

Original article

A review of the southern African ‘non-spitting’ cobras (Serpentes: Elapidae: *Naja*)

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Abstract.—We analysed the systematics of the ‘non-spitting’ cobras of southern Africa, paying particular attention to the *Naja annulifera* complex. Multivariate morphometric analyses demonstrate that the taxa *annulifera* and *anchietae* are consistently distinct and homogenous over their respective ranges, and their distributions overlap in western Zimbabwe, with only limited intergradation. Sequences of the mitochondrial cytochrome *b* gene indicate that they are separated by considerable genetic distances. These results suggest that these two taxa are morphologically and genetically distinct evolutionary lineages, and should be considered as two separate evolutionary species, *N. annulifera* and *N. anchietae*.

Key words.—*Naja*, taxonomy, multivariate morphometrics, phylogeny, zoogeography, Africa.

The three cobras considered here have had a chequered history. The Cape Cobra was described as *Coluber niveus* by Linnaeus in 1758, but was redescribed as *Naja flava* by Merrem in 1820, *N. gutturalis* by Andrew Smith in 1838 and *N. intermixta* by Duméril & Bibron in 1854. Subsequently Smith (1842), Peters (1870) and other authors assigned Cape Cobras to *N. haje* of North Africa, while Jan (1863) used *N. haje* var. *capensis*. Boulenger (1887) recognised the distinctness of the species, but used the name *Naia flava*. Although Andersson (1899) examined the type in the Royal Museum in Stockholm and stated that the correct name for this species was *Naia nivea* (L.), subsequent authors continued to use *Naja flava* until Flower (1929) again used *Naja nivea*, which then gradually came into general use.

Naja annulifera was described as a variety of *N. haje* by Peters in 1854, but was not recognised by Boulenger (1896), however he only

had typical *N. haje* from Egypt and Morocco at his disposal. This taxon was revived as a subspecies by Broadley (1968b) and subsequently recognised as an evolutionary species (Broadley 1995).

Naja anchietae was described by Bocage in 1879, and because it had only 15 or 17 scale rows on the neck, Boulenger (1896) grouped it with the ‘hoodless cobras’ *Naja goldii* and *Naja guentheri*. The latter two species were subsequently placed in the genus *Pseudohaje* Günther by Bogert (1942), while *anchietae* was treated as a subspecies of *N. haje* (Mertens 1937; Bogert 1943), and later as a subspecies of *N. annulifera* (Broadley 1995). Angel (1921) erected the name *Naia Anchietae* var. *barotseensis* for a specimen from western Zambia with only 15 scale rows at midbody.

Following records of sympatry between *N. a. annulifera* and *N. a. anchietae* at Livingstone, Zambia (Haagner *et al.* 2000) and in the

Hwange District of Zimbabwe (Broadley unpubl.), it was decided to investigate the status of these taxa, using the parapatric species *N. nivea* for comparative purposes. Until now, the distinction between *N. a. annulifera* and *N. a. anchietae* has been based almost entirely on midbody and neck scale counts. Here, we use multivariate analysis of multiple morphological characters and comparative sequencing of a part of the mitochondrial gene for cytochrome *b* to investigate the population systematics of the *N. annulifera* complex and, specifically, the contact zone between *N. a. annulifera* and *N. a. anchietae*.

MATERIALS AND METHODS

We used a three-pronged approach to the question of the interrelationships between *N. a. annulifera* and *N. a. anchietae*: the analysis of patterns of variation in individual morphological characters; multivariate morphometrics, to elucidate patterns of variation in generalised phenotype; and comparative mitochondrial DNA sequencing to determine whether there is evidence of independent phylogenetic lineages within these snakes.

The morphological analysis was based on most of the material available in museums in southern Africa, Europe and the United States, examined by the first author over a period of 35 years. These specimens are listed in an appendix, together with relevant literature records. Institutional acronyms follow Leviton *et al.* (1985) and Leviton & Gibbs (1988), except that NMWN is used for the National Museum of Namibia (formerly the State Museum, SMWN), TM is used for the Transvaal Museum (= Northern Flagship Institution, Pretoria), while AJL = A.J. Lambiris Collection, Hillcrest, KwaZulu-Natal; EBM = Estação de Biologia Marítima, Inhaca Island, Mozambique; HF = Helmut Finkeldey Collection, Windhoek (now incorporated into

NMWN); JDV = J.D. Visser Collection, Jeffreys Bay; JPT = J.P. Tello Collection (? destroyed in Mozambique); PM = Peterhouse Museum, Marondera, Zimbabwe. The specimens examined in the Museu Bocage, Lisbon (MBL), were subsequently destroyed by fire, while many uncatalogued specimens in the National Museum of Namibia (denoted in parentheses by numbers with a "B" prefix) were lost when their alcohol drum was stolen.

In order to investigate the nature of the contact zone between *N. a. annulifera* and *N. a. anchietae*, we used Canonical Variates Analysis (CVA), one of the most widely used multivariate techniques in venomous snake systematics (e.g., Slowinski & Wüster 2000; Wüster *et al.*, 1995), which maximises the separation between groups relative to the within-group variance, taking into account the within-group correlation between characters (Thorpe 1976, 1980). Since the inclusion of insignificant characters can reduce the power of a multivariate analysis (Thorpe 1985), we first used analysis of variance (ANOVA) to determine which characters display significant between-group variation.

Both ANOVA and CVA require specimens to be grouped *a priori* into operational taxonomic units (OTUs). When constructing OTUs, it is important to avoid forming groups of specimens that contain intergrades or that include specimens mis-assigned to the "wrong" group. Moreover, simply grouping all putative *N. a. annulifera* and all putative *N. a. anchietae* into a single OTU each would be circular, as the resulting CVA would not be able to represent any possible clinal variation, but would instead provide the artificial impression of categorically distinct taxa. Our approach was therefore to establish the discriminant function of the CVA using two OTUs, consisting of unambiguous *N. a. anchietae* and *N. a. annulifera* populations, and allow the analysis to place the specimens from intervening localities, particularly the

Table 1. Specimens used for DNA analysis and their localities.

| Species | Genbank Accession no. | Locality, origin and voucher (if available) | Sample size |
|---------------------------|-----------------------|---|-------------|
| <i>Naja kaouthia</i> | AF217835 | Burma: Ayeyarwady Div.; CAS 206602 | 1 |
| <i>Naja nigricollis</i> | AF399746 | Ghana - Liverpool School of Tropical Medicine, live collection | 1 |
| <i>Naja nivea</i> | AF217827 | Unknown, no voucher (Slowinski & Keogh 2000) | 1 |
| <i>Naja haje</i> | AY463032 | Morocco - Liverpool School of Tropical Medicine, live collection | 1 |
| <i>Naja haje</i> | AY463031 | Egypt - Liverpool School of Tropical Medicine and Latoxan 98110004 and 98140015, live collections | 3 |
| <i>Naja haje</i> | AY463030 | Kenya: Athi River and Naivasha - BioKen, live collection nos. BK 10043 and 10197 | 2 |
| <i>Naja a. annulifera</i> | AY463028 | South Africa: Mpumalanga Province: Phalaborwa | 1 |
| <i>Naja a. annulifera</i> | AY463029 | Zimbabwe: Bulawayo. NMZB 16066 | 1 |
| <i>Naja a. anchietae</i> | AY463027 | Namibia: Okahandja | 1 |
| <i>Naja a. anchietae</i> | AY463026 | Namibia: Caprivi Strip: Silumbi | 1 |

putative contact zone, without any *a priori* assignment to any group.

Previous studies (Broadley 1983, 1995) placed the contact zone between *N. a. annulifera* and *N. a. anchietae* in western Zimbabwe, eastern Botswana and southern Zambia. Consequently, all populations west of 20° E were considered as unambiguous *N. a. anchietae* and assigned to OTU 1, and all populations east of 30° E, as well as those from North West Province, South Africa, from 27-30° E, were considered as unambiguous *N. a. annulifera* and assigned to OTU 2. Specimens from the intervening area from 20-30° E, containing the contact zone between *N. a. annulifera* and *N. a. anchietae*, were grouped into OTU 3.

We used 2-way analysis of variance (2-way ANOVA) of OTUs 1 and 2, using locality and sex as the grouping variables, to identify characters that display significant geographic and sexual variation between “typical” populations of *N. a. annulifera* and *N. a. anchietae*. Specimens with missing data were excluded from all multivariate analyses. Characters that did not show significant variation between the two groups were not considered in further analyses.

We then used CVA of the remaining characters to investigate the nature of the contact zone between *N. a. annulifera* and *N. a. anchietae*. The discriminant function was established using solely OTUs 1 and 2. Specimens from the OTU 3, comprising the likely contact zone, were entered into the discriminant function *a posteriori*. Analyses were initially carried out separately for males and females, and then for both jointly. Since sexual dimorphism did not affect the patterns revealed by the joint analysis, we present only the results of the combined analysis of both sexes in this paper.

In addition to morphological data, we obtained mitochondrial DNA sequence data from several specimens of the *Naja haje* complex from different parts of its distribution, as well as related species for outgroup comparison (Table 1). We amplified and sequenced a 758 b.p. fragment of the mitochondrial cytochrome *b* gene. All laboratory procedures followed the protocols of Wüster & Broadley (2003). For phylogenetic analysis, we used existing sequences from *Naja nigricollis* and *Naja kaouthia* (GenBank accession nos. AF399746 and AF217835, respectively) as outgroups for the rooting of all trees. A sequence of *N. nivea* (AF 217827), shown to be the closest relative

of the *N. haje* complex in preliminary analyses, was included but not assigned to the outgroup. All phylogenetic analyses were carried out using the program PAUP*4.0b10 (Swofford 2002), unless stated otherwise. Maximum parsimony analysis (MP) was carried out using the exhaustive search algorithm of PAUP. Non-parametric bootstrapping (Felsenstein 1985) involved 10,000 pseudoreplicates and branch-and-bound searching. Branch support (Bremer 1994) was calculated using the reverse-constraint option in PAUP*. In order to calculate genetic distances between the different haplotypes of the *N. haje-annulifera* complex, we identified the most appropriate model of sequence evolution for our data using the software Modeltest (Posada & Crandall 1998), and then calculated between-haplotype genetic distances using that model in PAUP*.

RESULTS AND DISCUSSION

CHARACTER ANALYSIS

1. Shape of rostral shield: all three forms have the rostral about as broad as deep, but *N. nivea* has a rounded snout, *N. annulifera* a more pointed one, while in adult *N. anchietae* the rostral becomes even more prominent (Figs. 1 & 2).

2. Head shields: the *N. haje* complex is usually distinguished from *N. nivea* (Fig. 1) by the presence of subocular scales separating the third and fourth supralabials from the eye (Fig. 2). However, both labials entered the eye in *N. anchietae* MBL 1988 from Galanga (Broadley 1983) and one (usually third) or two labials enter the eye in several specimens of *N. annulifera* and *N. anchietae* examined subsequently. The posterior chin shields are normally widely separated in all three forms, temporal patterns are similar and the number of nuchals and cuneates is variable.

3. Dorsal scale rows: *Naja nivea* usually has 21-23 (rarely 19) scale rows on the neck 21 (rarely 19 or 23) at midbody and 15 (rarely 13) before the vent. *Naja annulifera* has 19 (rarely 17 or 21) rows on the neck and at midbody, reducing to 13 or 15 before the vent. *Naja anchietae* has 15 or 17 rows on the neck, 17 (rarely 15) at midbody, reducing to 13 (rarely 11) before the vent. So *N. nivea* tends to have an increase in the number of scale rows on the neck, in *N. annulifera* the counts on the neck and at midbody are the same, while in *N. anchi-*

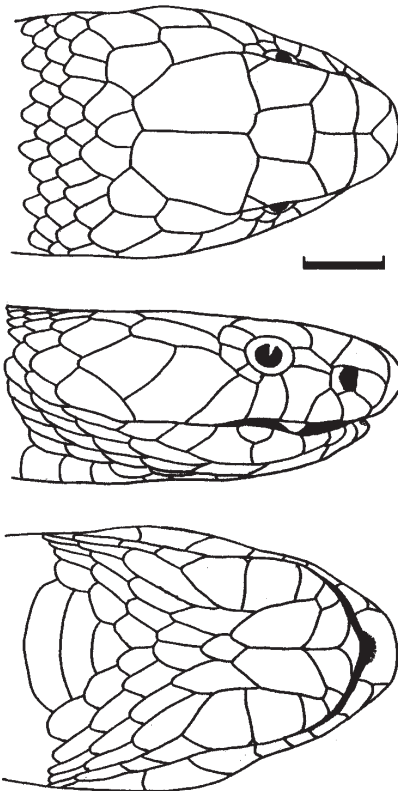


Figure 1. Dorsal, lateral and ventral views of the head of *Naja nivea* (NMZB-UM 9525 - 65 km NW of Lephepe, Botswana). The line indicates 10 mm to scale.

etae there is often a decrease in the number of scale rows on the neck and the scales are consequently larger in size.

4. Throat banding pattern: A single black throat band or ring is clearly defined in juveniles. With age, it is completely lost in *N. nivea*, while in *N. annulifera* and *N. anchietae* it becomes dark brown, but may be obscured by general ventral darkening. In *N. nivea*, the black band is centred on ventral 14 and usually covers v 6-18. In *N. annulifera*, the dark band is displaced posteriorly and usually covers at

least ventrals 14-19, while in *N. anchietae* it moves slightly further back and usually covers at least v 13-22.

MULTIVARIATE ANALYSIS

The 2-way ANOVAs indicated nine characters that showed significant between-group geographic variation. These were: 1. Dorsal scale rows around neck; 2. Difference between dorsal scale rows around neck and around mid-body; 3. Dorsal scale rows at vent; 4. Ventral scales; 5. Subcaudal scales; 6. Infralabials; 7.

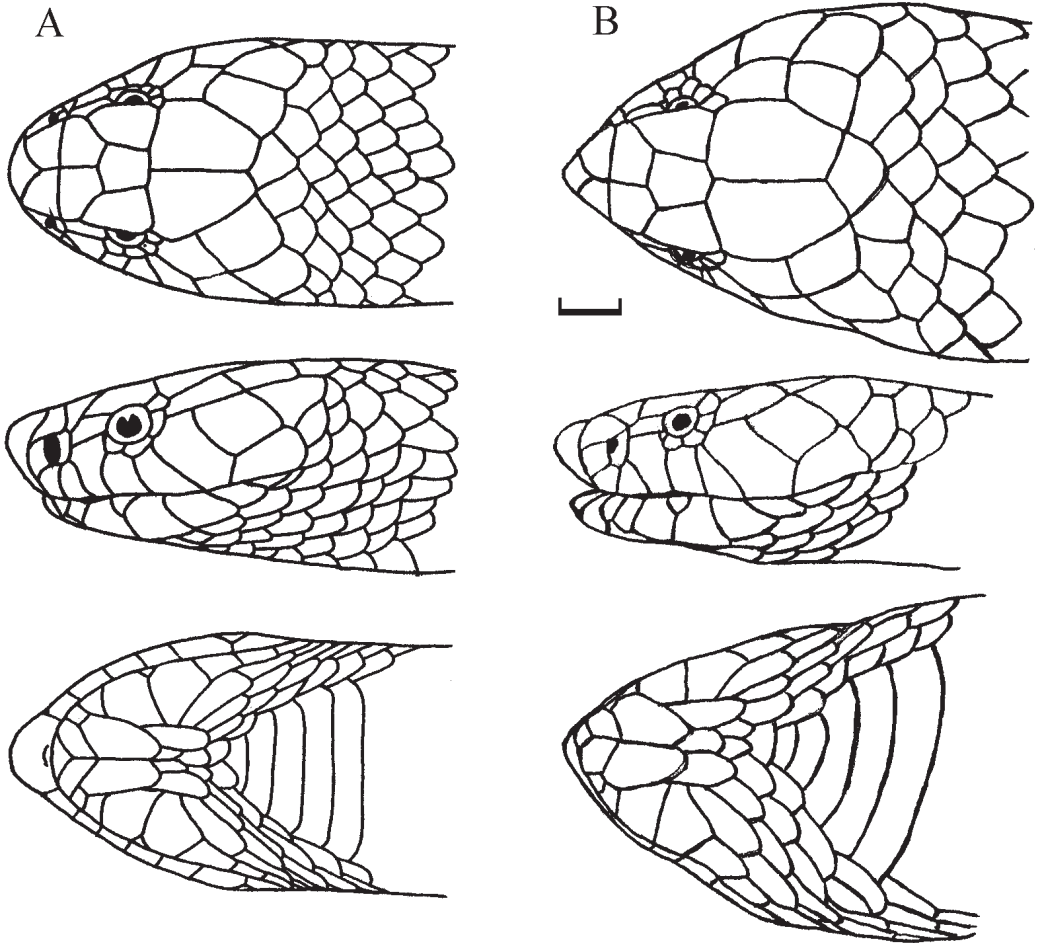


Figure 2. Dorsal, lateral and ventral views of the heads of: A. *Naja annulifera* (NMZB-UM 32421 - Darwendale, Zimbabwe). B. *Naja anchietae* (NMZB-UM 18169 - Maun, Botswana). The lines indicate 10 mm to scale.

Preoculars; 8. Postoculars; 9. Cuneates. The remaining characters were excluded from further analyses.

The CVA (Fig. 3) shows a very clear bimodal distribution of canonical variate scores, illustrating a distinct morphological discrepancy between an eastern and a western morphological type. The two characters most strongly associated with separation along the canonical variate were midbody dorsal scale rows and the difference between midbody and neck scale counts. There was no overlap in canonical variate score between OTUs 1 and 2. Specimens of OTU 3 also displayed a bimodal distribution of canonical variate scores, most specimens falling into a similar distribution of scores as OTUs 1 and 2. Specimens were deemed to be of intermediate morphology if their CV score was morphologically intermediate between the scores of OTU 1 and 2, and more than 2.5 within-group standard deviations away from the mean of OTUs 1 and 2, since in a normal dis-

tribution, 99% of specimens are expected to fall within 2.5 SD of the group mean. In total, out of 393 specimens, including 165 in OTU 3, only nine had canonical variate scores intermediate between *annulifera* and *anchietae*. Almost all these morphologically intermediate specimens come from the Hwange and Bulawayo areas of western Zimbabwe. These two areas were the only localities where specimens with *annulifera* and *anchietae* phenotypes occur in sympatry. The only other morphologically intermediate specimens were one from Gobabis (Namibia), and one from Mutare, eastern Zimbabwe.

MOLECULAR ANALYSIS

We aligned 650 b.p. of the mitochondrial cytochrome *b* (*cytb*) gene by eye for all taxa. Of these, 171 were variable and 90 parsimony-informative. Translation of the nucleotide sequences into amino acid sequences revealed no gaps, frameshifts or nonsense codons. All

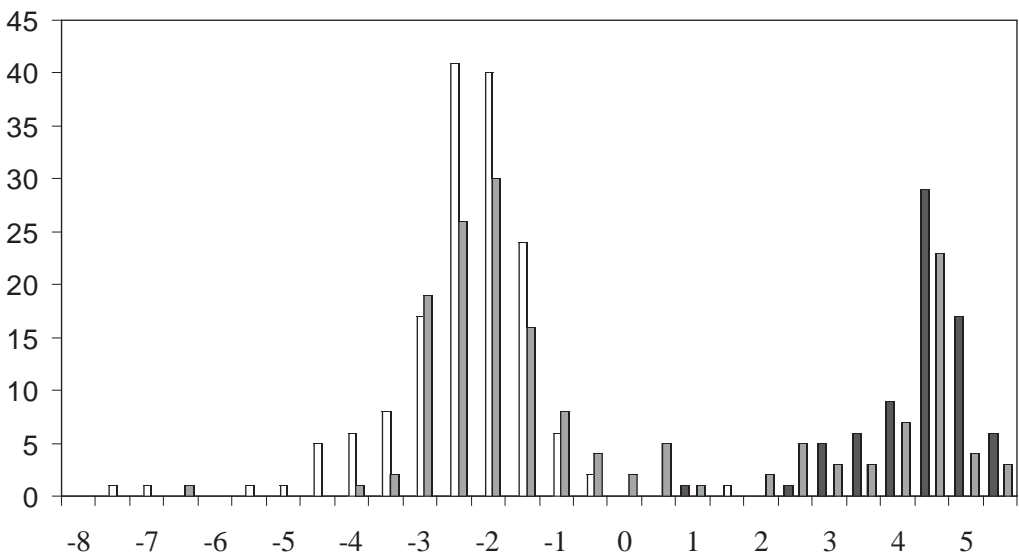


Figure 3. Distribution of canonical variate scores for specimens of OTUs 1 (western *anchietae*; darkest bars), 2 (eastern *annulifera*; clear bars) and 3 (affinities not assumed *a priori*). Note bimodal distribution of values, including those of OTU3.

sequences have been submitted to GenBank (accession numbers AY463026-032).

Maximum parsimony analysis of the data yielded a single most parsimonious tree (MPT) (Fig. 4) with a length of 241 steps. The distribution of tree lengths was significantly left-skewed ($g1 = -1.107115$), rejecting the null hypothesis of no significant phylogenetic signal in the data (Hillis & Huelsenbeck 1992). The MPT supported the reciprocal monophyly of north and east African *N. haje* and the southern African *N. annulifera-anchietae* group, and the monophyly of the latter with high levels of bootstrap and branch support.

Modeltest identified the TIM + I model as optimal for our sequence data. Between-haplotype sequence divergences are shown in Table 2. The two samples of *N. annulifera*, from widely separated parts of the range, differed by only a single base pair, whereas there were two differences between the two *anchietae* sequences. However, *N. annulifera* and *N. anchietae* differ from each other by a ML distance of 0.043-0.046, and from our *N. haje* sequences by 0.056-0.072. A ML tree calculated with the same model (not shown) was topologically identical to the MP tree.

DISCUSSION

The multivariate analyses demonstrate that the taxa *annulifera* and *anchietae* constitute taxa that are highly distinct and largely homogenous throughout their large ranges in southern Africa. Only nine out of 393 specimens analysed were phenotypically intermediate between “typical” *annulifera* and *anchietae*. Out of these, seven originated from the Hwange and Bulawayo areas of western Zimbabwe, the contact zone for the two taxa. In both the Hwange and Bulawayo areas, specimens with unambiguous *annulifera* and/or *anchietae* phenotypes were also found. In the

Hwange area, eight out of 12 specimens displayed the *anchietae* phenotype, two the *annulifera* phenotype, and two were intermediate, whereas in the Bulawayo area, 88 out of 94 displayed the *annulifera* phenotype, five were intermediate, and only one displayed the *anchietae* phenotype. The southeasternmost specimen with the *anchietae* phenotype originated from Esigodini (NMZB 928), but displayed 17 dorsal scale rows on neck and at midbody, thus lacking the two-row difference between neck and midbody that is typical of *anchietae*, and may thus be an aberrant specimen of *annulifera*. The next most southeasterly *anchietae* was NMZB 6117, from 50 km NNW of Bulawayo. The westernmost Zimbabwean records of specimens with the *annulifera* phenotype are from 15 km west of Ngamo Pan (NMZB 23239) and Lupane (NMZB 16936). Haagner *et al.* (2000) reported a specimen from Livingstone, Zambia, but this could be a waif, as cobras are prone to stow away in vehicles and disembark in urban areas! Only two specimens with intermediate phenotypes originated from outside the Hwange and Bulawayo areas: NMWN 3583 originated from Gobabis District, Namibia, and NMZB-UM 33549 from Mutare, eastern Zimbabwe. In both cases, these are almost certainly specimens of *anchietae* and *annulifera*, respectively, with abnormal scale counts (17 on neck, 19 at midbody, and 17 on neck and at midbody, respectively).

Our mtDNA sequence data, although based on very limited sampling, are consistent with the picture emerging from the morphological analyses. First, they support Broadley’s (1995) elevation of *Naja annulifera* to the status of a full species separate from *Naja haje*, as *N. annulifera* and *N. haje*, from various extremes of their respective ranges, display reciprocally monophyletic haplotypes. Second, the taxa *anchietae* and *annulifera* present considerable sequence differences, but both appear to be homogenous across much of their respective ranges. The level of divergence between our

Table 2. Genetic distances between taxa of the *Naja haje* complex, calculated by maximum likelihood.

| | <i>N. anchietae</i> Silumbi | <i>N. anchietae</i> Okahandja | <i>N. annulifera</i> Mpumalanga | <i>N. annulifera</i> Bulawayo | <i>N. haje</i> Kenya | <i>N. haje</i> Egypt | <i>N. haje</i> Morocco |
|---------------------------------|--------------------------------|----------------------------------|------------------------------------|----------------------------------|-------------------------|-------------------------|---------------------------|
| <i>N. anchietae</i> Silumbi | - | | | | | | |
| <i>N. anchietae</i> Okahandja | 0.00319 | - | | | | | |
| <i>N. annulifera</i> Mpumalanga | 0.04273 | 0.04329 | - | | | | |
| <i>N. annulifera</i> Bulawayo | 0.04478 | 0.04587 | 0.00154 | - | | | |
| <i>N. haje</i> Kenya | 0.06512 | 0.06062 | 0.07191 | 0.07046 | - | | |
| <i>N. haje</i> Egypt | 0.06275 | 0.05613 | 0.06254 | 0.06571 | 0.01610 | - | |
| <i>N. haje</i> Morocco | 0.06102 | 0.05664 | 0.06086 | 0.06400 | 0.01622 | 0.00311 | - |

annulifera and *anchietae* sequences is similar to that found in cytochrome *b* or other genes evolving at similar rates between pairs of morphologically distinct sister species in other snake taxa, including pythons and other elapids (e.g., Keogh *et al.* 2001, 2003). Moreover, the genetic distance between these two forms is comparable to that between them and *N. haje*, and much greater than between our three geographically disparate samples of *N. haje* (Table 2). This substantial sequence divergence between *anchietae* and *annulifera* suggests that they represent two morphologically differentiated lineages with a considerable history of independent evolution.

In summary, our molecular and multivariate analyses show that the taxa *annulifera* and *anchietae* represent two taxa that are morpho-

logically and genetically homogenous across their respective distributions, show only very limited intergradation in their narrow contact zone, and represent separate lineages with a considerable history of independent evolution. In view of these results, we regard them as two distinct evolutionary species, *Naja annulifera* Peters 1854 and *N. anchietae* Bocage 1879.

ZOOGEOGRAPHY

When the distributions of *N. nivea*, *N. anchietae* and *N. annulifera* are plotted on the same map (Fig. 5), it can be seen that they are complementary. *Naja nivea* does not seem to be sympatric with either of the others and there are only a few records of sympatry between *N. anchietae* and *N. annulifera* in the Hwange District of Zimbabwe. Here the former seems to be largely restricted to Kalahari sand areas, being replaced by *N. annulifera* further west, but on the sandstone substrates around Hwange town, there are no records of either species, apparently the only local cobra being *N. mossambica*.

The relict populations of *N. anchietae* around Lake Bangweulu must represent part of the Palaeo-upper Zambezi—Chambeshi fauna (Broadley & Cotterill 2004). The specimen from the Katanga pedicle was sympatric with *N. mossambica* (MRAC 4515, see Laurent 1956, pl. xxviii, fig. 4).

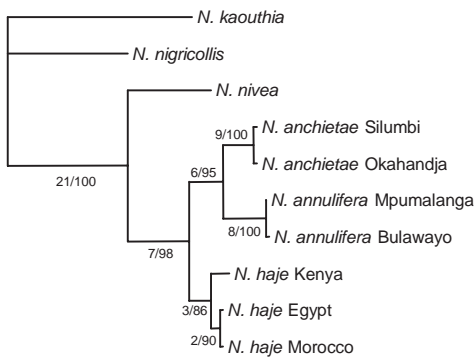


Figure 4. Maximum parsimony phylogram of cytochrome *b* sequences. Numbers on branches are Bremer branch support / bootstrap support.

SYSTEMATIC ACCOUNT

NAJA NIVEA (LINNAEUS) (Fig. 1)
CAPE COBRA

Coluber niveus Linnaeus 1758, Syst. Nat., ed. 10, 1: 223 & 1766, ed. 12, 1: 384. Type locality: “in Africa” [= Cape of Good Hope], type NHRM 91.

Vipera (Echidna) flava Merrem 1820: 154.

Naja nivea Boie 1827: 557; Flower 1929: 251; Mertens 1937: 15; Hewitt 1937: 67; Bogert 1943: 288; Rose 1950: 286 & 288; Pringle 1954: 16; Perkins 1954: 230 & 1955: 262; Mertens 1955: 111; Rose 1955: 124; Isemonger 1955: 83; FitzSimons, V. 1957: 391 & 1962: 297; Gaerdes 1962: 12; Klemmer 1963: 325; FitzSimons V. 1966: 73; Visser, 1966: 19; Broadley 1968a: 412 & 1968b: 5; FitzSimons, V. 1970/74: 158/157; Mertens 1971: 100; Visser 1972: 58; Maclean 1973: 242; Rippey *et al.* 1976: 1874; De Waal 1978: 121; Visser & Chapman 1978: 44;

Branch 1979: 219; Visser 1979, No. 27; Elzen, 1980: 352; Stuart 1980: 10; Welch 1982: 190; Broadley 1983: 286; Buys & Buys 1983: 32; Auerbach 1985: 41 & 1987: 197; Golay 1985: 47; Baard *et al.* 1988: 31; Branch 1988: 93; Branch *et al.* 1988: 14; Branch & Braack 1989: 32; Jacobsen 1989: 1115; Morgan & Haagner 1992: 87; Branch *et al.* 1993: 40; Broadley 1993: 190; Burger 1993: 4; Haagner & Branch 1996: 42; Bates 1996: 42 & 1997: 21; Branch 1998a: 93 & 1998b: 17; Griffin 2000: 84; Clauss & Clauss 2002: 98; Griffin 2003: 118; Wüster & Broadley 2003: 347.

Naja haje var. Schlegel 1837: 471; Jan 1859: 129.

Naja gutturalis A. Smith 1838: 92.

Naja haje (not Linnaeus) A. Smith 1842: pls xviii, xix & xxi; Peters 1870: 117; Fischer 1888: 12; Fleck 1894: 85.

Naja haje (part) Duméril & Bibron 1854: 1298; Günther 1858: 225; Boettger 1894: 92.

Naja intermixta Duméril & Bibron 1854: 1298.

Naja haje var. *capensis* Jan 1863: 119.

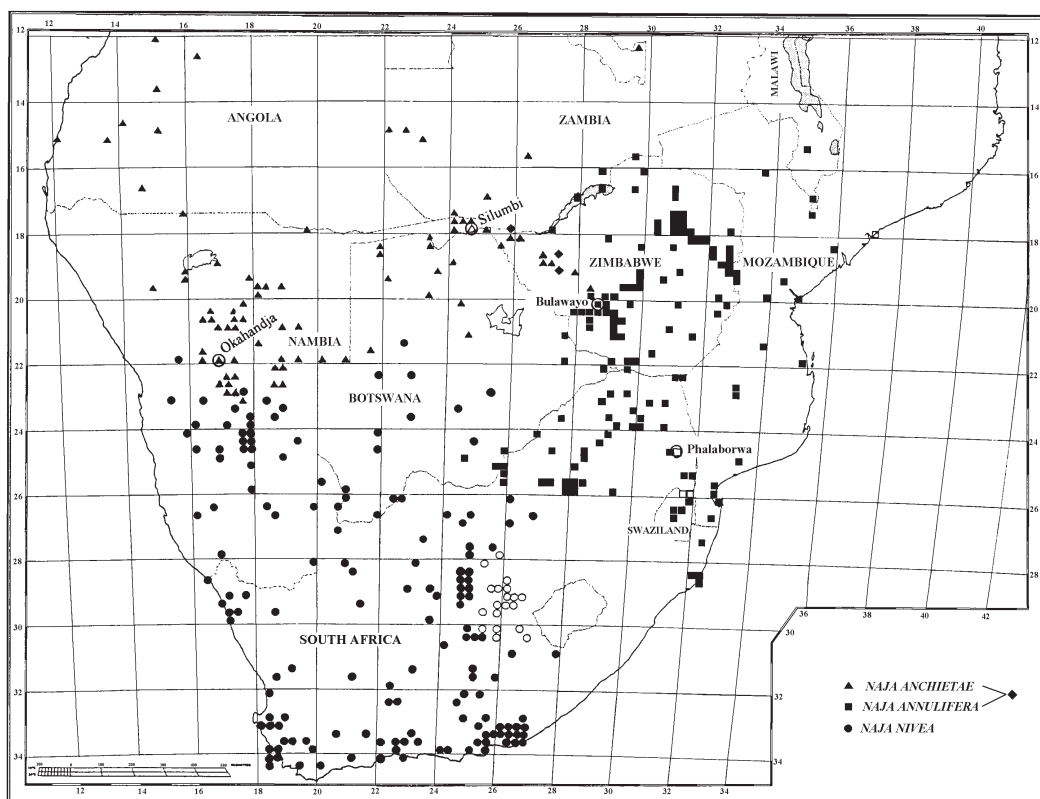


Figure 5. Distribution of *Naja nivea*, *N. annulifera* and *N. anchietae* by quarter degree cells. Open symbols denote literature records. Localities for which mtDNA samples were available are encircled and named.

Naia flava Boulenger 1887: 179 & 1896: 376; Sclater 1898: 101; Roux 1907: 739; Mitchell & Pocock 1907: 791; Gough 1908: 35; Boulenger 1910: 517; Werner 1910: 364; Gilchrist 1911: 234; FitzSimons, F.W. 1912: 164, 171; Hewitt & Power 1913: 164; Werner 1915: 366 & 1923: 181; Flower 1925: 972; Rose 1929: 168; Lawrence 1929: 21, 27.

Naia nivea Andersson, 1899: 64.

Naja flava Sternfeld 1910a: 32; Lampe 1911: 203; Falk 1923: 8; FitzSimons, V. 1935: 323; Christensen 1955: 2; Pitman 1958: 100.

Variation.—Dorsal scale rows on neck 21-23 (very rarely 19 or 25; mean 22.34 in ♂♂, $N = 176$; 21.99 in ♀♀, $N = 85$); at midbody 21 (very rarely 19 or 23; mean 21.03 in ♂♂, $N = 176$; 21.07 in ♀♀, $N = 85$); before vent 15 (very rarely 13 or 17; mean 14.83 in ♂♂, $N = 178$; 15.05 in ♀♀, $N = 86$); ventrals 186-215 in ♂♂ (mean = 202.88, $N = 173$); 193-228 in ♀♀ (mean = 210.13, $N = 85$); cloacal entire; subcaudals 52-68 in ♂♂ (mean = 59.69, $N = 160$); 50-67 in ♀♀, (mean = 57.63, $N = 82$); nuchals bordering parietals 6-9, usually 7; supralabials 7 (very rarely 6 or 8), the 3rd and 4th (very rarely 2nd & 3rd, 3rd only or 4th & 5th) entering the orbit; infralabials 9 (rarely 8 or 10), the first 4 (rarely 3) in contact with the anterior sublinguals; cuneates 1-3, very rarely absent (mean 1.47 in ♂♂, $N = 176$; 1.65 in ♀♀, $N = 84$); preocular 1 (very rarely 2); postoculars 3 (very rarely 4); temporals 1 + 2 or 1 + 3, rarely 2 + 2, 2 + 3 or 2 + 4.

Colouration.—Juveniles are yellow with a black band on the throat covering approximately ventrals 6 to 18, this fades to brown in subadults and disappears completely in adults. Specimens from the Kalahari sands of Botswana, central Namibia and northern Namaqualand are uniform yellow apart from a dark tail tip and sometimes a few scattered brown dorsal speckles. Further south the amount of brown speckling increases above and below and eventually dominates over yellow, there is also a uniform golden brown phase. A uniform black phase has been report-

ed from the Western Cape Province, but no voucher specimens have been examined and many of these reports are probably based on the Black Spitting Cobra *N. nigricincta woodi*.

Size.—Largest ♂ (PEM - Port Elizabeth, Eastern Cape Province) 1510 + 290 = 1800 mm (Branch 1998b, specimen now lost); largest ♀ (NMWN 2487 - Aus, Namibia) 1430 + 240 = 1670 mm. Branch (1998b) recorded a larger female (PEM 6441), but this proved to be a *N. nigricincta woodi*.

Distribution.—Central and southern Namibia, southwestern Botswana, and the western provinces of South Africa, just entering western Lesotho.

NAJA ANNULIFERA PETERS (FIG. 2A)
SNOUTED COBRA

- Naja haje* var. *annulifera* Peters 1854: 624. Type locality: "Tette" [= Tete, Mozambique], type ZMB 2813.
- Naja haje* (not Linnaeus) Peters 1882: 137; Symonds 1887: 488; Breijer 1915: 114; Pringle 1954: 18; Christensen 1955: 2; Pitman 1958: 100 (part); Wapnick *et al.* 1972: 139; Broadley 1975: 21; Broadley & Cock 1975: 51.
- Naia haie* Boulenger 1887: 179 & 1896: 374 (part); Sclater 1898: 101; Boulenger 1902: 18 & 1908: 230; Gough 1908: 35; Chubb 1909a: 596 & 1909b: 36; Hewitt 1910: 57; Boulenger 1910: 517; FitzSimons, F.W. 1912: 164; Hewitt & Power 1913: 164; Cott 1935: 970; Tasman 1953: 21.
- Naia haie* var. *annulifera* Chubb 1909a: 597 & 1909b: 36.
- Naja nigricollis* (not Reinhardt) Curtis 1911: pl. xvi.
- Naja haie* var. *annulifera* Power 1931: 44; Hewitt 1937: 71.
- Naja haje haje* (not Linnaeus) Bogert 1943: 288 & 64 (part); Loveridge 1953: 286; FitzSimons, V. 1958: 97; Broadley 1959: 61 & 1962: 839; FitzSimons, V. 1962: 293; Klemmer 1963: 320 (part); Pooley 1965: 53; FitzSimons, V. 1966: 73; Pienaar 1966: 206; Visser 1966: 19; Broadley 1968a: 410 (part); FitzSimons, V. 1970: 157.
- Naja haie* Rose 1950: 289 & 1955: 132; Isemonger 1955: 83.
- Naja haje annulifera* Broadley 1968b: 4 & 1971: 95; Visser 1972: 55; FitzSimons, V. 1974: 156; Stevens 1974: 19; Bourquin 1977: 47; Pienaar 1978: 192;

Visser & Chapman 1978: 42; Branch 1979: 216; Broadley & Blake 1979: 13; Visser 1979, No. 26; Welch 1982: 189; Broadley 1983: 286; Pienaar *et al.* 1983: 210; Auerbach 1985: 41 & 1987: 196; Golay 1985: 44; Branch 1988: 92; Els 1988: 52; Bourquin 1989: 21; Jacobsen 1989: 1109; Haagner 1990: 47; Kelly 1991: 4; Rasmussen 1991: 27; Boycott & Culverwell 1992: 40; Broadley 1993: 186; Haagner 1993: 39; Mackie 1994: 22.

Naja annulifera annulifera Broadley 1995: 29; Branch 1998a: 107; Schmidt 2002: 19.

Naja annulifera Haagner *et al.* 2000: 19; Clauss & Clauss 2002: 96 (part); Broadley *et al.* 2003: 107.

Variation.—Dorsal scale rows on neck 19 (very rarely 17 or 21; mean 19.04 in ♂♂, $N = 312$; 18.79 in ♀♀, $N = 191$); at midbody 19 (very rarely 17 or 21; mean 19.02 in ♂♂, $N = 312$; 19.06 in ♀♀, $N = 191$); before vent 13 or 15 (very rarely 11; mean 13.63 in ♂♂, $N = 314$; 14.06 in ♀♀, $N = 205$); ventrals 169-208 in ♂♂ (mean = 189.32, $N = 308$); 180-206 in ♀♀ (mean = 195.36, $N = 190$); cloaca entire; subcaudals 48-67 in ♂♂ (mean = 57.84, $N = 274$); 48-69 in ♀♀ (mean = 59.08, $N = 168$); nuchals bordering parietals 5-10, usually 7; supralabials 7 (very rarely 6 or 8), labials normally excluded from orbit by suboculars (very rarely the 3rd, 4th, or 3rd and 4th entering the orbit); infralabials 8 or 9 (rarely 7 or 10), the first 4 (rarely 3) in contact with the anterior sublinguals; cuneates 0-1, very rarely 2 (mean 0.46 in ♂♂, $N = 301$; 0.85 in ♀♀, $N = 188$); preoculars 1-2; suboculars 1-2; postoculars 2; temporals 1 + 2 or 1 + 3, very rarely 2 + 3.

Colouration.—Juveniles are yellow or greenish yellow above, usually with dark scale margins that may form irregular transverse lines, there is usually a broad black band encircling the neck; yellow below. Adults gradually darken to grey-brown or black, sometimes with lighter mottling or scattered white spots, but a few remain yellow or orange, the dark band on the back of the neck fades out. The venter is usually yellow, heavily blotched with dark brown, and the throat band, covering ca. ventrals 12-20, becomes purple-brown, but is often

obscured by general darkening posteriorly, becoming uniform blue-black on the tail.

A banded phase occurs throughout the range of the species, the banding is hardly discernable in hatchlings, but by the time a snake attains a length of 600 mm, it is black with seven to nine yellow bands on the body and one or two on the tail. The light bands are usually about half the width of the dark ones and may be divided by a narrow black transverse line. The yellow bands may encircle the body, but are frequently mottled with black ventrally. A few specimens have a single yellow band on the neck and several more caudad. One skin examined (from Mutare) had a series of yellow dorsal blotches instead of bands. One Bulawayo cobra had the broad bands golden-brown instead of black. This banded phase has been recorded in 27% of ♂♂ and 18% of ♀♀.

Size.—Largest ♂ (NMZB-UM 23838 - Hippo Valley, Zimbabwe) 2125 + 320 = 2445 mm; largest ♀ (NMZB 7673 - Chewore Safari Area, Zimbabwe) 1975 + 345 = 2320 mm.

Distribution.—The Gwembe (middle Zambezi) valley of Zambia, southern Malawi, Zimbabwe, central and southern Mozambique (on the coast not known north of Quelimane - Kelly 1991), eastern Botswana, the northeastern provinces of South Africa, and Swaziland.

NAJA ANCHIETAE BOCAGE (FIG. 2B) ANCHIETA'S COBRA

Naja anchietae Bocage 1879: 89 & 98. Type locality: Caconda, Angola, lectotype (destroyed) MBL 1987 (D.G.B.); Bocage 1895: 133; Werner 1903: 382; Peracca 1910: 4; Sternfeld 1910a: 33 & 1910b: 57; Falk 1923: 9; Pitman 1934: 299; Monard 1937: 137, 138; FitzSimons, V. 1938: 159; Rose 1950: 291 & 1955: 133; Isemonger 1955: 84; Christensen 1955: 2; Klemmer 1963: 320; Griffin 2000: 84 & 2003: 116; Broadley *et al.* 2003: 111.

Naja haje (not Linnaeus) Boettger 1887: 164; Pitman 1934: 298; Pike 1964: 38; Griffin *et al.* 1989: 37.

Naja anchietae Boulenger 1896: 387; Sclater 1898:

101; Boulenger 1910: 517; FitzSimons, F.W. 1912: 164; Werner 1923: 181, 183; Lawrence 1929: 21, 27; FitzSimons, V. 1935: 325.

Naja haie var. *annulifera* (not Peters) Sternfeld 1910a: 32; Falk 1923: 8.

Naja haie anchietae Mertens 1937: 15.

Naja haje anchietae Bogert 1940: 90 & 1943: 288; De Witte 1953: 276; Mertens 1955: 109; Broadley 1959: 65 & 1962: 839; Gaerdes 1962: 12; FitzSimons, V. 1962: 296 & 1966: 73; Visser 1966: 19; Broadley 1968a: 410 & 1968b: 4; FitzSimons, V. 1970/1974: 158/157; Broadley 1971: 95; Mertens 1971: 98; Visser 1972: 55; Visser & Chapman 1978: 42; Branch 1979: 217; Broadley & Blake 1979: 13; Visser 1979, No. 26; Elzen 1980: 351; Welch 1982: 189; Buys & Buys 1983: 40; Golay 1985: 44; Auerbach 1987: 197; Branch 1988: 92; Branch *et al.* 1988:14; Broadley 1993: 186.

Naja annulifera anchietae Broadley 1995: 31; Branch 1998a: 107.

Naja annulifera (not Peters) Clauss & Clauss 2002: 96 (part).

Variation.—Dorsal scale rows on neck 15 or 17 (mean 15.41 in ♂♂, n =110; 15.55 in ♀♀, N= 80); at midbody 17 (very rarely 15 or 19; mean 16.95 in ♂♂, N= 111; 17.06 in ♀♀, N= 80); before vent 13 (very rarely 11 or 15; mean 12.82 in ♂♂, N= 111; 13.05 in ♀♀, N= 80); ventrals 171-196 in ♂♂ (mean = 185.39, N= 104); 177-200 in ♀♀ (mean = 190.38, N= 77); cloacal entire; subcaudals 51-65 in ♂♂ (mean = 55.88, N= 98); 49-66 in ♀♀ (mean = 57.36, N= 70); nuchals bordering parietals 5-9, usually 7; supralabials 7 (very rarely 6 or 8), labials normally excluded from orbit by suboculars (very rarely the 3rd, or 3rd and 4th, entering the orbit); infralabials 8 or 9 (rarely 7 or 10), the first 4 (very rarely 3 or 5) in contact with the anterior sublinguals; cuneates 0-2, very rarely 3 (mean 0.85 in ♂♂, N= 105; 1.32 in ♀♀, N = 78); preoculars 1- 2; suboculars 1-2; postoculars 2-3; temporals 1 + 2 or 1 + 3, very rarely 2 + 2 or 2 + 3.

Colouration.—Juveniles are yellow above and below, dorsally with dark scale margins forming irregular transverse lines and a broad black band encircling the neck. Adults gradually

darken to light or dark brown, the dark band on the neck fades out. The venter is usually yellow, heavily blotched with dark brown, and the throat band, covering ca. ventrals 12-23, becomes purple-brown.

A banded phase sometimes occurs in the southern part of the species range, black with six to eight yellow bands on the body and one to three on the tail. The light bands are usually as wide or wider than the dark ones. This banded phase has been noted in 13% of ♂♂ and 22% of ♀♀.

Size.—Largest ♂ (NMWN 9734 - Windhoek, Namibia) 1990 + 320 = 2310 mm; largest ♀ (NMZB-UM 31521 - 25 km S of Shakawe, Botswana) 1870 + 310 = 2180 mm.

Distribution.—Southern Angola, western Zambia (with an isolated population around Lake Bangweulu, including the Katanga pedicle), northern Namibia, northern Botswana and northwestern Zimbabwe (where narrowly sympatric with *N. annulifera*).

ZOOGEOGRAPHY

When the distributions of *Naja nivea*, *N. anchietae* and *N. annulifera* are plotted on the same map (Fig. 5), it can be seen that they are complementary. *Naja nivea* does not seem to be sympatric with either of the others and there are only a few records of sympatry between *N. anchietae* and *N. annulifera* in the Hwange District of Zimbabwe. Here the former seems to be largely restricted to Kalahari sand areas, being replaced by *N. annulifera* further west, but on the sandstone substrates around Hwange town there are no records of either species, only *N. mossambica*.

The relict populations of *N. anchietae* around Lake Bangweulu seem to represent part of the Palaeo-upper Zambezi - Chambeshi herpetofauna (Broadley & Cotterill 2004). The speci-

men from the Katanga pedicle was sympatric with relict *Naja mossambica* (MRAC 4515, see Laurent 1956, pl. xxvii, fig. 1).

ACKNOWLEDGEMENTS

We are particularly indebted to Mathilda Awases for facilities granted at the National Museum of Namibia in Windhoek and Mike Griffin for depositing there long series of *Naja anchietae* and *Naja nivea*. For help with tissue samples, we thank W.R. Branch (Port Elizabeth Museum), Mike Griffin, H.-W. Herrmann (CRES, Cameroon), Liverpool School of Tropical Medicine (P.D. Rowley and R.D.G. Theakston) and BioKen, Watamu, Kenya (R. Taylor and A. Childs), also, for help in the lab, G.J. Duckett, A.J. Dumbrell, C.E. Ercolani, C.E. Pook and A.G. Stenson. The curators of the following museums also provided access to specimens for morphological analysis: Transvaal Museum (W.D. Haacke), Port Elizabeth Museum (W.R. Branch), South African Museum, Cape Town (D. Drinkrow), McGregor Museum, Kimberley (B. Wilson), Natal Museum, Pietermaritzburg (J. Pringle), Field Museum of Natural History, Chicago (H. Marx, A. Resetar), United States National Museum, Washington (G.R. Zug), California Academy of Sciences, San Francisco (R.C. Drewes, J. Vindum), Museum of Vertebrate Zoology, University of California at Berkeley (H.W. Greene); Museum of Comparative Zoology, Harvard (J.P. Rosado), Carnegie Museum, Pittsburgh (C.J. McCoy), American Museum of Natural History, New York (C.W. Myers), Museu Bocage, Lisbon (G. Sacarrão), Natural History Museum, London (A.G.C. Grandison, C.J. McCarthy), Institut Royal des Sciences Naturelles de Belgique, Brussels (G.-F. de Witte), Muséum National d'Histoire Naturelle, Paris (J. Guibé), Zoologisches Museum der Universität, Berlin (R. Günther) and Naturhistorisches Museum zu Wien, Vienna (J. Eiselt).

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Received: 3 March 2004;

Final acceptance: 27 May 2004.

APPENDIX

Material examined and specimens for which reliable data were available from the literature. Countries are listed from north to south and west to east.

NAJA NIVEA: **NAMIBIA**. Achenib/Nina crossroad, Windhoek TM 47092; Ameib Nord NMWN 3447; Arabi 401, Keetmanshoop TM 79270; 20 km S of Arenos NMWN 3958; Aus NMWN 2487; Bitterwasser 116, Rehoboth TM 44123; Damaraland SAM 20528; Dordabis, Windhoek NMWN 2475; Eava 383, Gobabis NMWN 2491; Estcourt, Maltahöhe NMWN 7950; Hardap Dam NMWN 2484; Haribes, Mariental NMWN 2480; Kub South 2, Mariental NMWN 2485; Kuzikus 37, Gobabis TM 44120; Leonardville, Gobabis NMWN 2479; Maltahöhe NMWN 7219; Mariental NMWN 3526; M'bela 200, Mariental NMWN 2472-4, 2488, 2636; Mooilaagte 175, Stampriet TM 44796; Mooirivier 160, Maltahöhe TM 41496; Nelsip 34, Lüderitz NMWN 2478; 38 km E of Rehoboth NMWN (B24); Skraplip, Keetmanshoop TM 54517; Solitaire, Windhoek NMWN (B13); Spitzkoppe, Keetmanshoop NMWN (B107); Tumasberg, Namib-Naukluft Park NMWN 9103; Twilight 113, Mariental NMWN 2477; Uhlenhorst 114, Mariental NMWN 2476. **BOTSWANA**. Jwaneng NMZB 13927; Kang ZMB 22875; Kuke Pan FMNH 17656; Lekuru Pan NMZB-UM 22486-9; 65 km NW of Lephepe NMZB-UM 9725; Okwa valley NMZB-UM 30407; Tshabong SAM 45166; 25 km SE of Tshabong NMZB-UM 13157-8; Tshane NMZB 11321; 10 km S of Tshane NMZB-UM 14789; Vloorskop NMZB-UM 13164, 13166. **SOUTH AFRICA**. Adcocks Farm, Port Elizabeth PEM 9857; Albany District SAM 3561; Albion (De Waal, 1978); Alice PEM 1166; Alicedale PEM 9886; Andalusia TM 22241; Andries Vosloo Nat. Res. PEM 8180; Anyberg Nat. Res. PEM 7022; Auob River near Twee Rivieren TM 26449-50; Bathurst TM 21404; Beaufort West NMZB-UM 11527; USNM 162442; Beginseldam (De Waal, 1978); Bloemfontein NMBO 6177; Burghersdorp SAM 11136; Brak Kloof, Grahamstown NMP 438; Brazil Farm, Kleinsee TM 71218; Bultfontein 32, Pretoria TM 71508; Campbell MMK 710; Cape of Good Hope Nat. Res. SAM 47036, USNM 7509 (2); Cape Town CM 69375; TM 71201; Clanwilliam TM 14911; Coerney SAM 46878; Coronation, Alexandria PEM 8254; De Aar MMK 631/2; SAM 9494; De Wet TM 19669; Divgat 195, Namaqualand TM 82093; Doornhoek

Dam, Mountain Zebra Nat. Park PEM 3113, 11851; Doornkloof Nat. Res. PEM 7752; Doornlaagte (De Waal 1978); Dronfield Farm MMK 628/3; Dunbrody NMZB 13933; PEM 9846-7, 9849; Dunedin, Beaufort West SAM 44887-8; Enslin MMK 627/7; Formosa Cons. Area, Nooitgedacht Witelsbos PEM 13821; Gamkaskloof PEM 13808; Garaas Farm, Carnarvon TM 49799; Geelhoutkoom, Lorie Dam Nat. Res. PEM 10208; Goukamma Nat. Res. PEM 1148; Graaf Reinets IRSNB 10117; Grahamstown MCZ 21351; PEM 9851-2, 9854, 10423, 10938, 18815; TM 5796; Graspan NMBO 7214; Grasslands NMBO 5261; Groenkloof (De Waal 1978); 4 km E of Hankey PEM 7028; Heilbron (De Waal 1978); Hex River East, Worcester SAM 1614; Hofmeyr PEM 1164; Holme's Dale (De Waal 1978); Hooplaagte, Alexandria PEM 11005; Hot Springs PEM 1170; Hout Bay TM 54046; Inkbosch Pan, Gordonia TM 37894; Jacobs Rush MMK 631/3; Joubertsberg PEM 3571; Kalahari Gemsbok Nat. Park TM 24201-2, 24649; Kalkfontein, Boshof TM 63772; Kalkfontein Dam Nature Res. (Bates, 1996); Kareedouw Pass PEM 13707; Kenton-on-Sea PEM 9853; Kernemelksrivier, Heidelberg TM 68252; Kimberley MMK 54/1, 627/1, 628/2, 629/2, 909; 50 km W of Kimberley TM 28064; Kini Bay, Port Elizabeth PEM 2515; Kleinmond, Caledon TM 64922; Kleinsee SAM 43358; TM 56118, 68735, 69496; Kloof Nek, Cape Town TM 57335; Kraaifontein, Cape Town JDV 5474; Kranzkloof Farm, Somerset West PEM 1725; Kreefbaai SAM 43357; Krugersdrift Dam (De Waal 1978); Kuruman MMK 627/4; 160 km N of Kuruman PEM 1152; Ky Ky MMK 627/9; Landesdowne SAM 18906; Langebaan SAM 44810; Langhoogte TM 57645, 81872; 20 km N of Lekkerseng TM 35490; Lemoenboord (De Waal 1978); Letskraal PEM 1167, 1723; Lichtenburg TM 52431; Loatla, Postmasburg TM 65070; Lower Molopo MMK 627/8, 628/1; Magdalen (De Waal 1978); Magersfontein MMK 709; Mitchells Plain SAM 46554; Modder River MMK 633/1-2; Modderkop, Klerksdorp TM 64852; Mossel Bay MMK 628/4; Nieuwoudtville, Calvinia SAM 47386; Nossob River NE of Twee Rivieren MVZ 69426; Observatory SAM 1837; Orange Free State NMZB 3943; Ottosdal TM 33607; Oudtschoorn SAM 47199; Paardeberg Road MMK 539; Paarl PEM 11; Penrock, Modderfontein PEM 9855; Pigott's Bridge, Helsőort Pass PEM 7027; P.K. le Roux Dam SAM 44812; Port Alfred PEM 9856; TM 54015; Port Elizabeth MCZ 21424-5, MVZ 65335, 65338,

63542; SAM 9024; TM 5894; USNM 63589; Port Nolloth NMWN 6928; SAM 11420; TM 26060; 50 km N of Prieska TM 28063; Ribblesdale NMBO 6907; Riebeeck East PEM 10939; Riverton MMK 629, 632; Rondevlei Lakes Cons. Stn PEM 1493, 1521; Roodeflee, Bredasdorp TM 65073-5; Rooduin, Namaqualand TM 69029; Rudesheim MMK 627/5; St. Clair, Douglas SAM 2859; Sandveld Nature Res. NMBO 6737; Sannapos NMBO 5622; Scoombe, Steynsburg MMK 631/4; Sea Point SAM 43227; Selborne, Sam Knott Nat. Res. PEM 1171; Showan, Albany PEM 9848; Signal Hill SAM 1845, 43356; Smithfield MCZ 11915; Southwell. Albany PEM 9858; Sparrowfront, Jacobsdal MMK 54/2; Spreeuwfontein MMK 53/2; Steenkampspuits, Gordonia TM 67827; Steinkopf, 23 km to Richtersveld TM 51364; Stella, Vryburg TM 67951; Stolshoek, Karoo Nat. Park PEM 4758; Strandfontein SAM 18913; TM 66010; Strydenburg TM 13116, 13118; Sweet Home (De Waal 1978); Table Valley SAM 1832; Tamboerkloof SAM 44496; Taungs MMK 627/3; Tokai TM 5768-9; 5 km N of Trakas Kuillen PEM 1724; Trappes Valley IRSNB 10119; Tushilow 71, Barkly East TM 49616; 115 km S of Tweerivieren PEM 12931; Tygerberg SAM 47362; Uitenhage NMZB-UM 6663; Uniondale NMZB 13934; Upington SAM 11234; Usherwood NMBO 7118; Vaal River Diggings MMK 627/6; Vaalkoppies, Beaufort West TM 66348; 20 km N of Vanrhynsdorp SAM 44889; Vet River/Bloemhof Dam confl. (De Waal 1978); Victoria West PEM 9883-5, 9887; TM 5767; Vlakteplaas, Oudtshoorn PEM 1168-9; Vondeling PEM 1165; Vrolijkheid, Robertson SAM 45247, 45414; Vryburg TM 41453; Waaierstertplaat, Karoo Nat. Park PEM 7706; Wellington TM 68741; Western Cape Province NMZB 3571-2, 13935-6; Whitney, Albany PEM 9850; Woodlands, Alexandria PEM 11008.

NAJA ANNULIFERA: ZAMBIA. Chakwenga, Zambezi NMZB 4529; Chezia Confl, Kariba Lake NMZB 3286; 30 km W of Chirundu NMZB 16907; Kariba Lake NMZB 3130. **MALAWI.** Nsanje USNM 137552. **BOTSWANA.** Francistown NMZB-UM 11951; Gaborone ZFMK 18914; Gesond Farm, Macloutsie/Limpopo Confl. TM 31227; Kgomodi-kae NMZB-UM 13155; Mmadinare NMZB-UM 8669; Moeding College NMZB 11331; Sunnyside Farm, Otse NMZB 7854. **ZIMBABWE.** Amalinda Camp, Matobo NMZB 15417; Amandas, Mazowe TM 14344; Arcturus

SAM 14238; Baddeley NMZB-UM 25488; Balu Estate NMZB 7990; Beatrice NMZB-UM 25510; Bembesi NMZB 2329, 2852; NMZB-UM 11997; Birchenough Bridge NMZB-UM 2524, 4707, 25724, 32518; Border Ridge Farm, Beitbridge NMZB 11067; Borrowdale, Harare NMZB 7545; NMZB-UM 33014; Borrowdale Brook, Harare NMZB-UM 31263, 32818-9; Boulder Beacon Farm, Somabhula NMZB 11029; Bromley NMZB-QVM 409; NMZB-UM 25496, 27916; Bubi NMZB 1965; Buena Vista Farm, Bulawayo NMZB-UM 7116; Bulawayo MVZ 176496; NMZB 18, 64, 70, 371, 380, 469, 618, 734, 897, 936, 2328, 2720, 5405, 5511, 5513, 5682, 5727, 5836, 5847-9, 5909, 5912, 6047, 6225, 6313, 6315, 6393, 6449, 6721, 6732, 6743, 6944, 6969, 7107, 7162-3, 7202, 7204, 7229, 7747, 7760, 7769, 7992, 8106, 8266, 8635, 8637, 8739, 8877, 8910-1, 8980, 9441, 9469, 9499-500, 9608, 9778, 10254, 10816, 10987, 11034, 11184-5, 11593-4, 12064-5, 12109, 13145-6, 13725, 13765, 13811-2, 13816, 13824, 15429, 15563, 15767, 15978, 16066, 16651, 16904, 16943, 16947, 16953; NMZB-UM 1734, 5387, 5787, 6399-400, 7056, 9724, 10904, 17886, 21625, 21636, 26667, 29071, 31523-7, 31859-60, 32231, 32530, 32905, 33553, 33557-9, 33563-4, 33675; 10 km N of Bulawayo NMZB 393; 15 km S of Bulawayo 353, 591, 1782, 3408, 3618; Butler North, Mutare NMZB-UM 16549; Calgary, Harare NMZB-UM 32613; Chikwarakwara NMZB 16286; Chipinge NMZB-UM 18562, 30286; Chiredzi NMZB-UM 25582; Chishawasha, Harare SAM 14034, 14315; Chivero Lake NMZB-UM 6231; Christon Bank NMZB-UM 28441; Colleen Bawn NMZB 6048; Daisyfield, Gweru NMZB 8740; Darwendale NMZB-UM 32632; Dovenby Farm, Umguza NMZB-UM 21611; Eiffel Flats NMZB 11112; Elston Farm, Norton NMZB 7547; Esigodini NMZB 470, 737, 928, 1072, 1957, 8579; Fairlands Farm, Bulawayo NMZB 7542; Fern Hill, Mutare NMZB-UM 30311; Fern Valley, Mutare NMZB-UM 31097, 31711, 32534; Feruka NMZB-UM 3821, 6665, 13396; Figtree NMZB 1772; Filabusi NMZB 2708; 5 km NW of Filabusi NMZB 11030; Gem Farm, Beitbridge NMZB 14337; Glendale NMZB-UM 18315; 10 km N of Glenlivet, Masvingo NMZB-UM 31842; Gokwe NMZB-UM 18521; Grand Reef, Mutare NMZB-UM 8720, 8897; Guinea Fowl, Gweru NMZB-UM 21637; Gwanda NMZB 6441; Gweru NMZB 278, 3944, 7965, 8789; NMZB-UM 31371; Halfway House Hotel, Lupane NMZB 16936; Harare AMNH 65538; NMZB 7418, 9537-8;

NMZB-QVM 41, 43-4, 620; NMZB-UM 2628, 4790, 6233, 7204, 10145, 10148, 17891, 18199, 18233, 18242, 18257-8, 18274, 18280, 18286, 18291, 18297, 20019, 20021, 20601, 23358, 23377, 23894, 24281, 25497, 25511, 26580, 26791, 27049, 27850, 27928, 28141, 29247, 29254-6, 29289, 29314, 29508, 29566, 32614, 32655, 32820, 33278-9; Heany NMZB-UM 16353; Hippo Valley, Chiredzi NMZB-UM 23838; Hope Fountain NMZB 5845, 5911; Horseshoe Block NMZB 10121; NMZB-QVM 69; Hunters Road, Kwekwe NMZB-UM 5790; Hunyani TM 5875; Imbeza NMZB 7237; NMZB-UM 17973; Inyokene, Umuza NMZB 9420, 13852, 13930, 13943; Irisvale, Umzingwane NMZB 1783; Jelf Estate, Mutare NMZB-UM 17985; Chewore Safari Area NMZB 7673; 25 km NNW of Karoi NMZB-UM 31938; 7 km S of Kezi NMZB 12367; Lochard NMZB 2298; Lower Vumba, Mutare NMZB-UM 27425; Macheke NMZB-UM 27866; Makore Farm, Mutare NMZB-UM 6556-7, 19514, 27053; Manyera Farm, Mutare NMZB-UM 11626; Marondera NMZB 3910; PM 15, 54; Matopos NMZB 937; Matopos Dam NMZB 16622, 16951; Mkonono Farm, Zvimba NMZB-UM 32421; Morgenster Farm, Gweru NMZB 6730; Mount Hampden NMZB-QVM 42; NMZB-UM 18311, 25498; Mususa, Zambezi TM 22626; Mutare NMZB 4167, 7238, 12522-3; NMZB-UM 873, 3820, 4727, 5388, 5791, 7332, 8440, 11359, 12786, 12901, 17900-1, 18861, 19518, 19624, 19880, 20030, 20254, 20580, 23088, 23272, 23410, 23489, 23755, 24061, 25716, 26982, 27549, 27860, 27964, 27984, 28167, 28249, 28270, 28340-1, 28408, 28598, 29044, 29057, 29090, 29319, 30333, 30358, 31099-100, 31322, 31342, 31355, 31373, 31401, 31882, 31911, 32105, 32107, 32197, 32300, 32402, 32475, 32797, 32801, 32804, 32898, 32900, 32925, 33068, 33137, 33426, 33537, 33549, 33627, 33789; Mvuma NMZB-UM 17914, 18179; Ncema Dam NMZB 289; 15 km W of Ngamo Pan NMZB-UM 23239; Ngundu NMZB-UM 2525; Nharira, Chikomba NMZB 15817; Norton NMZB 7546; Nottingham Ranch, Beitbridge NMZB 6387; NMZB-UM 13384; Nyabira NMZB-UM 28440; Nyamandhlovu NMZB 1373, 9896; Nyamazi, Nyanga NMZB-UM 6558, 32660; Nyanyadzi NMZB-UM 22744; Nyazura NMZB-UM 6295-6; Odzani NMZB-UM 31431; Odzi NMZB 427; NMZB-UM 8299, 10321, 23692, 28194-5, 29356, 31447, 32187; Old Mutare, Mutasa NMZB 12521; NMZB-UM 2620, 3062, 3191, 10564, 28664, 32249, 32802; Palm Block, Mvurwi NMZB-UM 26927; Penhalonga NMZB 7973-4, 23263; NMZB-UM 31364, 32377, 32671, 33108, 33743; Plumtree NMZB 498, 13884, 15709, 16988; Redbank NMZB 1029; Rupisi Hot Springs NMZB-UM 29368; Rusape NMZB-UM 6282, 26659, 28158; Ruwa NMZB-QVM 659; Save Experiment Stn, Chipinge NMZB-UM 33660; Sanyati Basin, Kariba Lake NMZB-UM 24156; Selborne, Nyanga NMZB-UM 17196; Shambayetu Farm, Beitbridge NMZB-UM 33676; Shangangwe, Insiza NMZB 12111; Siesta Farm, Bulawayo NMZB 927; St Mary's Mission, Nyanga NMZB-UM 16399, 17987, 19005, 20039; Stanmore, Gwanda NMZB 5512, 6045; Syringa NMZB 12564; The Park Farm, Mutare NMZB-UM 11616; Trelawney TM 21692-3; Tuli NMZB 10219; Umwindsdale, Harare NMZB 6339; Vumba Mtn NMZB 912; NMZB-UM 20318, 30191, 32189, 32511; Weirmouth, Mutare NMZB 7977; West Nicholson NMZB 17077; Westacre, Bulawayo NMZB 1900, 15764; Zambezi/Sebungwe Confl. NMZB 985; Zimunya, Mutare NMZB-UM 9899.

MOZAMBIQUE. Acampamento Ruiz, Banhinhe JPT 1432; Banhinhe JPT 1834; Bigabe TM 5890; Charre BMNH 1934.4.6.30; Chimonzo TM 29397; Delagoa Bay MCZ 29143; SAM 461, 1662; Inhaca Island EBM C (2); TM 24955; Jorge NMZB-UM 25765; Kasumbabedza, Tete MCZ 51566; Lamego NMZB-UM 9707, 13395; Manga, Sofala NMZB-UM 8384; Marromeu PEM 15496-7; Pambarra NMZB 11248; Rikatla MMK 634/2, 638; Tete ZMB 2813 (type of annulifera Peters); Zalala (Kelly 1991); Zinave NMZB-UM 30696.

SOUTH AFRICA. Acornhoek TM 11631; Amsterdam Farm, Zoutpansberg TM 39455; Blouberg TM 24080; Bokfontein 448JQ CAS 125654, 125675; Brandfort (?) MMK 634; Brits TM 26442; Broederstroom, Haenertsberg TM 5883, 34838; Buffelshoek TM 5900; Bynespoort, Pretoria TM 5874; De Wildt, Pretoria TM 35951; Donkerhoek TM 34825; Ellisras TM 29996; Groenkloof, Rustenburg TM 5873; Hammanskraal TM 15039; Hartebeespoort Dam TM 31244; Hectorspruit TM 5879; Hennops River, Pretoria TM 5887, 13021, 24704; Kameeldrift, Pretoria TM 39911; Komatipoort NMZB-UM 2368; TM 5862, 5868-9; Letaba TM 22147-8; Linokana MMK 639; Manaba TM 13766; Marico-Crocodile Colfl. TM14776; Middelburg TM 26818; Monzi TM 67727, 67840; Mtubatuba TM 71241; Nylstroom PEM 1155; TM 5872; Pafuri TM 26145; Pietersburg TM 5881; Politsi TM 28724; Potgietersrust TM 5860, 5870, 29990-1; Pretoria MCZ 41962; TM 5861, 5874, 5878-9, 5886, 5889, 5892-3, 5895,

5899, 12641, 24637, 25047, 26415, 34623, 34826; 15 km W of Pretoria TM 27425; 20 km E of Pretoria TM 37626; Pyramid TM 5885-6, 5889; Richards Bay TM 68919; Rooiberg- Thabazimbi MVZ 63525; Rustenberg PEM 1150; TM 5866-7, 5888, 5891, 24627; Str. Lucia TM 68257; Selati TM 5901; Soekmakaar PEM 1157-9; Tshakoma, Zoutpansberg TM 14220; Vygeboompoort, Waterberg TM 5778; Warmbaths TM 5880; Waterkloof, Pretoria TM 28677; Waterpoort CM 69365; Zandfontein, Rustenburg TM 5865, 5871, 5896-7. **SWAZI-LAND.** Dinedor Farm, Mafutseni TM 78878; Manzini TM 22994, 24133, 24355, 71855, 78875; Tshaneni FMNH 206233-4; NMZB-UM 32753-4.

NAJA ANCHIETAE: **ANGOLA.** Alto Chicapa MD 5372; Alto Cuilo MD 5289; Caconda BMNH 1906.8.24.77; MBL 1986-7, 1990: Caçula to Negala NMZB-UM 28066; Capelongo AMNH 51810; Galanga MBL 1988; Huila MBL 1984; Humbe MBL 1985; 5 km N of João de Almeida TM 45165; Missao di Dondi, Bella Vista MCZ 32480; Ponanghuma, Mossamedes BMNH 1917.6.29.50-1. **ZAMBIA.** Chilubi Island (Pike 1964); Kalabo NMZB-UM 4848, 20928; Kalimankonde (Pike 1964); Lealui MNHN 1920-110 (type of barotseensis Angel); Livingstone NMZB 1934, 3131, NMZL 1507-8; SAM 9413; Machile Forest Stn NMZB 3800-1, 4266; Mwananawa FMNH 133058; Namwala NMZB-UM 1696. **D.R.C. (KATANGA).** S of Lake Bangweulu MRAC 4497 (De Witte 1953: 276, Fig. 98). **NAMIBIA** [ENWC = specimens from the Eastern National Water Carrier, see Griffin *et al.* 1989]. No precise locality FMNH 64480-1; USNM 154160; Autabid Sud 100, Windhoek HF3; TM 44124; Bergland, Windhoek NMWN 2495; Bethlehem, Windhoek TM 54804; Brakwater 48, Windhoek TM 45092; Colorado Oos, Otjiwarango NMWN 5278; De Hoek 878, Omaheke NMWN 2496-7; Dei Gratia (ENWC) NMWN 9779; Eava 383, Gobabis HF 24; NMWN 2481, 2491, 2494; TM 79294; Epata, Tsumkwe TM 82305; Friedrichswald, Swakop River FMNH 74057; Gobabis ZMB 28527; Grootfontein (ENWC) NMWN 7511, 7519-21; Herrenhofen, Gobabis TM 65570; Kalizo Lodge, Zambezi River NMWN 9602, 9738; Kamanjab SAM 17565; Kapaku, Okavango NMWN 2490; Katima Mulilo NMWN (B23,25,27); TM 47164-5, 47707; 15 km WSW of Katima Mulilo NMZB-UM 21288, 22804; Kehoro South 160, Gobabis NMWN 2486, 2492; Keres 39, Windhoek NMWN 2489, 2493; Klein Hamakari NMWN 9777; Klein

Okapulua, Windhoek TM 67871; Labora 436, Gobabis TM 33496, 33676; Leeubron, Etosha Nat. Park NMWN (B34); Lianshulu Lodge NMWN (B26); Lichtenstein, Windhoek ZMB 27650; Mpacha, Caprivi TM 55881; Namutoni TM 5780; Oamites, Rehoboth TM 30463; Okahandja FMNH 61644, 81617; MCZ 21016; PEM 2368; TM 71261; ZMB 21596; Okakarara NMWN 6795, 6797; Okamukaru 258, Gobabis TM 80385; Okanjindi 970 (ENWC) NMWN 9782; Okaukuejo NMWN 9735, 9774, 9776, 9780; TM 37643; Omatako (ENWC) NMWN 7541-3; Ombika, Etosha Nat. Park NMWN 9781; Ombujomatamba ZMB 35524; Ondeka, Etosha Nat. Park NMWN 9523; Ondekaremba, Windhoek NMWN 4325; Onjoka 333, Otjiwarongo NMWN 5297; Oshikango TM 17095; Otjinine NMWN 4338; Otjiwarongo NMWN 2482; 9 km S of Otjiwarongo TM 71526; 60 km S of Otjiwarongo NMWN (B12); Otjiwarongo to Grootfontein (ENWC) NMWN 7470, 7484, 7489, 7510, 7552, 7583, 7586-95, 7613-5, 7619-20; Plaas Maitland NMWN 7520; Rietfontein North TM 5882; Rodenstein, Otjiwarongo TM 68597; Schönhausen (ENWC) NMWN (B28); Shinkara NMWN 9778; Talismanis area SMWN 6616; Wilhelmstal, Okahandja FMNH 75702; Windhoek NMWN 2483, 9734; Windhoek- 20 km to Okahandja NMWN 9775; Windhoek Airport NMWN 6607, 6629, **BOTSWANA.** Bushman Pits NMZB-UM 10487; 15 km SSE of Gomare NMZB-UM 16193; Kasane NMZB 13336; Khwae NMZB-UM 28216; Kwando River NMZB-UM 23266; Maun FMNH 17659-60; NMZB-UM 17660, 18076, 18969-71, 20172, 20758; TM 14725-6; Mongalatsetla, Ghanzi BMNH 1931.2.3.4; Shakawe TM 31098; 25 km S of Shakawe NMZB-UM 31521; Toromoja NMZB-UM 26799. **ZIMBABWE.** Dete NMZB-UM 31324; Kazuma Depression (W) NMZB 9203, 9251, 12059; 3km WNW of Kenmaur NMZB 6887; Main Camp, Hwange Nat. Park NMZB 13373; NMZB-UM 29616-8; Maraposa, Umguzo NMZB 6117; Matetsi River Bridge NMZB-UM 585; Ngamo, Hwange Nat. Park NMZB-UM 28092; Nyamandhlovu Pan, Hwange Nat. Park NMZB-UM 1156; Umtshibi, Hwange NMZB 16699; Victoria Falls NMZB 13880; 25 km SE of Victoria Falls NMZB-UM 388.

NAJA ANNULIFERA x *ANCHIETAE*: **ZIMBABWE.** Bulawayo NMZB 296, 3948, 7491; Dete NMZB-UM 31324; Main Camp, Hwange Nat. Park NMZB-UM 852; Matobo South NMZB-UM 11996.