

Systematics of African *Nycteris* (Mammalia: Chiroptera) Part III. The *Nycteris thebaica* group

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Abstract. In this paper, the systematics of the African *N. thebaica* group is discussed. Based on multi- and univariate statistical tests, two species are retained within this group: *N. thebaica*, which occurs over almost the entire African continent and the Arabian Peninsula, and *N. gambiensis*, which is limited to West Africa. Based on literature data, the species status of *N. vinsoni* is confirmed. Literature data, measurements and lists of material examined are presented for each of these species. Unfortunately, even the vast amount of specimens available for this study is still insufficient to decide definitely the status of forms such as *brockmani* and *damarensis*, which at present are considered synonyms of *N. thebaica*.

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

Introduction

In two previous papers (Van Cakenberghe & De Vree 1985, 1993b) the systematics of the three other African species groups, belonging to the genus *Nycteris* Geoffroy

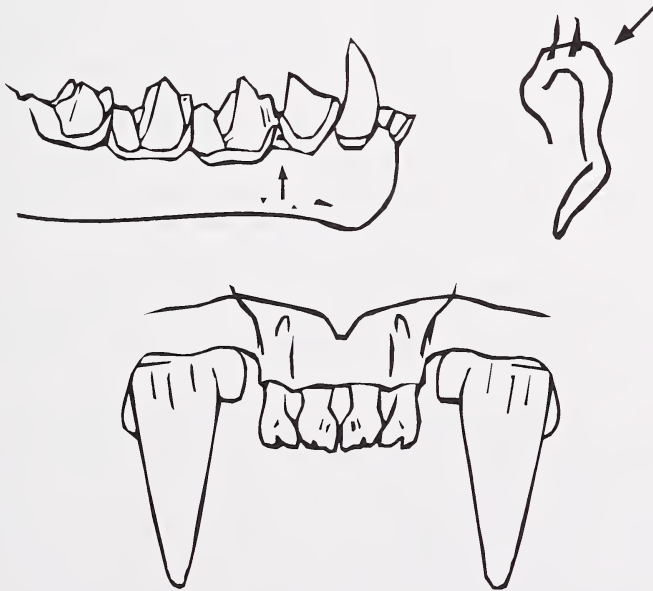


Fig. 1: Morphological characters of the members of the *N. thebaica* group.

& Cuvier, 1795 were discussed. This paper will deal with the fourth and final group as conceived by Andersen (1912): the *Nycteris thebaica* group. Figure 1 shows the morphological characters, which are common to all members of this species group: bicuspid upper incisors, a small second lower premolar (less than half the height of the first one) and a tragus, which has an inverted pearshape. This latter character is the only morphological distinction between the members of the present group and those belonging to the *N. macrotis* group (see Van Cakenberghe & De Vree 1985: 57, fig. 4).

The *N. thebaica* group is the most common of all African groups. In this group, many forms are described, of which the pan African *thebaica* Geoffroy, 1813 and the West African *gambiensis* K. Andersen, 1912 are the most important. The status of some 18 other forms will also be discussed more thoroughly in the systematic accounts section

Material and Methods

For this part of the study, 2243 specimens belonging to the *N. thebaica* group were examined. These originated from the following collections, the curators of which we would like to thank:

British Museum (Natural History), London, G. B. (BM): J. E. Hill; Carnegie Museum, Pittsburgh, U.S.A. (CM): S. B. McLaren & D. A. Schlitter; Harrison Zoological Museum, Sevenoaks, G. B. (HZM): D. L. Harrison & P. Bates; 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; Museum of Comparative Zoology, Harvard University, Cambridge, U.S.A. (MCZ): M. E. Rutzmoser; Muséum d'Histoire Naturelle, Genève, Switzerland (MHNG): V. Aellen; 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 Civico di Storia Naturale di Milano, Italy (MSNM): L. Gagnolaro; Museo Zoologico de "la Specola", Firenze, Italy (MZUF): M. L. Azzaroli; Naturhistorisches Museum, Wien, Austria (NMW): F. Spitzenberger & K. Bauer; Nationaal Natuurhistorisch Museum (formerly Rijksmuseum van Natuurlijke Historie), Leiden, The Netherlands (RMNH): C. Smeenk; Oklahoma State University, Stillwater, U.S.A. (OSU): M. Douglas; 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, D.C., U.S.A. (USNM): M. D. Carleton & C. B. Robbins; Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn, Germany (ZFMK): R. Hutterer; Zoologisches Institut und Zoologisches Museum, Hamburg, Germany (ZMH): H. Schliemann; Zoologisk Museum Universitet København, Denmark (ZMUC): H. J. Baagøe.

During this study, 11 cranial and 9 external variables were measured on all adult specimens, as far as possible. The measurements taken were: 1: Gl = 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-m₁ = Length of the upper toothrow, 8: c-c = Width across the upper canines, 9: m³-m³ = Width across the upper third molars, 10: Mand = Mandibular length, 11: c-m³ = Length of the lower toothrow, 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 = Tibia length.

More details on the measurements and on the statistical techniques are presented in previous papers (Van Cakenberghe & De Vree 1985, 1993a).

Results

Since recent authors still do not agree on the status of the West-African *N. gambiensis*, the following analyses will primarily deal with this problem. The abundant material from the Smithsonian Institution (USNM) enabled us to carry out numerous analyses, even on material from individual countries.

Figure 2 illustrates the presence of two different forms in Senegal by means of a principal components analysis on the skull measurements of 56 specimens. All 11 original variables are weakly (0.54 for Mast) to very strongly (0.96 for Gl_s) correlated with the first principal component (P.C.₁). This shows that P.C.₁ is a good indicator for size. Gl_s, Mast, c-m³ and Mand are positively correlated with P.C.₂ but all correlations are very weak, except for this of Mast (0.83). The Senegalese material is clearly separated into two groups, one with 44 specimens and another with 12 animals. Group "1" includes specimens from Koular and Saboya (together 14 specimens), Diattacounda and Gamon (1 each) and Dialocote (28, including the holotype of *N. gambiensis* ["3"]). The second group ("2") consists of 5 specimens from Diattacounda, 4 from Saboya, 2 from Bandia and 1 from M'Bour. The presence of the holotype of *N. gambiensis* makes it possible to identify the specimens of the first group as *N. gambiensis*. These are clearly smaller than the other specimens, which represent *N. thebaica*. Because of the sympatric occurrence of the forms in Diattacounda, specific separation is suggested. A similar picture is obtained from an analysis on the external measurements, although only 19 specimens could be measured completely.

Unfortunately, these differences are not everywhere as clear as in Senegal. However, an analysis on the skull measurements of 99 specimens from Burkina Faso shows that also in that country both forms occur sympatric: 7 specimens from Oulo belong to *N. thebaica* and 10 to *N. gambiensis*. The skull measurements of 65 specimens from Ghana could be analyzed, and these belong almost uniquely to *N. gambiensis*. Only one specimen out of nine from Damongo (USNM 467930) is somewhat different, and represents *N. thebaica*.

All West African material was lumped together for the next canonical analysis on the tooth measurements of 420 specimens. In figure 3, 12 groups are defined (between brackets the number of specimens in each group is given): 1 = Senegal (16), 2 = Burkina Faso (80), 3 = Morocco (13), 4 = Nigeria (26), 5 = Cameroon (12), 6 = Senegal (58), 7 = Burkina Faso (83), 8 = Ghana (80), 9 = Nigeria (17), 10 = Guinea (14), 11 = Gambia (11) and 12 = Togo (10). Two groups are defined for Senegal, Burkina Faso and Nigeria, since analyses on the specimens from these countries indicated the presence of two size classes. The analysis reveals that all original variables show a very strong correlation with the first canonical variate (C.V.₁): from 0.89 for c-c (represented by "v8") to 0.99 for Mand ("v10"). The upper jaw variables are positively correlated with C.V.₂ and those of the lower jaw negatively. Two clusters of groups can be recognized in figure 3 of which groups

1 to 5 are found to represent *N. thebaica* and groups 6 to 12 *N. gambiensis*. Both clusters show a small overlap, which primarily results from countries where only one species was found.

A discriminant analysis to separate both species in West Africa is performed on the tooth measurements of 343 specimens belonging to *N. gambiensis*: Benin (54), Gambia (16), Guinea-Bissau (2), Ghana (80), Guinea (10), Burkina Faso (83), Ivory Coast (14), Nigeria (17), Senegal (57) and Togo (10), and 132 *N. thebaica* specimens from Benin (1), Guinea (4), Burkina Faso (80), Cameroon (12), Morocco (13), Nigeria (4) and Senegal (18). This results in the following function for all five variables:

$$X = 4.031 * c\text{-}m^3 + 0.363 * c\text{-}c + 4.642 * m^3\text{-}m^3 + 6.563 * \text{Mand} + 3.288 * c\text{-}m_3.$$

This formula gives a Mahalanobis distance of 12.262 and a chance for misclassification of 3.99 %. The Hotelling T^2 is 1168.848, with a F-value of 231.792 and 5 and 469 df., ****. For the above formula, 153.761 is the discriminating value. The best separating measurement is the length of the lower jaw. For this one variable, the discriminant function is: $X = 10.591 * \text{Mand}$, which has a Mahalanobis distance of 9.692 and 5.98 % chance for misclassification. The Hotelling T^2 amounts to 923.908, which is equal to the F-value, with 1 and 473 df., ****. This function produces a discriminating value of 124.654, which results in a mandibular length of 11.76 mm. Some misclassifications, essentially for *N. gambiensis*, can result from this simple function. Only one *N. thebaica* specimen has a smaller value.

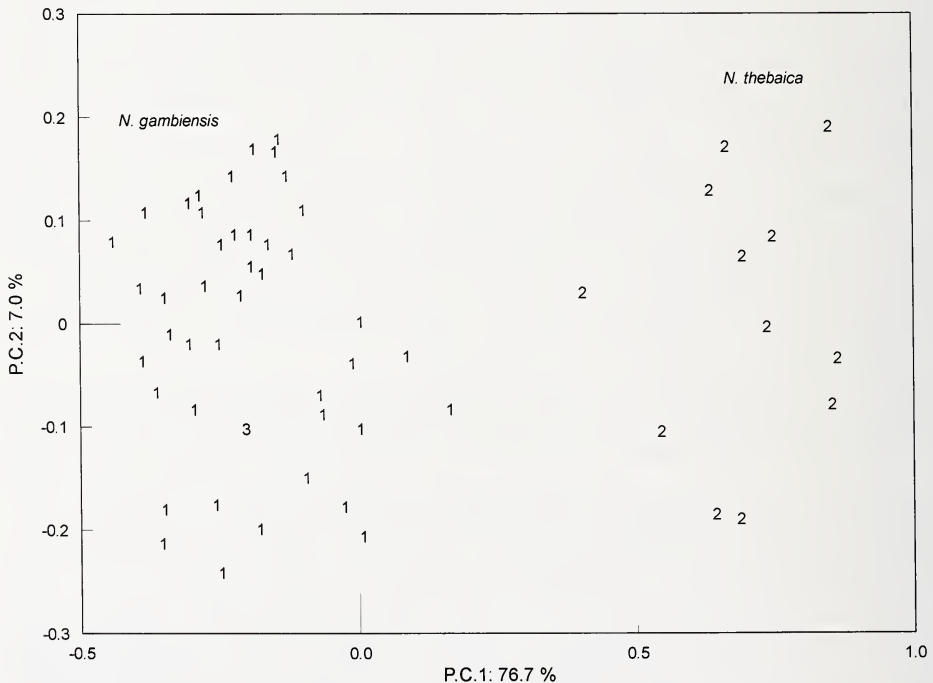


Fig. 2: Principal components analysis on the skull measurements of animals from Senegal (1: *N. gambiensis*, 2: *N. thebaica*, 3: holotype of *N. gambiensis*).

Univariably, the West African representatives of both species are significantly different in all their measurements if both sexes are grouped together. Males are not significantly distinct for 3 ph 2 ($F = 2.807$ with 1 and 65 df.), whereas females are not significantly distinct for 5 ph 2 ($F = 2.993$ with 1 and 78 df.).

The large amounts of material available made it possible to examine the relation between *N. gambiensis* and *N. thebaica* univariably for a number of separate countries such as Senegal, Burkina Faso and Nigeria. There was even material enough to perform analyses on two separate localities: Koular-Saboya in Senegal and Oulo in Burkina Faso. For all of these groups, the sexes could be examined separately. Except for 5 ph 2 ($F = 0.689$ with 1 and 18 df.) all variables are significantly distinct (****) for animals from Senegal. Similar results are obtained for the analyses on the Senegalese females. No significant distinction is found for 5 ph 2, whereas the distinction for Mast ($F = 9.919$, with 1 and 32 df., ***) and 3 ph 2 ($F = 11.552$ with 1 and 9 df., **) is less significant. The males are significantly distinct for all 20 variables. For Koular-Saboya, only the skull measurements and the forearm length could be compared. These data indicate that for both sexes combined, all variables, except Sw ($F = 4.630$ with 1 and 19 df.), are significantly distinct. The absence of significant distinction for Sw ($F = 0.191$ with 1 and 7 df.) can be traced to the females. All their other variables are significantly distinct. In the males from both species, all variables are significantly distinct.

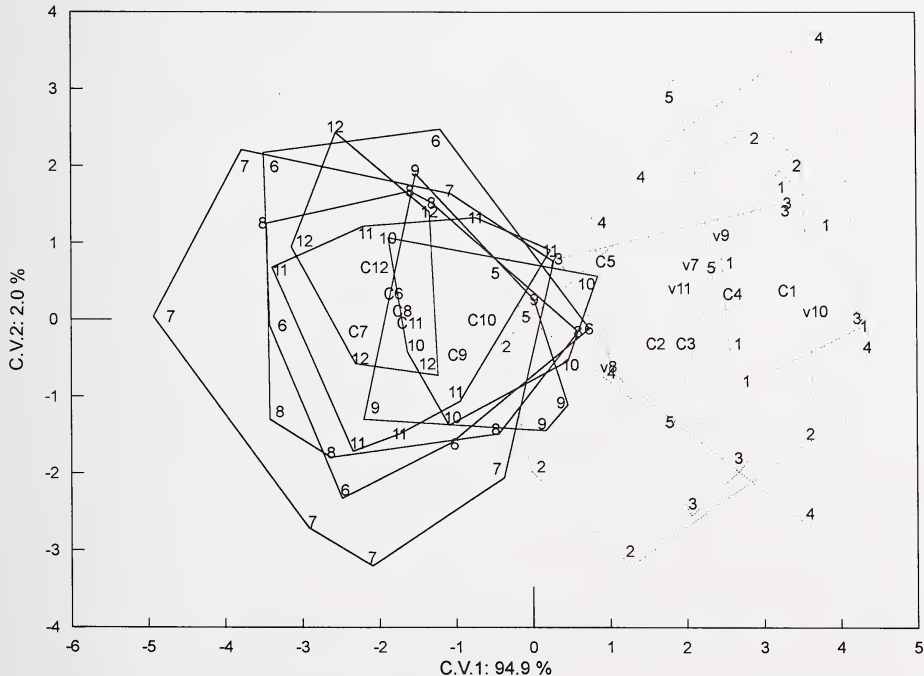


Fig. 3: Canonical analysis on the tooth measurements of 422 West African specimens divided by country (full lines: *N. gambiensis*; dashed lines: *N. thebaica*).

3 ph 2 and 5 ph 2 are the only variables for which the Burkina Faso material (males and females separately and combined) is not significantly distinct. For the females, 3 ph 1 is not significantly distinct either ($F = 2.444$ with 1 and 24 df.). The Oulo material gives almost the same results as for all of the Burkina Faso material, except that the external measurements, excluding Fa, are not significantly distinct. Sw is the only non-significant skull measurement ($F = 2.757$ with 1 and 21 df.).

The Sw is also not significantly distinct in the material from Nigeria. Neither sex of the Nigerian material shows differences for 5 ph 2 ($F = 0.0385$ with 1 and 19 df.). In contrast to the other groups, the males show the largest differences. Besides Sw ($F = 6.033$ with 1 and 17 df.), both Mast ($F = 5.925$ with 1 and 16 df.) and Brain ($F = 5.987$ with 1 and 17 df.) are not significantly distinct.

The previous analyses clearly prove the presence of two distinct species in West Africa: *N. thebaica* and *N. gambiensis*.

An area where many forms have been described is Northeast Africa and the Arabian peninsula. Figure 4 shows the results of a principal components analysis on the external measurements of 77 specimens from northeast Africa, including 39 specimens from Egypt ("1"), 11 from Somalia ("2", including the holotype of *brockmani* ["T1"]), 18 from Sudan ("3"), 6 from South Yemen ("4", including the holotype of *adana* ["T2"]) and 3 from Saudi Arabia ("5", including the holotype ["T3"] and a paratype of *najdiya* ["T4"]). All original variables are positively correlated with P.C., from 0.62 for Tib to 0.93 for Meta 5, indicating that the size of the specimens

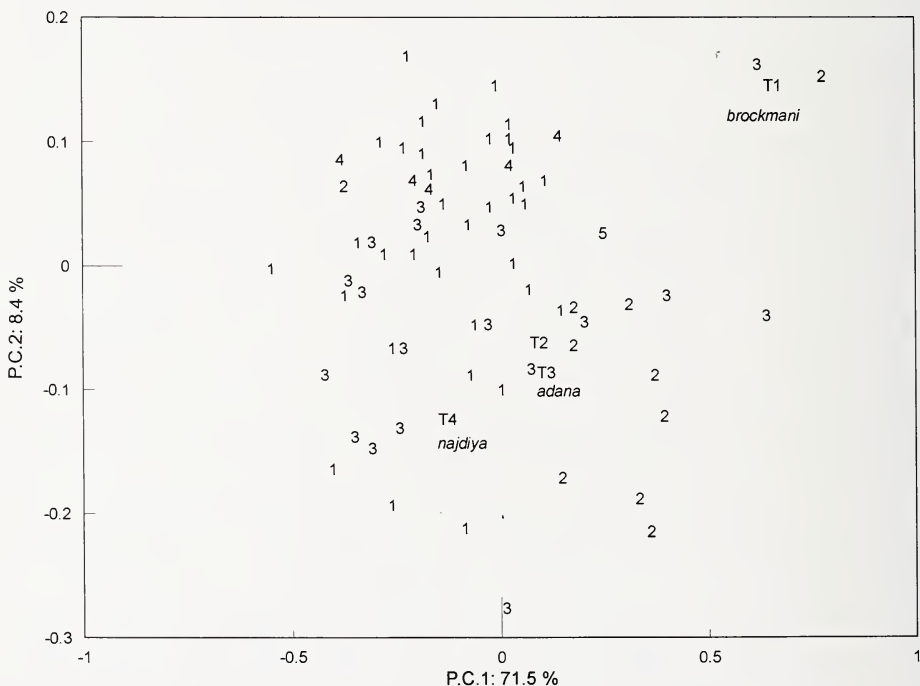


Fig. 4: Principal components analysis on the external measurements of 77 specimens from Northeast Africa (for further details see the text).

increases from left to right. 3 ph 2, 5 ph 1, 5 ph 2 and Tib are correlated positively with P.C.₂, whereas all other variables are correlated negatively with this axis. The graph shows that specimens from Egypt, South Yemen and Saudi Arabia are very uniform, and resemble one another close by. Both type specimens of *najdiya* closely resemble the one from *adana*, suggesting that both forms should be considered synonyms. Most specimens from Somalia and Sudan can also be found in the same area of the graph. However, one specimen from Sudan and two specimens from Somalia — including the holotype of *brockmani* — score very high on both P.C.₁ and P.C.₂. This indicates that these specimens are exceptionally large and possibly different from all other *N. thebaica* forms from this area.

For northeast Africa, one can conclude that *adana* and *najdiya* are conspecific. Furthermore, *brockmani* might represent a different form, but because of a lack of material, its status cannot be adequately determined.

The literature on southern African *N. thebaica* regularly refers to two major forms: a larger *damarensis* and a slightly smaller *capensis*, both of which were considered valid species at one time. Our analyses on specimens from the Republic of South Africa and Botswana revealed the possible presence of two size classes in both countries. In the first country, 8 specimens from Kersbos Farm and a few others from neighbouring localities are slightly larger than most of the remaining specimens. In Botswana, larger specimens were found to occur in Drodsky cave. These larger specimens might represent *damarensis*.

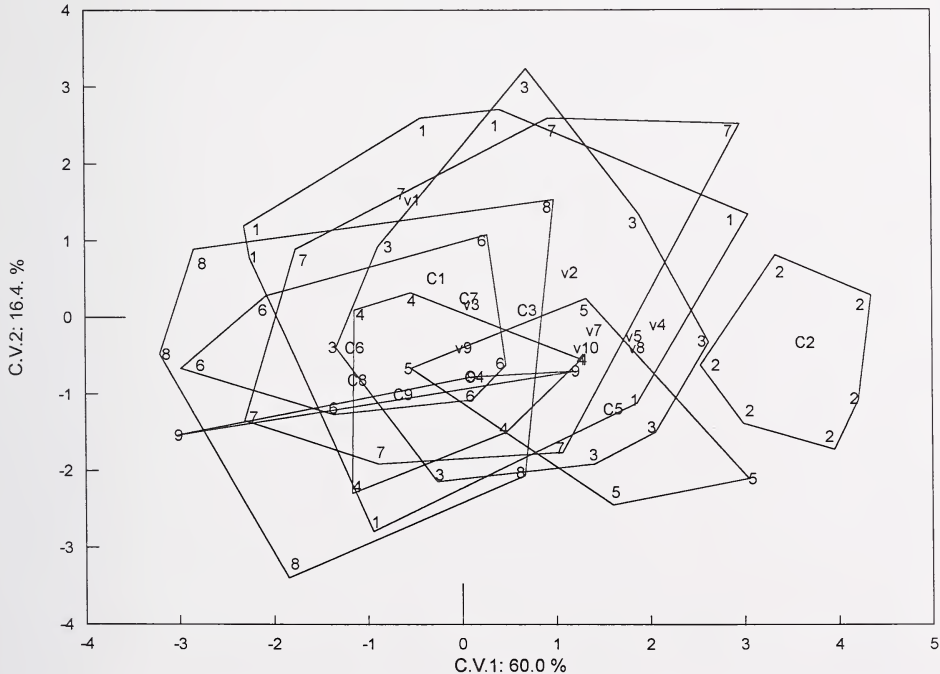


Fig. 5: Canonical analysis on the skull measurements of 283 specimens from southern Africa, divided by country.

All of the available specimens from the southern African region were used in a canonical analysis on the skull measurements. The groups in figure 5 represent the following countries (with the number of specimens in the group given between brackets): 3 = Namibia (44), 6 = Zambia (12), 7 = Zimbabwe (41), 8 = Mozambique (54), and 9 = Angola (3). For the reason mentioned above, the specimens from the Republic of South Africa and Botswana are divided into two separate groups. These groups are: 1 = South Africa: small specimens (92), 2 = South Africa: Kersbos Farm et al. (15), 4 = Botswana: Drodsky Cave (10), and 5 = Botswana: small specimens (12). Most of the original variables are correlated positively with C.V.₁ — from 0.21 for c-m³ to 0.98 for Mand. Cbl, Zyg and Mast are correlated negatively with this axis. The positive and negative correlation values indicate that the first axis does not represent size.

Figure 5 also shows most groups largely overlap, even both groups from Botswana. Only the two groups from South Africa do not overlap, more specific the Kersbos Farm group scores highest of all on C.V.₁. However, since almost all the members of this group are females, the aberrant position of this group could result from an extreme sexual dimorphism rather than from a form difference.

The most important specimens from the East African region originate from Tanzania, and are subjected to a principal components analysis on the skull measurements. Figure 6 includes a total of 73 specimens: 1 = Bagamoyo (7), 2 = Iraku (4),

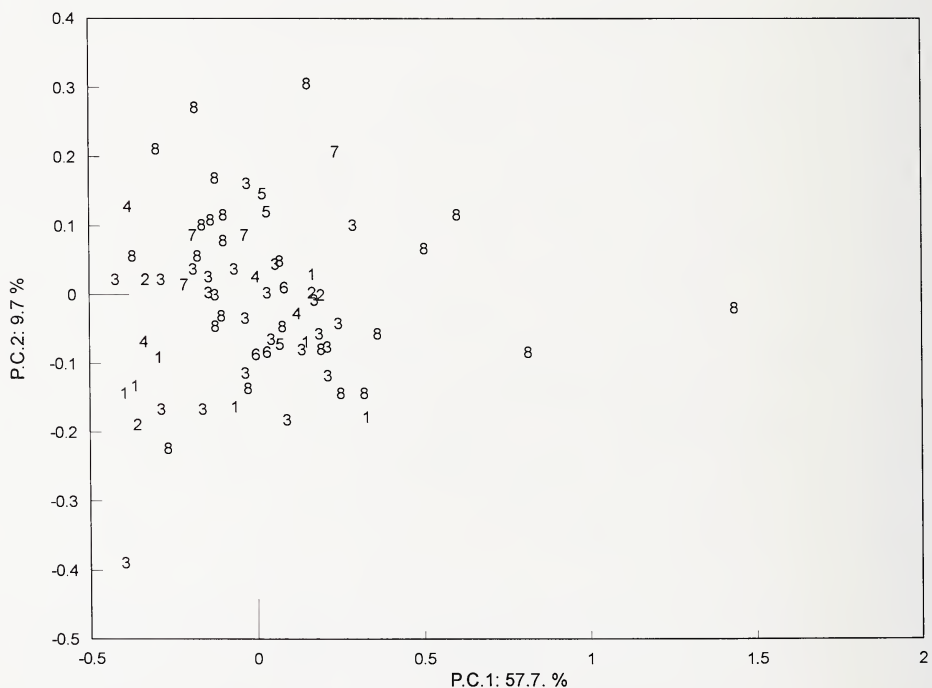


Fig. 6: Principal components analysis on the skull measurements of 74 specimens from Tanzania.

3 = Mikindani (23), 4 = Taveta (4), 5 = Kampi ya mawe (3), 6 = Ol donyo Sambu (3), 7 = Kilosa (4), 8 = 25 specimens from a variety of localities with each less than 3 specimens. The analysis indicates that all original variates are positively correlated with P.C.₁: from 0.44 for Mast to 0.86 for Mand, illustrating that the x axis is an indicator for size. Except for of m^3 - m^3 , all width measurements are positively correlated with P.C.₂.

With the exception of one specimen, which scores very high on P.C.₁, the animals from Tanzania are very similar to one another. This one specimen was collected in the St. Andrews College at Minaki (KU 89943) and all of its measurements are considerably larger than those of the other Tanzanian material. It even falls within the range of *N. macrotis*. However, the shape of the tragus clearly indicates that this specimen belongs to *N. thebaica*.

No significant distinction could be found between the different localities along P.C.₁. Along P.C.₂, the specimens from Kilosa differ significantly from those from Bagamoyo, Iraku and Mikindani. Both sexes, however, are significantly distinct along both P.C.₁ and P.C.₂.

A final canonical analysis is performed on the skull measurements of 818 specimens and is illustrated by figure 7. The group division is as follows: 1 = *N. thebaica* from West Africa (n = 111), 2 = *N. thebaica* from northeast Africa (n = 67), 3 = *N. thebaica* from southern Africa (n = 294), 4 = *N. thebaica* from East Africa (n = 108)

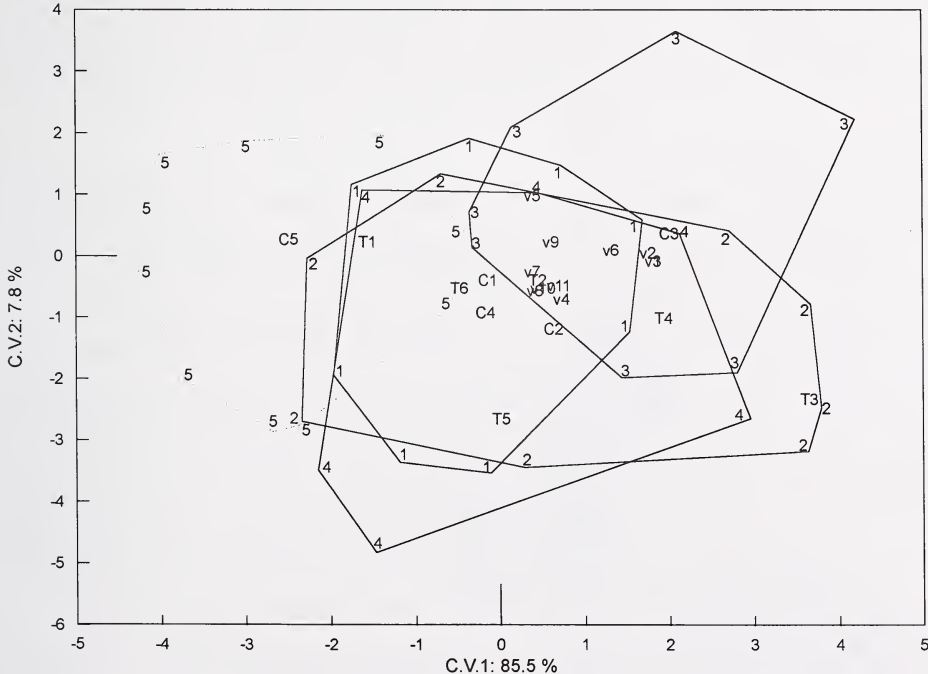


Fig. 7: Canonical analysis on the skull measurements of 818 specimens divided by species and region (dashed line = *N. gambiensi*, full line = *N. thebaica*).

and 5 = *N. gambiensis* from West Africa ($n = 238$). Separately indicated are: the holotypes of *najdiya* ("T2"), *brockmani* ("T3"), *media* ("T4"), *adana* ("T5") and *gambiensis* ("T1") and a paratype of *najdiya* ("T6"). Except for Sw (-0.84), all variables are correlated positively with C.V.₁, from 0.57 for Zyg to 0.99 for Gl_s and Cbl. Gl_s, Cbl, Sw, Mast, Brain and m^3 - m^3 are correlated positively with C.V.₂. With the exception of southern Africa, which scores rather high on C.V.₂, the different regional groups of *N. thebaica* show a large overlap. *N. gambiensis* shows a considerable overlap with three regional *N. thebaica* groups. The position of the holotype of *brockmani* ("T3"), on the extreme right of the figure, reflects its large size.

Systematic account

As already mentioned in the introduction, the members of the *Nycteris thebaica* group are characterized by bicuspid upper incisors, a low second lower premolar and a uniformly inverted pearshaped tragus. This latter character is the only difference with the *N. macrotis* group.

The members of the *N. thebaica* group have the widest distribution of any African species in the genus *Nycteris*. Except for the rain forest and the centre of the Sahara, they occur in all vegetation types, even in the deserts of the Arabian peninsula.

Three species are distinguished, although for one we lacked material to perform analyses (see further). The two most important species, *N. thebaica* Geoffroy, 1813 and *N. gambiensis* (K. Andersen, 1912), occur sympatrically in ten localities, distributed over six different countries: Guene in Benin, Damongo in Ghana, Nyembaro in Guinea, Afon in Nigeria, Natiaboani, Orodara and Oulo in Burkina Faso, and Diattacounda, Saboya and Koular in Senegal. Based on the very elaborate discussion by Kock (1969), we accept *N. vinsoni* as a third distinct species in this group.

Nycteris thebaica Geoffroy, 1813

Nycteris Thebaicus Geoffroy-Saint-Hilaire, 1813. Description de l'Egypte. Histoire Naturelle. Tome Second: 119–123. — Type locality: Egypt.

Nycteris Geoffroyi Desmarest, 1820. Mammalogie ou description des espèces de Mammifères. Première partie, Paris: 127–128. — Type locality: Podor, Senegal.

Nycteris capensis A. Smith, 1829. Zool. J., 4: 434. — Type locality: Interior of South Africa.

Nycteris affinis A. Smith, 1829. Zool. J., 4: 434–435. — Type locality: South Africa.

Nycteris albiventer Wagner, 1840. Die Säugethiere in Abbildungen nach der Natur, mit Beschreibungen. Suppl. I., Leipzig: 439–440. — Type locality: Nubia.

Nycteris discolor Wagner, 1840. Die Säugethiere in Abbildungen nach der Natur, mit Beschreibungen. Suppl. I., Leipzig: 440–441. — Type locality: Ecklon, South Africa.

Nycteris fuliginosa Peters, 1852. Naturwissenschaftliche Reise nach Mossambique, Berlin: 46–48. — Type locality: Boror, Mozambique.

Nycteris labiata Heuglin, 1861. Nov. Acad. Caes. Leop.-Carol., 28 (8): 5–6. — Type locality: Cheren, Bogos.

Plecotus aethiopicus Heuglin & Fitzinger, 1866. Sber. Akad. Wiss. Wien (Math. naturw. Classe), 54 (6): 546. — Type locality: Bahr et Abiat (White Nile).

Nycteris geoffroyi Var. *senegalensis* Hartmann, 1868. Zeitschr. Gesellschaft Erdkde., Berlin, 3: 44. — Type locality: Sennaar, Sudan.

Nycteris angolensis Peters, 1870. Monatsb. k. preuss. Akad. Wiss., Berlin: 903–904. — Type locality: Caconda, Biballe and Rio Coroca, Angola.

Nycteris damarensis Peters, 1870. Monatsb. k. preuss. Akad. Wiss., Berlin: 905. — Type locality: Otjimbingue, Namibia.

Nycteris Revoilii Robin, 1881. Bull. Soc. Pholim. Paris, (7) 5: 90–91. — Type locality: Somalia.

Petalia thebaica adana K. Andersen, 1912. Ann. Mag. nat. Hist., (8) 10: 548. — Type locality: Myba, near Aden.

Petalia damarensis brockmani K. Andersen, 1912. Ann. Mag. nat. Hist., (8) 10: 548. — Type locality: Upper Sheikh, Somalia.

Petalia damarensis media K. Andersen, 1912. Ann. Mag. nat. Hist., (8) 10: 548. — Type locality: Harer, Ethiopia.

Petalia (Nycteris) thebaica aurantiaca de Beaux, 1923. Atti Soc. ital. Sci. nat., 62: 91–96. — Type locality: Archers Post, Kenya.

Nycteris thebaica Koopman, 1975. Bull. Amer. Mus. nat. Hist., 154 (4): 379. [Lapsus].

Nycteris thebaica najdiya Nader & Kock, 1982. Senckenberg. biol. 63: (1/2): 9–15. — Type locality: Dir'iyah, Saudi-Arabia.

N. thebaica has the largest distribution of any species of the genus: it occurs over almost the entire African continent with the exception of the centre of the Sahara and the rain forest (figure 8). This species is found even in the deserts of the Arabian peninsula up to Israel and is the easternmost *Nycteris* species of the Ethiopian region. Its distribution on the African continent is also remarkable. It ranges along the Nile to the Mediterranean Sea. However, its occurrence in Morocco is very difficult to explain. Probably Moroccan localities are a result of an upward distribution from Senegal. Only very few collections have been made in the countries between Senegal and Morocco. Only Qumsiyeh & Schlitter (1981) report on some details of specimens from Mauritania, but their collection only contains *N. hispida*.

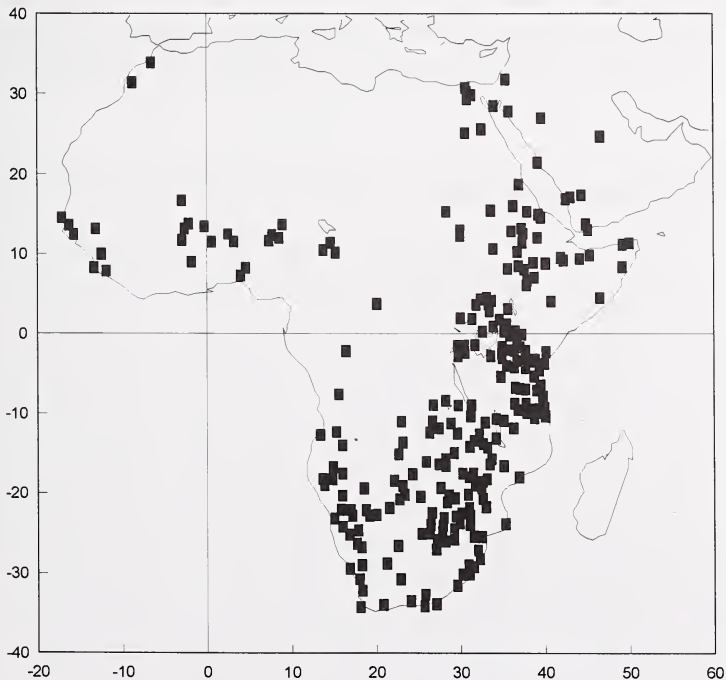


Fig. 8: Distribution map of *Nycteris thebaica* Geoffroy, 1813.

The presence of *N. thebaica* on the island of Corfu (Ellerman, Morrison-Scott & Hayman 1953, Toschi & Lanza 1959, Koopman 1970, Atallah 1977, Van den Brink 1978) can be traced to a misclassified specimen in the Naturhistorisches Museum in Vienna (NMW 27873, collected on 11 april 1914 by dr. R. Lohr). The specimen label bears a correction, changing the locality in "Egypt".

The colour of this species is very variable: from light grey, sometimes almost albino white on the belly of animals collected in deserts and semi-deserts (e.g., Egypt, Sudan, Saudi Arabia, Yemen, Botswana and Senegal), over beige (e.g., Egypt, Ethiopia, Ghana, Guinea, Burkina Faso, Morocco, Mozambique, Nigeria, Kenya, Senegal, Namibia, Benin and Togo) and reddish brown (e.g., Kenya, Mozambique, Zimbabwe and South Africa) to dark brown for animals from Ethiopia, Egypt, Guinea, Burkina Faso, Malawi, Sudan and Zambia. Therefore, the conclusion is that the colour of *N. thebaica* does not follow a certain geographical pattern. The only possible conclusion is that animals from dryer areas are lighter.

Table 1 shows that the forearm length is considerably smaller than usually accepted in literature: 34.2 to 50.7 mm as opposed to 42 to 53 mm (Hayman & Hill 1971) and 42.5 to 49 mm (Ellerman, Morrison-Scott & Hayman 1953). The ranges of measurements given by Rosevear (1965) for Fa and Gl's are also higher than our data for West Africa (see table 3); whereas those for Zyg agree very well with the ones given by Rosevear: Gl's: 19–20 mm; Zyg: 10.5–11.5 mm; c-m³: 6.2–6.9 mm and m³-m³: 6.8–7.5 mm.

Tables 2 and 3 indicate that most forms resemble each other for the measurements taken. Only *brockmani* is somewhat larger, in skull as well as external measurements. The forearms of the syntype of *fuliginosa* from the BM and the holotype of *dama-rensensis* are a little longer than the forearm of *brockmani*. The *damarensensis* specimen

Table 1: Measurements of *N. thebaica* (in mm).

Var	Mean	SD	Min	Max	# ind
Gls	19.12	0.67	17.0	21.2	869
Cbl	16.90	0.65	15.1	18.7	816
Sw	7.50	0.39	6.1	9.0	834
Zyg	11.12	0.43	9.8	12.9	823
Mast	8.93	0.46	6.1	10.1	856
Brain	8.62	0.35	7.5	9.6	899
c-m ³	6.26	0.32	5.0	7.5	1016
c-c	4.65	0.25	3.7	6.0	982
m ³ -m ³	7.04	0.34	4.7	8.5	979
Mand	12.52	0.47	10.6	14.4	974
c-m ₃	6.87	0.32	6.0	8.4	994
Fa	44.52	2.32	34.2	50.7	1164
Meta 3	33.02	2.13	28.0	39.7	456
3 ph 1	23.74	1.51	19.4	27.6	447
3 ph 2	23.27	1.84	17.0	27.8	435
Meta 4	35.12	2.12	26.4	40.7	441
Meta 5	35.50	1.97	28.2	42.1	438
5 ph 1	12.71	0.90	9.4	15.4	435
5 ph 2	11.30	0.97	8.4	14.4	429
Tib	21.99	1.37	16.8	26.5	627

even has the longest first phalange of the third finger (3 ph 1). However, the remaining measurements of these specimens are smaller and agree with those of the other type specimens. The syntype of *fuliginosa* from the RMNH is relatively small: c-m³, m³-m³, Mand, c-m₃ and Fa have the smallest value of all types, whereas c-c only has a smaller value for the holotype of *capensis* and *damarensis*.

Table 2: Measurements of the type material of *N. thebaica*. Part I. 1: *thebaica*, 2: *capensis*, 3: *fuliginosa* (RMNH), 4: *fuliginosa* (BM), 5: *labiata*, 6: *damarensis*.

Var	1	2	3	4	5	6
Gls	----	----	----	----	----	----
Cbl	----	----	----	----	----	----
Sw	----	----	----	7.1	----	----
Zyg	----	----	----	----	----	----
Mast	----	----	----	----	----	----
Brain	----	----	----	----	----	----
c-m ³	----	----	5.9	6.2	6.0	6.8
c-c	----	4.0	4.2	4.6	4.7	4.0
m ³ -m ³	----	6.8	6.8	7.0	7.1	7.0
Mand	----	----	11.2	12.0	12.2	13.2
c-m ₃	----	7.0	6.4	6.6	6.6	7.5
Fa	43.7	43.7	42.5	46.4	44.3	48.8
Meta 3	----	34.5	----	33.5	----	37.8
3 ph 1	----	24.8	----	23.0	----	25.4
3 ph 2	----	21.0	----	22.2	----	24.0
Meta 4	----	37.0	----	----	----	34.9
Meta 5	----	35.8	----	36.2	----	38.7
5 ph 1	----	11.5	----	12.8	----	12.7
5 ph 2	----	10.6	----	----	----	11.5
Tib	----	19.4	----	24.5	----	21.4

Table 3: Measurements of the type material of *N. thebaica*. Part II. 7–8: paratypes *revoilii*, 9: *adana*, 10: *brockmani*, 11: *media*, 12: holotype *najdiya*, 13: paratype *najdiya*.

Var	7	8	9	10	11	12	13
Gls	----	----	18.5	20.8	19.6	19.3	18.8
Cbl	----	----	16.6	18.4	17.4	17.2	16.9
Sw	----	----	7.3	7.9	7.6	7.9	7.9
Zyg	----	----	11.3	12.1	11.6	11.0	10.6
Mast	----	----	8.4	9.1	8.8	8.5	8.3
Brain	----	----	8.4	9.0	8.8	8.3	8.0
c-m ³	----	----	6.6	7.1	6.3	6.4	6.4
c-c	----	----	4.6	5.0	4.7	4.5	4.4
m ³ -m ³	----	----	7.4	7.6	7.1	7.4	7.0
Mand	----	----	12.6	13.9	12.7	12.9	12.4
c-m ₃	----	----	7.4	7.6	6.8	7.0	6.9
Fa	45.0	44.7	45.3	45.5	44.8	44.7	43.7
Meta 3	----	----	33.9	38.2	34.2	35.0	32.1
3 ph 1	----	----	22.7	25.1	24.8	23.0	23.3
3 ph 2	----	----	23.6	26.2	22.2	24.0	23.2
Meta 4	----	----	36.0	39.7	35.9	36.4	34.0
Meta 5	----	----	36.0	40.1	36.1	36.9	34.1
5 ph 1	----	----	12.5	14.0	13.7	11.5	11.0
5 ph 2	----	----	11.2	13.8	11.3	10.9	11.1
Tib	----	----	21.7	25.2	24.6	22.0	20.0

Since this species is distributed over such a vast area, tables 4 through 8 present the standard statistical data for specimens from the various African regions.

The very large distribution of this species and the very large range of colours has resulted in the description of numerous different forms. Besides *N. thebaica*, only *N. gambiensis* and *N. vinsoni* are here retained as valid species.

Table 4: Measurements of *N. thebaica* from West Africa (in mm).

Var	Mean	SD	Min	Max	# ind
Gls	18.68	0.43	17.7	19.6	154
Cbl	16.51	0.40	15.6	17.5	155
Sw	7.42	0.29	6.6	8.2	153
Zyg	10.81	0.32	10.0	11.8	134
Mast	8.80	0.40	7.4	9.5	161
Brain	8.31	0.27	7.7	9.0	163
c-m ³	6.18	0.25	5.3	6.9	172
c-c	4.56	0.18	4.0	5.1	166
m ³ -m ³	6.94	0.23	6.3	7.9	165
Mand	12.38	0.31	11.7	13.3	168
c-m ₃	6.77	0.23	6.0	7.4	171
Fa	43.98	1.31	39.2	47.4	187
Meta 3	33.05	1.34	28.4	36.1	63
3 ph 1	22.71	0.96	20.1	24.7	62
3 ph 2	21.99	1.36	17.1	25.0	60
Meta 4	34.35	1.48	30.1	38.5	62
Meta 5	34.64	1.32	30.6	38.0	61
5 ph 1	12.59	0.58	10.9	14.0	60
5 ph 2	10.92	0.67	8.4	12.5	60
Tib	22.24	1.06	19.4	24.9	63

Table 5: Measurements of *N. thebaica* from northeast Africa (in mm).

Var	Mean	SD	Min	Max	# ind
Gls	19.01	0.73	17.4	20.8	99
Cbl	16.80	0.76	15.1	18.5	96
Sw	7.50	0.41	6.3	8.4	93
Zyg	11.04	0.51	10.0	12.2	100
Mast	8.67	0.42	7.7	9.6	100
Brain	8.42	0.36	7.8	9.3	106
c-m ³	6.23	0.35	5.1	7.1	123
c-c	4.69	0.26	4.0	5.4	122
m ³ -m ³	7.02	0.36	6.0	8.3	122
Mand	12.51	0.62	10.9	14.1	118
c-m ₃	6.89	0.37	6.1	7.9	122
Fa	43.46	2.61	34.2	50.4	193
Meta 3	32.21	2.20	28.0	39.7	124
3 ph 1	23.19	1.53	19.4	27.5	120
3 ph 2	23.09	1.79	17.0	27.8	117
Meta 4	34.11	2.02	30.4	40.0	119
Meta 5	34.85	1.91	30.9	40.0	119
5 ph 1	12.25	0.88	9.8	14.9	120
5 ph 2	11.23	1.00	8.8	14.4	118
Tib	21.90	1.42	17.8	26.2	136

Although most authors mention 1818 as date of description for *N. thebaica*, it should be 1813 (e.g., Anderson & De Winton 1902, Kock 1969). In that year, Geoffroy published two papers (1813a, 1813b), in which he mentions the name *N. thebaica*, although the description in “De l’organisation et de la détermination des Nyctères, une des familles de Chauve-souris” (1813b) is very brief.

Table 6: Measurements of *N. thebaica* from East Africa (in mm).

Var	Mean	SD	Min	Max	# ind
Gls	18.56	0.48	17.0	20.6	156
Cbl	16.34	0.43	15.3	18.0	141
Sw	7.38	0.40	6.5	8.6	157
Zyg	10.94	0.40	10.0	12.9	151
Mast	8.63	0.42	7.2	9.5	151
Brain	8.49	0.27	7.8	9.4	163
c-m ³	6.03	0.27	5.0	7.0	189
c-c	4.53	0.24	3.7	5.6	176
m ³ -m ³	6.77	0.32	4.7	8.3	179
Mand	12.15	0.37	10.6	13.7	172
c-m ₃	6.64	0.26	6.1	8.0	180
Fa	42.85	1.59	37.3	47.0	211
Meta 3	31.91	1.52	28.4	36.7	92
3 ph 1	23.15	1.03	20.9	25.9	89
3 ph 2	22.50	1.40	19.4	26.8	87
Meta 4	34.36	1.63	30.9	38.4	88
Meta 5	34.83	1.52	31.6	38.9	88
5 ph 1	12.49	0.73	9.4	14.5	86
5 ph 2	10.93	0.86	9.1	12.9	86
Tib	22.24	1.62	18.9	26.5	89

Table 7: Measurements of *N. thebaica* from Central Africa (in mm).

Var	Mean	SD	Min	Max	# ind
Gls	18.68	0.46	17.9	19.9	21
Cbl	16.24	0.33	15.7	17.0	19
Sw	7.51	0.36	6.8	8.4	20
Zyg	11.13	0.52	10.5	12.8	24
Mast	8.43	0.38	7.9	9.4	20
Brain	8.62	0.30	8.2	9.6	24
c-m ³	6.04	0.36	5.5	7.1	27
c-c	4.61	0.42	4.2	6.0	25
m ³ -m ³	6.97	0.45	6.5	8.5	26
Mand	12.34	0.60	11.8	14.4	27
c-m ₃	6.77	0.47	6.3	8.4	27
Fa	42.72	1.58	36.6	45.5	30
Meta 3	31.98	1.40	29.2	35.1	21
3 ph 1	23.45	0.77	21.6	24.7	22
3 ph 2	21.93	1.02	20.3	24.4	20
Meta 4	34.86	1.41	32.5	37.6	22
Meta 5	34.63	1.47	32.3	37.4	22
5 ph 1	12.40	0.75	11.2	14.0	20
5 ph 2	10.94	0.72	9.1	12.5	21
Tib	21.48	1.20	19.3	23.9	24

Nycteris geoffroyi Desmarest, 1820 seems to have posed a problem for many authors. Allen (1939) says that *N. geoffroyi* might possibly include *N. thebaica* and *N. macrotis*. Rosevear (1965) and Kock (1969) make *N. geoffroyi* a synonym of the later *N. macrotis* Dobson, 1876, which is nomenclatorically inappropriate. The holotype of *N. geoffroyi* cannot be located and is presumed lost (see already Andersen 1912). The original description is very vague on the shape of the tragus, here found to be a key character:

"=... oreillon petit, appliqué au bord interne du dedans de la conque, de forme arrondie ou en cuiller, en étant deux fois aussi large que haut, sa face antérieure étant velue; ...".

"=... tragus small, connected to the inner side of the ear, rounded or spoonshaped and twice as wide as long, its front side is hairy ...".

The rounded shape could indicate a resemblance with *N. thebaica*, because the tragus of *N. macrotis* always has a clearly flattened top. The collection site of the type specimen does not reveal any additional information, because both species occur in Senegal. The presence of a very old specimen of *N. thebaica* in the RMNH (nr 27933), originating from the "Red Sea" and labelled *N. geoffroyi* might lead to a solution for the problem. Another old specimen of *N. thebaica* in the BM (nr 7.1.1.336), identified as "*N. senegalensis*", also has an inverted pearshaped tragus. "*N. senegalensis*" was originally described as *N. geoffroyi* Var. *senegalensis* by Hartmann in 1868, although he refers to Desmarest (1820). However, in the latter paper, no indication of *senegalensis* could be found. The above data appear to indicate that *geoffroyi* Desmarest, 1820 as well as *senegalensis* Hartmann, 1868 are synonyms of *N. thebaica* Geoffroy, 1813. It is further remarkable that neither Kock (1969), nor Koopman (1975) mention this form.

Table 8: Measurements of *N. thebaica* from southern Africa (in mm).

Var	Mean	SD	Min	Max	# ind
Gls	19.52	0.51	18.0	21.2	432
Cbl	17.31	0.50	15.9	18.7	400
Sw	7.57	0.39	6.1	9.0	405
Zyg	11.30	0.34	9.8	12.3	408
Mast	9.18	0.34	8.1	10.1	418
Brain	8.83	0.24	8.2	9.5	435
c-m ³	6.40	0.28	5.5	7.4	494
c-c	4.73	0.22	3.9	5.4	481
m ³ -m ³	7.20	0.29	6.2	8.4	476
Mand	12.71	0.39	11.2	14.0	478
c-m ₃	7.00	0.27	6.2	7.7	482
Fa	45.87	1.97	37.5	50.7	532
Meta 3	34.84	1.57	30.6	38.6	147
3 ph 1	25.04	1.12	22.2	27.6	145
3 ph 2	24.61	1.55	20.8	27.8	143
Meta 4	36.82	1.82	26.4	40.7	142
Meta 5	37.02	1.75	28.2	42.1	141
5 ph 1	13.35	0.79	11.4	15.4	139
5 ph 2	11.82	0.96	9.1	13.7	136
Tib	21.97	1.33	16.8	26.1	306

Only Smith (1829) and Wagner (1855) consider *N. affinis* Smith, 1829 as a valid species. More recent authors always regarded it as a synonym of *N. capensis* Smith, 1829, *N. capensis capensis* Smith, 1829 or *N. thebaica capensis* Smith, 1829, according to the status they gave to *N. capensis*. Wagner (1840) claimed it to be a synonym of *N. hispida* (Schreber, 1774), but expressed some reservation. This is confirmed in his later work (Wagner 1855), in which he regards *N. affinis* as a valid species.

Already in 1855, Wagner claimed *N. albiventer* Wagner, 1840 to be a synonym of *N. thebaica* Geoffroy, 1813. Thereafter only Aharoni (1944) accepted it as a valid subspecies of *N. thebaica* Geoffroy, 1813.

Hartmann (1868) is the first to make *N. discolor* Wagner, 1840 a synonym of *N. thebaica* Geoffroy, 1813. Subsequent authors considered *N. discolor* to be a synonym of *N. capensis* Smith, 1829 or of *N. thebaica capensis* Smith, 1829. Wagner himself, already proposed that *discolor* might belong to *N. capensis* (Wagner 1840).

Dobson (1880) claimed *N. fuliginosa* Peters, 1852 to be a synonym of *N. angolensis* Peters, 1870, probably because the material is almost exclusively from Angola, a decision that is nomenclatorically inappropriate. Other authors place *fuliginosa* in the synonymy of *N. capensis* Smith, 1829 or *N. thebaica capensis*, Smith 1829.

Allen (1939) makes *N. labiata* Heuglin, 1861 a synonym of *N. revoilii* Robin, 1881, which does not agree with the regulations of nomenclature on priority. Most other authors accept *labiata* as a subspecies of *N. thebaica* Geoffroy, 1813.

As mentioned in an earlier paper (Van Cakenberghe & De Vree 1985), Anderson & De Winton (1902: 109–110) and Kock (1969: 94) are followed, who consider *Plecotus aethiopicus* Heuglin & Fitzinger, 1866 — a nomen nudum — to be a synonym of *N. thebaica* Geoffroy, 1813.

Allen (1939) claims *N. angolensis* Peters, 1870 to be a synonym of *N. thebaica thebaica* Geoffroy, 1813, whereas other authors (e.g., Ellerman, Morrison-Scott & Hayman 1953, Kock 1969) still believe it to be a valid subspecies of *N. thebaica* Geoffroy, 1813.

Only Allen & Lawrence (1936) consider *revoilii* Robin, 1881 as a valid subspecies of *N. thebaica* Geoffroy, 1813. More recent authors mention *N. revoilii* as synonym of *N. thebaica labiata* Heuglin, 1861 or of *N. thebaica thebaica* Geoffroy, 1813.

Except for the type locality, no other records are available for *N. damarensis media* (K. Andersen, 1912). Kock (1969) and Koopman (1975) consider this form as synonym of *N. thebaica brockmani* (K. Andersen, 1912).

Hayman & Hill (1971) consider *aurantiaca* (de Beaux, 1923) to be a synonym of *N. thebaica* Geoffroy, 1813. Kock (1969) and Koopman (1975) claim it to be a synonym of *N. thebaica labiata* (Heuglin, 1861), whereas Rosevear (1965) says it is only a colour phase, lacking even subspecific value.

Hayman & Hill (1971) consider *N. madagascariensis* Grandidier, 1937 to be an island form of *N. thebaica* Geoffroy, 1813. In a previous paper (Van Cakenberghe & De Vree 1985), we showed it to be a synonym of *N. macrotis* Dobson, 1876.

Literature citations

In this section, we try to give a complete summary of all literature data found on the representatives of *Nycteris thebaica*, with an accent on the distributional data. All records are given under the combination of names given by the different authors, without any interpretation.

We do refer to remarks made by other authors, but these might be criticized as well as the original references. If the author did not mention the name *Nycteris*, this is indicated by "(as *Petalia*)". For every combination or names, all references are given in a chronological order. For every author the country and the locality of origin of the material are indicated. The data, for which an older reference was given, are indicated by e.g., "(see Seabra 1909)".

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

Nycteris affinis Smith, 1829

Smith (1829): Republic of South Africa: TYPE — Wagner (1840): *affinis* = *hispida* (?) — Wagner (1855): Republic of South Africa: Cape — Peters (1871): *affinis* = *capensis* — Dobson (1878): *affinis* = *capensis* — Allen (1939): *affinis* = *capensis* — Roberts (1951): *affinis* = *capensis capensis* — Ellerman, Morrison-Scott & Hayman (1953): *affinis* = *thebaica capensis* — Kock (1969): *affinis* = *thebaica capensis*.

Nycteris albiventer Wagner, 1840

Wagner (1840): Nubia = Dongola according to Koopman 1975: TYPE — Wagner (1855): *albiventer* = *thebaica* — Heuglin & Fitzinger (1866): Sudan: Sennaar, Nubia — Hartmann (1868): *albiventer* = *thebaica* — Dobson (1878): *albiventer* = *thebaica* — Anderson & de Winton (1902): *albiventer* = *thebaica* — Cabrera (1903): *albiventer* = *thebaica* — Allen (1939): *albiventer* = *thebaica thebaica* — Bodenheimer (1958): *albiventer* = *thebaica* — Harrison (1964a): *albiventer* = *thebaica* — Rosevear (1965): *albiventer* = *thebaica* — Kock (1969): *albiventer* = *thebaica thebaica* — Koopman (1975): *albiventer* = *thebaica thebaica*.

Nycteris angolensis Peters, 1870

Peters (1871): Angola: Caconda, Biballa, Rio Coroca: TYPE — Dobson (1878): *angolensis* = *thebaica* — Peters (1879): Zanzibar: Ndi (Taita) — Dobson (1880): *angolensis* = *thebaica* — Giglioni (1888): *angolensis* = *thebaica* — Anderson & de Winton (1902): *angolensis* = *thebaica* (?) — Allen (1939): *angolensis* = *thebaica thebaica* — Ellerman, Morrison-Scott & Hayman (1953): *angolensis* = *thebaica angolensis* — Hayman (1967): *angolensis* = *thebaica* — Kock (1969): *angolensis* = *thebaica angolensis* — Hayman & Hill (1971): *angolensis* = *thebaica*.

Nycteris capensis Smith, 1829

Smith (1829): Interior of South Africa and East coast — Wagner (1855): Interior of South Africa and East coast — Peters (1871): Republic of South Africa: Port Natal, Kaffer country — Dobson (1878): Republic of South Africa: Damaraland, Zambesi river, East Africa, Natal, Zanzibar, Caffraria (*capensis* might be a synonym of *thebaica*, but larger amounts of material are necessary) — Dobson (1880): *capensis* = *thebaica* — Anderson (1881): *capensis* = *thebaica* — Jentink (1888): Republic of South Africa: Cape; Mozambique: Boror (ex *fuliginosa*) — Thomas (1897b): Malawi: Ruarwe — Noack (1889): southern Africa — Neumann (1900): Zanzibar: Mojon; Tanzania: Usandawe, Irangi, Kilimadjaru — Thomas & Schwann (1905): Republic of South Africa: Jususie valley — Thomas & Wroughton (1908): Mozambique: Tette (as *Petalia*) — Chubb (1909): Zimbabwe: Bulawayo; Zambia: Mazeppa Mine, Gwanda — Seabra (1909): Mozambique: Mocamedes — Andersen (1912): from Zambesia to Transvaal, Zululand, Natal, Pondoland; Angola: Mocamedes, Benguela (as *Petalia*) — Roberts (1913): Republic of South Africa: Port St Johns, Malvern, Fountain Grove, Pretoria, Metlapetsi river — Roberts (1917): Republic of South Africa: Pretoria, Rooikrans, Rustenberg; Mozambique: Guja, lower Limpopo — Jordan & Rothschild (1921): Republic of South Africa: Mfongosi — Kershaw (1922): Malawi: Chiromo — De Beaux (1923): Angola: Quissenge, Rio Coroca, Humbe; Cape province (as *Petalia*) — Loveridge (1923): British East Africa: Kilosa, Itende, Igulwe, Suna, Gwao's — Hewitt (1931): Republic of South Africa: Eastern Cape province (as *Petalia*) — Bedford (1932): Republic of South Africa: Mfongosi (Zululand), Albany district (Cape province) — Monard (1935): Angola: Mupanda, Humbe, Sangeué — Cowles (1936): Republic of South Africa: Natal, Umzumbe valley — Jordan (1936): Namibia: Klipfontein — Allen (1939): Republic of South Africa; Mozambique: Boror, 12 mi NW Quellimane — Jobling (1939): Republic of South Africa: near Port Elisabeth, Natal — Asdell (1946): Southern Africa — Swynnerton & Hayman (1951): Tanzania: Zanzibar coast, Amani, Bagiro, Mkangazi, Kilosa, Kilimanjaro, Irangi, Sandawe, Gulwe, Itende, Suna,

Zagayu — Garnham & Heisch (1953): Kenya; Zanzibar — Hopkins & Rothschild (1953): Republic of South Africa: Klipfontein — Lawrence & Loveridge (1953): Malawi: Mtimbuka — Frechkop (1954): Democratic Republic of Congo: Mabwe, Kaswabilenga, Kateke, Munoi, Kiamokoto — Dekeyser (1955): Republic of South Africa; Angola; Tanzania; S-Cameroon? — Lips & Rodhain (1956): Kenya (see Garnham & Heisch 1953) — Theodor (1957): Namibia: Okahandja; Zimbabwe: Mareppa Mine (Gwanda); Republic of South Africa: Pietermaritzburg — Pienaar (1964): Republic of South Africa: Kruger Park — Hayman, Misonne & Verheyen (1966): *capensis* = *thebaica* — Hayman (1967): *capensis* = *thebaica* — Verschuren (1967): Uganda: Kisoro; Democratic Republic of Congo: Sinda, Rutshuru, Basse Tumbwe — Kock (1969): *capensis* = *thebaica capensis* — Anciaux de Faveaux (1971): Republic of South Africa: Bishopstowe Cave — Hayman & Hill (1971): *capensis* = *thebaica* — Koopman (1975): *capensis* = *thebaica capensis* — Anciaux de Faveaux (1978a): *capensis* = *thebaica*.

Nycteris capensis brockmani (K. Andersen, 1912)

De Beaux (1923): Eritrea; Somalia (as *Petalia*).

Nycteris capensis capensis Smith, 1829

Shortridge (1934): Republic of South Africa: Worcester, Grahamstown, Klipfontein, Anenous — Roberts (1951): Republic of South Africa: Klipfontein, Anenous, Insusie valley, Hectorspruit, Swellendam, Knysna, Natal, Zululand, Swaziland, Transvaal; Zimbabwe; Mozambique; Malawi; Zambia; Ovamboland.

Nycteris capensis damarensis Peters, 1870

De Beaux (1923): Damaraland, Namaqualand, Lake Ngami, Tette (as *Petalia*) — Shortridge (1934): Namibia: East Caprivi area (Mashi river), Between Chobe valley and Mababa Flats (= Gemsbok Pan + Goho Hills), Karibib, Ukualukasi — Hill & Carter (1941): Angola: Capelongo; Gambos, Humbe (see Bocage 1889), Mossamedes (see Seabra 1909); Mupanda, Sanguene (see Monard 1935) — Roberts (1951): Republic of South Africa: Oranje river, Damaraland, Kaokoveld, Ngamiland, Louisvale, Karibib, Windhoek, Sandfontein, Karolinenhof, Nuitsas, Quickborn Farm, Lake Ngami — Aellen (1952): Damaraland, Namaqualand; Angola; Botswana; Mozambique; Tanzania; Cameroon (see Eisentraut 1941) — Sanborn & Hoogstraal (1953): Yemen: Al 'Asr — Radford (1954): Ethiopia: Asmara — Vercammen-Grandjean & Fain (1958): Ethiopia: Asmara (see Radford 1954) — Vercammen-Grandjean (1964): Ethiopia: Asmara.

Nycteris capensis var. *fuliginosa* Peters, 1852

Seabra (1909): Angola: Mossamedes.

Nycteris capensis media (K. Andersen, 1912)

De Beaux (1923): Ethiopia: Harar (as *Petalia*).

Nycteris damarensis Peters, 1870

Gray (1843): Republic of South Africa: Damaraland (Nomen Nudum) — Peters (1871): Otjibingue: TYPE — Dobson (1878): *damarensis* = *capensis* — Dobson (1880): Damaraland — Andersen (1912): Damaraland, Namaqualand, Lake Ngami, Tette (as *Petalia*) — Thomas (1929): Kaokoveld — Ferris (1930): Namibia: Kaokoveld — Bedford (1932): Namibia: Kaokoveld (see Ferris 1930) — St. Leger (1936): Namibia: Klein Winkhoek — Jobling (1939): Namibia Kaokoveld — Eisentraut (1941): Cameroon (these animals probably belong to *N. arge*, see Aellen 1952, Eisentraut 1956 retains them as *N. major*) — Toschi (1956): *damarensis* = *thebaica damarensis* — Hayman (1967): *damarensis* = *thebaica* — Kock (1969): *damarensis* = *thebaica damarensis* — Hayman & Hill (1971): *damarensis* = *thebaica*.

Nycteris damarensis brockmani (K. Andersen, 1912)

Andersen (1912): Somalia: Upper Sheikh: TYPE; Ethiopia (as *Petalia*) — De Beaux (1923): *damarensis brockmani* = *capensis brockmani* — Allen & Lawrence (1936): Kenya: Voi — Allen (1939): Somalia: Upper Sheikh; from Somalia to Ethiopia — Funaioli (1959): *damarensis brockmani* = *thebaica brockmani* — Hayman (1967): *brockmani* = *thebaica* — Kock (1969): *brockmani* = *thebaica brockmani* — Hayman & Hill (1971): *damarensis brockmani* = *thebaica brockmani* — Koopman (1975): *brockmani* is at least a subspecies of *thebaica*.

Nycteris damarensis damarensis Peters, 1870

Andersen (1912): Damaraland; Namaqualand to Lake Ngami and Tette (as *Petalia*) — Allen & Loveridge (1933): Tanzania: Saranda (Ugogo) — Allen (1939): Namibia: Otjimbingue, Damaraland — Swynnerton & Hayman (1951): Namibia: Otjimbingue; Tanzania: Saranda.

Nycteris damarensis media (K. Andersen, 1912)

Andersen (1912): Ethiopia: Harar: TYPE (as *Petalia*) — De Beaux (1923): *damarensis media* = *capensis media* — Allen (1939): Ethiopia: Harar; Abyssinia — Hayman (1967): *media* = *thebaica* — Kock (1969): *damarensis media* = *thebaica brockmani* — Hayman & Hill (1971): *media* = *thebaica* — Largen, Kock & Yalden (1974): *damarensis media* = *thebaica brockmani* (?) — Koopman (1975): *damarensis media* = *thebaica brockmani*.

Nycteris discolor Wagner, 1840

Wagner (1840): Republic of South Africa: Cape: TYPE — Wagner (1855): Republic of South Africa: Cape — Heuglin & Fitzinger (1866): N-Nubia; Batn-el-Hadjar — Hartmann (1868): *discolor* = *thebaica* — Peters (1871): *discolor* = *capensis* — Dobson (1878): *discolor* = *capensis* — Allen (1939): *discolor* = *capensis* — Roberts (1951): *discolor* = *capensis capensis* — Ellerman, Morrison-Scott & Hayman (1953): *discolor* = *thebaica capensis* — Kock (1969): *discolor* = *thebaica capensis* — Koopman (1975): *discolor* = *thebaica capensis*.

Nycteris fuliginosa Peters, 1852

Peters (1852): Mozambique: Boror, 12 mi NW Quellimane: TYPE — Wagner (1855): Mozambique: Boror — Peters (1866): Zanzibar Coast — Peters (1869): Zanzibar coast — Peters (1870): Angola: Rio Coroca, Biballe, Caconda (= *angolensis*, see Peters 1871) — Peters (1871): Shupanga (Zambesi), Zanzibar coast — Dobson (1878): *fuliginosa* = *capensis* — Dobson (1880): *fuliginosa* = *thebaica* — Jentink (1888): *fuliginosa* = *thebaica* — Noack (1889): *fuliginosa* = *capensis* — Neumann (1900): *fuliginosa* = *capensis* — Thomas & Wroughton (1908): *fuliginosa* = *capensis* — Moreau & Pakenham (1940): *fuliginosa* = *capensis* — Ellerman, Morrison-Scott & Hayman (1953): *fuliginosa* = *thebaica capensis* — Kock (1969): *fuliginosa* = *thebaica capensis*.

Nycteris geoffroyi Desmarest, 1820

Desmarest (1820): Senegal: Podor: TYPE — Wagner (1840) (1855): *geoffroyi* = *thebaica* — Heuglin & Fitzinger (1866): Sudan: Sennaar; (Here *N. geoffroyi* Var. *senegalensis* Desm. Mammal. p. 127 is mentioned as synonym, but this name does not occur in Desmarest 1820) — Hartmann (1868): Sudan: Sennaar — Peters (1871): *geoffroyi* = *thebaica* — Dobson (1878): *geoffroyi* = *thebaica* — Giglioni (1888): *geoffroyi* = *thebaica* — Jentink (1888): *geoffroyi* = *thebaica* — Anderson & de Winton (1902): *geoffroyi* = *thebaica* — Cabrera (1903): *geoffroyi* = *thebaica* — Allen (1939): *geoffroyi* = *macrotis* — Rosevear (1965): *geoffroyi* = *macrotis* or *thebaica* — Kock (1969): *geoffroyi* = *thebaica* (?).

Nycteris labiata Heuglin, 1861

Heuglin (1861): Ethiopia: Cheren, Bogos: TYPE — Hartmann (1868): Ethiopia: Cheren — Peters (1871): *labiata* = *thebaica* — Dobson (1878): *labiata* = *thebaica* — Jentink (1888): *labiata* = *thebaica* — Anderson & de Winton (1902): *labiata* = *thebaica* — Cabrera (1903): *labiata* = *thebaica* — Allen (1939): *labiata* = *revoilii* !!! — Moreau, Hopkins & Hayman (1946): Ethiopia: Cheren — Kock (1969): *labiata* = *thebaica labiata* — Koopman (1975): *labiata* = *thebaica labiata*.

Nycteris revoilii Robin, 1881

Robin (1881): Somalia: TYPE — Anderson & de Winton (1902): *revoilii* = *thebaica* — Trouessart (1904): northern Somalia — Allen (1911): Kenya: Guaso Nyiro (as *Petalia*) — Andersen (1912): Ethiopia; Somalia; British East Africa; Uganda; (maybe *revoilii* = *labiata*) (as *Petalia*) — Lönnberg (1916): British East Africa: Juja Farm — Loveridge (1922): British East Africa: Morogoro, Mpapua — Kershaw (1924): Ethiopia: Bahr dar Giorgis (south Lake Tsana) — Allen & Loveridge (1933): Tanzania: Unyangayi (Turu), Madehani mountains — Allen (1939): Somalia; Ethiopia: Keren — Rode (1941): Somalia — Moreau, Hopkins & Hayman (1946): northern Somalia, north of 10 degrees N. — Swynnerton & Hayman (1951): Tanzania: Morogoro, Mpwapwa, Unyang'anyi, Madehani — Harrison (1960): Kenya: Guaso Nyiro,

Elgoni, Kirui — Anonymous (1965): Uganda: Mbale, Bugisu — Hayman (1967): *revoilii* = *thebaica* — Kock (1969): *revoilii* = *thebaica labiata* — Hayman & Hill (1971): *revoilii* = *thebaica* — Largen, Kock & Yalden (1974): *revoilii* = *thebaica labiata* — Koopman (1975): *revoilii* = *thebaica thebaica* — Kock (1981a): *revoilii* = *thebaica*.

Nycteris thebaica Geoffroy, 1813

Geoffroy (1813a): Egypt: TYPE (as *N. thebaicus*) — Smith (1834): Egypt; Republic of South Africa — Wagner (1840) (1855): from Egypt to Senegal — Rüppell (1842): North-Africa — Gray (1843): Egypt — Hartmann (1863): Egypt: Denderah; Nubia; Bir-el-Gabrah — Gray (1866): Africa — Heuglin & Fitzinger (1866): Egypt; Nubia — Hartmann (1868): Egypt: Denderah, Thebe, Qom-Ombû, Edfu, Wād i-Siba'a, Dindir; Sudan: Kitchland — Peters (1871): Ethiopia: Keren — Dobson (1878): Egypt — Dobson (1880): Egypt; Abyssinia; Angola; Pokomoland; Damaraland; Zambezi; Natal; Zanzibar; Mozambique — Anderson (1881): Egypt: Karnak; South and East Africa — Rochebrune (1883): Senegal: Thionk, Sorres, Leybar, Gandiole, Dagana, Podor — Dobson (1885): Aden — Nehring (1886): Northeast Africa; Arabia; Egypt — Monticelli (1887): Aden, Dahlak archipelago, Massaua — Giglioni (1888): Ethiopia: Assab — Jentink (1888): Egypt; Abyssinia; Azum (ex *labiata*); Red Sea (ex *geoffroyi*) — Bocage (1889): Angola: Quanza, Quissanga, Rio Caroca, Caconda, Gambos, Humbe — Noack (1889): entire Africa — True (1892): Tanzania: Kilimandjaro — Matschie (1895): Tanzania: Tanga, Bagamoyo, Vikindo in Usaramo, Kilimandjaro, Klein-Aruschua, Derema, Irangi (see Neumann), Usandawi, Wualaba, Bukoba and West Africa — Yerbury & Thomas (1895): South Yemen: Aden, Lahej — Pousarges (1896): Congo: Kemo — Matschie (1897): Zanzibar and the continental coast and the innerlands and the east coast of Lake Victoria; Lake Nyasa — Sjöstedt (1897): Cameroon: Yaounde — Thomas (1897a): Somalia: Lugh — Seabra (1900): Angola: Galanga, Umpungoana (Manica), Quissange — Thomas (1900): South Yemen: Myba — Anderson & de Winton (1902): Egypt: Karnak, Khayzan, Luxor, Gizeh, Thebe; Sudan: Sennaar, Kordofan, Dongola; Saudi Arabia: Hadramut; Somalia: Mount Wagga — Cabrera (1903): Rio Muni (= Equatorial Guinea; according to Cabrera 1908 these animals belong to *N. arge*) — Trouessart (1904): Northeast Africa; Egypt; Abyssinia — Senna (1905): Ethiopia: Agordat, Godeflassi, Adi Guhebo, Adi Ugri, Adi Caie, Cheren, Dahlak Archipelago (see Monticelli 1887); Assab (see Giglioni 1888); Angola; Zanzibar; Sinai; Arabia; Aden — Schwann (1906): Botswana: Kuruman — Lönnberg (1908): British East Africa: Kibonoto, Ngare na nyuki — Bonhote (1909): Egypt: Fayum — Seabra (1909): Mozambique: Cazengo, Mossamedes — Drake-Brockman (1910): Somalia: Upper-Sheikh (Guban) — Thomas (1910): Tanzania: Taveta (as *Petalia*) — Hollister (1918): Kenya: Kilimandjaro — Thomas & Hinton (1921): Egypt: Farniso near Cairo; Niger: Zinder — De Beaux (1923): Egypt: Cairo, Sinai; Korosco; Somalia: Lugh; Zanzibar; Kere; Setit; Agordat; Nora ilsand (as *Petalia*) — De Beaux (1924): Somalia: Lugh — Ruxton (1926): Kenya: River Kerio Suk — De Beaux (1930): Ethiopia: Agordat — Zammarrano (1930): Somalia: Basso Giuba — De Beaux (1931): Ethiopia: Rorom — Monard (1935): Angola: Galangè, Catumbela (see Seabra 1900) — Zimara (1935): Senegal: Tabadienke — Flower (1932): Egypt: Thebe, Karnak, Khayzan (see Anderson & de Winton 1902), Giza, Fayum, Birket Qarum — Braestrup (1935): Mali: Timbuktu — Jeannin (1936): Cameroon — Moreau & Pakenham (1940): Zanzibar — Eisentraut (1941): Cameroon: Mubenge-Isongo — Rode (1941): Egypt — Allen & Loveridge (1942): Tanzania: Mbanje (these animals might belong to *N. thebaica fuliginosa*) — Ellerman, Morrison-Scott & Hayman (1953): Republic of South Africa: Cape province, Klein Namaqualand (Goodhouse, Klipfontein, Port Nolloth, Garies), near Lambertsbaai, Swellendam, Knysna, Louisvale, Kuruman, Zululand, Natal, Swaziland, Transvaal (Rustenberg, Pietersburg, Pretoria, Hectorspruit, Kruger Park [Skukuza]); Namibia; Angola; Zimbabwe; Zambia; Malawi; Mozambique; Tanzania; Kenya; Somalia; Ethiopia; Zaire; Egypt; Palestina; Arabia; Corfou — Rosevear (1953): from Gambia to Aden and Angola — Ellerman (1954): Republic of South Africa: Cape province, Namaqualand (Garies, Goodhouse, Port Nolloth, Klipfontein), near Lambertsbaai, Swellendam, Knysna, Louisvale, Kuruman, Natal, Zululand, Transvaal (Pietersburg, Pretoria, Rustenburg, Hectorspruit), Skukuza — Stresemann (1954): Egypt: Alexandria, Bulak — Wassif & Hoogstraal (1954): Egypt: Sinai, Khayzan, Giza, Faiyum — Dekeyser (1955): Arabia; Egypt; Angola; Cameroon; Northern Nigeria; Ghana; Gambia and the area of the great lakes — Felten (1956): Namibia: 140 km SE of Windhoek — Möhres & Kulzer (1956): Egypt — Davis (1957): Tongaland — Verschuren (1957): Zaire: Tunga river, Mabwe, Kaswabilenga, Kateke, Munoi, Kiamakoto — Bodenheimer (1958): Israel: Beit Shan — Chapman (1958): Tanzania: Rukwa valley — Funaioli (1959): Somalia: Basso and Alto Giuba (see Thomas 1897a, De Beaux 1924 and Zammarrano 1930) — Harrison (1959): Zimbabwe: 30 mi E of Chirundu, Belingwe, Wallaby Claims, Filabussi, Makwiro, Sebakwe, Bulawayo, Kasempa Boma, 20

mi NW of Eshowe — Toschi & Lanza (1959): Egypt; Arabia; Israel; Sudan; Kenya; Somalia; Angola; Nigeria; Congo; Cameroon; Corfu; Morocco — Ansell (1960): Zambia: to Barotse — Harrison (1961): Zambia: Chilanga — Blanc, Delage & Ascione (1962): Morocco: Cherrat, Goulimine — Kulzer (1962): Kenya: Lembeni — Brosset (1963): Morocco: near Rabat (see Panouse 1958) — Hanney (1963): Malawi — Wassif & Madkour (1963): Egypt — Rees (1964): Tanzania: Ulanga district — Child (1965): Tanzania: Kilimandjaro — Coetzee (1965): Republic of South Africa: Lydenburg-Nelspruit, Rooiberg-Monscha-neng, Kimberley-Kuruman-Upington, King Williamstown-Uitenhage; Namibia — Ingles (1965): Zambia: Chimbembe Pontoon — Rosevear (1965): Egypt; Nubia; Sudan; Cameroon: Buea, Yaoundé; Nigeria: Kano; Niger: Zinder; Namibia: 90 mi SE of Windhoek — Verschuren (1965a): Rwanda: Kagera Park, Kionga, Kakitumba, Mishushu — Verschuren (1965b): Tanzania: Musabi, Ngelehek, Bologonja, Grum-metti, Handajega — Hayman, Misonne & Verheyen (1966): Rwanda: Kionja, Kisenyi, Muluchu, Kagera Park; Zaire: Kaswabilenga, Kateke river, Tschambi, Rutshuru, Sindo river, Tumbwe, Kakanda, Kapolowe, Kasenga Road (km 67), Mukuen, Tungu, Kakitumba, Albert Park — Hayman (1967): Morocco; Egypt; from Guinea to Cape and Arabia, Israel, Corfu — Verschuren (1967): Zaire: Kisenyi, Mutwanga — Harmsen & Jabbal (1968): Kenya: Olorgesailie — Maa (1968): Mozambique: Jangamo, Muchena, Vila Gamito; Botswana: Drodsky Cave — Kock (1969): Egypt: Cairo, 80 km S of Cairo, Saqqara; Sudan: Nubia, Kordofan; Ethiopia: Lake Langano; Namibia: Kowas, Mariënthel; Tanzania: Arusha, Ol Donyo Sambu, Madabo, Mbamba, Iraka, Mikindani; Zaire: Kapolowe, Lubudi — Koopman (1970): Tropical Africa; Morocco; Egypt; SW-Asia; Corfu — Lanza & Calloni (1970): Somalia — Bourquin, Vincent & Hitchins (1971): Republic of South Africa: Hluhluwe Game Camp, Umfolozi Game Reserve — Funaioli (1971): Somalia — Grubb (1971): Ghana: Weila — Hayman & Hill (1971): Morocco; Egypt; from Guinea to Cape and Arabia, Israel, Corfu — Hill & Morris (1971): Ethiopia: Lake Chamo — Poulet (1972): Senegal: Nord Ferlo — Barus (1973): Egypt — Fain (1974): Namibia: Khomas Heights — Largen, Kock & Yalden (1974): Ethiopia: Keren, Nora island, Assab, Asam river, Agordat, Godolefassi, Adi Guhebo, Adi Ugri, Adi Caie, Harar, Setit river, Rorum plains, Saganeiti, Bahr der Giorgis, Asmara, 4 km S of Dire Dawa, Lake Langano, Mabil + 10 km W, Gondar, Ghibbey Valley, Gallabat, NE Lake Chamo, Didessa river Bridge — Seal & Makey (1974): Africa and Arabia — Viellard (1974): Chad: Zouar (Tibesti) (see Toschi 1954) — Fenton (1975): Zimbabwe: Atlantica Ecological Research Center. — Khalil (1975): Tanza-nia: Kisarawe — Koopman (1975): Sudan: Torit, 36 mi S of Torit, Murukurun, Mura, Loa, Nimule, Katuluru, Lobira, Terangole, Madial, Nagichot, Tungu, Luem, Lokwi, Shukole, Lawudo, Lake Nyibor, Senaar, Nubakka, Jebel Toro, Erkovit, Gallabat, Dongola (see Anderson & de Winton 1902), Batn-el-Hadjar (see Heuglin & Fitzinger 1866) (Koopman uses the name *N. thebaica*) — Lynch (1975): Republic of South Africa: Christiana — Peterson & Nagorsen (1975): Zimbabwe: Triumph Mine near Lake McIlwaine, Umtali, 112 km W of Birchenough bridge, Garden cave (Zimbabwe Nat. Park) — Adam & Hubert (1976): Senegal: Rosso, Bandia, Saboya, M'Bour, Badi (see Aellen 1965) — Makin (1976): Israel — Anciaux de Faveaux (1976): Rwanda; Zaire: Katanga — Overal & Wingate (1976): Republic of South Africa: Doornhoek Cave, 12 km E Pietermaritzburg — Smithers & Tello (1976): Mozambique: Tete, N of Quellimane, Vila de Martica, Zinave, Limpopo river — Whitaker & Black (1976): Zambia: 10 km NW of Lusaka — Atallah (1977): South of the tropic of Cancer, Morocco, Egypt, Arabia, Israel, Corfu — Fenton et al. (1977): Zimbabwe: Thriumph Mine, 32 km W of Salisbury — Saoud & Ramadan (1977): Egypt: Abu Rawash — Anciaux de Faveaux (1978a): Zaire: Tantara cave, Kondo cave, Lubid cave, Kasende Road (km 60 en 67), Mount Mukwene, Kapolowe, Kiwakishi cave, Kaswabilenga, Kateke, Mabwe, Munoi (see Frechkop 1954); Rwanda: Butare, Birambo cave, Kisenyi, Kamitumba (see Verschuren 1965a); Kenya: Kirui, Elongyi (see Allen & Lawrence 1936); Tanzania: Hadajega (see Verschuren 1965b), Kibonoto (see Lönnberg 1908), Mojoni (see Neumann 1900), Saranda (see Allen & Loveridge 1933), Mkamba bay (see Ansell 1967); Zambia: Chikwa (see Ansell 1967), Luangwa valley (see Ansell 1967), Kasempa (see Ansell 1960), Luambe (see Ansell 1960), Mfuwe, Missale Old Mine (see Ansell 1967); Zimbabwe: Mazeppa Mine (see Chubb); Namibia: Karibib, Ukualukasi (see Shortridge 1934); Egypt: Karnak, Dandara (see Gaisler, Madkour & Pelikan 1972) — Anciaux de Faveaux (1978b): Zaire: Ruisseau cave, Kondo, Lusolo, Lubum-bashi, Mount Mukween, Kapolowe — Ansell (1978): Zambia: Mukuen (see Hayman, Misonne & Verheyen 1966), Mount Kapsuku, Kasane (see Smithers 1971) — Gaisler & Barus (1978): Egypt: Dandara — Koop-man, Mumford & Heisterberg (1978): Burkina Faso: Barga, Dio, Djpologo, Founzan, Koutoura, Natiaboani, Nayouré, Orodara, Oulo, Tatarko; Niger; Mali; Ghana — Rautenbach (1978): forest of southern Africa, the southern treesavannah, the Namib desert and the southern arid areas — Van den Brink (1978): Corfu — Wingate (1978): Republic of South Africa: Doornhoek mine (16 km E of Pietermaritzburg) — Delany & Happold (1979): Senegal: Fété-Olé (see Poulet 1972) — Fenton & Fullard (1979): Zimbabwe:

Sengwa Wildlife Research Area — Howell (1979): Tanzania: Pugu Hills — Corbet & Hill (1980): south of the Sahara, Morocco, Egypt, Israel, Arabia — Fenton & Thomas (1980): Zimbabwe: Sengwa Wildlife Research Area — Howell (1980): Tanzania: Near Kisarawe — LaVal & LaVal (1980): Republic of South Africa: Umdoni Park — Pienaar, Rautenbach & De Graaff (1980): Republic of South Africa: Kruger Park — Robbins (1980): Benin: Guene, Zizonkame — Swanepoel, Smithers & Rautenbach (1980): Southern Africa — Demeter (1982): Ethiopia: Awash National Park — Goff (1982): Tanzania: Kisarawe — Koopman (1982): Egypt: Thebe; Namibia; Israel; Sinai; Egypt; Morocco; Senegal; Benin; Somalia; Kenya; to Republic of South Africa in open vegetation zones; Zanzibar; Pemba — Nader (1982): Saudi Arabia: Dir'yiah — Nader & Kock (1982): Sudan: Nubia, Erkowit, Kordofan, Jebel Toro; Ethiopia: 4 km W Didessa Settlement, Lake Langano, Doki Riv. Bridge; Kenya: Mt. Suswa, Gedi Nat. Park 10 km S Diani Beach, Bushwackers Safari Camp; Tanzania: Iraki area, Mikindani, Ol Donyo Sambu, Arusha, Madaba, Mbemba — Fenton et al. (1983): Zimbabwe: Sengwa Wildlife Research Area — Findley & Black (1983): Zambia: Lusaka — Ogen-Odoi (1983): Uganda: Entebbe peninsula — Baeten, Van Cakenberghe & De Vree (1984): Rwanda: Bugarama, Muhabura, Rukira — Herselman & Norton (1985): Republic of South Africa: Abbotsburg, Alice, Amalinda, Atherstone, Bakleisdrijf, Blouputs, Brakkloof, Brandkaros, Compagnies Drift, De Hoop, Despatch, Doringkraal, Doringpoort River, Driefontein, Forest Ranch, Fort Brown, Garies, Glenlea, Goodhouse, Graaff-Reinet, Grahamstown, Grootvadersbos, Hawston, Hester Malan, Hex river, Keikamspoor, Kersbos, Kleinpoort, Kroomie, Lessendrum, Manley Flats, McGregor, Moneysworth, Montagu Cave, Okiep, Port Alfred, Port Elisabeth, Port St Johns, Rangerton, Salem, Sanderg, Sewefontein, Skrik van Rondon, Spitskop, Stones Hill, Twee Rivieren, Vrolijkheid, Welbedacht Mine, Wondergat — Feiler (1986): Angola: Luanda — McLellan (1986): Sudan: Barh-el-Ghazal Province, Wau — Bell (1987): Zimbabwe: near Sengwa Wild Life Research Institute — Happold, Happold & Hill (1987): Malawi: Blantyre, Chiwipina near Chilwa, Ekwendeni Station, Fort Johnston, Karonga, Lengwe N.P., Limbe, Mapera, Mzuzu, Zomba, Chimpeni Estate — Van der Merwe (1987): Republic of South Africa: near Thabazimbi and Potgietersrust (see Rautenbach 1982) — Aldridge et al. (1990): Zimbabwe: Mana Pools National Park — Fenton et al. (1990): Zimbabwe: Mana Pools National Park — Sidiyene & Tranier (1990): Mali: Kidal — McDonald, Rautenbach & Nel (1991a, 1991b): Republic of South Africa: De Hoop Provincial Nature Reserve — Rautenbach & Fenton (1992): Zimbabwe: Mana Pools National Park (see Aldridge et al. 1990), Sengwa, Pafuri — Yom-Tov, Makin & Shalmon (1992): Israel: En Gedi, Neot HaKikar.

Nycteris thebaica adana (K. Andersen, 1912)

Andersen (1912): Myba, Aden: TYPE (as *Petalia*) — De Beaux (1923): Aden (as *Petalia*) — De Beaux (1934): Somalia: Bender Cassim — Scortecci (1937): Somalia: Bender Cassim — Morrison-Scott (1939): Saudi Arabia: Jidda, Najran — Hayman (1941): Jebel Harir — Harrison (1956): Arabia — Funaioli (1959): Somalia: Migiurtinia (see De Beaux 1934, 1937) — Harrison (1964a): Mybar, Jeddah, near Jeddah, Buraiman, Najran, Jizan, Sabiya, Lahej, Dhala, 90 mi N of Aden, Jebel Harir, Aden, Khalla, N of Dhala — Ellerman & Morrison-Scott (1966): south Arabia — Funaioli & Simonetta (1966): Somalia — Kock (1969): *thebaica adana* = *thebaica labiata* — Nader (1975): Saudi Arabia: Jeddah, Najran (see Morrison-Scott 1939), Sabiya, Jizam (see Harrison 1964) — Scaramella (1975): South Yemen; Arabia; Aden; Djibouti; E Ethiopia; Somalia; Kenya — Nader & Kock (1982): Saudi Arabia: Jeddah, Buraiman, Mothra, Ben Yeshdan, Abha, Ahad Rufaida, Sabiya, Jizan Al Jowa, Najran; Yemen: Al Asr; South Yemen: Khalla, Sheikh Othman, near Myba (= Mybar), Lahej, Aden — Harrison & Bates (1989): Oman: Jifjif — Al-Safadi (1991): Yemen: Al-Kadan area.

Nycteris thebaica albiventer Wagner, 1840

Aharoni (1944): Israel: Beisan Plain.

Nycteris thebaica angolensis Peters, 1870

Seabra (1900): Angola: Rio Coroca, Caconda, Catumbella (as *N. thebaica*, Geoffroy, var. *angolensis*, Peters) — Trouessart (1904): Congo; Angola; Pekono; Taita — Monard (1935): Angola: Rio Coroca, Caconda, Huila — Frechkop (1938): Democratic Republic of Congo — Hill & Carter (1941): Angola: Hanha; Rio Coroca, Bibale, Caconda (see Peters 1871); Quissanga (see Bocage 1889), Catumbella (see Seabra 1900), Serra de Seles (see Seabra 1905), Mossamedes, Cazengo (see Seabra 1909) — Schouteden (1947): Democratic Republic of Congo: Lualaba area (see Matschie).

Nycteris thebaica aurantiaca (De Beaux, 1923)

De Beaux (1923): Kenya: Archer's Post: TYPE (as *Petalia (Nycteris) thebaica aurantiaca*) — Frechkop (1938): Kenya — Allen (1939): Kenya: Archer's Post — Monard (1939): Kenya (see De Beaux 1923) — Allen & Loveridge (1942): Kenya: Northern Guaso Nyiro (see De Beaux 1923) — Swynnerton & Hayman (1951): Tanzania: Tanga, Vikindu, Mbanja, Ndarema, Arusha Chini, Kibongoto, Kilimanjaro, Engare Nanyuki, Irangi, Sandawe, Bukoba, Zanzibar, Bagamoyo — Harrison (1960): Kenya: Archer's Post, Guaso Nyiro, Shimoni, Nairobi, Magadi, Cherangani Hills, Kirio Suk river, Loldyka Hills near Nanyuki, Mount Mombassa, Machakos district, Kiambu, Lake Naivasha, Marsabit mountains, Athi river, Gilgil, Mrima Hills, Lake Elmenteita, Voi, Elgon caves, Ol Kalou, Langata — Hayman (1967): *aurantiaca* (de Beaux, 1923) = *thebaica* — Kock (1969): *thebaica aurantiaca* (de Beaux, 1923) = *thebaica labiata* — Hayman & Hill (1971): *aurantiaca* (de Beaux, 1923) = *thebaica* — Koopman (1975): *thebaica aurantiaca* (de Beaux, 1923) = *thebaica labiata* — Cagnolaro (1976): Kenya: Archer's Post (TYPE destroyed).

Nycteris thebaica brockmani (K. Andersen, 1912)

Toschi (1956): Somalia: Candala, Guriasamo (Ahl Mascot) — Funaioli (1959): Somalia: Somalia settle (see Toschi 1956) — Funaioli & Simonetta (1966): Somalia — Largen, Kock & Yalden (1974): Ethiopia: Metahara.

Nycteris thebaica capensis Smith, 1829

Trouessart (1904): Southern Africa from Zambezi to Cape — Wettstein (1918): Sudan: Nubbaka — Ellerman, Morrison-Scott & Hayman (1953): Republic of South Africa: Cape province, Zululand, Transvaal; Zimbabwe; Mozambique; Malawi; Zambia; Tanzania — Davis (1957): Republic of South Africa: Lake Simbu — Skead (1958): Republic of South Africa: Uitenhage and Cradock districts — Swynnerton (1958): Tanzania: Serengeti National Park — Till (1958): Republic of South Africa: Between Tete Pan and Pongola river (Ubombo district, Zululand) — Kulzer (1959): Tanzania: Ol Donyo Sambu (30 km N of Arusha), Arusha — Anonymous (1960): Republic of South Africa: Skukuza, Kruger Park — Krampitz & Anciaux de Faveaux (1960): Kenya coast and Zanzibar (see Garnham & Heisch 1953) — Meester (1960): Republic of South Africa: Loskop Dam National Park — Bateman (1961): Republic of South Africa: Uitenhage, Bredasdorp, Swellendam — Hatt (1963): Zimbabwe: Atlantica Ecological Research Center — Harrison (1964b): Zimbabwe: Zambesi-Cherowe river confluence — Dalquest (1965): Mozambique: Zinave — Ansell (1967): North coast of Lake Kariba, Kapombo, Luambe Game Camp, Mfuwe Game Camp, Petauke, Chikwa, Luangwa valley, Fort Jameson, Missale Old Mine, Livingstone, Kalabo, Lusongazi, Nkamba Bay — Dalquest (1968): Mozambique: Zinave — De Sousa Diaz (1968): Zambesia — Ansell (1969): Zambia: Ngwerere Siding, Namatombwa Hill, Naleza (Blue Lagoon), Leopard's Hill Cave, Chunga, Kalala island — Keymer (1971): Zambia; Kenya (see Garnham & Heisch 1953) — Smithers (1971): Botswana: Drotsky's Cave, Gweta, Kwaai, Livingstone's Cave, Maun, Molopolole, Ngoma, Nokaneng, Satuvi, Sepopa, Serowe — Ansell (1973): Zambia: Chief Chitanda, Muckle Neuk — Laycock (1973): Republic of South Africa: Bishopstowe Tunnel — Wilson (1975): Zimbabwe: Wankie Nat. Park, Shapi, Main Camp — Smithers & Wilson (1979): Zimbabwe.

Nycteris thebaica damarensis Peters, 1870

Seabra (1900): Angola: Gambos, Humbe — Trouessart (1904): South and East Africa, Damaraland — Monard (1935): Angola: Gambos, Humbe (see Bocage 1889) — Ellerman, Morrison-Scott & Hayman (1953): Republic of South Africa: Oranje river, Kaokoveld, Damaraland, Ngamiland, Klein Namaqualand; S. Angola; Tanzania — Harrison (1956): Arabia — Hoesch & Lehmann (1956): Namibia: Okahandja, Otjimbojo/Omaruru — Bauer & Niethammer (1959): Namibia: de Valle, Naukluft — Meester (1962): Namibia: Djab Farm — Hoogstraal & Kohls (1967): Namibia: Uis Tin mine — Smithers (1968): Botswana: Francistown, Serowe, Nokanang, Gweta, Sevuti — Roer (1970): Namibia: Gobabeb — Anciaux de Faveaux (1971): Ethiopia: Asmara — Roer (1971): Namibia: Gobabeb stat. — Roer (1972): Namibia: Khomas heights (E of Windhoek), Neuhof-Kowas Farm (near Windhoek) — Stuart (1975): Namibia: Kuiseb, Gobabeb.

Nycteris thebaica fuliginosa Peters, 1852

Seabra (1900): Angola: Quissange — Trouessart (1904): Mozambique; Zanzibar — Monard (1935): Angola: Quissanges.

Nycteris thebaica labiata Heuglin, 1861

Hill & Morris (1971): Ethiopia: Mabil, 10 mi W of Mabil — Largen, Kock & Yalden (1974): Ethiopia: Gura, east coast Lake Abiata, W coast Lake Langano, Abella, N coast Lake Abaya, Ambo, 6 mi W of Asmara, Dorfu, Torat, Abbyssinia — Koopman (1975): Central and Southern Sudan — Schlitter et al. (1983): Central African Republic: Manovo, Gounda, St.-Floris National Park, 11,5 km NW Koumbala Camp — Aggundey & Schlitter (1984): Kenya: Ndi (see Peters 1878), Taveta (see Thomas 1910), Archer's Post (see De Beaux 1923), Guaso Nyiro (see Allen 1911), Voi (see Allen & Lawrence 1936), Elgonyi (see Allen & Lawrence 1936), Kirui (see Allen & Lawrence 1936), Shimoni, Nairobi, Magadi, Cherangani Hills (see Ruxton 1926), River Kerio Suk (see Ruxton 1926), Ladyka Hills, Machakos, Tanganyika, Kiambu, Lake Naivasha, Rongai, Molo, Karen, Eldoret, Marsabit Mountains, Athi river, Gilgil, Yatta Escarpment, Mrima Hill, Lake Elmenteita, Elgon Caves, Ol Kalou, Langata Forest, Ngong Hills, Molo River, Konza, Soysambu, Malindi, Lokori, Watamu, Mount Suswa (see Nader & Kock 1983), Nakuru, Kibwezi, Kijabe, Msambweni Cave, Karibiti, Juja Farm (see Lönnberg 1916), Masalani (see O'Shea & Vaughan 1981), Gedi National Park (see Nader & Kock 1983), 10 km S Diani Beach (Nader & Kock 1983), Ologesailie (Harmsen & Jabbal 1968), Bushwacker's Safari Camp (Nader & Kock 1983).

Nycteris thebaica najdiya Nader & Kock, 1982

Nader & Kock (1982): Saudi Arabia: Dir'iyah.

Nycteris thebaica revollii Robin, 1881

De Beaux (1923): Northern Somalia (as *Petalia*) — Allen & Lawrence (1936): Kenya: Elgonyi, Kirui.

Nycteris thebaica thebaica Geoffroy, 1813

Andersen (1912): Egypt + Sinai (as *Petalia*) — Wettstein (1918): Egypt: Karnak (see Anderson & de Winton 1902) — De Beaux (1934): Somalia — Allen (1939): Egypt; Nubia; Angola: Caconda, Biballe, Rio Coroca; Corfu — Malbrant & Maclatchy (1949): from Egypt to Angola (see Allen 1939); Congo (see Pousargues 1896); Cameroon (see Jeannin 1936) — Aellen (1952): Egypt; North Arabia; Corfou; Angola; Congo (see Pousargues 1896); Cameroon: Yaoundé, Buea (see Sjöstedt 1897; Jeannin 1936); Somalia (see De Beaux 1934); Nigeria: Farniso (see Thomas & Hinton 1921) — Toschi (1954): Egypt; Centre of the Sahara; Zounar (Tibesti) — Sanborn & Hoogstraal (1955): Egypt: Faiyum, Giza, Beheira, Minufiya — Harrison (1956): Arabia — Hoogstraal (1956): Sudan — Aellen (1957): Red Sea; Sudan; Ethiopia; Somalia; Zambia; Egypt; Corfou; Arabia; Palestina — Anciaux de Faveaux (1958): Zaire: Kapolowe — Eisentraut (1958): Tanzania: Dar es Salaam — Panouse (1958): Morocco: Cherrate Wadi — Kulzer (1959): Egypt: Cairo — Macy et al. (1961): Egypt: Abu Sir, Abu Rauwash — Heyneman & Macy (1962): Egypt: Abu Rawash, Abu Sir, Giza; Sudan; Palestina; N Arabia — Hoogstraal (1962): Egypt: Faiyum, Giza, Beheira, Minufiya province — Radovsky & Yunker (1963): Egypt: Abu Rawash — Harrison (1964a): Mount Sinai — Anciaux de Faveaux (1965): Zaire: Tshamakale = Kamishinka (near Mwela Pande, Tenke) near Lubudi-Lusulo, Kyasala, Mototo, Kapolowe — Aellen (1966): Zaire: Mount Né, Tantara — Ellerman & Morrison-Scott (1966): Egypt; Palestina; Corfu; N Arabia — Kock (1969): Egypt: Dendera, Upper Egypt, Thebe, Kom Ombo, Edfu, Wadi Sibaa, Sinai, Khayzan, Karnak, Birket el Quarum, Korosko, Gizeh, Seila, Bahr el Roda, Alexandria, Bulak; Chad: Zounar; Sudan: Nubia, Bajuda steppe, Batn el Hadjar, Sennar, Dinder river, Kitch country, Dungola, Nubbaka, Mount Tungu, Erkowit, Jebel Toro, Mesakim Qisar, Nuba mountains — Hill & Morris (1971): Egypt; Sudan: Gondar, Gallabat, Ghibbey Valley — Gaisler, Madkour & Pelikan (1972): Egypt: Karnak, Dandara, Mount Sinai, Alexandria, Buhaira, Minufiya province, Giza, Cairo, Abu Rawash, Abu Sir, Seila, Birket el Qarun, Bahr el Roda, Faiyum, Thebe, Khayzan near luxor, Edfu, Kom Ombo, Wadi Sibaa near Korosko, Karnuk — Koopman (1975): Northern Sudan — Atallah (1977): Israel: Beit Shean (see Aharoni 1944); Egypt: Sinai (see Anderson & de Winton 1902); NW Arabia; Corfu — Nader & Kock (1982): Israel: Sulam near Merhavia; Egypt: Abu Rawash, Bulac el Dakrur, Giza, Gizeh zoological Garden, Lake Moeris, Upper Egypt, Seila, Cairo, Saqqara, 20 km S Cairo — Qumsiyeh (1985): Egypt: El Khatatba, Kafr Dawud Kom Hamada, Wadi El Natrun 12 mi W, Bulaq El Dakrur, Cairo, Abu Rawash, Gizeh, Gizeh Pyramids, Saqqara, Wardan, Kom Oshim, Lake Qarun, Seila, Dandara, Luxor, Korosko, Mt Sinai; Israel: Jericho, Merhavva, Ein Yahav; Sudan: Erkowit.

Specimens examined

Nycteris thebaica E. Geoffroy, 1813

Angola: 8 specimens: Benguela (BM: 1); Bungo (BM: 3); Humbe (MHNG: 1, MSNG: 1); Mount Moks (BM: 1); Sanguéve (MHNG: 1);

Benin: 2 specimens: Guéne (USNM: 2);

Botswana: 97 specimens: Dibete (SMNS: 1); Drodsky Cave (SMF: 2, USNM: 51); Gemsbok Pan (TM: 1); Ghanzi, 20 mi NE (USNM: 1); Gweta, 18 mi S (HZM: 1); Kanye (ZFMK: 9); Kuruman (BM: 2); Maun (USNM: 4); Mohembo (KU: 4); Lake Ngami (BM: 1); Ngoma, Chobe river (HZM: 1); Sepopa (USNM: 3); Serowe (HZM: 2); Serule (USNM: 3); Toteng (SMNS: 1); Xugana (USNM: 10);

British East Africa: 1 specimen: Jaraungu (BM: 1);

Burkina Faso: 132 specimens: Barga, 9 km NE (USNM: 1); Dio (USNM: 9); Natiaboani (USNM: 74); Orodara, 27 km ENE (USNM: 1); Oulo (USNM: 30); Tatarko (USNM: 17);

Cameroon: 13 specimens: Mokolo (KMMA: 1); Sir (KMMA: 9); Waza (KMMA: 1); Yagoua (KMMA: 2);

Egypt: 94 specimens: ? (BM: 1, NMW: 1, RMNH: 1, SMF: 2, SMND: 1); Abu Rawash (HZM: 1, USNM: 14); Bulaq (BM: 1); Cairo (SMF: 1, USNM: 1); Cairo, 20 km S (SMF: 3); Egypt (RMNH: 2, SMF: 1, ZFMK: 1); Egypt (Holotype *thebaica*, MNHN: 1); Gizeh (BM: 8); Gizeh province (SMNS: 2); Jabal Musa (BM: 1); Kafr Dawud (USNM: 5); Karnak (BM: 2); Khayzan (BM: 1); Kom Hamada (USNM: 5); Komo Shim (USNM: 2); Luxor (BM: 1); Lake Moeris (BM: 1); Saqqara (SMF: 9, USNM: 12); Seila (BM: 8); Thebe (BM: 1); Zokila (USNM: 4);

Ethiopia: 58 specimens: Lake Abaya, N coast (BM: 1); Abella (BM: 1); Abessynia (RMNH: 1, SMF: 1); Lake Abiata, E coast (BM: 1); Adi Caie (MZUF: 4); Agordat (MZUF: 7); Azam (Paralectotype or syntype *labiata*, RMNH: 1); Bahr der Giorgis (BM: 2); Lake Chamo, NE of (BM: 3); Didessa river (BM: 1); Didessa Settlement (SMF: 1); Dire Dawa, 3 km S (OSU: 3); Doki river bridge (SMF: 5); Ghibbey valley (BM: 1); Gondar (BM: 1); Harer (Holotype *media*, BM: 1); Lalibela (MZUF: 4); Lake Langanu (BM: 1, SMF: 2); Lake Langanu, W coast (BM: 1); Mabil (BM: 5); Mabil, 10 km W (BM: 3); Mekinissa (CM: 1); Metahara (BM: 1); Saganeiti (MSNG: 1); Torat (MSNM: 3); Woliso (HZM: 1);

Ghana: 1 specimen: Damongo (USNM: 1);

Guinea: 5 specimens: Nyembaro (SMNS: 4, ZFMK: 1);

Israel: 2 specimens: Jericho, a few miles N (USNM: 1); Sulam (HZM: 1);

Kenya: 80 specimens: Athi river (HZM: 1, USNM: 2); Bushwackers Safari Camp (SMF: 2); Diani Beach, 10 km S (SMF: 1); Diani Forest (RMNH: 1); Eldoret (HZM: 1); Garsen (BM: 1); Gedi national park (SMF: 1); Gilgil (HZM: 1); Karen (BM: 1, HZM: 1); Karen, 10 mi SW (USNM: 5); Karen, 10 mi W (USNM: 2); Karibiti (CM: 3); Mount Kenya (BM: 1); Kerio Suk river (BM: 1); Kiambu (HZM: 3); Kilifi (BM: 4, USNM: 1); Kitale (BM: 1, USNM: 2); Kitale, 18 mi SW (USNM: 2); Kivondo Forest (BM: 1); Kivumoni Forest (BM: 1); Konza (RMNH: 1); Kyangili (RMNH: 1); Laikipia (BM: 1); Lodwar, 100 km S (SMNS: 1); near Loldyka Hills (HZM: 1); Machakos district (BM: 1, KMMA: 2); Magadi (HZM: 1); Marsabit (HZM: 1); Molo river (BM: 1, HZM: 1); Mrima Hill (HZM: 1); Murri (BM: 1); Muumandu (RMNH: 1); Nairobi (NMW: 2); Lake Naivasha (HZM: 4, USNM: 4); Ndi (USNM: 1); Ngombeni (USNM: 1); Ngong (USNM: 3); Rongai (HZM: 1); Shimba Hills (KMMA: 1); Shimoni (CM: 1); Mount Suswa (SMF: 1); Taita (BM: 3); Tamkal Camp (BM: 1); Trans-Nzoia (BM: 1); Yatta Escarpment (HZM: 1);

Malawi: 14 specimens: Chiromo (BM: 8, KU: 2); Livingstonia (BM: 1); Nkhota-Kota (KM: 3);

Mali: 1 specimen: Tombouctou (ZMUC: 1);

Morocco: 21 specimens: Chichaoua (USNM: 7); Chichaoua, 20 km S (USNM: 6); Tagonidert (BM: 1); Tiflet, 21 km W (USNM: 7);

Mozambique: 85 specimens: ? (BM: 1); Boror (BM: 1, syntypes *fuliginosa*, BM: 1, RMNH: 1, RMNH: 1); Guja (TM: 1); Jongamo (USNM: 21); Massangena (USNM: 2); Milepa (BM: Muchena, 10 mi E Massamba (USNM: 2); Tete, 2 mi SE (USNM: 12); Tette (BM: 5); Vila Gamito, 10 km N (TM: 10, USNM: 26); Vila Gouveia (USNM: 1);

Namibia: 153 specimens: ? (SMNS: 3); Arnhem (TM: 6); Berseba (USNM: 5); De Valle/Naukluft (ZFMK: 5); Felsenack/Naukluft (ZFMK: 6); Gobabeb (TM: 2, USNM: 9); Grootfontein (ZMH: 1); Kaoko-Otavi (KM: 1); Karibib (BM: 2, KM: 2); Karolinenhof (BM: 2, KM: 3); Keetmanshoop (USNM: 1, ZMH: 1); Klein Windhoek (BM: 2); Marienthal (SMF: 1); Neuhof-Kowas (SMF: 2); Ngweze (KM: 1); Nuitsas (BM: 9, KM: 8); Oas (BM: NMW: 3); Okahandja (ZFMK: 4, ZMH: 1); Ombombo (BM: 2);

Ondangwa (BM: 2, KM: 1); Oshikanga (TM: 4); Otjimbingue (TM: 2); Otjimbojo (ZFMK: 2); Otjitundua (BM: 21, HZM: 1, KM: 11); Outjo (BM: 3, SMNS: 2); Quickborn (TM: 1); Sandfontein (KM: 1); Swartbooisdrif (BM: 1; KM: 3); Ukualuisi (BM: 3, KM: 3); Ukualukasi (BM: 2, KM: 4); Windhoek (BM: 1, KM: 1);

Niger: 5 specimens: I-N-Gall (KMMA: 1); Park W, 2 km E Tapoa (USNM: 1); Zinder (BM: 3);

Nigeria: 32 specimens: Afon (USNM: 2); Farniso (BM: 1); Ibadan (USNM: 1); Karaduwa (USNM: 3); Panisau (USNM: 19); Sokoto, 12 mi N (USNM: 6);

Republic of South Africa: 213 specimens: ? (BM: 1, OSU: 1); Babanango, 15 km NNW (TM: 2); Bishopstowe Cave, Pietermaritzburg (TM: 2); Blyde river canyon national reserve (TM: 1); Bordeaux Farm (TM: 4); Cape (RMNH: 1); Cape of Good Hope (NMW: 1); Cape province (NMW: 1); Damaraland (Syntype *damarensis*, BM: 1); Dordrecht Farm (TM: 2); Duivelskloof (TM: 1); Durban (BM: 1, KBIN: 1); Dzundwini (TM: 1); Eshowe (TM: 1); Fountain Grove, Pretoria (BM: 1, TM: 4); Fountains, Pretoria (USNM: 1); Garies (KM: 1); Goodhouse (KM: 5, TM: 1); Graaff Reinet, 23 mi SE (USNM: 1); Greefswald Farm (TM: 3); Grootvadersbosch (TM: 5); Hectorspruit (TM: 8); Hillaries, nr Durban (HZM: 6); Hluhluwe (ZFMK: 3); Huwi Private Nature Reserve (CM: 1; TM: 6); Ingwavuma (TM: 1); Insuzi river (BM: 8); Itala Game Reserve (TM: 2); Kaap river (BM: 1); Keikamspoort Farm (TM: 3); Kersbos Farm (TM: 8); Kleinpoort Grahamstown (TM: 10); Klipfontein (BM: 2); Komatipoort (TM: 1); Kruger Park (TM: 2); Lamberts Bay (KM: 3); Letaba Ranch (TM: 9); Levuvhu Hippopool (TM: 1); Leydsdorp (TM: 3); Loskopdam Nature Reserve (TM: 6); Louisvale (BM: 4, KM: 1); Malensan Singwetse nature reserve (TM: 4); Malvern (BM: 1, TM: 2); Mayirli, Durban (HZM: 1); Matupa Cave, Pretoriuskop area, KNP (TM: 1); Messina (TM: 1); Moketsi (TM: 4); Mooigenoeg Farm (TM: 5); Mooiplaas Farm (TM: 1); Mutale river (TM: 1); Natal (TM: 3); Nduму Game Reserve (TM: 2); Olifantspoort Farm (TM: 2); Ottershoop (USNM: 1); Pietermaritzburg (SMF: 3); Port Alfred (NMW: 1); Port Elisabeth (NMW: 1); Port Nolloth, 15 mile inland (KM: 1); Port St Johns (BM: 2); Port St Johns district (TM: 5); Potchefstroom (BM: 2); Pretoria (TM: 1); Punda Mana Camp, KNP (TM: 1); Rochdale Farm (TM: 1); Rooikrans Rustenburg (TM: 5); Rooikrans Waterberg (TM: 4); Sabi Riv. (BM: 2); Ten Bosch Estates (TM: 5); Thabazimbi, 16 mi SE (USNM: 10); Transvaal (BM: 1); Welgevonden Farm (TM: 5); Zebediela, Howell Davies Cave (TM: 1);

Rwanda: 16 specimens: Akagera Park (KBIN: 10); Butare (KBIN: 2); Kidaho (KMMA: 2); Muhabura (KMMA: 1); Rukira (KMMA: 1);

Saudi Arabia: 20 specimens: Buraiman (BM: 1); Dir'iyah (Holotype and paratype *najdiya*, SMF: 2); Jeddah (BM: 4); Jizan (BM: 2); near Khalla (HZM: 7); Najran (BM: 3); Sabiya (BM: 1);

Senegal: 22 specimens: ? (BM: 1); Badi (MHNG: 1); Bandia (ZFMK: 3); Diattacounda (ZFMK: 7); Koular (MNHN: 1); M'Bour (MHNG: 1); Saboya (MNHN: 8);

Sierra Leone: 2 specimens: Freetown, Hillstation (BM: 1); Mongberi (BM: 1);

Somalia: 29 specimens: Bender Cassim (MSNM: 4); Callis (MZUF: 8); Candala (MSNM: 1); El-Bur (MSNM: 1); Hargeisa (BM: 2); Mijertein (MSNM: 1); Ruspoli (BM: 1); Somalia (MNHN: 1); Somalia (Paratype *revoilii*, MNHN: 2); Upper Sheikh (BM: 7, Holotype *brockmani*, BM: 1);

South Yemen: 25 specimens: Aden (BM: 5); Dhala, 90 mi N of Aden (BM: 1); Lahej (BM: 4); Myba (BM: 4); Myba (Holotype *adana*, BM: 1); Sheikh Othman (HZM: 9); Wadi Sawawin (HZM: 1);

Sudan: 49 specimens: En Nabbaka (NMW: 1); Erkovit (BM: 3); Gallabat (BM: 2); Imatong (SMNS: 2, ZMUC: 1); Jebel Toto (SMF: 1); Khartoum of Sennaar (NMW: 2); Kordofan (SMF: 3); Loa (ZMUC: 2); Lobira (ZMUC: 3); Luem (ZMUC: 1); Madial (ZMUC: 1); Nagishot (ZMUC: 1); Sennaar (NMW: 1); Torit (ZMUC: 15); Torit, 80 km E (SMNS: 1); Mount Wagga (BM: 9);

Swaziland: 2 specimens: Balegane (BM: 1); Big Bend (TM: 1);

Tanzania: 281 specimens: Amani (TM: 1); Arusha (SMF: 2); Bagamoyo (RMNH: 20); Banagi Hill (BM: 2); Bologonja (KBIN: 1); Bugagi, Zanzibar (BM: 1); Bungi, Zanzibar (BM: 2); Dar es Salaam (KMMA: 2, ZFMK: 3, ZMH: 1); Grummetti (KBIN: 1); Gulwe Station (BM: 2); Handajega (KBIN: 4); Ikungi (BM: 1); Iraku (SMF: 10); Itende (BM: 4); Kampi ya Mawe (BM: 4); Karugu (BM: 4); Kilondoni (BM: 4); Kilosa (BM: 2, HZM: 4, KM: 2, USNM: 1); Kilwa (HZM: 9); Kisarawe (BM: 2, USNM: 5); Kizimkazi, Zanzibar (BM: 3); Lembeni district (ZFMK: 1); Likawage (BM: 1); Lipumba (SMND: 1); Liwale (BM: 2, HZM: 17, SMF: 1); Madaba (SMF: 1); Mangangachi (BM: 1); Lake Manyara (BM: 2); Mayjombo (BM: 1); Mbemba (HZM: 1, SMF: 2); Mbeni, Zanzibar (BM: 3); Mount Meru (BM: 2); Mikindani (SMF: 39, ZFMK: 11); Mikumi (KMMA: 1); Mikumi-Morogoro Road (HZM: 2); Minaki, St Andrews College (KU: 1); Morogoro (BM: 2); Mto-wa-Mbo (BM: 2); Muhange (BM: 1); Muheza (ZMUC: 16); Musabi (KBIN: 2); Mwaya (BM: 1); Nachingwea (HZM: 1); Nakibou (BM: 1); Namumbulu (BM: 4); Ndara Hills (BM: 3); Ngelehek (KBIN: 1); Noamania (BM: 1); Ol Donyo Sambu (SMF: 7); Pugu Forest (ZMUC: 10); Rondo

Flat (KMMA: 1); Sagaya (BM: 1); Same (SMNS: 1); Seronera (BM: 1); Soga (ZFMK: 3); Songomano (BM: 2); Southern province (BM: 3); Suna (BM: 1); Takaungu (BM: 1); Tandamanga (BM: 7); Tanganika (BM: 1); Taveta (BM: 5); Tendaguro (BM: 2); Tengeru (BM: 1); Ulanga (HBM: 2); Unyanganyi (MCZ: 7); Zanzibar (BM: 1); Zinga (BM: 2);

Uganda: 13 specimens: Amiel (BM: 3); Bulaganya, 3 mi S (BM: 1); Burisifwe Gombolola (BM: 1); Kama Tin Mine (BM: 1); Kampala (BM: 1); Karamoja district, S of (BM: 1); Mbale (BM: 3); Moruita (BM: 1); Moyo (BM: 1);

Democratic Republic of Congo: 29 specimens: Albert Park (KBIN: 6); Kakanda (BM: 1, KMMA: 1); Kakyelo (KMMA: 3); Kapolowe (KMMA: 4, SMF: 2); Kasenga Road, km 36 (KMMA: 1); Kasenga Road, km 67 (KMMA: 1); Kaswabilenga (KBIN: 1); Kateke KBIN: 1; Lubudi (SMF: 1); Mahagi Port (BM: 1); Mukwen (KMMA: 1); Ndwa (KMMA: 1); Mount Ne (BM: 1, MHNG: 1); Tantara (MHNG: 1); Tungu (KBIN: 1);

Zambia: 80 specimens: Balovale (BM: 1, KM: 1); Chibembe Pontoon, 1/2 mi S (BM: 5); Chikundulu river (BM: 1); Chilanga (HBM: 1); Chinzombo (SMF: 2); Chipata (KM: 5); Chisorwe, Luano valley (BM: 1); Dzala Cave, 14 mi NE of Lusaka (BM: 1); Kafue river (HBM: 1); Kasama (HBM: 3); Luambe Game Camp (HBM: 1); Luangwa (HBM: 1); Luangwa Myamadzi (HBM: 2); Lunga Pontoon (BM: 2, KM: 2); Lunzi river (BM: 1); Lusaka (HBM: 3); Lusingazi Game Camp (BM: 1); Mansa (HBM: 1); Masali Mine (BM: 5); Mbala (HBM: 7, KM: 1); Missale Old Mine (BM: 1, HBM: 6); Monze (BM: 4, KM: 5); Mporokuso-Mweruwanitipa (HBM: 3); N'Dola (BM: 3); Ndulumina (HBM: 1); Ngwerere Cave (SMF: 1); Petauke (BM: 1, KM: 1); Solwezi Boma (BM: 3); Wenela (BM: 2);

Zimbabwe: 80 specimens: Bindura (HBM: 1); Bulawayo (USNM: 1); Chipangayi river (HBM: 1); Chirinda Forest (USNM: 1); Chirisa Cave (TM: 1); Falls Road (TM: 16); Filabusi, 14 mi W (HBM: 3); Gourlay Block (BM: 1); Gwanda (BM: 2); Haroni-Lusitu confluence (HBM: 1); Mount Kapovka (BM: 1); Kyle Game Reserve (USNM: 12); Mazoe (BM: 9); Lake Mcllwaine (HBM: 2); Odzi district (BM: 1); Porte-Angwa Junction (HBM: 1); Rhodos Inyanga Nature Park (TM: 1); Between Rusape and Inyanga (HBM: 1); Rusito Forest (TM: 1); Mount Selinda (USNM: 1); Sinoia (BM: 1); Umtali district (BM: 1);

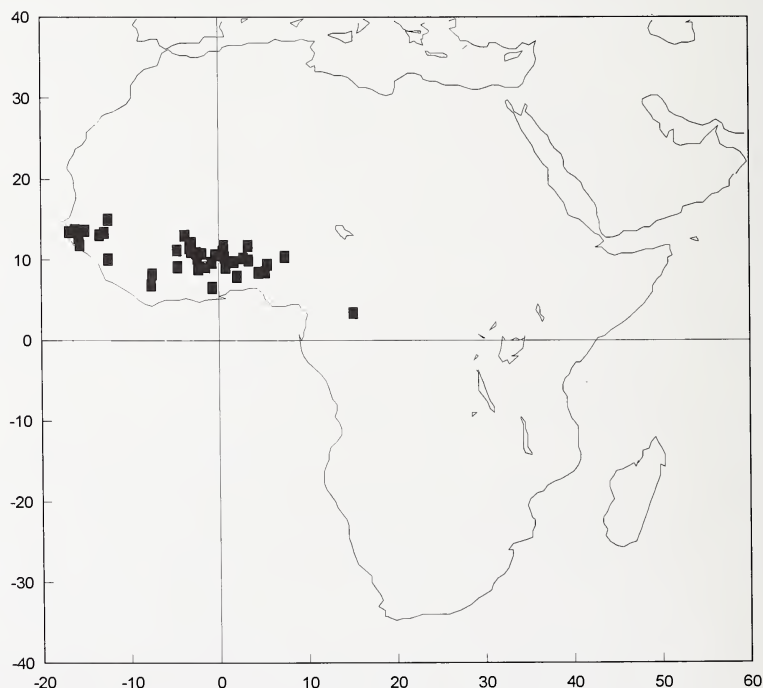


Fig. 9: Distribution map of *Nycteris gambiensis* (K. Andersen, 1912).

Umtali Old Mine (TM: 14); Vumba Road (HZM: 2); Wallaby Claims, Filabusi (BM: 1); Zambesi-Cherowe Junction (HZM: 2); Zambesidal, Matabeleland (SMNS: 1);

Unknown country: 20 specimens: ? (BM: 3, KBIN: 1, RMNH: 2, USNM: 1); ? (Holotype *capensis*, BM: 1); Afrique du Sud (KBIN: 1); E Africa (BM: 1, NMW: 1); Goho Hills (TM: 1); Jebel Harir (BM: 2); Matubatuba, Zululand (TM: 1); N Africa (SMNS: 1); Nubia (SMF: 1); Red Sea (RMNH: 1); Red Sea (*geoffroyi*) (RMNH: 1); Shupanga (BM: 1);

Nycteris gambiensis (K. Andersen, 1912)

Petalia gambiensis K. Andersen, 1912. Ann. Mag. nat. Hist. (8) 10: 548. — Type locality: Dialocote, Senegal.

The distribution area (see figure 9) of *N. gambiensis* is more limited than this of *N. thebaica*. It only occurs in the West African savannas, where both species are found sympatrically in a number of localities.

The colour of *N. gambiensis* is less variable than that of *N. thebaica*, varying between dark beige and dark brown (see also Rosevear 1965).

Our measurements of the forearm length (35.1 to 44.0 mm, see also table 9) indicate much lower values than those given in the literature: Rosevear (1965) and Hayman & Hill (1971) mention 39 to 43 mm, Eisentraut & Knorr (1957) 40 to 42.5 mm and Monard (1939) 40 to 43 mm. This is also true for the greatest length of the skull: (Gls — 16.6 to 18.5 mm) as opposed to 18 to 19 mm (Rosevear 1965) and 18 to 18.9 mm (Eisentraut & Knorr 1957).

The very large overlap between the measurements of *N. gambiensis* and *N. thebaica* from West Africa (see tables 4 and 9), makes it sometimes difficult to separate these species. Some authors (e.g., Kock 1969 and Koopman 1975) consider *gambiensis* as a synonym of *N. thebaica*, because of the even larger overlap between *N. gambiensis* and northeast African *N. thebaica* (table 5). Koopman (1982) reconsiders this and lists *gambiensis* again as a separate species. However, the clear multivariate

Table 9: Measurements of *N. gambiensis* (in mm).

Var	Holotype	Mean	SD	Min	Max	# ind
Gls	17.7	17.58	0.36	16.6	18.5	321
Cbl	15.8	15.40	0.36	14.2	16.5	315
Sw	6.9	7.22	0.26	6.4	8.0	335
Zyg	10.1	10.19	0.29	9.2	11.0	290
Mast	8.2	8.49	0.29	7.1	9.2	323
Brain	8.0	7.88	0.25	7.1	8.7	330
c-m ³	5.4	5.66	0.19	5.2	6.2	376
c-c	4.5	4.23	0.17	3.5	4.7	355
m ³ -m ³	6.4	6.41	0.20	5.8	6.9	353
Mand	11.5	11.46	0.29	10.4	12.7	366
c-m ₃	6.0	6.20	0.23	4.6	7.0	370
Fa	37.9	40.15	1.44	35.1	44.0	458
Meta 3	28.3	29.24	1.26	26.4	32.1	92
3 ph 1	19.0	21.41	0.94	19.0	23.6	90
3 ph 2	21.9	21.17	1.19	17.7	23.8	85
Meta 4	32.4	31.45	1.19	28.7	34.0	91
Meta 5	32.4	32.15	1.22	29.8	35.3	90
5 ph 1	11.3	11.60	0.65	9.9	13.1	90
5 ph 2	10.8	10.50	0.78	8.4	12.3	89
Tib	18.7	19.87	0.99	17.0	22.3	90

separation in West Africa confirms that *N. thebaica* and *N. gambiensis* are both valid species. The significantly lower values for measurements of *N. thebaica* in northeast Africa might result from the absence of a second closely allied species. Because of this, *N. thebaica* can occupy a larger number of "niches" in this area and consequently achieve a greater morphological range.

Literature citations

Nycteris gambiensis (K. Andersen, 1912)

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Nycteris thebaica gambiensis (K. Andersen, 1912)

De Beaux (1923): Gambia (as *Petalia*) — Ingoldby (1929): Ghana: Elima, Sekondi — Sanborn (1936): Senegal: Kedougou — Cansdale (1948): Ghana — Aellen (1956): Senegal: Badi — Booth (1959): Ghana: Accra Plain.

Specimens examined

Nycteris gambiensis (K. Andersen, 1912)

Benin: 72 specimens: Bimbereke (USNM: 26); Guene (USNM: 29); Nikki (USNM: 1); Soubroukou (USNM: 8); Zizonkane (USNM: 8);

Burkina Faso: 143 specimens: Djipologo (USNM: 18); Founzan (USNM: 22); Konankira (USNM: 18); Koutoura, 5 km SW (USNM: 6); Natiaboani (USNM: 4); Orodara, 27 km ENE (USNM: 4); Oulo (USNM: 71);

Cameroon: 1 specimen: near Yokadouma (1: MNHN);

Gambia: 26 specimens: ? (BM: 1); Banjul, 8 mi W (USNM: 1) Kudang (USNM: 3); Kuntaur, 10 mi SE (BM: 2); Makka (BM: 1); Toniataba (USNM: 18);

Ghana: 136 specimens: Bangweli Camp, Mole National Park (BM: 1); Bangwon (USNM: 20); Damongo (USNM: 9); Gambaga (USNM: 3); Nabogo (USNM: 1); Nkawaw (ROM: 1); Pirisi (USNM: 71); Pulima (USNM: 24); Sakpa (USNM: 4); Samole (BM: 1); Sawla, 15 mi E (BM: 1);

Guinea: 12 specimens: Kolente (SMF: 1, ZFMK: 2); Nyembaro (SMF: 2, SMNS: 4); Tahire (SMNS: 3);

Guinea-Bissau: 5 specimens: Ponta Robalo (KMMA: 2, MHNG: 3);

Ivory Coast: 27 specimens: Kong (USNM: 24); Tyenko (USNM: 3);

Nigeria: 46 specimens: Afon (USNM: 36); Alabe (BM: 1); Kaduna (BM: 1); Kudu (USNM: 8);

Senegal: 79 specimens: Bakel (BM: 1); Dialocote (USNM: 58, Holotype *gambiensis*, BM: 1); Diattacounda (ZFMK: 2); Gamon (USNM: 2); Koular (MNHN: 4); Saboya (MNHN: 11);

Togo: 12 specimens: Baoule (KMMA: 1); Binaparba (KMMA: 1); Dapango (USNM: 6); Namoundjoga (KMMA: 4).

Nycteris vinsoni Dalquest, 1965

Nycteris vinsoni Dalquest, 1965. J. Mamm., 46 (2): 254–255. — Type locality: Zinave, Mozambique.

Only very few data are available for this species, which might be a result of its “fairly recent” description. The literature only provides information about its type locality. Only Kock (1969) and Koopman (1975) discuss the status of this species. Kock gives an extensive analysis of the two known specimens, although he did not examine them, but based his conclusions on observations by W. W. Dalquest, J. K. Jones and C. K. Phillips (see Kock 1969: 96). Table 10 gives the measurements for *N. vinsoni* (after Kock 1969: 97). Besides these measurements, Kock also comments on a number of morphological characters, from which he concludes that *N. vinsoni* is a member of the *N. macrotis* group and more precisely a synonym of *N. macrotis luteola*.

The presence of bicuspid upper incisors in the paratype excludes affinity with the *N. hispida* group. According to Kock, the most important character is the size and the position of the second lower premolar (p_4). In both specimens, this tooth is small and pressed toward the lingual side of the toothrow; this would exclude relationship with both the *N. arge* group and the *N. thebaica* group. The lingual position of p_4 suggests an affinity with the *N. macrotis* group. Koopman (1975) does not agree with this decision, because of the extreme variability of the position of p_4 in the toothrow. Therefore, this character is unlikely to have the decisive value claimed by Kock. Our observations, especially on material of *N. thebaica*, confirm Koopman’s finding that the position of p_4 in the toothrow is very variable, even in animals from the same locality. Therefore, we cannot exclude the *N. thebaica* group.

Kock also mentions that one of the tragi of the holotype is very badly preserved, whereas the other one is probably pyriform. This then would indicate a relationship with the *N. thebaica* group. However, Kock immediately rejected this idea because of the above mentioned thesis on the position of the lower premolar. On the contrary, Koopman (1975) judges that the pyriform tragus justifies the inclusion of *vinsoni* in the *N. thebaica* group.

Table 10: Comparison of the measurements of *N. vinsoni* (after Kock, 1969: W. D. = measurements by Walter W. Dalquest, K. J. = measurements by J. Knox Jones Jr.) with *N. macrotis* and *N. thebaica*.

Var	<u><i>N. macrotis</i></u>			<u><i>N. vinsoni</i></u>			<u><i>N. thebaica</i></u>		
	mean	min	max	holotype W.D.	para K.J.		mean	min	max
Ear	----	----	----	22.0	----	22.0	----	----	----
Fa	48.19	40.0	54.1	50.6	----	----	44.52	34.2	50.7
Tib	22.68	18.1	26.0	----	24.8	----	21.99	16.8	26.5
					25.8				
Gls	20.52	19.0	22.2	22.0	21.9	22.1	19.12	17.0	21.2
Cbl	17.98	16.4	19.6	----	19.5	19.5	16.90	15.1	18.7
Mast	9.41	7.7	10.3	----	9.9	9.4	8.90	6.1	10.1
Brain	8.88	7.9	10.0	10.0	9.5	9.2	8.62	7.5	9.6
Zyg	12.52	10.4	13.8	13.3	13.3	13.5	11.12	9.8	12.9
c-c	5.66	4.5	6.5	5.8	----	5.4	4.65	3.7	6.0
m'-m ¹	8.13	7.1	9.1	8.8	9.1	8.6	7.04	4.7	8.5
c-m ³	6.99	5.6	7.9	7.8	7.8	7.6	6.26	5.0	7.5
Mand	14.02	11.8	15.4	15.0	----	15.0	12.52	10.6	14.4
c-m ₃	7.85	6.3	8.9	8.4	----	8.3	6.87	6.0	8.4

The ear length (not measured in this study) excludes, according to Kock, the *N. thebaica* group. As all other measurements also exclude *woodi* and *parisii* from the *N. macrotis* group, Kock concludes that *N. vinsoni* is a synonym of *N. macrotis luteola*.

Besides the measurements of *N. vinsoni*, table 10 also includes measurements of both *N. macrotis* and *N. thebaica*. The table shows that some measurements of both the holotype and the paratype of *N. vinsoni* are larger than those for *N. thebaica*: Gl, Cbl, Zyg, m^3-m^3 , $c-m^3$ and Mand. All measurements fall within the range of *N. macrotis*. The width of the braincase (Brain) and the width across the upper molars (m^3-m^3) of the holotype are as large as the maximum for *N. macrotis*.

Two very large specimens of *N. thebaica* from East Africa scored very aberrantly in the multivariate analyses (see figure 6). These were collected at the St. Andrews college in Minaki, Tanzania (KU 89943) and at Garsen, Kenya (BM 75.2446 — not explicitly referred to in this paper). However, their dimensions are considerably smaller than those given by Kock, e.g., Gl: Minaki = 20.5 mm and Garsen = 19.5 mm, Cbl: Minaki = 17.5 mm and Garsen = 17.2 mm, Fa: Minaki = 46.1 mm and Garsen = 44.7 mm. A comparison with *N. thebaica* from Mozambique, the country where the type specimens of *vinsoni* originated from, shows that the latter have a larger forearm than the former (48.2 mm for BM 8.4.3.94 from Tete). Additionally, the length of the skull (Gl = 20.6 mm and Cbl = 17.9 mm for BM 8.4.3.94 from Tete, and Gl = 20.2 mm and Cbl = 17.4 mm for USNM 365174 from Vila Gamito) is even 2 mm smaller.

The combination of the morphological characters and the metrical data allow the conclusion that *N. vinsoni* must be considered as a valid species of the *N. thebaica* group. Further data should test this conclusion.

Recently, however, Koopman (1992) reexamined the tragus of the holotype, and concluded it to be semilunate instead of pyriform. Therefore, he is inclined to recognize *vinsoni* provisionally as a subspecies of *N. macrotis*.

Literature citations

Nycteris vinsoni Dalquest, 1965

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Zusammenfassung

In dieser Arbeit wird die Systematik der afrikanischen *Nycteris thebaica*-Gruppe diskutiert. Aufgrund multi- und univariater statistischer Untersuchungen werden zwei Arten dieser

Gruppe beibehalten: *N. thebaica*, die fast auf dem ganzen afrikanischen Kontinent und der arabischen Halbinsel vorkommt, und *N. gambiensis*, die auf Westafrika beschränkt ist. Der Artstatus von *N. vinsoni* wird nach Literaturangaben bestätigt. Literaturdaten, Maße und Listen des untersuchten Materials werden für jede Art angegeben. Leider reicht selbst das für diese Studie vorliegende umfangreiche Material nicht aus, den Status von z. B. *brockmani* und *damarensis* endgültig zu bestimmen, die z. Z. als Synonyme zu *N. thebaica* gelten.

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