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In praise of subgenera: taxonomic status of cobras of the genus *Naja* Laurenti (Serpentes: Elapidae)

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Abstract

The genus *Naja* Laurenti, 1768, is partitioned into four subgenera. The typical form is restricted to 11 Asian species. The name *Uraeus* Wagler, 1830, is revived for a group of four non-spitting cobras inhabiting savannas and open formations of Africa and Arabia, while *Boulengerina* Dollo, 1886, is applied to four non-spitting African species of forest cobras, including terrestrial, aquatic and semi-fossorial forms. A new subgenus is erected for seven species of African spitting cobras. We recommend the subgenus rank as a way of maximising the phylogenetic information content of classifications while retaining nomenclatural stability.

Key words: *Naja, Uraeus, Boulengerina, Afronaja* subgen. nov., taxonomy, Africa, Asia

Introduction

The scientific nomenclature of life serves the key function of providing labels for the cataloguing of the Earth's biodiversity and thus for information retrieval. In order to make a system of classification predictive, it is generally agreed that a classification should reflect the current state of knowledge about the evolutionary relationships within a group, which, in the case of a nested, hierarchical system of nomenclature, means recognizing only monophyletic groups as named taxa. However, this creates the dilemma that, whereas the function of information retrieval ideally requires stability of names, our developing understanding of the Tree of Life requires changes in nomenclature, to reflect new insights into patterns of relationships provided by ongoing research. This issue is particularly acute at low taxonomic levels, where novel insights into the phylogeny of relatively closely related groups of organisms may reveal long-established genera to be non-monophyletic: a change in genus allocation of a species changes the scientific name of the species itself, thus impeding information retrieval. As a result, changes in genus allocation are often slow to percolate into the non-systematic literature (e.g., Wüster & McCarthy, 1996) or may encounter resistance (e.g. Orlov *et al*., 2004), particularly if multiple studies propose different arrangements in relatively quick succession (e.g., Pizatto *et al*., 2008). This matters particularly in the case of high profile species, such as those of medical importance, where nomenclatural confusion can seriously hamper later research.

This situation exemplifies the dilemma between using nomenclature as an information retrieval and cataloguing system, and also to represent organismal phylogeny. Smith & Chiszar (2006) highlighted the usefulness of the rank of subgenus in these circumstances: where a large monophyletic genus contains well-defined lineages that could usefully be endowed with scientific names, the subgenus rank provides the opportunity to do so without altering the binomial name of the animal, which would interfere with information retrieval, thus increasing the overall information content of the classification. The rank of subgenus has been relatively little-used in recent herpetological taxonomy, particularly among snakes (but see Tokar, 1989, for

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Eryx; Lenk *et al*., 1999, for *Bitis;* Kharin, 2004, for *Hydrophis),* although it was previously used in the 19th Century (e.g., Peters, 1860, 1861; Jan & Sordelli, 1860-1881; Jan, 1863; Steindachner, 1867; Duméril *et al*., 1870–1909). Here, we revisit the taxonomy of the genus *Naja* in the light of recent advances in our understanding of the phylogeny of the genus, and apply the rank of subgenus to highlight the main lineages of phylogenetic, biogeographical and/or morphological interest within the genus.

Systematics

Cobras are among the most widely known of all snakes, and yet, despite their popular notoriety, their taxonomy has long remained poorly understood. Within the genus *Naja,* the number of species recognized has risen from six (Klemmer, 1963) to 23, through a series of revisions (Broadley, 1968, 1995; Wüster 1996; Slowinski & Wüster 2000; Broadley & Wüster, 2004; Wüster *et al*., 2007). Additionally, several recent molecular phylogenetic studies have provided evidence for the paraphyly of *Naja* with respect to *Boulengerina* and *Paranaja*, prompting the synonymization of these two genera with *Naja* (Slowinski & Keogh, 2000; Nagy *et al*., 2005; Wüster *et al*., 2007).

As a result, there are currently 26 extant species of terrestrial Old World cobras assigned to the genus *Naja,* of which 11 inhabit Asia and 15 occur in Africa. This number does not include the four extinct species assigned to *Naja* nor the distantly related African arboreal cobras (*Pseudohaje*), shield cobras (*Aspidelaps*), desert cobras (*Walterinnesia*) or the rinkhals (*Hemachatus*).

Bogert (1943) demonstrated a significant difference between the more derived dentition of Asiatic *Naja* in comparison with that of African *Naja,* the Asiatic taxa having 0–1 solid maxillary teeth and the African species having 2–3, exceptions representing a small minority of cases (see below). Szyndlar & Rage (1990) and Wüster & Thorpe (1992a) noted that *Naja oxiana* shares the derived condition of other Asian species *(contra* Bogert, 1943). Furthermore, Szyndlar & Rage (1990) also noted that the Asian species share the derived characteristic of a Vidian canal that is opened extracranially (vs. intracranially), and Underwood (*in* Szyndlar & Rage, 1990) reported differences in the form of the premaxilla, with the Asiatic group being more derived.

Wüster *et al.* (2007) demonstrated that cobras of the genus *Naja* form three separate evolutionary lineages, one of them with two major sublineages: 1) an Asiatic lineage represented by *N. kaouthia, N. naja, N. siamensis,* and *N. sputatrix,* 2) an African non-spitter lineage composed of two sister lineages, one including *N. annulifera, N. haje,* and *N. nivea*, the other *N. melanoleuca* plus *Boulengerina annulata* and *Paranaja multifasciata,* and 3) an African spitter lineage composed of *N. ashei, N. katiensis, N. mossambica, N. nigricincta, N. nigricollis, N. nubiae,* and *N. pallida* (Fig. 1). In the interest of nomenclatural stability, since members of the genus *Naja* are large and dangerously venomous snakes with an important medical and taxonomic literature based on the generic name, Wüster *et al.* (2007) (like Nagy *et al.*, 2005, in the case of *Boulengerina*) synonymized the African water cobras *(Boulengerina)* and the African burrowing cobra *(Paranaja),* snakes that are quite different in size, external morphology, internal anatomy, diet, behaviour, and habitat preference (Loveridge, 1944; Spawls & Branch, 1995; Wallach, 1998; Chippaux, 2006). However, this leaves the genus *Naja* as a large and somewhat heterogeneous genus containing a considerable diversity of species, and also multiple, well defined clades that differ in anatomy, distribution and ecology, and may thus warrant nomenclatural recognition. The rank of subgenus is ideally suited to highlight our new understanding of the phylogeny of the group while retaining the nomenclatural stability of a group of iconic species.

In choosing to erect subgenera within the genus *Naja* to reflect its phylogenetic structure, we have elected to recognize four larger groups that fulfil the criteria that (i) their monophyly is strongly supported in previous phylogenetic studies (Wüster *et al*., 2007), and (ii) that they represent lineages with morphological and/or distributional or ecological characteristics that can be suitably underscored through recognition as subgenera. On that basis, the four major clades of *Naja* recognised as subgenera are as follows: 1) the 11 species of Asiatic *Naja*; 2) six species of open-formation non-spitting African cobras (the *N. haje* group, *N. nivea),* 3)

four species of forest-dwelling African non-spitting cobras (*N. annulata, N. christyi, N. melanoleuca, N. multifasciata*), and 4) the seven species of African spitting *Naja*.

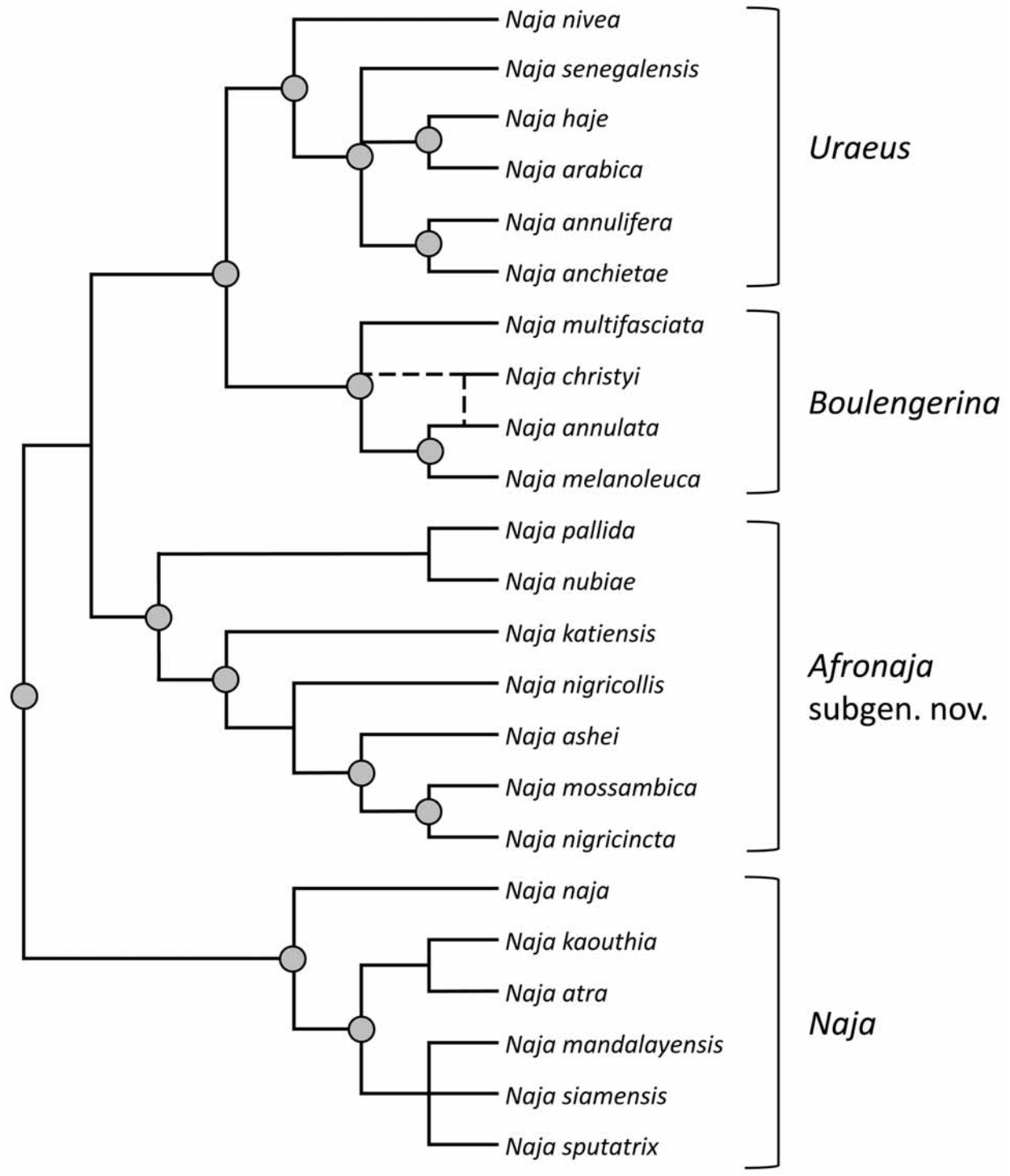

FIGURE 1. Schematic representation of the phylogeny of the genus *Naja*, indicating the subgenera recognised here. Redrawn from Wüster *et al.* (2007). Grey circles indicate nodes with ≥ 95% Bayesian posterior probability support. The position of taxa not included in that study was inferred from Slowinski & Wüster (2000 – *N. atra*, *N. mandalayensis*), Broadley & Wüster (2004 – *N. annulifera*) and Trape *et al.* (2009 – *N. arabica*, *N. senegalensis*). *Naja christyi* has never been included in a rigorous phylogenetic analysis. It is tentatively placed in this tree based on prior classification (Bogert, 1943).

While this paper was in preparation, Raymond Hoser, one of several recent amateur herpetologists who have chosen to publish evidence-free taxonomic papers in self-published outlets or in the unreviewed hobbyist literature (see Williams et al., 2006, for a review), named two new genera, for the *Naja haje* group and the African spitting cobras, in his privately edited, online publication Australasian Journal of Herpetology (Hoser, 2009). Hoser (2009) provided no new data, and his generic diagnoses and descriptions are replete with errors: for instance, he overlooked the existing name *Uraeus* Wagler 1830, which takes precedence over his genus *Wellsus*; Asian *Naja* have 15–25 midbody dorsal scale rows (not 21–25), 19–37 scale rows around the hood (not 25–35), 36–71 subcaudal scales (not 43–56), 153–210 ventral scales (not 164–200) (Wüster, 1990; Wüster & Thorpe, 1989, 1992a; Wüster *et al*, 1997); the fourth as well as the third supralabial enter the eye; the solid maxillary teeth number 0 or 1, not 1–3 (Bogert, 1943; Szyndlar & Rage, 1990); many Asian *Naja* have highly modified spitting fangs, just like African spitting cobras (Bogert, 1943; Wüster & Thorpe, 1992b; Wüster *et al*., 1997); and important skeletal characters (Szyndlar & Rage, 1990) were ignored. Other counts are confusing and difficult to attribute to specific taxa recognized by Hoser.

More importantly from the nomenclatural point of view, this online publication does not constitute a published work according to Articles 8.1.3, 8.6, 9.7 and 9.8 of the International Code of Zoological Nomenclature (ICZN, 1999) (hereafter referred to as "the Code). The new names published therein are therefore unavailable under the rules of the Code. Article 8.6 states that "For a work produced after 1999 by a method other than printing on paper to be accepted as published under the meaning of the Code, it must contain a statement that copies (in the format that it is published) have been deposited in at least five major publicly accessible libraries which are identified by name in the work itself." Although Hoser claims the existence of a printed version of his journal, we have found evidence of only one single copy, deposited in the Australian National Library (ANL). Article 9 of the Code (What does not constitute published work) includes: "9.7 copies obtained on demand of an unpublished work [Art. 8], even if previously deposited in a library or other archive." On 9 May 2009, one of us (VW) received printed copies of all issues of the *Australasian Journal of Herpetology.* Unlike the ANL copy of Issue 7, all these issues are printed on one side only, and give the appearance of having been printed on demand at the same time: all have a pair of longitudinal white lines along the midline of the entire page: issue 1 has the lines spaced about 2 mm apart but all the other issues have the lines spaced 5 mm apart, suggesting that they were printed at the same time. These lines are not present in the ANL copy of Issue 7. All the issues received by us are bound by a single large staple in the upper, left hand corner. We conclude that the *Australasian Journal of Herpetology* is an online publication that fails to fulfill the requirements of Articles 8.1.3 and 8.6, any printed copies are printed on demand and therefore do not constitute published work under the provisions of Article 9.7, and the electronic versions available from Hoser's website are not published under the provisions of Article 9.8. The same almost certainly applies to the previous six issues of the journal published at the time of writing.

Since Hoser's 2009 paper is unavailable under the provisions of the Code, we therefore propose the following nomenclatural changes regarding the genus *Naja:* the subgeneric name *Naja* must be applied to the Asiatic cobras, whose type species is *Naja naja* Linnaeus; the non-spitting African cobras are assigned to the subgenera *Uraeus* Wagler (1830), with *Naja haje* as the type species, and *Boulengerina* Dollo (1886), with *Naja annulata* as the type species, while the African spitters are placed in a new subgenus with *Naja nigricollis* as the type species.

Genus *Naja* Laurenti, 1768

Subgenus *Naja* Laurenti, 1768

Naia Merrem, 1820: 147 (unjustified emendation of *Naja* Laurenti, 1768)
Aspis Wagler, 1830: 173 (not Laurenti) (type species *Coluber naja* Linnaeus, 1758)
Tomyris Eichwald, 1831: 171 (type species *Tomyris oxiana* Eichwald, 1831)

Naga Nicholson, 1874: 104 (unjustified emendation of *Naja* Laurenti, 1768)
†*Palaeonaja* Hoffstetter, 1939: 57 (type species †*Palaeonaja romani* Hoffstetter, 1939)

Type species: *Naja lutescens* Laurenti, 1768 (= *Coluber naja* Linnaeus, 1758), by subsequent designation (Leviton, 1968).

Gender: feminine.

Etymology: derived from the Sinhala *Naya*, cobra.

Distribution: southern and south-eastern Asia and the East Indies, from Transcaspia to the Philippines and the Lesser Sunda Islands.

Content: eleven species:

Naja (Naja) atra Cantor, 1842: 482
Naja (Naja) kaouthia Lesson, 1831: 122
Naja (Naja) mandalayensis Slowinski & Wüster, 2000: 260
Naja (Naja) naja (Linnaeus, 1758: 221)
Naja (Naja) oxiana (Eichwald, 1831: 171)
Naja (Naja) philippinensis Taylor, 1922: 265
Naja (Naja) sagittifera Wall, 1913: 247
Naja (Naja) samarensis Peters, 1861: 690
Naja (Naja) siamensis Laurenti, 1768: 91
Naja (Naja) sputatrix Boie, 1827: 557
Naja (Naja) sumatrana Müller, 1890: 277

Diagnosis: Extracranial (ventral) anterior Vidian canal position, 0–1 solid maxillary teeth in all species (Wüster, 1990—only 6 out of 650 specimens examined in that study had 2 solid maxillary teeth), seven supralabials with penultimate (sixth) shield low, combination of single preocular and two (occasionally three) anterior temporals, rostral broader than deep; internasals shorter than prefrontals; fang structure variable, all species except *N. naja* and *N. oxiana* have some degree of adaptation to spitting (Wüster & Thorpe, 1992b). We tentatively include the extinct †*Naja* (*Naja*) *romani* (Hofstetter, 1939) in this subgenus based on the shared derived condition of the basisphenoid morphology and the vestibular window, despite the possession of two solid maxillary teeth (Szyndlar & Rage, 1990).

Comments: this is a morphologically relatively conserved, but ecologically highly adaptable subgenus that appears to be the result of a single colonization event of Asia from an African origin (Slowinski & Wüster, 2000; Wüster *et al*., 2007; Wüster, unpublished data).

The issue of the type species of *Naja* has a complex background. Laurenti's (1768) *Naja* was based upon six species from Seba (1734–1735), all of which Linnaeus (1758) included in his synonymy of *Coluber naja* (in addition to 1735: pl. 85, fig. 1 and 1735: pl. 94, fig. 1): *N. brasiliensis* (1735: pl. 89, fig. 4) = *Naja naja*, *N. fasciata* (1735: pl. 89, fig. 3) = *Naja naja*, *N. lutescens* (1734: pl. 44, fig. 1) = *Naja naja*, *N. maculata* (1735: pl. 90, fig. 2) = *Naja naja*, *N. non Naja* (1735: pl. 90, fig. 1) = *Naja kaouthia*, and *N. siamensis* (1735: pl. 89, figs. 1–2) = *Naja siamensis*. *Naja naja* (Linnaeus) has been considered the type species of *Naja* by tautonymy, monotypy, and subsequent designation of Stejneger (1936: 140), M. Smith (1943: 426), Oshima (1944: 204), and others. However, David & Vogel (1996: 146) suggested that those assumptions were incorrect and that the only valid type species designation was that of Williams & Wallach (1989: 97), who selected *Naja lutescens*. However, Leviton (1968: 547) designated *Naja lutescens* Laurenti (=*Coluber naja* Linnaeus) as the type species of *Naja* Laurenti and several earlier nomenclatural acts precede this action. Cantor (1847: 1038) could be considered the first revisor as he synonymized *Naja lutescens* with *Coluber naja* Linnaeus. Deraniyagala (1945: 108–109) then restricted the name *Naja lutescens* to the race of cobras inhabiting India south of 20° N Latitude. The type locality of Seba's (1735) pl. 44, fig. 1 was given as "India Orientali." Deraniyagala (1945) recognized *Naja naja lutescens* as a subspecies and designated the type locality as Madras, with *N. fasciata* and *N. maculata* as synonyms.

Subgenus *Uraeus* Wagler, 1830

Type species: *Coluber haje* Linnaeus, 1758, by monotypy.

Gender: masculine.

Etymology: derived from the Egyptian *uraeus*, a symbol of the goddess Wadjet in the shape of a cobra with a spread hood, which formed part of the head-dress of Egyptian divinities and kings.

Distribution: open formations in most of Africa and southern Arabia.

Content: six species:

Naja (Uraeus) anchietae Bocage, 1879: 89
Naja (Uraeus) annulifera Peters, 1854: 624
Naja (Uraeus) arabica Scortecci, 1932: 47
Naja (Uraeus) senegalensis Trape, Chirio & Wüster in Trape et al, 2009: xxx
Naja (Uraeus) haje (Linnaeus, 1758: 225)
Naja (Uraeus) nivea (Linnaeus, 1758: 223)

Diagnosis: Intracranial (dorsal) anterior Vidian canal position, almost always 2–3 solid maxillary teeth (one specimen out of 21 examined by Bogert [1943] and Szyndlar & Rage [1990] had one solid maxillary tooth on each side), seven supralabials with penultimate (sixth) shield high, combination of one preocular and one anterior temporal, rostral as broad as deep, internasals as long as prefrontals, dorsal scales matt or moderately shiny, and fangs not adapted for spitting.

Comments: This is a morphologically relatively conserved lineage that occupies open formations in much of Africa and the southern Arabian Peninsula. The most basal cladogenic split separates *Naja (Uraeus) nivea*, a species largely restricted to southern African areas with winter rainfall, from the remaining species, which occupy primarily tropical or subtropical formations (Wüster *et al.*, 2007).

Subgenus *Boulengerina* Dollo, 1886

Limnonaja Schmidt, 1923: 124 (type species *Boulengerina christyi* Boulenger, 1904)
Paranaja Loveridge, 1944: 231 (type species *Naja anomala* Sternfeld = *Naia multifasciata* Werner, 1902)

Type species: *Boulengerina stormsi* Dollo, 1886 (= *Naja annulata* Buchholz & Peters *in* Peters, 1876), by monotypy.

Gender: feminine.

Etymology: dedicated to George Albert Boulenger, famous Belgian herpetologist, and curator of reptiles at the British Museum (Natural History) in London from 1881 to 1920.

Distribution: forested regions of western, central, eastern and south-eastern Africa.

Content: four species:

Naja (Boulengerina) annulata Buchholz & Peters *in* Peters, 1876: 119
Naja (Boulengerina) christyi (Boulenger, 1904: 14)
Naja (Boulengerina) melanoleuca Hallowell, 1857: 61
Naja (Boulengerina) multifasciata Werner, 1902: 347

Diagnosis: Intracranial (dorsal) anterior Vidian canal position, 2–4 solid maxillary teeth, penultimate (sixth) supralabial high, combination of one preocular and one anterior temporal (except *N. christyi*, which sometimes has two anterior temporals), rostral much broader than deep, internasals shorter than prefrontals, dorsal scales highly polished, fangs not modified for spitting.

Comments: This subgenus is morphologically and ecologically highly diverse, including species at both the large (*Naja melanoleuca*) and small (*Naja multifasciata*) extremes of the size spectrum of the cobra clade,

and semi-fossorial, terrestrial and aquatic forms. However, they are united by their restriction to forest and forest edge habitats, and their distribution is centred on the central African forests, with only *N. melanoleuca* extending significantly into West and East Africa.

Subgenus *Afronaja* subgen. nov.

Type species: *Naja nigricollis* Reinhardt, 1843, by present designation.

Gender: feminine.

Etymology: from Africa, referring to the distribution of the subgenus, and the Sinhala *Naya*, snake or cobra.

Distribution: open formations and forest edges throughout sub-Saharan Africa and Nile Valley north to central Egypt.

Content: seven species:

Naja (Afronaja) ashei Wüster & Broadley, 2007: 58
Naja (Afronaja) katiensis (Angel, 1922: 40)
Naja (Afronaja) mossambica Peters, 1854: 625
Naja (Afronaja) nigricincta Bogert, 1940: 89
Naja (Afronaja) nigricollis Reinhardt, 1843: 269
Naja (Afronaja) nubiae Wüster & Broadley, 2003: 348
Naja (Afronaja) pallida Boulenger, 1896: 379

Diagnosis: Intracranial (dorsal) anterior Vidian canal position, 2–3 solid maxillary teeth, six supralabials (except some *N. nubiae* and *N. pallida*) with penultimate (fifth or sixth) shield low, combination of two preoculars and two or three anterior temporals, rostral as broad as deep; internasals as long as prefrontals, dorsal scales matte or moderately shiny, and fangs adapted for spitting.

Comments: A morphologically and ecologically relatively conserved lineage occupying a wide variety of open formations in most of sub-Saharan Africa, but not rainforests themselves; the most basal division in the phylogeny separates two north-east African species (*N. nubiae* and *N. pallida*), occurring primarily in relatively arid areas, from the remainder of the subgenus (Wüster *et al*., 2007).

Naja incertae sedis

Three of the four currently recognized extinct cobra species, †*Naja antiqua* Rage, 1976, †*Naja iberica* Szyndlar, 1985, and †*Naja robusta* Meylan, 1987, cannot be allocated to any subgenus with confidence, as identifying synapomorphies are lacking (Rage, 1976; Szyndlar, 1985; Meylan, 1987). They are therefore placed in *Naja incertae sedis.*

Key to the subgenera of African and Asian cobras (extant species only)

1a. Solid maxillary teeth behind fangs 0–1; 1 preocular **and** 2–3 anterior temporals ..... *Naja*
1b. Solid maxillary teeth behind fangs 2–3; normally **either** 1 preocular **or** 2–3 anterior temporals..... 2
2a. Penultimate (usually 5th, sometimes 6th) supralabial low, not enlarged, not contacting postocular scales; two or more anterior temporal shields; fangs adapted for spitting .....*Afronaja* subgen. nov.
2b. Penultimate (6th) supralabial high, enlarged, contacting postocular scales; normally one anterior temporal shield; fangs not adapted for spitting..... 3
3a. Rostral as broad as deep; internasals as long as the prefrontals; dorsal scales matte or moderately shiny..... *Uraeus*
3b. Rostral much broader than deep; internasals shorter than prefrontals; dorsal scales highly polished..... *Boulengerina*

Conclusion

We believe that our reclassification of the cobras of the genus *Naja* illustrates the usefulness of the underused rank of subgenus in zoological nomenclature. As advocated by Smith & Chiszar (2006), the use of the subgenus rank allows the representation of improved phylogenetic resolution of the genus *Naja* while reducing the disruptive effect of nomenclatural changes on other disciplines of biology that are less closely linked to systematics and phylogeny. The subgenera recognised here serve as formal nomenclatural labels for robustly supported lineages of cobras united by morphological and/or ecological characteristics, while the formal generic name of each species remains unchanged, thus facilitating information retrieval. We suggest that increased use of the subgenus rank would be welcomed by a substantial proportion of the wider biological community.

As a final note, the authors find it profoundly disconcerting that, 25 years after the controversy surrounding the publications of Wells & Wellington (1984, 1985 – see Thulborn, 1986), taxonomy remains as vulnerable to acts of nomenclatural vandalism as it was then. In the middle of the current biodiversity crisis, taxonomists should be able to devote their time to studies of taxonomy rather than cleaning up after evidence-free taxonomic acts perpetrated in self-published, un-reviewed publications. We urge the International Commission on Zoological Nomenclature to give the fight against nomenclatural vandalism highest priority as part of its stated mission, 'achieving stability and sense in the scientific naming of animals'.

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References

Angel, F. (1922) Sur une collection de reptiles et de batraciens, recueillis au Soudan français par la mission du Dr. Millet Horsin. *Bulletin du Muséum national d'Histoire naturelle de Paris* 28, 39–41.

Bocage, J.V.B. Du (1879) Subsidios para a fauna das possessões portuguezas d'Africa occidental. *Jornal de sciencias mathematicas, physicas, e naturaes da Academia Real das Sciencas de Lisboa*, 7, 85–96.

Bogert, C.M. (1940) Herpetological results of the Vernay-Angola Expedition, with notes on African reptiles in other collections. I. Snakes, including an arrangement of African Colubridae. *Bulletin of the American Museum of Natural History*, 77, 1–107.

Bogert, C.M. (1943) Dentitional phenomena in cobras and other elapids with notes on adaptive modifications of fangs. *Bulletin of the American Museum of Natural History*, 81, 285–360.

Boie, F. (1827) Bemerkungen über Merrem's Versuch eines Systems der Amphibien. Erste Lieferung: Ophidier. *Isis von Oken*, 20, col. 508–566.

Boulenger, G.A. (1896) *Catalogue of the Snakes in the British Museum (Natural History)* 3. British Museum (Natural History), London, 727 pp.

Boulenger, G.A. (1904) Descriptions of two new elapine snakes from the Congo. *Annals and Magazine of Natural History*, 7, 453–456.

Broadley, D.G. (1968) A review of the African cobras of the genus *Naja* (Serpentes: Elapinae). *Arnoldia Rhodesia*, 3, 1–14.

Broadley, D.G. (1995) The snouted cobra, *Naja annulifera*, a valid species in southern Africa. *Journal of the Herpetological Association of Africa*, 44, 26–32.

Broadley, D.G. & Wüster, W. (2004) A review of the southern African 'non-spitting' cobras (Serpentes: Elapidae: *Naja*). *African Journal of Herpetology*, 53, 101–122.

Cantor, T.E. (1842) General features of Chusan, with remarks on the flora and fauna of that island. *Annals and Magazine of Natural History*, 1, 265–277.

Cantor, T.E. (1847) Catalogue of reptiles inhabiting the Malayan Peninsula and islands, collected or observed by Theodore Cantor. Venomous serpents. *Journal of the Asiatic Society of Bengal*, 16, 1026–1078.

Chippaux, J.-P. (2006) *Les serpents d'Afrique occidentale et cenrale.* Institut de Recherche pour le Développement (IRD), Paris, 311 pp., 16 Pls.
David, P. & Vogel, G. (1996) *The snakes of Sumatra: an annotated checklist and key with natural history notes.* Edition Chimaira, Frankfurt am Main, 260 pp., 8 Pls.
Deraniyagala, P.E.P. (1945) Some new races of the python, *Chrysopelea,* binocellate cobra, and tith-polonga inhabiting Ceylon and India. *Spolia Zeylanica,* 24(2), 103–112.
Dollo, L. (1886) Note sur les reptiles et batraciens recueillis par M. le Capitaine Em. Storms dans la region du Lac Tanganyika. *Bulletin du Musée Royal d'Histoire Naturelle de Belgique,* 4, 151–160.
Duméril, A.H.A., Bocourt, F. & Mocquard, F. (1870–1909) *Recherches zoologiques pour servir a l'histoire de la faune de l'Amérique Centrale et du Mexique. Troisième partie. – 1re section. Études sur les reptiles.* Imprimerie Impériale, Paris, 1012 pp., 77 Pls.
Eichwald, E. (1831) *Zoologia specialis quam expositis animalibus tum vivis, tum fossilibus potissimum Rossiae in universum, et Poloniae in species, in usum lectionum publicarum in Universitate Caesareae Vilnensi habendarum. Part 3.* Josephi Zawadski, Vilnius, 396 pp.
Hallowell, E. (1857) Notice on a collection of reptiles from the Gaboon country, West Africa, recently presented to the Academy of Natural Sciences in Philadelphia by Dr. Henry A. Ford. *Proceedings of the Academy of Natural Sciences of Philadelphia,* 9, 48–72.
Hoffstetter, R. (1939) Contribution à l'étude des Elapidae actuels et fossiles et de l'ostéologie des ophidiens. *Archives du Muséum d'Histoire Naturelle de Lyon,* 15, 1–78, 2 Pls.
Hoser, R. (2009) A reclassification of the true cobras; species formerly referred to the genera *Naja, Boulengerina* and *Paranaja. Australasian Journal of Herpetology,* 7, 1–15.
ICZN (1999) *International Code of Zoological Nomenclature. Fourth edition.* International Commission on Zoological Nomenclature, London, 306 pp.
Jan, G. (1863) *Elenco sistematico degli ofidi descritti e disegnati per l'Iconografia Generale.* A. Lombardi, Milano, 143 pp.
Jan, G. & Sordelli, F. (1860–1881) Iconographie générale des ophidiens. Tome I–III. Georges Jan et Ferdinand Sordelli, Milan, 39 pp., 300 Pls.
Kharin, V.E. (2004) Review of sea snakes of the genus *Hydrophis* sensu stricto (Serpentes: Hydrophiidae). *Russian Journal of Marine Biology* 30, 387–394.
Klemmer, K. (1963) Liste der Rezenten Giftschlangen. *In: Die Giftschlangen der Erde (Behringwerke–Mitteilungen).* N. G. Elwert, Marburg, pp. 255–464.
Laurenti, J.N. (1768) *Austriaci Viennensis Specimen Medicum, Exhibens Synopsin Reptilium Emendatam Cum Experimentis Circa Venena et Antidota Reptilium Austriacorum.* J.T. De Trattern, Viennae, 214 pp.
Lenk, P., Herrmann, H.-W., Joger, U. & Wink, M. (1999) Phylogeny and taxonomic subdivision of *Bitis* (Reptilia: Viperidae) based on molecular evidence. *Kaupia,* 8, 31–38.
Lesson, R.P. (1831) Catalogue des reptiles qui font partie d'une collection zoologique recueillie dans l'Inde continentale ou en Afrique et rapportée en France par M. Lamare-Piquot. *Bulletin des Sciences Naturelles et de Géologie, Paris,* 25, 119–123.
Leviton, A.E. (1968) The venomous terrestrial snakes of East Asia, India, Malaya, and Indonesia. *In:* Bücherl, W., Buckley, E.E. & Deulofeu, V. (Eds.), *Venomous animals and their venoms. Volume I. Venomous vertebrates.* Academic Press, New York, pp.529–576.
Linnaeus, C. von. (1758) *Systema Naturae per Regna Tria Naturae secundum Classes, Ordines, Genera, Species cum Characteribus Differentiis, Synonymis, Locis.* Stockholm, Laurentii Salvii, 824 pp.
Loveridge, A. (1944) Further revisions of African snake genera. *Bulletin of the Museum of Comparative Zoology,* 95(2), 121–247.
Merrem, B. (1820) *Versuch eines Systems der Amphibien.* Johann Christian Krieger, Marburg, xv + 191 pp., 1 Pl.
Meylan, P.A. (1987) Reptiles and birds. Fossil snakes from Laetoli. *In:* Leakey, M.D. & Harris, J.M. (Eds.), The Pliocene site of Laetoli, northern Tanzania, Oxford University Press, Oxford, pp. 78–82.
Müller, F. (1887 [1890]) Fünfter Nachtrag zum Katalog der herpetologischen Sammlung des Basler Museums. *Verhandlungen der naturforschenden Gesellschaft in Basel,* 8, 249–296.
Nagy, Z.T., Vidal, N., Vences, M., Branch, W.R., Pauwels, O.S.G., Wink, M. & Joger, U. (2005) Molecular systematics of African Colubroidea (Squamata: Serpentes) *In:* Huber, B.A., Sinclair, B.J. & Lampe, K.H. (Eds.), *African Biodiversity: Molecules, Organisms, Ecosystsms.* Proceedings of the 5th International Symposium on Tropical Biology, Museum Koenig, Bonn. Springer Verlag, Berlin, pp. 221–228.
Nicholson, E. (1874) *Indian snakes. An elementary treatise on ophiology with a descriptive catalogue of the snakes found in India and the adjoining countries.* Second edition. Higginbotham and Company, Madras, 188 pp., 20 Pls.
Orlov, N.L., Ryabov, S.L., Thanh, B.N. & Cuc, H.T. (2004) A new species of *Trimeresurus* (Ophidia: Viperidae: Crotalinae) from Karst region in Central Vietnam. *Russian Journal of Herpetology,* 11, 139–149.
Oshima, M. (1944) *"Poisonous snakes in East and South Asia."* Hokuryukan, Tokyo, 330 + 19 pp., 18 Pls. [in Chinese]

Peters, W.K.H. (1854) Diagnosen neuer Batrachier, welche zusammen mit der früher (24. Juli und 17. August) gegebenen Übersicht der Schlangen und Eidechsen mitgetheilt werden. *Bericht über zur Bekanntmachung geeignete Verhandlungen der Königlichen Preussischen Akademie der Wissenschaften zu Berlin*, 1854, 614–628.

Peters, W.K.H. (1860) Über eine zu der Gattung *Onychocephalus* gehörige Wurmschlange, *Onychocephalus macrurus*, und ein Vergleich mit den bisher von dieser Gattung bekannt gewordenen Arten. *Monatsberichte der Königlichen Preussischen Akademie der Wissenschaften zu Berlin*, 1860, 77–83.

Peters, W.K.H. (1861) Eine zweite Übersicht (vergl. Monatsberichte 1859 p. 269) der von Hrn. F. Jagor auf Malacca, Java, Borneo und den Philippinen gesammelten und dem Kgl. Zoologischen Museum übersandten Schlangen. *Monatsberichte der Königlichen Preussischen Akademie der Wissenschaften zu Berlin*, 1861, 683–691.

Peters, W.K.H. (1876) Eine zweite Mittheilung über die von Hrn. Professor D. R. Buchholz in Westafrika gesammelten Amphibien. *Monatsberichte der Königlichen Preussischen Akademie der Wissenschaften zu Berlin*, 1875, 117–123.

Pizatto, L., Chilt, T. & Shine, R. (2008) Why be diurnal? Shifts in activity time enable young cane toads to evade cannibalistic conspecifics. *Behavioral Ecology*, 19, 990–997.

Rage, J.-C. (1976) Les squamates du Miocène de Beni Mellal. *Géologie Méditerranéenne*, 3(2), 57–69.

Reinhardt, J.T. (1843) Beskrivelse af nogle nye Slangearter. *Det Kongelige Danske Videnskabernes Selskabs Naturvidenskabelige og Mathematiske Afhandlinger*, 10, 233–277.

Schmidt, K.P. (1923) Contributions to the herpetology of the Belgian Congo based on the collection of the American Museum Congo Expedition, 1909–1915. Part II. Snakes, with field notes by Herbert Lang and James P. Chapin. *Bulletin of the American Museum of Natural History*, 49, 1–146.

Scortecci, G. (1932) Rettili dello Yemen. *Atti della Società Italiana di Scienze Naturali*, 71, 39–49.

Seba, A. (1734–1735) *Locupletissimi rerum naturalium thesauri accurata descriptio, et iconibus artificiosissimis expressio, per universam physices historiam.* Tomus I-II. Janssonio-Waesbergios, J. Wetstenium & Gul. Smith, Amstelaedami, 178 pp., 111 Pls. & 154 pp., 114 Pls.

Slowinski, J.B. & Keogh, S. (2000) Phylogenetic relationships of elapid snakes based on cytochrome *b* mtDNA sequences. *Molecular Phylogenetics and Evolution*, 15, 157–164.

Slowinski, J.B. & Wüster, W. (2000) A new cobra (Elapidae: *Naja*) from Myanmar (Burma). *Herpetologica*, 56, 257–270.

Smith, H.M. & Chiszar, D. (2006) Dilemma of name-recognition: why and when to use new combinations of scientific names. *Herpetological Conservation and Biology*, 1, 6–8.

Smith, M.A. (1943) *The fauna of British India, Ceylon and Burma, including the whole of the Indo-Chinese sub-region. Reptilia and Amphibia. Vol. III.—Serpentes.* Taylor & Francis, London, 583 pp.

Spawls, S. & Branch, W.R. (1995) *The dangerous snakes of Africa: natural history, species directory, venoms and snakebite.* Ralph Curtis Books, Sanibel Island, 192 pp.

Steindachner, F. (1867) *Reise der Österreichischen Fregatte Novara um die Erde in den Jahren 1857, 1858, 1859 unter den Befehlen des Commodore B.von Wüllerstörf-Urbair. Zoologischer Theil. Erster Band. Reptilien.* Kaiserlich-Königliche Hof- und Staatsdruckerei, Wien, pp. 1–98, 3 Pls.

Stejneger, L. (1936) Types of the amphibian and reptilian genera proposed by Laurenti in 1768. *Copeia*, 1936(3), 133–141.

Szyndlar, Z. (1985) Ophidian fauna (Reptilia, Serpentes) from the uppermost Miocene of Algora (Spain). *Estudios Geologicos*, 41, 447–465.

Szyndlar, Z. & Rage, J.-C. (1990) West Palearctic cobras of the genus *Naja* (Serpentes: Elapidae): interrelationships among extinct and extant species. *Amphibia-Reptilia*, 11, 385–400.

Taylor, E.H. (1922) *The Snakes of the Philippine Islands*. Bureau of Printing, Manila, 312 pp.

Thulborn, T. (1986) Taxonomic tangles in Australia. *Nature*, 321,13–14.

Tokar, A.A. (1989) Revision of the genus *Eryx* (Serpentes, Boidae) based on osteologial data. *Vestnik Zoologii*, 4, 46–55.

Trape, J.-F., Chirio, L., Broadley, D.G. & Wüster, W. (2009) Phylogeography and systematic revision of the Egyptian cobra (Serpentes: Elapidae: *Naja haje*) species complex, with the description of a new species from West Africa. *Zootaxa*, in press.

Wagler, J. (1830) Natürliches System der Amphibien, mir Vorangehender Classification der Säugethiere und Vögel. Ein Beitrag zur Vergleichenden Zoologie. J.G. Cotta, München, 354 pp.

Wall, F. (1913) A popular treatise on common Indian snakes. *Naia tripudians* (Merrem). The cobra. *Journal of the Bombay Natural History Society*, 22, 243–259.

Wallach, V. (1998) The lungs of snakes. *In*: Gans, C. & Gaunt, A.S. (Eds.), *Biology of the Reptilia. Volume 19 (Morphology G). Visceral organs*. Society for the Study of Amphibians and Reptiles, Ithaca, pp. 93–295.

Wells, R.W. & Wellington, C.R. (1984) A synopsis of the class Reptilia in Australia. *Australian Journal of Herpetology*, 1, 73–129.

Wells, R.W. & Wellington, C.R. (1985) A classification of the Amphibia and Reptilia of Australia. *Australian Journal of Herpetology Supplementary Series*,1, 1–61.

Werner, F. (1902) Über westafrikanische Reptilien. *Verhandlungen der Zoologischen und Botanischen Gesellschaft in*

Wien, 52, 332–348.
Williams, D., Wüster, W. & Fry, B.G. (2006) The good, the bad and the ugly: Australian snake taxonomists and a history of the taxonomy of Australia's venomous snakes. *Toxicon*, 48, 919–930.
Williams, K.L. & Wallach, V. (1989) *Snakes of the world. Volume I. Synopsis of snake generic names.* Krieger Pubishing Company, Malabar, 234 pp.
Wüster, W. (1990) *Population evolution of the Asiatic cobra (*Naja naja*) species complex*. PhD Thesis, University of Aberdeen.
Wüster, W. (1996) Taxonomic changes and toxinology: systematic revisions of the Asiatic cobras (*Naja naja* species complex). *Toxicon*, 34, 399–406.
Wüster, W. & Broadley, D.G. (2003) A new species of spitting cobra from northeastern Africa (Serpentes: Elapidae: *Naja*). *Journal of Zoology, London*, 259, 345–359.
Wüster, W. & Broadley, D.G. (2007) Get an eyeful of this: a new species of giant spitting cobra from eastern and north-eastern Africa (Squamata: Serpentes: Elapidae: *Naja*). *Zootaxa*, 1532, 51–68.
Wüster, W., Crookes, S., Ineich, I., Mané, Y., Pook, C.E., Trape, J.-F. & Broadley, D.G. (2007) The phylogeny of cobras inferred from mitochondrial DNA sequences: evolution of venom spitting and the phylogeography of the African spitting cobras (Serpentes: Elapidae: *Naja nigricollis* complex). *Molecular Phylogenetics and Evolution*, 45, 437–453.
Wüster, W. & McCarthy, C.J. (1996) Venomous snake systematics: implications for snakebite treatment and toxinology. *In:* Bon, C. & Goyffon, M. (Eds.), *Envenomings and their Treatments*. Fondation Mérieux, Lyon, pp. 13–23.
Wüster, W. & Thorpe, R.S. (1989) Population affinities of the Asiatic cobra (*Naja naja*) species complex in south-east Asia: reliability and random resampling. *Biological Journal of the Linnean Society*, 36, 391–409.
Wüster, W. & Thorpe, R.S. (1992a) Asiatic cobras: population systematics of the *Naja naja* species complex (Serpentes: Elapidae) in India and Central Asia. *Herpetologica*, 48, 69–85.
Wüster, W. & Thorpe, R.S. (1992b) Dentitional phenomena in cobras revisited: fang structure and spitting in the Asiatic species of *Naja* (Serpentes: Elapidae). *Herpetologica*, 48, 424–434.
Wüster, W., Warrell, D.A., Cox, M.J., Jintakune, P. & Nabhitabhata, J. (1997) Redescription of *Naja siamensis* Laurenti, 1768 (Serpentes: Elapidae), a widely overlooked spitting cobra from Southeast Asia: geographic variation, medical importance and designation of a neotype. *Journal of Zoology*, 243, 771–788.