	****	****	****	****	****
MAU	****	****	ns	****	ns	ns	***	***	****	*	**
GHA	*	***	***	***	ns	ns	*	****	**	****	***
BFA	*	****	****	*	ns	ns	***	****	****	****	****
Arly	ns	ns	ns	ns	ns	ns	ns	ns	ns	*	ns
Goden	ns	****	****	ns	ns	ns		ns		****	
Orodara	***	***	*	*		ns		****		****	
BEN	ns	*	ns		ns	**	ns	ns	*	ns	ns
TOG	ns	**	ns	ns	ns	ns	ns	ns	***	ns	ns
Nanergou	ns	ns	ns	ns	***	ns	ns	ns	ns	ns	ns
NIG	**	****	*	ns	ns	ns	ns	ns	ns	*	ns
CAM	****	****	****	***	ns	ns	****	****	***	****	****
Gueme	****	****	****	ns	ns	ns	***	***	ns	****	*
Waza	ns	**	ns	ns	ns	ns	ns	ns	ns	****	ns
Yagoua	****	****	ns	ns	ns	ns	ns	ns	**		
SEN	ns	ns	ns	**	ns	ns	ns	ns	ns	****	ns
IVC	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Kong	ns	ns	ns	*	ns	****	ns	ns	ns	ns	ns

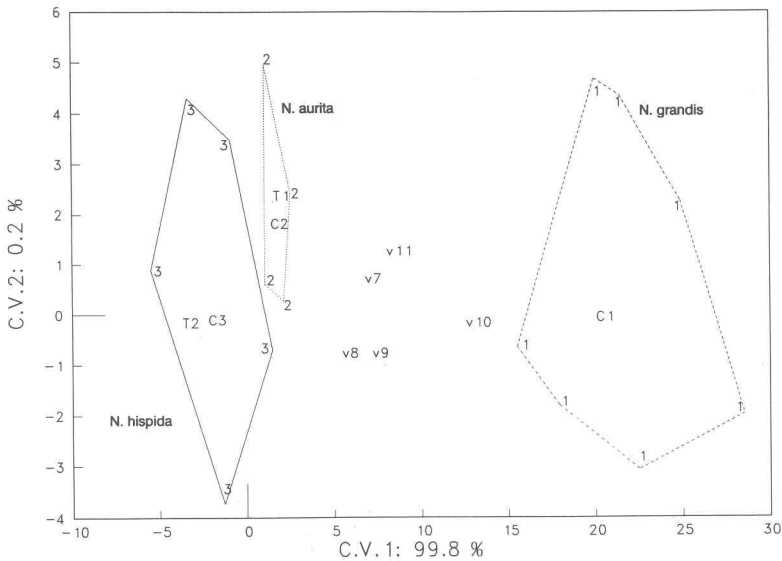


Fig. 6: Canonical analysis on the tooth measurements of 818 specimens belonging to the *N. hispida* group, divided by species.

southern African specimens (8 males and 6 females) are only for m^3 - m^3 significantly distinct.

These univariate analyses indicate that one must be very careful when indicating sexual dimorphism in a certain species. The analyses clearly show that geographic variation might obscure the picture.

For confirmation of the species identity of the *N. hispida* group, the results of a final multivariate analysis are given by figure 6. All available specimens of the *N. hispida* group were entered, including the very large *N. grandis*. The 818 specimens were divided into three groups: 1 = *N. grandis* (67), 2 = *N. aurita* (18) and 3 = *N. hispida* (733). All variables are positively correlated with C. V. 1, ranging from 0.997 for c-c to 0.999 for Mand. Therefore, the first axis is a very good indicator for size. The graph indicates that *N. grandis* is clearly larger than both other species. However, it is also important that even on this scale *N. aurita* is still significantly distinct from *N. hispida* ($F = 283.94$ with 1 and 749 df., ****).

This leads to the conclusion that three species are recognized in the *N. hispida* group: a very large *N. grandis*, the large size of which lets it readily be distinguished from two smaller species: *N. hispida* and *N. aurita*, which can only be separated by means of skull measurements.

Systematic Accounts

Three species are retained in the *N. hispida* group: *N. hispida*, *N. aurita* and *N. grandis*, all having tricuspid upper incisors, a small second lower premolar and a small tragus, which has an equal width over its entire length.

Nycteris hispida (Schreber, 1774)

Vespertilio hispidus Schreber, 1774. Die Säugethiere in Abbildungen nach der Natur mit Beschreibungen: 169–170. — Type locality: Senegal.

Nycteris Daubentonii E. Geoffroy, 1813. Ann. Mus. Hist. Nat., Paris, 20: 19. — Type locality: Senegal.

Nycteris poensis Gray, 1843. Catalogue of the Spec. Mammals of the British Museum, London: 24. — Type locality: Fernando Po.

Rhinolophus Martini Fraser, 1843. Proc. zool. Soc. Lond.: 25–26. — Type locality: Fernando Po.

Nycteris villosa Peters, 1852. Naturwissenschaftliche Reise nach Mossambique, Berlin: 48–50. — Type locality: Inhambane, Mozambique.

Nycterops pilosa Gray, 1866. Proc. zool. Soc. Lond.: 83. — Type locality: Africa.

Nycteris pallida J. A. Allen, 1917. Bull. Amer. Mus. Nat. Hist., 37: 425. — Type locality: Faradje, Zaire.

Although most authors indicate 1775 as date of description, it must be 1774.

N. hispida is the most common species of this group (see figure 7), therefore its distribution agrees with the range of the entire group.

The distribution of *N. hispida* in southern Africa is most peculiar. This species is very common southward to 10° S. Further south, there are a few records from Mozambique and Botswana up to 20° S, followed by a large gap. In the Republic of South Africa, an area which has been sampled intensively, only a few specimens were collected, almost on the southernmost point of the continent: Cape of Good Hope (1 in BM and 1 in MSNG). A third record is extensively discussed by Herselman & Norton (1985), who, however, believe that the specimen of Port St Johns (see Ellerman, Morrison-Scott & Hayman 1953) is a juvenile representative of *N. thebaica*. They base their conclusion on the fact that Shortridge collected several *N. thebaica* specimens at the same time and that the smaller size and different colour agrees with those of juvenile specimens caught at the same time of the year. The existence of two *N. hispida* specimens from the Cape of Good Hope make it very likely that this one specimen is indeed a member of the same species.

Also the records of *N. hispida* on Sicily (see e. g. Doderlein 1871 and 1881; Toschi & Lanza 1959 and Van den Brink 1978) are surprising. All these records can be traced back to the very vague record by Malherbe in 1843. Unfortunately, the specimen mentioned by Malherbe has been lost. The suggestion of Toschi & Lanza (1959) that this might be a vagrant of *N. thebaica* from Egypt is probably correct. Malherbe (1843) might have called this specimen *N. hispidus*, because he was not aware of the “recent” description of *N. thebaica* by Geoffroy in 1813.

The pelage colour of *N. hispida* is very variable, but dark beige and dark brown are the most common colour tints. The dominance of these dark tones is mainly due to its common occurrence in the forests.

N. daubentonii is considered a valid taxon by Geoffroy (1813b) only. In his other work, dating from the same year (Geoffroy 1813a), he already mentioned a “Nyctère de Daubenton”, without a scientific name, which he claims to be a representative of *N. hispida*. Wagner (1840) was the first to make *daubentonii* a synonym of *N. hispida* on a formal basis.

After Gray (1843), all subsequent references cite *N. poensis* Gray, 1843 as a synonym of *N. hispida* (Schreber, 1774). Eisentraut (1964) even claims it to be a synonym of *N. hispida hispida*.

Only two references (Fraser 1843 and Wagner 1855), report *Rhinolophus martini* as such, but according to Peters (1871), Dobson (1878), Elliot (1907), Cabrera (1908),

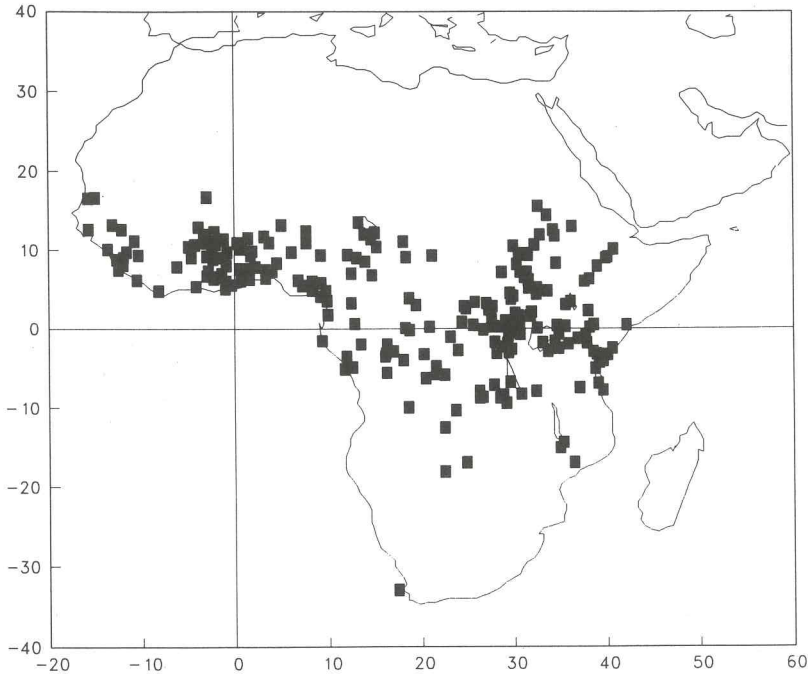


Fig. 7: Distribution map of *Nycteris hispida* (Schreber, 1774).

Allen (1939) and Rosevear (1965), it is clearly a member of the genus *Nycteris*. Most authors put this name in synonymy with *N. hispida* (Schreber, 1774). Braestrup (1935) accepts *N. martini* as a subspecies of *N. hispida*, occurring in the south Sudanese forest area, as counterpart of *N. hispida hispida*, occurring from Senegal to central Sudan. Koopman (1975) could not distinguish these subspecies in the Sudan. The dubious holotype in the BM also confirms it to be a *Nycteris*, but since this specimen is indicated to be the holotype of either *R. martini* or *N. poensis*, its affinity remains puzzling.

Except for the specimen mentioned by Gray (nomen nudum), *N. pilosa* Gray, 1866 is generally considered to be a synonym of *N. hispida* (Schreber, 1774).

N. pallida is widely accepted as a synonym of *N. hispida* (Schreber, 1774), also because all specimens believed to belong to *pallida* were males and these are usually a little smaller than females. The smaller measurements given for *N. pallida* therefore might reflect sexual dimorphism rather than taxonomic differences. Koopman (1965) suggested that a study of topotypical material of *N. hispida* from Senegal might be necessary to determine whether *pallida* can be retained as a valid subspecies of *N. hispida* (Schreber, 1774) as proposed by Braestrup (1935). From his study of Sudanese material Koopman (1975) found *pallida* to be identical with *N. hispida hispida*.

This study indicated that the form *pallida* cannot be separated from the other forms. We follow Verschuren (1957), Koopman (1965, 1975), Rosevear (1965),

Hayman, Misonne & Verheyen (1966), Kock (1969) and Hayman & Hill (1971) in regarding *pallida* to be a synonym of *N. hispida*.

It has not been possible to examine specimens of the southern form *villosa*. The few southern African specimens, which were identified as *hispida*, were intermediate in size. One specimen from the Cape of Good Hope is remarkably larger than the others. Roberts (1951) indicated that the locality record for South Africa might be wrong, therefore this Cape of Good Hope specimen might not represent *villosa*. The lack of material makes it impossible to go into this problem more thoroughly.

Our analyses (see figure 5) indicate that *N. hispida* is very uniform throughout its entire distribution area and therefore cannot be divided into subspecies.

Table 3 shows the standard statistical data for all adult representatives of *N. hispida*. Included are the measurements of the paratype of *pallida* and the holotype of either *poensis* or *martini* (It is uncertain to which of these two forms the latter holotype relates). The limits of measurements of the forearm length (Fa: 33.5 to 43.9 mm) are somewhat smaller than those given by Rosevear (1965) and Hayman & Hill (1971), who give 36 to 45 mm. The lower limit is appreciably smaller than the figure given by other authors: 39 to 43 mm (Allen 1959); 39.3 to 43.7 mm (Kulzer 1962); 38 to 41 mm (Ellerman, Morrison-Scott & Hayman 1953); 40.6 to 42.3 mm (Jones 1971); 40 to 41 mm (Hill & Carter 1941); 39 to 42 mm (Monard 1939); 40 to 43.5 mm (Allen 1917) and 36 to 45 mm (Kingdon 1974). The greatest length of the skull (Gls: 15.3 to 18.4 mm) also shows an extension of the lower limit of the range compared with the data found in the literature: Rosevear (1965): 17 to 18.5 mm and Allen (1917): 17.4 to 18.4 mm. The range of other measurements given by Rosevear (1965) includes

Table 3: Measurements of *N. hispida* (in mm).

Var	paratype <i>pallida</i>	<i>poensis</i> or <i>martini</i>	Mean	SD	Min	Max	n
Gls	—	15.8	16.45	0.39	15.3	18.4	748
Cbl	—	13.7	14.13	0.36	12.8	15.7	704
Sw	—	6.7	7.17	0.31	5.8	8.1	793
Zyg	—	9.6	10.10	0.29	8.8	12.0	678
Mast	—	7.9	7.89	0.36	6.3	8.7	746
Brain	—	7.3	7.54	0.25	6.3	8.5	794
c-m ³	5.0	5.0	5.28	0.21	4.6	6.7	870
c-c	4.0	4.0	4.10	0.18	3.5	4.8	814
m ³ -m ³	6.0	6.1	6.34	0.23	5.3	7.5	839
Mand	10.6	10.7	10.84	0.33	9.9	13.4	841
c-m ₃	5.7	5.8	5.90	0.21	5.1	7.6	860
Fa	—	38.0	38.72	1.65	33.5	43.9	742
Meta 3	—	29.0	29.85	1.70	24.1	34.4	253
3 ph 1	—	20.3	21.57	1.16	16.1	24.8	251
3 ph 2	—	17.6	20.82	1.68	11.2	24.3	247
Meta 4	—	30.7	31.72	1.79	26.2	36.3	249
Meta 5	—	30.7	31.93	1.66	26.9	36.6	246
5 ph 1	—	10.6	11.55	0.75	9.4	13.3	250
5 ph 2	—	8.0	9.43	0.82	7.4	12.0	246
Tib	—	18.0	18.12	1.25	13.8	23.5	258

larger minimum and smaller maximum values: Zyg: 10.0–11.0 mm; c-m³: 5.4–6.3 mm and m³-m³: 5.5–7.0 mm.

Literature citations

All records listed below are mentioned in the combination of names given by the different authors, without any interpretation. If the author mentioned another generic name, this is indicated by "(as *Petalia*)". For every combination of names, all references are given in a chronological order. For every author the country and the locality of origin of the material is indicated. The data, for which an older reference was given, are indicated by e. g. "(see Andersen 1923)".

The synonymy proposed by the author is also mentioned in the list, e. g.: "*poensis* = *hispidus hispidus*", meaning that the author regards *N. poensis* as a synonym of *N. hispidus hispidus*; "*aurita* = *hispidus aurita*" means that the author retains *N. aurita* only as a subspecies of *N. hispidus*.

Nycteris daubentonii E. Geoffroy, 1813

Geoffroy (1813 b): Senegal: TYPE — Desmarest (1820): without locality — Wagner (1840) (1855): *daubentonii* = *hispidus* — Peters (1871): *daubentonii* = *hispidus* — Dobson (1878): *daubentonii* = *hispidus* — Rochebrune (1883): *daubentonii* = *hispidus* — Trouessart (1904): *daubentonii* = *hispidus* — Elliot (1907): *daubentonii* = *hispidus* — Cabrera (1908): *daubentonii* = *hispidus* — Allen (1939): *daubentonii* = *hispidus* — Rosevear (1965): *daubentonii* = *hispidus*.

Nycteris hispidus (Schreber, 1774)

Schreber (1774): Senegal: TYPE (as *Vespertilio hispidus*) — Wagner (1840) (1855): Senegal — Malherbe (1843): Sicily — Doderlein (1871) (1881): Sicily — Peters (1871): Senegal; Fernando Po; Ghana: Accra, Dongola; Sudan: Port Rek — Dobson (1878): Khartoum; Fernando Po; Old Calabar; Lagos; Angola; Zanzibar; Cape of Good Hope — Dobson (1879): Zanzibar — Peters (1879): Kenya: Kitui — Dobson (1880): Kenya: Kitui — Rochebrune (1883): Senegal: Thionk, Sorres, Leybar, Gandiole, Dagana, Podor (as *N. hispidus*) — Pagenstecher (1885): British East Africa: Maurui — Jentink (1887 a): Zaire: Banana — Jentink (1887 b): Liberia: Schieffelinville — Jentink (1888): Liberia: Schieffelinville (= *N. arge*, see Kuhn 1965); Zaire: Banana — Noack (1889): Angola: Mocamedes (see Jentink 1887); Liberia — Bocage (1890): Guinea Bissau: Bolama — Matschie (1892): Kenya: Pangani; Zanzibar: Ukamba; Sudan: Port Reck; Dongola; Accra; Tschintchoscho; Aguapim — Matschie (1893): Togo: Bismarckburg — True (1893): Sudan: Tana river — Matschie (1894): Cameroon — Matschie (1895): Maurui on the Pangani and West Africa — Thomas (1896): Malawi: Fort Johnston — Matschie (1897): Zanzibar and continental coast — Sjostedt (1897 a) (1897 b): Cameroon: Itoki, Kitta — Neumann (1900): Muansu — Thomas (1901): Sudan: Kaka, Renk — Anderson & de Winton (1902): Sudan: Khartoum — Cabrera (1903): Fernando Po — Trouessart (1904): Egypt — Elliot (1907): Upper Shiré river — Cabrera (1908): Fernando Po; Rio Muni (= Equatorial Guinea) — Sassi (1908): Sudan: Khor Attar, Mongalla — Seabra (1909): Mozambique: Mossamedes — Thomas & Wroughton (1910): Mokia, Mubuku valley (Ruwendzori) (as *Petalia*) — Andersen (1912): Egypt; Sudan; British East Africa; Uganda; Malawi: Fort Johnston; Upper Shiré river; Angola; Guinea; Gambia (as *Petalia*) — Alluaud & Jeannel (1914): Kenya: Kulumuzi caves — Thomas (1915): Zaire: Medje, Poko — Allen (1917): Zaire: Boma, Stanleyville, Avakubi, Medje — Hollister (1918): Sudan: Bor; Kenya: Nairobi, Tana river (as *Petalia*) — Wettstein (1918): Sudan: Tonga, White Nile — Hinton & Kershaw (1920): Sudan: Kongor, Duk Fagwil, Duk Fadiat, Dinka Country — Schwarz (1920): Duma, Melfi, Koloka, Poko (as *Petalia*) — De Beaux (1922): Uganda: Koba (Lake Albert), Entebbe, Bugala island, Bubeke island, Bukasa island, Kitobo island, Gondokoro (as *Petalia*) — Kershaw (1922): Malawi: Chiromo — Kershaw (1923 b): Zaire: Eala, Kwamouth — Loveridge (1923): Tanzania: Madazani — Rodhain (1923): Zaire: Boma — De Beaux (1924): Somalia: Bardera, Afgoi — Kershaw (1924): Sudan: Malek — Cabrera & Ruxton (1926): Zaire: Luluabourg — Rodhain (1926): Zaire: Boma — Cabrera (1929): Rio Muni (= Equatorial Guinea) — Ingoldby (1929): Ghana: Upper Bibianaha, Kumasi, Kintampo — Allen & Coolidge (1930): Liberia: Schieffelinville, Du river (as *Petalia*) — Zammarano (1930): Somalia: Bardere-Afgoi — Hewitt (1931): Republic of South Africa: E Cape province (as *Petalia*) — Allen & Lawrence (1936): Kenya: Kaimosi, Ngatama — De Beaux (1937): Somalia: Belet Amin, Ola Uager — St. Leger (1937): Kenya: Lodwar — Frechkop (1938): Zaire — Allen (1939): Senegal; Mozambique: Inham-

bane; Fernando Po — Monard (1939): Guinea Bissau: Mansoa, Echalé, Bagingara, Catlo, Bolama (see Bocage 1890) — Moreau & Pakenham (1940): Zanzibar — Sanderson (1940): Cameroon: Mamfe, Nko — Hill & Carter (1940): Angola: Mossamedes (see Seabra 1909), Mt Moco (see St. Leger 1936) — Matthews (1941): Tanzania: Mto-wa-mbo — Nash (1942): Nigeria: Gadau — Frechkop (1943): Zaire: Mutwanga — Asdell (1946): Central and West Africa — Schouteden (1947): Zaire: Boma, Kunungu, Kasenga, Luluaburg, Mweka, Boende, Karawa, Stanleystad, Avakubi, Makala, Fundi, Buta, Djamba, Panga, Medje, Poko, Mulungu, Mutwanga, Mongbwalu, Moliro, Pweto; Duma, Koloka (see Schwarz 1920) — Cansdale (1948): Ghana — Malbrant & Maclatchy (1949): Mozambique (see Allen 1939); Zaire: Boma (see Lang & Chapin 1917), Kwamouth, Eala, Kunungu (see Schouteden 1947); Congo: Fougamou, Brazzaville, Ngabé — Sanborn (1950): Angola: Dundo — Swynnerton & Hayman (1951): Tanzania: Maurui, Bagiro, Madazini, Mwanza, Zanzibar — Aellen (1952): Egypt and Sudan to Malawi, Kenya, Uganda, Tanzania, Angola and Gambia; Cameroon: Itoki, Kitta (see Sjostedt 1897 a), Mamfe (see Sanderson 1940), Campo, Ndikinimeki, Tibati, Fernando Po — Basilio (1952): Rio Muni (= Equatorial Guinea) — Ellerman, Morrison-Scott & Hayman (1953): Republic of South Africa: Port-St-Johns (see Hewitt 1930); Mozambique: Inhambane; Angola: Mocamedes, Mount Moco; Tanzania; Kenya; from South Sudan West to Senegal — Garnham & Heisch (1953): Zaire: Boma (see Rodhain 1926) — Hopkins & Rothschild (1953): Ghana — Fain (1953): Zaire: Mount Korovi, Kawa, Mongbwalu (see Schouteden 1947) — Rosevear (1953): from Senegal to Angola and Sudan — Ellerman (1954): Republic of South Africa: Port-St-Johns (see Hewitt 1930) — Hayman (1954): Zaire: Banana, Beno, Paulis, Kasaji; Rwanda: Astrida — Dekeyser (1955): Mozambique; East and Central Zaire; Cameroon; Fernando Po; Nigeria; Ghana; Senegal; Guinea Bissau — Lips & Rodhain (1956): Zaire — Harrison (1957): Tanzania: Tumba — Verschuren (1957): Zaire: Gangale-na-Bodio, Cel II, Bagunda, Kasai, Maleli, Haute Makpe, PPK. 56, Ndelele, Nadegebe, PPK. 72, Nampume, PFSK-8, PFSK-17, Meridi, Aka, Utukuru, Moko — Benoit (1958): Tanzania: Shirati; Rwanda: Musha — Blancou (1958): Central African Republic: Ndelé — Chapman (1958): Tanzania: Rukwa valley — Booth (1959): Ghana: Accra Plain — Funaioli (1959): Somalia: Alto and Basso Giuba (see De Beaux 1924, 1939 and Zammarano 1930) — Toschi & Lanza (1959): Sicily (see Malherbe 1843 and Doderlein 1871, 1881); Egypt; Sudan; Kenya; Uganda; Tanzania; Malawi; Angola; Gambia — Ansell (1960): Zambia: Chavuma, Kabompo, Limalunga — Kuhn (1962): Liberia: Harbel — Kulzer (1962): Kenya: Lembeni — Rahm & Christiaensen (1963): Zaire: Nyambasha — Lehmann (1964): Upper Nile — Koopman (1965): Zaire: Avakubi, Medje, Stanleyville, Boma, Irumu, Kasenyi, Luluabourg — Rosevear (1965): Republic of South Africa: Port-St-James; Senegal: Dialoco; Nigeria: Panyam, Zaria; Zaire: Garamba; Sierra Leone: Njala — Verschuren (1965): Tanzania: Serengeti Park — Brosset (1966a): Congo: Sibiti — Brosset (1966b): Gabon: Makokou — Ellerman & Morrison-Scott (1966): Senegal — Hayman, Misonne & Verheyen (1966): Rwanda: Astrida, Kisenyi; Zaire: Avakubi, Bambesa, Banana, Bokuna, Bolobo, Boma, Buta, Djamba, Djeka, Eale, Faradje, Fundi, Ikela, Lake Kisale, Kamituga, Karawa, Kasanga, Kiambi, Mount Korovi, Koteli, Kunungu, Kwamouth, Leverage, Leopoldstad, Lukonzolwa, Luluaburg, Makala, Makengo, Medje, Moliro, Mongbwalu, Mukishi, Mulungu river, Mushie, Mutwanga, Mweka, Nyambasha, Paulis, Poko, Pweto, Rutshuru, Stanleyville, Aka, Bagunda, Gangala na Bodio, Goma, Kaswabilenga, Lake Kivu, Kyangvinionge, Mabwe, Makpe river, Maleli, Meridi, Moka, Musosa, Mutsora, Nampume, Ndelele, PPK. 56, PPK. 72, PPK. 8, PPK. 17, Garamba National Park, Teturi, Tshambi, Utukuru, Vitshumbi, Yangambi, Mayumbe, Zobia, Cel II, Bukavu, Irumu, Ishango, Kakungu, Kassi, Kamande, Kasaka, Kissisile, Lake Katanda, Kiavikere, Kitonga, Makpe river, Murambi, Mutsora, Nadegebe, Nampume, Beno, Samboko, Vankerckhoveville — Rahm (1966): Zaire: Kisanga — Rahm & Christiaensen (1966): Zaire: Malambo — Ansell (1967): Zambia: Salujinga, Chunga, Lochinvar Ranch — Verschuren (1967): Zaire: Bukavu, Kamande, Kasaka, Ishango, Kitonga, Lake Katanga — Williams (1967): East Africa — Krampitz (1968): Uganda: Tororo — Lanza & Calloni (1970): Somalia — Niort (1970): Burundi: Bujumbura, Kiremba — Fain (1971): Zaire: Rutshuru — Funaioli (1971): Somalia: Giohar — Grubb (1971): Ghana: Achimota, Bole, Kintampo (Saunders Falls) — Anciaux de Faveaux (1971): Rwanda: Butare — Jones (1971): Rio Muni (= Equatorial Guinea): Ikunde — Keymer (1971): Zaire — Ansell (1973): Zambia: Kalabo — Ansell (1974): Zambia: Nyansowe river, Sakeji Headwaters, Sumbu — Howell (1974): Tanzania: Lake Rudolf, Fergusons Gulf (see also Harrison 1960), Central Island — Seal & Makey (1974): from southern Africa to Senegal — Vielliard (1974): Nigeria: Baga-Kawa; Chad: Djiboulboul, Chari-delta, Logone-Gana — Fenton (1975): Zimbabwe — Jeffrey (1975): Ghana: Pampramase — Adam & Hubert (1976): Senegal: Rosso, Sangalkan, Kedougou, Badi (see Aellen 1956) — Verschuren (1976): Guinea: Nimba (see Aellen) — Bergmans (1977): Nigeria: Ibadan, Shaguna — Rautenbach (1978): southern Africa (forest) — Delany & Happold (1979): Gabon: Makokou (see Brosset 1966c); Uganda:

Ruwenzori Park; Kenya: Loraki (see Coe 1972) — Corbet & Hill (1980): from Senegal to Ethiopia and Republic of South Africa — Van den Brink (1978): Sicily — Swanepoel, Smithers & Rautenbach (1980): southern Africa — Verschuren (1980): Burundi: Rusizi Delta — Kock (1981 b): Burundi: Kayanza — Qum-siyeh & Schlitter (1981): Mauretania: Garak — Koopman (1982): from Senegal to Somalia to Angola and Republic of South Africa, Zanzibar, Bioko — Anciaux de Faveaux (1983): Zaire: Shaba, Upemba Park; Rwanda — Brosset (1984): Guinea: Mount Nimba (see Aellen) — Herselman & Norton (1985): Republic of South Africa: Port St Johns (probably juvenile *N. thebaica*) — Infuta (1985): Zaire: Bafwasenda Road, km 44, near Kisangani — Feiler (1986): Angola: Between Funda and Luanda — Koopman (1986): Sudan: Bangangai Forest — Happold, Happold & Hill (1987): Malawi: Fort Johnston, Kota Kota, Livingstonia, Upper Shire valley, (all see W. F. H. Ansell) and Zoa Estate (?) — Lee, Bickham & Schlitter (1989): Somalia: 1.5 km S, 0.5 km E of Giohar.

Nycteris hispida hispida (Schreber, 1774)

Braestrup (1935): Nigeria: Mopti, Kabar; Sudan: Tonga, Bor. (*N. hispida hispida* is the race from Northern Sudan) — Aellen (1956): Senegal: Badi — Eisentraut (1956) (1957): Cameroon: Buea — Perret & Aellen (1956): Cameroon: Mintyamiyumin, Foullassi, Bangwa, Yaoundé — Anciaux de Faveaux (1958): Zaire: Pweto, Mukishi (see Schouteden 1947), Kasaji (see Hayman 1954) — Swynnerton (1958): Tanzania: Serengeti National Park — Vercammen-Grandjean & Fain (1958): Rwanda: Astrida — Aellen (1963): Liberia: Ziéla, Zougouépo — Eisentraut (1964): Fernando Po (see Dobson 1878) — Vercammen-Grandjean (1964): Rwanda: Astrida — Kuhn (1965): Liberia: Du river, Harbel — Aellen (1966): Rwanda: Nyarutovu — Funaioli & Simonetta (1966): Somalia — Hayman (1967): from Angola to Zaire, Zanzibar, Tanzania, W-Kenya, Uganda, Sudan, Somalia, west to Senegal — Hill (1968): Cameroon: Nyasoso, Mount Kupe — De Vree, De Roo & Verheyen (1969): Togo: Ahoué-houé, Atakpame, Nanergou Nuatja, Paio — Kock (1969): Sudan: Subeigh Forest Reserve, Buram, Angola, Dongola, Port Req, Khartoum, Renk, Kaka, Tonga, Bor, Duk Fadiat, Duk Fagwil, Kongor, Gondokoro, Malek, Meridi, Lake No, Hellet Nuer, Bahrel-Zeraf, Wad Medani, Fora, Dilling, Khor Attar, Mongalla, 40 mi N of Bor, Lado; Zaire: Duma, Koloka; Chad: Melfi; Kenya: Sala; Burkina Faso: Nouna — De Vree, Hulselmans & Verheyen (1970): Togo: Togoville, Namoundjoga — De Vree (1971): Ivory Coast: Adiopodoumé — De Vree, Van der Straeten (1971): Togo: Borgou — Hayman & Hill (1971): from Angola to Zaire, Zanzibar, Tanzania, W-Kenya, Uganda, Sudan, Somalia, west to Senegal — Roche (1971): Guinea Bissau: Sérédou — Eisentraut (1973): Fernando Po; Cameroon: Mount Cameroon, Kupe — Largen, Kock & Yalden (1974): Ethiopia: Bahadu, Filwoha, Awash Falls, Gambela, Bulcha Forest, 10 mi N of Lake Rudolf, W coast of Lake Abaya, W coast of Lake Chamo, Pokwo — Koopman (1975): Sudan: Torit, Terangole, Logurun, Parajok, Palwar, Kapoeta, Nimule, Mongalla, Lafon, Meridi, 100 mi N of Wau, Lake Nyibor, Tonj, Kongor, Bor, Tonga, Khor Attar, Kaka, Lake No, Renk, Malek, 40 mi N of Bor, Duk Faiwil, Disa, Subeigh Forest Reserve, Buram, Angola, Khartoum, Duk Fadiat (see Hinton & Kershaw 1920), Wad Medani, Meshra er Req, Dilling, Fora, Dongola (see Kock 1969) — Gallagher & Harrison (1977): Zaire: Scierie Forest (30 km S of Kindu), Avakubi, Ankoro — Koopman, Mumford & Heisterberg (1978): Burkina Faso: Arly National Park, Djipologo, Founzan, Goden, Konikira, Koutoura, Nobéré, Orodara, Oulu, Sideradougou; Mali: Togo; Ghana; Ivory Coast — Robbins (1980): Togo: Agou, Dapango; Benin: Guene, Nikki, Segbana, Zizonkame — Schlitter et al. (1983): Central African Republic: Gounda Camp, St-Floris National Park, Birao, Nola, Manovo — Hill (1983): Central African Republic.

Nycteris hispida martini (Fraser, 1834)

Braestrup (1935): this name might be retained for the dark forest form — Koopman (1965): subspecies of South Sudan (see Braestrup 1935).

Nycteris hispida pallida J. A. Allen, 1917

Braestrup (1935): S Sudan — Koopman (1965)?: Zaire: Faradje, Vankerckhoveville.

Nycteris hispida villosa Peters, 1852

Dobson (1878): Mozambique: Inhambane (as var. a.) — Noack (1889): southeast Africa — Trouessart (1904): Central and East Africa — Roberts (1951): Republic of South Africa: Cape of Good Hope (see Smith) — Hayman (1967): Republic of South Africa; Mozambique — De Sousa Diaz (1968): Mozambique: Inhambane — Hayman & Hill (1971): Republic of South Africa; Mozambique — Smithers & Tello (1976): Mozambique: S of Villa Gouveia, Cabora Bassa, Inhambane — Bruton (1978): Republic of South Africa: Manzengeyena Forest Station — Smithers & Wilson (1979): Zimbabwe: Pungwe river.

"Rhinolophus martini" Fraser, 1843

Fraser (1843): Fernando Po: TYPE — Wagner (1855): Fernando Po — Peters (1871): *martini* = *hispidia* — Dobson (1878): *martini* = *hispidia* — Elliot (1907): *martini* = *hispidia* — Cabrera (1908): *martini* = *hispidia* — Allen (1939): *martini* = *hispidia* — Rosevear (1965): *martini* = *hispidia*.

Nycteris pallida J. A. Allen, 1917

Allen (1917): Zaire: Faradje: TYPE; Vankerckhoveville — Gyldenstolpe (1928): Zaire: Irumu — Braestrup (1935): *pallida* = *hispidia* — Frechkop (1938): Zaire — Allen (1939): Zaire: Faradje; from northeast Zaire to Liberia (see Allen 1917) — Schouteden (1947): Zaire: Leopoldville, Kwamouth, Mushie, Leverageville, Luluabourg, Eala, Stanleyville, Avakubi, Djamba, Koteli, Mukishi, Faradje, Vankerckhoveville (see Allen 1917), Irumu (see Gyldenstolpe 1928) — Malbrant & Maclatchy (1949): from northeast Zaire to Liberia; Zaire: Kinshasa, Kwamouth — Aellen (1952): Chad: Mangeigne (see Malbrant 1952) — Dekeyser (1955): Liberia; northeast Zaire; southeast Chad — Verschuren (1957): *pallida* = *hispidia* — Blancou (1958): Central African Republic: Manguaigne — Koopman (1965)?: *pallida* = *hispidia* — Rosevear (1965): *pallida* = *hispidia* — Hayman, Misonne & Verheyen (1966): *pallida* = *hispidia* — Hayman (1967): *pallida* = *hispidia* — Kock (1969): *pallida* = *hispidia hispidia* — Hayman & Hill (1971): *pallida* = *hispidia* — Vielliard (1974): Chad: Manguaigne (see Malbrant 1952) — Koopman (1975): *pallida* = *hispidia*.

Nycteris pilosa (Gray, 1866)

Gray (1866): Africa: TYPE Nomen Nudum (as *Nycterops pilosa*) — Peters (1871): *pilosa* = *hispidia* — Dobson (1878): *pilosa* = *hispidia* — Elliot (1907): *pilosa* = *hispidia* — Cabrera (1908): *pilosa* = *hispidia* — Allen (1939): *pilosa* = *hispidia* — Rosevear (1965): *pilosa* = *hispidia*.

Nycteris poensis Gray, 1843

Gray (1843): Fernando Po: TYPE Nomen Nudum — Peters (1871): *poensis* = *hispidia* — Dobson (1878): *poensis* = *hispidia* — Allen (1939): *poensis* = *hispidia* — Eisentraut (1964): *poensis* = *hispidia hispidia* — Rosevear (1965): *poensis* = *hispidia*.

Nycteris villosa Peters, 1852

Peters (1852): Mozambique: Inhambane: TYPE — Wagner (1855): Mozambique: Inhambane — Peters (1871): Mozambique: Inhambane — Allen (1939): *villosa* = *hispidia* — Rosevear (1965): *villosa* = *hispidia* — Kock (1969): *villosa* = *hispidia villosa*.

Specimens examined

Nycteris hispidia (Schreber, 1774)

- Angola: 3 specimens: Alto Chicapa (BM: 1); Dundo (BM: 2);
 Benin: 48 specimens: Guene (USNM: 4); Nikki (USNM: 10); Segbana (USNM: 2); Zizonkane (USNM: 32);
 Botswana: 4 specimens: Xugana (USNM: 4);
 Burkina Faso: 149 specimens: Arly (USNM: 62); Djipologo (USNM: 9); Founzan (USNM: 22); Goden (USNM: 35); Konankira (USNM: 2); Koutoura, 5 km SW (USNM: 14); Nobere, 1 km S (USNM: 4); Nouna (SMF: 1); Orodara, 27 km ENE (USNM: 24); Oulo (USNM: 3); Sideradougou (USNM: 17);
 Burundi: 1 specimen: Kayanza (SMF: 1);
 Cameroon: 236 specimens: ? (KMMA: 1); Bibundi (ZMH: 1); Biteye (BM: 5, KMMA: 2); Bota (BM: 1) Campement du Grand Capitaine (KMMA: 1); Djohong (KMMA: 2); Galim (KMMA: 1); Gueme (KMMA: 146); Mamfe (BM: 2); Mbongo (BM: 1); Mueli (ZFMK: 1); N'ko (BM: 1); Nyasoso (ZFMK: 1); Tisongo (USNM: 1); Touroua (KMMA: 1); Victoria (BM: 1); Waza (KMMA: 6, ZFMK: 12); Waza, 35 km N (ZFMK: 19); Yagoua (KMMA: 29);
 Central African Republic: 7 specimens: Gounda Camp (CM: 7);
 Chad: 8 specimens: Melfi (ZMH: 1); Melfi area (SMF: 5); N'Djamena (USNM: 1); Sarh (USNM: 1);
 Congo (Brazzaville): 1 specimen: Mayumbe (KBIN: 1);
 Equatorial Guinea: 4 specimens: Bata (KMMA: 1); Benito river (BM: 3);
 Ethiopia: 26 specimens: Arba Minch (SMF: 1); Aseita (USNM: 8); Bahadu (BM: 1); Bulcha (BM: 1); Filwoha (USNM: 1); Filwoha Awash (BM: 1); Gambela (BM: 1, CM: 1, ZFMK: 7); Lado (ZFMK: 1);

- Melka Were (ROM: 1); Pokwo (SMF: 2);
 Fernando Po: 2 specimens: ? (Holotype *poensis* or *martini*, BM: 1); ? (BM: 1);
 Gabon: 4 specimens: Makokou (MNHN: 1); Omboue (USNM: 3);
 Gambia: 4 specimens: Dialocote (BM: 4);
 Ghana: 122 specimens: Aburi (USNM: 1); Accra (BM: 1); Bangwon (USNM: 2); Bibiani (BM: 1);
 Damongo (BM: 1); Dormaa Ahenkro (BM: 3); Gold Coast (BM: 3, USNM: 1); Karoga (BM: 1); Kokofu
 (USNM: 1); Kumasi (BM: 1); Lovi Camp, Mole Game Reserve (BM: 1); Mampong (BM: 1); Mankesin
 (USNM: 1); Mole Motel, Damongo (BM: 4); Nabogo (USNM: 6); Oda (BM: 1); Pampramase (BM: 1);
 Pirisi (USNM: 27); Prang (BM: 2); Pulima (USNM: 18); Sakpa (USNM: 40); Sawla, 15 mi E (BM: 3);
 Sogakofe (BM: 1);
 Guinea: 1 specimen: Ouassou (NMW: 1);
 Ivory Coast: 27 specimens: Adiopodoumé (KMMA: 5, USNM: 1); Bouna (USNM: 3); Kong (USNM:
 16); Tule (USNM: 2);
 Kenya: 33 specimens: Athi river (USNM: 2); Benane (ROM: 1); Central island, Lake Turkana (BM: 1);
 Ferguson's Gulf (BM: 1); Keekevok (ROM: 1); Keekevok, Mara river (ROM: 1); Kilifi (ROM: 1, USNM:
 1); Kipkabu (BM: 1); Kisii (BM: 1); Kwale (RMNH: 1); Leopard Rock Lodge, Meru National Park (SMF:
 1); Lodwar (BM: 1); Machakos district (BM: 1); Malindi (BM: 1); Marsabit Road (USNM: 1); Mazeras
 (BM: 1); Molo (CAS: 1); Mumias (BM: 1); Murango (BM: 8); Nairobi (USNM: 1); Sala (SMF: 2); Tana
 river (USNM: 1); Tiwi (ROM: 1);
 Liberia: 3 specimens: Mount Barclay (BM: 1); Harbel (USNM: 1); Schieffelinville (RMNH: 1);
 Malawi: 4 specimens: Fort Johnston (BM: 2); Upper Shire river (BM: 1, SMND: 1);
 Mali: 1 specimen: Kabara (ZMUC: 1);
 Mauretania: 52 specimens: Garak (USNM: 52);
 Mozambique: 2 specimens: Quilimane (ZMH: 2);
 Namibia: 1 specimen: Nampini (KM: 1);
 Nigeria: 56 specimens: ? (BM: 1); Afon (USNM: 13); Araba (BM: 3); Asaba (BM: 3); Dikwa, 31 mi
 NE (USNM: 10); Ibadan (BM: 2); Igbo-Ora (USNM: 1); Karaduwa (USNM: 3); Lagos (BM: 2); Numan
 (BM: 1); Old Calabar (BM: 2); Panyam (BM: 1); Umuahia (BM: 4); Yo, Yobe river (BM: 6); Zaria (BM:
 1); Zungeru (USNM: 5);
 Republic of South Africa: 2 specimens: Cape of Good Hope (BM: 1, MSNG: 1);
 Rwanda: 8 specimens: Butare (KMMA: 2); Kisenyi (KMMA: 1); Rukara (KMMA: 5);
 Senegal: 38 specimens: Badi (KMMA: 1); Diattacounda (ZFMK: 15); Kedougou (USNM: 4); Podor
 (USNM: 18);
 Sierra Leone: 11 specimens: Bonthe (BM: 2, NMBE: 2); Makeni (BM: 1); Musaia (BM: 1); Njala (BM:
 4); Rokupr (BM: 1);
 Somalia: 3 specimens: ? (USNM: 1); Afmadu (MZUF: 2);
 Sudan: 119 specimens: Angolo (SMF: 7); Bor (USNM: 8); Bor, 40 mi N (BM: 1); Buram (SMF: 18);
 Dinka Country (Duk Fagul) (USNM: 1); Disa (BM: 3); Gallabat (NMW: 1); Hellet Nuer (ZFMK: 2); Kaka
 (BM: 6); Kapoeta (USNM: 2); Khartoum (BM: 1, NMW: 12); Khor Attar (NMW: 1); Kongor (BM: 4, KM:
 2); Lafon (ZMUC: 9); Mongalla (BM: 3, NMW: 3, ZMUC: 5); Lake No (ZFMK: 1); Renk (BM: 2);
 Shambe (ROM: 1); Subeigh Forest Reserve (SMF: 7); Tonga (BM: 1, NMW: 13); Tonj (BM: 1, ROM: 1);
 Torit (USNM: 1, ZMUC: 1); Wad Medani (ROM: 1);
 Tanzania: 13 specimens: Amani (TM: 1); Dar es Salaam (BM: 1); Grummetti (BM: 1); Ilonga Research
 and Training Centre (BM: 1); Kisarawe (BM: 1); Mikumi National Park H. Q. (BM: 1); Minaki, St.
 Andrews College (KU: 3); Seronera (KBIN: 1); Tanganika (NMW: 1); Ukara (BM: 2);
 Togo: 51 specimens: Agou (USNM: 1); Anonoe (KMMA: 3); Atakpame (KMMA: 1); Borgou (KMMA:
 2); Dapango (USNM: 2); Namoundjoga (KMMA: 2); Nanergou (KMMA: 38); Paio (KMMA: 1); Togo-
 ville (KMMA: 1);
 Uganda: 12 specimens: Budongo Forest (ROM: 1); Buligi (ROM: 1); Entebbe (BM: 3); Kasenyi (CAS:
 1); Katwe (CAS: 2, ROM: 1); Masindi (BM: 1); Mbarara (BM: 1); Wasa river, Chemliki valley (BM: 1);
 Zaire: 231 specimens: Albert Park (KBIN: 5); Avakubi (BM: 1, KMMA: 3); Bambesa (KMMA: 3);
 Banana (KMMA: 2); Boende (KMMA: 3); Bokuma (KMMA: 2); Bolobo (KMMA: 1); Boma (KMMA:
 1); Buta (KMMA: 7); Djeka (KMMA: 1); Duma (SMF: 2); Eala (KMMA: 1); Faradje (Paratype *pallida*,
 KMMA: 1); Fundi (KMMA: 1); Garamba Park (KBIN: 45, KMMA: 26); Goma (KBIN: 2); How . . . (E-
 ZAI) (RMNH: 1); Ikela (KMMA: 2); Irangi (RMNH: 1); IRSAC Labo, Lake Kivu (KMMA: 1); Ishango-
 Kiayinonge, road (KBIN: 1); Isiro (KMMA: 1); Kadin, Lake Kisale (KMMA: 1); Kakungu (KMMA: 1);

Kamituga (KMMA: 1); Kananga (BM: 8, KMMA: 3); Karawa (KMMA: 1); Kasaji (KMMA: 1); Kasenyi (KBIN: 1); Kasongo (KMMA: 1); Kassi river (KMMA: 1); Kaswabilenga (KBIN: 1); Kawa (BM: 2, KMMA: 1); Kiambi (KMMA: 1); Kingabwe (KMMA: 1); Kinshasa (KMMA: 1); Kisangani (KMMA: 3); Kisangani-Ituri (KMMA: 1); Lake Kivu (KBIN: 1); Mount Korovi (KMMA: 1); Koteli (KMMA: 1); Kunungu (KMMA: 1); Kwamouth (KMMA: 1); Kyavinionge (KBIN: 1, KMMA: 1); Leverville (KMMA: 1); Lukonzolwa (KMMA: 1); Lwiro (ZMZ: 1); Mabwe river (KBIN: 7); Makala (KMMA: 2); Makengo (KMMA: 1); Upper Makpe (KBIN: 2, KMMA: 3); Maleli (KBIN: 2, KMMA: 1); Medje (KMMA: 1); Meridi (KBIN: 1); Moko (KBIN: 2); Moliro (KMMA: 1); Mongbwalu (KMMA: 5); Mukishi (KMMA: 1); Murambi (KMMA: 2); Mushie (KMMA: 1); Musosa (KBIN: 1); Mutsora station (KBIN: 1, KMMA: 4); Mutwanga (KMMA: 2); Mweka (KMMA: 1); Nadegebe (KMMA: 2); Nampume (KBIN: 2, KMMA: 1); Ndelele (KBIN: 1); Ndwa (KMMA: 1); Nyambasha (KMMA: 4); Ogooue (ZMH: 1); PFSK 8 (KMMA: 3); Poko (BM: 1, KMMA: 3); Pweto (KMMA: 1); Rutshuru (KBIN: 1, KMMA: 2); Rutshuru-Ebene (NMW: 1); Tandala (USNM: 2); Teturi (KBIN: 1); Tschakala (KMMA: 1); Utu (KMMA: 1); Utukuru (KBIN: 1); Uvira (NMW: 2); Vitshumbi (KBIN: 1); Yalosemba (USNM: 1); Yangambi (KBIN: 1); Zambia: 2 specimens: Balovale (KM: 2); Unknown country: 15 specimens: ? (KMMA: 3, ROM: 1); Batunga (ZFMK: 2); Rukwa (KBIN: 2); Ruwenzori SE (BM: 4); Tropical Africa (ZMH: 2); Upper Nile (BM: 1).

Nycteris grandis Peters, 1865

Nycteris grandis Peters, 1865. Monatsb. k. preuss. Akad. Wiss. Berlin: 358–359. — Type locality: Guinea.

Nycteris baikii Gray, 1866. Monatsb. k. preuss. Akad. Wiss. Berlin: 672. — Type locality: Baikie, West Africa.

Nycteris marica Kershaw, 1923. Ann. Mag. Nat. Hist., (9) 12: 534–535. — Type locality: Tindiga, Kilosa, Tanzania.

Nycteris proxima Lönnberg & Gyldenstolpe, 1925. Ark. Zool., 17B: 1–2. — Type locality: Kartoushi, Zaire.

Nycteris gaudis Baker, Honeycutt & Van den Bussche, 1991. Bull. Am. Mus. Nat. Hist., 206: 46. [Lapsus].

The distribution of *N. grandis* is limited to the rain forests, as shown in figure 8. The species is also found in the coastal forests of East Africa. It is not surprising to find that dark beige to dark brown is the most dominant colour variation of the pelage in this species.

Due to its very large dimensions, *N. grandis* cannot be confused with any other species of the genus. Kock (1981 a) considers *marica* as a valid subspecies in East and southern Africa, however without mentioning the nominal subspecies. The other forms *N. baikii* Gray, 1866 and *N. proxima* Lönnberg & Gyldenstolpe, 1925 are considered to be mere synonyms of *N. grandis* Peters, 1865. Peters (1867) was already the first to point this out for *N. baikii*.

Our analyses indicate that *N. grandis* is very uniform throughout its entire distribution area. Therefore the proposed subdivision into subspecies is rejected.

Table 4 shows the standard statistical data for *N. grandis*. The forearm length of the paralectotype or syntype of *N. grandis* has been included, as are the measurements of the holotype of *marica*.

Whenever comparing *N. hispida*, *N. aurita* and *N. grandis*, the minimal values of *N. grandis* are always larger than the maximal values for *N. aurita*. *N. hispida* only shows a larger value for Zyg and 5 ph 2. The minimal value of the Zygomatic width of *N. grandis* seems to be exceptionally small and might have been measured on an aberrant specimen. The overlap for 5 ph 2 is a result of an extremely large specimen of *N. hispida*.

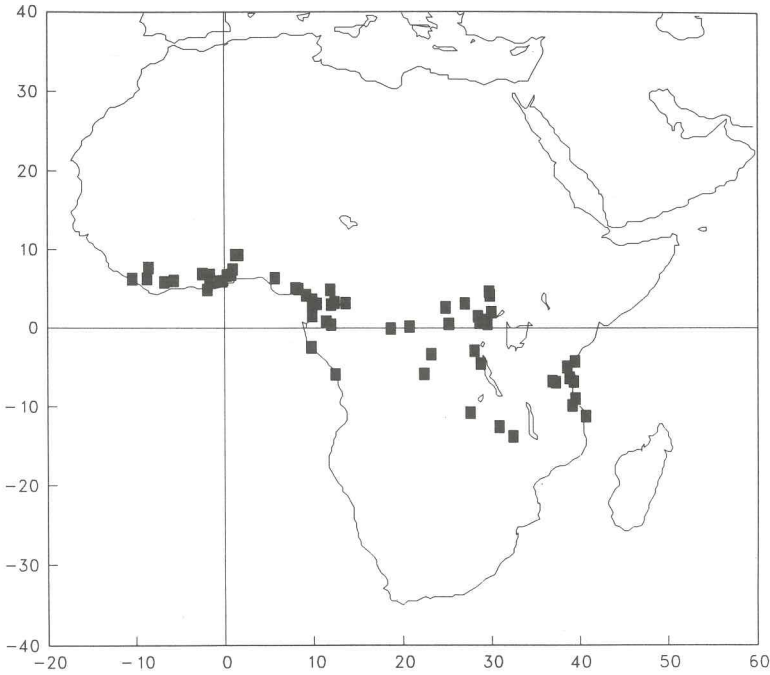


Fig. 8: Distribution map of *Nycteris grandis* Peters, 1865.

The measurements of the forearm length found in this study extend the lower limit of the known range as presented by Rosevear (1965); Hayman & Hill (1971) and Kingdon (1974): 57 to 66 mm. The same is true for all other measurements given by Rosevear (1965): Gls: 26.0–27.0 mm; Zyg: 16.0–17.0 mm; c-m³: 9.1–9.7 mm and m³-m³: 10.4–10.9 mm.

Literature citations

Nycteris baikii Gray, 1866

Gray (1866): Baikie, West Africa TYPE, Nomen Nudum — Peters (1867): *baikii* = *grandis* — Allen (1939): *baikii* = *grandis* — Rosevear (1965): *baikii* = *grandis*.

Nycteris grandis Peters, 1865

Peters (1865): Guinea: TYPE — Peters (1867): Baikie — Peters (1871): Guinea — Dobson (1878): Ghana: Accra; Guinean Coast — Dobson (1879) (1880): Zanzibar — Thomas (1880): Cameroon: Old Calabar — Jentink (1887b): Du Queah river — Jentink (1888): Liberia: Du-Queah river (Hilltown) — Noack (1889): Zaire: Netonna; West Africa (see Dobson 1878); Liberia (see Jentink 1887b) — Matschie (1893): Ghana; Zanzibar — Matschie (1895): Zanzibar; Comores; Guinea — Matschie (1897): Zanzibar — Trouessart (1904): West Africa and Zanzibar — Andersen (1912): Zanzibar to Congo and to Old Calabar (as *Petalia*) — Jordan & Rothschild (1914): Namibia: Spitzkoppe — Thomas (1915): Zaire: Poko — Schwarz (1920): Poko (see Thomas 1915) (as *Petalia*) — Cabrera & Ruxton (1926): Zaire: Luluaburg — Ingoldby (1929): Ghana — Allen & Coolidge (1930): Liberia: Du river (as *Petalia*) — Hayman (1935): Ghana: Goaso — Jordan (1936): Namibia: Spitzkopje — Frechkop (1938): Zaire — Allen (1939): Guinea, West Africa — Moreau & Pakenham (1940): Tanzania: Pemba, Zanzibar — Eisentraut (1941) (1956) (1957): Cameroon:

Table 4: Measurements of *N. grandis* (in mm).

Var	paralecto- or syntype <i>grandis</i>	Holotype <i>marica</i>	Mean	SD	Min	Max	n
Gls	—	25.0	25.20	0.74	23.3	27.5	70
Cbl	—	22.1	22.04	0.73	20.0	25.0	70
Sw	—	10.0	11.85	0.92	10.0	17.7	70
Zyg	—	16.0	16.17	0.82	11.5	17.4	64
Mast	—	11.0	11.26	0.44	9.7	12.1	69
Brain	—	10.9	10.80	0.39	10.0	11.8	69
c-m ³	—	8.7	8.80	0.30	7.9	9.7	79
c-c	—	6.8	7.13	0.36	6.3	8.5	74
m ³ -m ³	—	9.7	10.38	0.39	9.3	11.5	76
Mand	—	17.5	18.10	0.63	16.5	20.5	77
c-m ₃	—	9.8	10.15	0.36	9.2	11.2	77
Fa	56.0	58.5	58.25	2.60	51.6	64.5	85
Meta 3	—	44.9	43.35	2.54	36.7	48.8	32
3 ph 1	—	30.2	29.28	1.07	25.9	31.3	31
3 ph 2	—	29.0	30.28	1.53	25.6	33.3	31
Meta 4	—	47.2	46.02	2.33	40.7	51.0	31
Meta 5	—	52.3	50.14	2.39	44.3	55.8	32
5 ph 1	—	16.5	16.18	0.93	13.5	18.2	32
5 ph 2	—	13.6	14.01	0.98	11.3	15.6	32
Tib	—	30.0	30.13	2.21	24.6	34.6	33

Mubenge-Isongo — Schouteden (1947): Zaire: Poko, Beni, Netonna near Banana (see Noack 1889), Luluaburg (see Cabrera & Ruxton 1926); Cameroon: Bitey — Cansdale (1948); Ghana — Malbrant & Maclatchy (1949); Zaire: Bitey, Banana (see Schouteden 1947); Gabon — Swynnerton & Hayman (1951); Tanzania: Pemba, Zanzibar — Aellen (1952): from Zanzibar to Zaire and Ghana; Cameroon: Bitey, Mubenge-Isongo (see Eisentraut 1942) — Garnham & Heisch (1953); Liberia (see Theiler 1930) — Hopkins & Rothschild (1953); Namibia: Spitzkoppe — Rosevear (1953): from Ghana to Zaire — Dekeyser (1955): Ghana; South Nigeria; Cameroon; Zaire; Zanzibar — Perret & Aellen (1956); Cameroon: Mintyaminyumin, Ngam, Bitey (see Schouteden 1947) — Verschuren (1957); Zaire: Haute Magbwamu, Kalikimvua — Anciaux de Faveaux (1958); Zaire: Lusengi — Benoit (1958); Zaire: Lusengi — Blancou (1958); Central African Republic: Bangui — Harrison (1959); Zimbabwe: Chirundu — Kuhn (1962); Liberia: Freemantown — Aellen (1963); Liberia: Ziéla — Rees (1964); Tanzania: Ulanga district — Kuhn (1965); Liberia: Hilltown, Du river, Freemantown, Harbel — Rahm (1965); Zaire: Kisanga — Rosevear (1965); Guinea; Tanzania: Tingida, Kilosa; Nigeria: Benin — Brosset (1966a); Congo: Dimonika — Brosset (1966b); Gabon: Bélinga-Makokou (Loa-Loa) — Hayman, Misonne & Verheyen (1966); Zaire: Beni, Biyonga, Bokuma, Epulu, Omaniundu, Poko, Putnam Camp, Kilikimvua, Mogbwamu river, Djuma river, Makayva river, Ituri, Luluaburg, Mululo, Kartoushi — Rahm (1966); Zaire: Kisanga — Ansell (1967); Zambia: Luangwa valley; Zimbabwe: Chirundu (see Harrison 1959); Malawi: Liwonde (see Hanney 1963); Tanzania: Dar es Salaam; Congo: Benito river; Zaire: Ituri, Luluabourg; Benin; Gabon; Cameroon; Ghana — Hayman (1967); Guinea to Cameroon; Zaire; Uganda; Tanzania; Zanzibar; Zimbabwe; Malawi — Verschuren (1967); Zaire: Makayova, Haute Djuma — Ansell (1969); Zambia: Chisombo (Luangwa Valley) — De Vree, Hulselmans & Verheyen (1970); Togo: Pawa — Fain (1971); Zaire: Camp Putnam — Grubb (1971); Ghana: Ahafo-Gambia, Mangoasi, Mim, Tano Lodge — Hayman & Hill (1971); Guinea to Cameroon; Zaire; Uganda; Tanzania; Zanzibar; Zimbabwe; Malawi; Gabon — Keymer (1971); Zambia: Luangwa valley (see Ansell 1967) — Eisentraut (1973); Cameroon: Mubenge-Isongo — Seal & Makey (1974): from Guinea to Zambia — Fenton (1975); Zimbabwe — Adam & Hubert (1976); Senegal: Ziguinchor — Smithers & Tello (1976); Mozambique: Espungabera; Zambia: Luangwa valley — Verschuren (1976); Liberia: Gbapa — Bergmans (1977); Nigeria: Nikrowa Forest Reserve — Rautenbach (1978); Southern Africa (forest) — Robbins (1978): West of the

river Volta to east of the river Niger — Rosin, Landau & Hugot (1978): Gabon: Makokou — Ansell (1979): Malawi: Chirundu (see Harrison 1960); Zambia: Chizombo (see Ansell 1967) — Bergmans (1979): Congo: 5 km S from Pointe Noire — Delany & Happold (1979): Gabon — Smithers & Wilson (1979): Zimbabwe: Mana Pools, Haroni-Lusitu river confluence — Corbet & Hill (1980): from Guinea to Tanzania; Mozambique; Zimbabwe — Robbins (1980): Togo: Agou, Ezimé, Pawa — Swanepoel, Smithers & Rautenbach (1980): Southern Africa — Fenton, Thomas & Sasseen (1981): Zimbabwe: Mana Pools National Park — Kock (1981 a): Kenya: 10 km S from Diani Beach; Tanzania: Bagamoyo, Kikaboga (Kilosa), Mikindani (Mtwara district); Zambia: Chinzombo; Zaire: Netonna — Brosset (1982): Gabon: Ivindo — Koopman (1982): Guinea; from Senegal to Zaire and Kenya; Tanzania; Uganda; Malawi; Zimbabwe; Mozambique; Zanzibar; Pemba; Namibia? — Wolton et al. (1982): Liberia: Grassfield, Bona, South Nimba — Fenton et al. (1983): Zimbabwe: Mana Pools Nat. Park — Grubb (1983): West and Central rain forests; Pemba; Zanzibar; Tanzania; Malawi; Zimbabwe; Zambia; Mozambique (especially in the savannahs) — Aggundey & Schlitter (1984): Kenya: 10 km S Diani Beach (see Kock 1981 a) — Brosset (1984): Guinea: Mount Nimba (see Aellen, Verschuren, Wolton et al.) — Infuta (1985): Zaire: Bafwasenda Road, km 64, near Kisangani — Fenton et al. (1987): Zimbabwe: Mana Pools National Park — Happold, Happold & Hill (1987): Malawi: Liwonde, 10 mi down river from Liwonde, Liwonde National Park — Fenton et al. (1990): Zimbabwe: Mana Pools National Park — Baker, Honeycutt & Van den Bussche (1991): Gabon: Estuaire Province, 2 km SE Cap Esterias (as *N. grandis*) — Rautenbach & Fenton (1992): Zimbabwe: Mana Pools National Park (see Fenton et al. 1990).

Nycteris grandis marica Kershaw, 1923

Kock (1981 a): East and Southern Africa.

Nycteris marica Kershaw, 1923

Kershaw (1923 a): Tanzania: Tingida, Kilosa: TYPE — Loveridge (1923): Tanzania: Tindiga — Frechkop (1938): Tanzania — Allen (1939): Tanzania: Tindiga, Kilosa — Swynnerton & Hayman (1951): Tanzania: Tendigo — Rosevear (1965): *marica* = *grandis* — Hayman (1967): *marica* = *grandis* — Hayman & Hill (1971): *marica* = *grandis*.

Nycteris proxima Lönnberg & Gyldenstolpe, 1925

Lönnberg & Gyldenstolpe (1925): Zaire: Kartoushi: TYPE — Gyldenstolpe (1928): Zaire: Kartoushi — Frechkop (1938): Zaire — Allen (1939): Zaire: Kartoushi, Semliki valley — Moreau, Hopkins & Hayman (1946): Zaire: Kartoushi — Schouteden (1947): Zaire: Kartoushi (see Lönnberg & Gyldenstolpe 1925) — Hayman, Misonne & Verheyen (1966): *proxima* = *grandis* — Hayman (1967): *proxima* = *grandis* — Hayman & Hill (1971): *proxima* = *grandis*.

Specimens examined

Nycteris grandis Peters, 1865

Cameroon: 5 specimens: ? (KMMA: 1, ZFMK 2); Bipindi, 10 km W (ROM: 2); Bitey (BM: 4, KMMA: 1); Buea (ROM: 1); Kribi, 14 km N (ROM: 1); Kribi, 4 km E (ROM: 2); Kribi, 7 km E (ROM: 2); Kribi, 9 km N (ROM: 2); Lomie district (BM: 1); Lumbindu (BM: 1); Mintjamyumin (ZFMK: 1); Ndjole, 4 km N (ROM: 1); Ndjole, 6 km N (ROM: 2); Ngam (ZFMK: 1); Tisongo (USNM: 1);

Equatorial Guinea: 1 specimen: Benito river (BM: 1);

Gabon: 4 specimens: Beluiga (MNHN: 1); Booué (MNHN: 1); Mitzic (BM: 1); Sette Cama (BM: 1);

Ghana: 18 specimens: Bame (USNM: 5); Butre (USNM: 1); Goaso (BM: 1); Cold Coast (Paralecto- or syntype *grandis*, RMNH: 1); Kpeve (USNM: 3); Kumasi (BM: 1); Kumasi-Dunkwa Road (BM: 1); Oda (BM: 1); Ofinsu (BM: 1); Tsibu, 2 mi SSW (USNM: 2); Tutu (USNM: 1);

Ivory Coast: 6 specimens: ? (KMMA: 2); Gueboua (KMMA: 2); Soubre, 10 mi WNW (USNM: 2);

Kenya: 1 specimen: Diani Beach, 10 km S (SMF: 1);

Liberia: 6 specimens: Ghapa (KBIN: 1); Grassfield, Nimba (BM: 1); Hilltown (RMNH: 1); LTC Camp (KMMA: 1); North Beeton, Nimba (BM: 1); South Nimba (BM: 1);

Nigeria: 4 specimens: Alimbo Ferry Road, Calabar (BM: 1); Benin (BM: 2); Old Calabar (BM: 1);

Tanzania: 8 specimens: Amani West Forest Reserve (BM: 1); Bagamoyo (RMNH: 1); Dar es Salaam (BM: 1); Kiraboga (SMF: 1); Likawage (BM: 1); Mikindani (SMF: 1); Namithu Kilwa (BM: 1); Tindiga (Holotype *marica*, BM: 1);

Togo: 7 specimens: Agou (USNM: 1); Aledjo (KMMA: 1); Ezimé (USNM: 1); Pewa (USNM: 4);
 Zaire: 23 specimens: Albert Park (KBIN: 3); Beni (KMMA: 1); Biyonga (KMMA: 1); Boende (KMMA:
 1); Bokuma (KMMA: 1); Epulu (KMMA: 1); Ituri Forest (BM: 1); Kalikimvua (KBIN: 1); Kamituga
 (KMMA: 1); Kananga (BM: 2); Kisangani-Ituri (KMMA: 1); Mogbwamu river (KMMA: 1, KBIN: 1);
 Mulolo (BM: 1); Netonna (SMF: 1); Omaniundu (KMMA: 1); Poko (KMMA: 1); Putnam Camp (KMMA:
 1); Ukaika (NMW: 1); Yalosemba (USNM: 1);
 Zambia: 2 specimens: Chinzombo (SMF: 1); Chisenga (BM: 1);
 Zanzibar: 4 specimens: ? (BM: 1, KBIN: 1); Shakani (BM: 2);
 Zimbabwe: 1 specimen: Ngorima Reserve (USNM: 1);
 Unknown country: 1 specimen: ? (BM: 1).

Nycteris aurita (K. Andersen, 1912)

Petalia aurita K. Andersen, 1912. Ann. Mag. Nat. Hist., (8) 10: 547. — Type locality: Kitui, Kenya.

This species is the most controversial one of the *N. hispida* group. Most authors consider *N. aurita* to be a synonym of *N. hispida* or at most a subspecies. The major difference between both species was believed to be the length of the ear. However, Harrison (1957) discussed the status of both forms in East Africa, noting that specimens from the Rukwa valley in Tanzania show a very large variation for this character, namely from short *hispida*-like to large *aurita*-like. He also remarks that it is not always possible to be absolutely precise about the length of the ear. The skull measurements of *N. aurita* from Kenya were not always as large as the one measured on the typespecimen and revealed an intergradation between both forms. Therefore Harrison only retains *aurita* as a subspecies of *N. hispida*. Kock (1969) concurred with this option, but in a personal communication, he suggests that the size differences, especially in the skull, are large enough to justify recognition of species. Koopman (1975) also believes that *aurita* could be retained as a valid species, in contradiction to the conclusions formulated by Harrison (1957).

This study's analyses show that it is rather difficult to separate *N. aurita* from *N. hispida* on the basis of univariate statistics. However, both species are significantly distinct for the skull measurements and for some of the external ones. The two species can always be separated by multivariate analyses on skull measurements. However, the external measurements alone do not generate such clear differences.

The distribution of *N. aurita* is limited to East and northeast Africa (see figure 9), an area in which *N. hispida* also occurs. In two Kenyan localities, Kilifi and Tana River, both species occur sympatrically, whereas in the border area between Kenya and Tanzania a number of "almost sympatrical" localities were found. This sympatric occurrence confirms our opinion that *aurita* and *hispida* are valid species.

The most common colour of the fur of *N. aurita* is dark beige to dark brown, but also a number of lighter specimens were found. This again confirms that colour is not a good discriminative character in *Nycteris*.

Published measurements of *N. aurita* are very scarce, especially because most authors do not retain *aurita* as a valid species and mention the data along with *N. hispida*. Therefore, it is difficult to compare this study's measurements (see table 5) with those from the literature. Koopman (1975) gives a condylobasal length of 15.2 to 15.9 mm, for 15 specimens from North and East Kenya which agrees with our data. Harrison (1957) gives a forearm length of 39.9 to 43.6 mm, for a number of specimens from the area around Lake Rudolf, which falls well within the range of

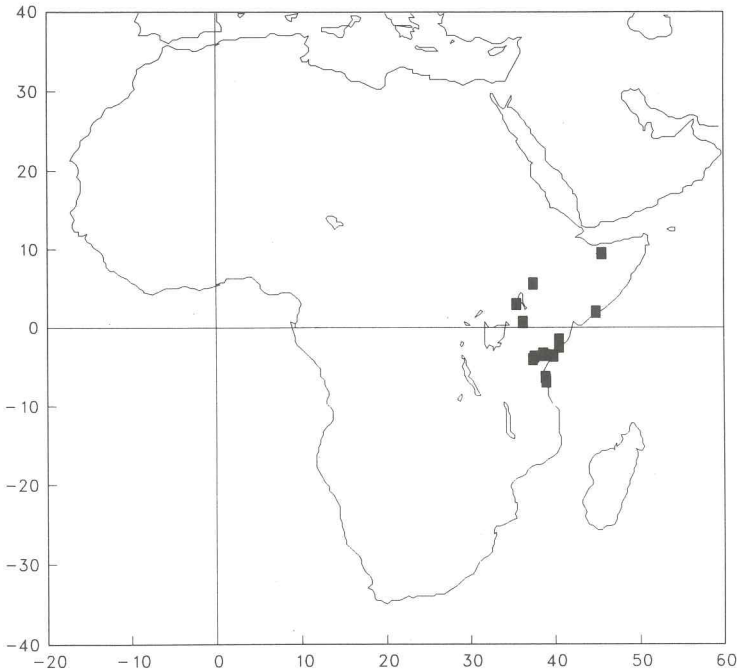


Fig. 9: Distribution map of *Nycteris aurita* (K. Andersen, 1912).

our data. His measurements of the greatest length of the skull (17.3 to 18 mm) also agree with these in table 5 as do those for the length of the upper toothrow (5.6 to 5.8 mm).

Literature citations

Nycteris aurita (K. Andersen, 1912)

Andersen (1912): Kenya: Kilifi: TYPE; British East Africa: Maungu; Somalia: Burao (as *Petalia*) — Hollister (1918): Kenya: Marsabit Road, Tana river (as *Petalia*) — De Beaux (1924): Somalia: Basso Giuba — Granvik (1924): Kenya: Mount Elgon — Zammarano (1930): Somalia: Basso Giuba — Allen & Lawrence (1936): Kenya: Ngatana, Tana river, Marsabit Road (see Hollister 1918), Mount Elgon (see Granvik 1924) — Frechkop (1938): British East Africa — Allen (1939): Kenya: Kilifi; from Somalia to Kenya — Percy, Percy & Ridley (1953): Kenya: Ijara — Harrison (1957): *aurita* = *hispida aurita* — Eisentraut (1958): Tanzania: Ras Dima island, Msala — Funaioli (1959): Somalia: Basso Giuba (see de Beaux 1924 and Zammarano, 1930) — Hayman (1967): *aurita* = *hispida* — Hayman & Hill (1971): *aurita* = *hispida* — Koopman (1975): *aurita* is at least a subspecies — Koopman (1982): *aurita* = *hispida*.

Nycteris hispida aurita (K. Andersen, 1912)

Ansell (1957): Zambia: Chavuma Falls, Zambesi river — Harrison (1960): Kenya: Nairobi, Tana river, Marsabit Road, Ferguson's Gulf, Lake Rudolf, Lodwar, Mumias, Elgon, Machakos, Mount Elgon, Kaimosi, Ngatana, Shimba Hills — Funaioli & Simonetta (1966): Somalia — Coe (1972): Kenya: Loraki, South Turkana — Ansell (1978): Zambia: Lukonzolwa, Pweto, Moliro (see Hayman, Misonne & Verheyen 1966), Nampini — Aggundey & Schlitter (1984): Kenya: Kitui (see Peters 1878, Dobson 1880), Sala (see Kock 1969), Nairobi (see Hollister 1914, Koopman 1975), Tana River (see True 1893, Hollister 1914, Koopman 1975), Marsabit Road (see Hollister 1914, Koopman 1975), Ferguson's Gulf (see Harrison 1957, Howell

Table 5: Measurements of *N. aurita* (in mm).

Var	Holotype	Mean	SD	Min	Max	n
Gls	17.8	17.90	0.35	17.2	18.3	13
Cbl	15.4	15.45	0.34	14.9	15.9	13
Sw	7.8	7.64	0.25	7.2	8.1	13
Zyg	10.6	10.74	0.26	10.1	11.1	13
Mast	8.3	8.55	0.21	8.2	8.9	13
Brain	7.9	7.85	0.21	7.4	8.1	13
c-m ³	6.0	5.92	0.12	5.7	6.2	14
c-c	4.4	4.44	0.18	4.1	4.8	19
m ³ -m ³	6.5	6.79	0.25	6.2	7.2	19
Mand	12.2	11.93	0.34	11.3	12.9	21
c-m ₃	6.7	6.74	0.22	6.4	7.5	21
Fa	42.5	41.63	1.72	37.3	44.5	24
Meta 3	32.0	29.24	1.71	27.1	32.9	20
3 ph 1	21.7	21.99	0.79	20.4	23.2	20
3 ph 2	22.4	22.06	1.21	19.9	24.6	20
Meta 4	34.0	31.76	1.85	29.0	36.2	20
Meta 5	35.1	32.86	1.88	29.0	36.2	20
5 ph 1	12.5	11.94	0.79	10.4	13.2	19
5 ph 2	9.3	9.77	0.58	9.0	11.0	19
Tib	19.8	20.25	1.17	17.9	22.1	20

1974), Lodwar (see St. Leger 1937), Mumias, Machakos, Mount Elgon (see Granvik 1924), Kaimosi (see Allen & Lawrence 1936, Koopman 1975), Wema (see Allen & Lawrence 1936, Koopman 1975), Shimba Hills, Stony Athi, Nakuru, Nginyang, Makeri, Voi (see Koopman 1975), Masabubu (see Koopman 1975), Galma Galla (see Koopman 1975), Kilifi (see Andersen 1912, Koopman 1975), Athi river, Maungu (see Andersen 1912), Njoro (see Lönnberg 1912), Central Island (see Howell 1974), Ijara (see Percy et al. 1953), Leopard Rock.

Specimens examined

Nycteris aurita (K. Andersen, 1912)

Ethiopia: 1 specimen: Gidole (SMF: 1);

Kenya: 14 specimens: Ijara (BM: 3); Kampi ya Samaki (ROM: 2); Kilifi (Holotype *aurita*, BM: 1); Kipini (ROM: 1); Lokiri, S Turkana (BM: 1); Maungu (BM: 1); Tana river (USNM: 4); Voi (ZMUC: 1);

Somalia: 7 specimens: Burao (BM: 1); Giohar (MZUF: 6);

Tanzania: 11 specimens: Bagamoyo (BM: 1); Lembeni (ZFMK: 4); Lake Manyara (BM: 1); Sam Deli (ZFMK: 1); Soga (ZFMK: 4).

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Zusammenfassung

Die vorliegende Untersuchung diskutiert auf der Grundlage multivariater statistischer Methoden die Systematik der *Nycteris hispida* Gruppe. Innerhalb dieser lassen sich drei Arten

unterscheiden: die sehr große *Nycteris grandis* Peters, 1865, und zwei kleine, *Nycteris hispida* (Schreber, 1774) und *Nycteris aurita* (K. Andersen, 1912). Die beiden letztgenannten Arten sind einander sehr ähnlich und lassen sich auf der Grundlage univariater statistischer Analyse von Körpermaßen kaum unterscheiden. Innerhalb keiner der drei Arten existiert eine die Auftrennung in Unterarten rechtfertigende geographische Variabilität. Außer den biometrischen Daten der drei Arten wird ihre Verbreitung diskutiert und eine Übersicht über alle Publikationen gegeben, die sich mit den betreffenden Formen befassen. Die Überprüfung auf Geschlechtsdimorphismus bei den drei Arten zeigte, daß dieser bei Herkunft der untersuchten Tiere aus einem geographisch großen Gebiet nicht sicher beurteilt werden kann.

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