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PSEUDOHAJE GÜNTHER, A VALID GENUS FOR TWO WEST AFRICAN ARBOREAL COBRAS¹

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While engaged in an investigation of the adaptive modifications of the fangs of cobras I have had occasion to examine the maxillae of nearly all African elapid genera. In the course of this work I chanced to notice that, whereas the snake described as Naja goldii usually had three teeth behind the fangs on each maxilla, all other species of African Naja normally have but two. Furthermore, it was noted that even though Naja quentheri had been listed as a synonym of N. goldii, it too possessed differences in the maxillary dentition. more extended investigation of the morphology, pattern and coloration of these cobras disclosed the fact that not only were two distinct species represented, but they differed sufficiently from all other snakes currently referred to Naja to warrant recognition of Pseudohaje, erected by Günther in 1858 for the species with thirteen midbody scale rows.

The nomenclature involving the two species herein referred to *Pseudohaje* is somewhat involved but not very complex. Günther diagnosed the genus in 1858, basing it on the species *nigra*, the only specimen of which was of unknown origin. Boulenger described *Naja goldii* in 1895 and the following year included both species in the third volume of his "Catalogue," referring *nigra* to the genus *Naja*. However, owing to the fact that the name *Naja*

nigra already had been applied to another elapid by Smith in 1838, Boulenger found it necessary to apply a new name, quentheri, to Günther's species and, supposedly upon the basis of its similarity to goldii, he listed the type from "West Africa?" No more definite locality was known for the species until 1897 when Boulenger mentioned a specimen from "Sierra Leone," the westernmost locality yet recorded. Naja yakomae was described by Mocquard in 1895, but he pointed out in a footnote that Boulenger's description of goldii had already appeared, and that, since his species was undoubtedly identical, Boulenger's name should be applied to it. 1900 Boulenger listed both N. yakomae and Pseudohaje nigra as well as his own designation, guentheri, as synonyms of N. goldii, and without presenting any evidence added. "I am now convinced that N. guentheri and N. goldii cannot be maintained as distinct species." Subsequent authors, particularly Schmidt (1923), for the most part accepted Boulenger's concept, although Sternfeld in 1910 listed two specimens from Togoland as quentheri, and Ferreira in 1930 listed guentheri in a key to African cobras that was essentially that provided in Boulenger's "Catalogue." This includes sufficient explanation for the more important references listed in synonymies below. It may be added, however, that two large specimens of goldii, from Niapu, Belgian Congo, were inadvertently listed by Schmidt (1923) as Naja melanoleuca, although the latter name is not listed as a partial synonym since Schmidt did not include any scalation data based on these specimens.

Since it is necessary to revive *Pseudohaje* for arboreal African cobras the species

ever, owing to the fact that the name Naja

1 For the loan of material I am indebted to Dr. Thomas Barbour and Arthur Loveridge, Museum of Comparative Zoölogy (MCZ), M. Graham Netting, Carnegie Museum (CM), and to K. P. Schmidt and Clifford H. Pope, Field Museum of Natural History (FMNH). The drawings accompanying the text were prepared by Mr. Dimitri Alexandroff, Mr. R. P. Thompson and Mr. Sidney Aberman. Their patient attention to detail in the preparation of the figures is gratefully acknowledged. Assistance in the preparation of the manuscript was furnished by the personnel of the Work Projects Administration, Official Project No. OP 265-1-97-16 W. P. 10.

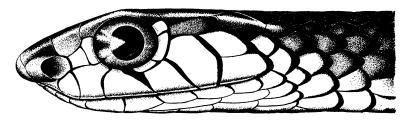
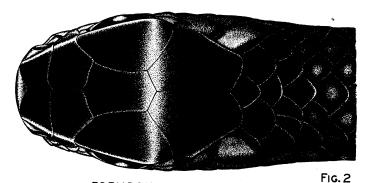
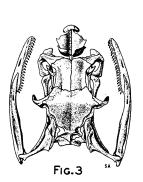


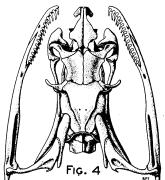
FIG. I



PSEUDOHAJE GUENTHERI A.M.N.H. NO. 31556, X 2







PSEUDOHAJE GUENTHERI NAJA MELANOLEUCA A.M.N.H. NO. 31708, X I A.M.N.H. NO. 63428, X 1.5

Figs. 1, 2. Lateral and dorsal view of *Pseudohaje guentheri*.

Figs. 3, 4. Dorsal views of the skulls of *Pseudohaje guentheri* and *Naja melanoleuca*, to show strong contrast in proportions. The skull of *N. melanoleuca* is characteristic of the genus *Naja*.

listed in the "Catalogue" by Boulenger as Naja guentheri, but originally described as Pseudohaie nigra, becomes the type species of the genus as the "single original species." The name nigra originally proposed by Günther, but suppressed by Boulenger as a homonym when the species was erroneously referred to Naja, unfortunately cannot be revived.

PSEUDOHAJE GÜNTHER, 1858

Diagnosis.—An elapid group, perhaps most closely allied to Naja Laurenti but differing from snakes of this genus in possessing more palatine, pterygoid and mandibular teeth and in having fewer rows of dorsal scales. Likewise it differs from snakes of the genus Naja in possessing a proportionately larger eye, a squamosal that extends hardly beyond the skull, a proportionately longer tail but relatively smaller fangs. Precise differences in skull shape and proportions may be observed in figures 3 and 4.

Maxilla with paired fang sockets (one fang in either socket normally ancylosed), followed after a gap by from two to four small, recurved, feebly grooved teeth. Palatine teeth 10 to 17; pterygoid teeth 24 to 41. Anterior ribs scarcely longer than those on posterior of body. Dorsal scale formula normally 15-13-11, with reduction to thirteen scales occurring either on the neck or posterior to the middle of the body. Ratio of tail to total length .21 to .24. Adult coloration black above. either yellowish or whitish on the venter, with black margins on posterior edges of the ventrals.

Pseudohaje guentheri (Boulenger)

Pseudohaje nigra Günther, 1858 (non Naja nigra Sмітн, 1838), "Cat. Colubrine Snakes Brit. Mus.," p. 222 ("Sine Patria").

Naia guentheri BOULENGER, 1896, "Cat. Snakes Brit. Mus.," III, p. 388, Pl. xxi ("West Africa?").—Boulenger, 1897, Ann. Mag. Nat. Hist., (6) XIX, p. 154 ("Sierra Leone").

Naja guentheri Sternfeld, 1910, Mitt. Zool. Mus. Berlin, IV, p. 220 (Misahöhe, Togo = Misa, Togoland).

Naja goldii Barbour and Loveridge, 1930 (non Boulenger, 1895), in R. Strong, "Report of the Harvard-African Expedition upon the African Republic of Liberia and the Belgian Congo," II, p. 773 (Totokwelli, Liberia).—

DITMARS, 1931, "Snakes of the World," pp. 171-172 (habits of captive specimens).

MATERIAL EXAMINED.—Four specimens in the American Museum (AMNH Nos. 31555-56, 31708, 29307) were received from the New York Zoological Park. Doubtless these specimens came from the west coast of Africa. A fifth specimen (MCZ No. 22531) is from Totokwelli. Liberia.

Lepidosis.—Cephalic scalation as depicted in figures 1 and 2, with minor variations: three specimens, like the type, have the sixth upper labial in contact with two lower postoculars instead of with one. The specimen depicted has the loreal separated from the preocular, as reported for the Togoland specimen briefly described by Sternfeld (supra cit.). All specimens examined have the third labial extending from the nasal to the eye, excluding the second labial from contact with the preocular or loreal (when the latter is present). Lower labials 8, the first four touching the anterior chin-shields, which are slightly longer than the posterior pair.

Dorsal scale row formula 15-13-11 on three specimens, 15-13-9 on two. five specimens examined the reduction to fifteen rows, through the loss of the third row, occurs between the 16th and 21st ventrals, while the reduction to eleven, through the loss of what has become the third row, occurs between the 112th and 123rd ventrals. Three females examined have, respectively, 180, 181, 184 ventrals; two males have 184 and 185; the male type also is reported to have 185, and the Togoland specimen, sex not mentioned, is reported to have 189. Caudals 74, 76 and 79 for three females, 81 and 77 for two males. The type is reported as having 74, the Togoland specimen 82. The mean for these seven specimens is 77.6. Tails terminate in a stout, but pointed, spine.

DIMENSIONS.—Largest specimen amined is a female (AMNH No. 31555) measuring 2,050 mm. over all, tail 450. Boulenger (supra cit.) reports the male type to be 2,130 mm., tail 470. Ratios of tail to total length vary from .21 to .22, with no indication of any difference between the sexes.

Dentition.—Of nine maxillae examined, eight contained two teeth behind the paired fangs, and one contained three teeth. Other features of the dentition were examined on both sides of three specimens and the following variations noted: palatine teeth 10 to 12, pterygoid teeth 24 to 27, mandibular teeth 21 to 22.

Hemipenis.—Examined as dissected from the tail on AMNH No. 29307. Extends to the eighth caudal, bifurcating at the seventh. Sulcus ventrad as in most snakes, dividing at the sixth caudal. At the fifth caudal the sulcus is flanked on either side by a fleshy protuberance comprised of one heavy spine around which several long slender spines are clustered. Laterally and distally, long slender spines are closely set in a diagonal row. Beyond these, smaller spines are present, diminishing in size to spinules on the tip of each lobe.

Coloration.—Above grayish or blackish, with darker margins apparent on most of the dorsal scales. The scales of the lower row on either side are scarcely darker than the ventrals; ventrals whitish and narrowly margined with black, except on the throat where only the lateral margins are black. Black margins on the caudals are apparent as far back as the middle of the tail, but posteriorly there is a gradual darkening of the caudals until no pattern is visible on the posterior third of the appendage.

Boulenger's description (1896) of the type as "brown beneath" is probably based upon a specimen discolored in preservation. Sternfeld (1910) describes a specimen 1,050 mm. long, as "Olive brown above, with irregular dark cross-bars." This description approximates the pattern of the Liberia specimen which is 825 mm. in length. The cross-bars undoubtedly represent the juvenile pattern since vestiges of cross-bars are present on juvenile *P. goldii*.

Range.—Published records indicate that *P. guentheri* inhabits the Western Forest Province from Sierra Leone on the west to western Togoland on the east.

Pseudohaje goldii (Boulenger)

Naja goldii Boulenger, 1895, Ann. Mag. Nat. Hist., (6) XVI, p. 34 (type locality "near Asaba," Nigeria).—Mocquard, 1895 (1896), C. R. Congr. Int. Zool., III, p. 234, footnote.— BOULENGER, 1896, "Cat. Snakes Brit. Mus.," III, p. 387, Pl. xx ("Mouths of the Niger," Nigeria).—Boulenger, 1900, Proc. Zool. Soc. London, p. 455 (Benito River, Gaboon).-STERNFELD, 1908, Mitt. Zool. Mus. Berlin, III, p. 415 (Buea, Bipindi, and Pungo Songo, Cameroon).—Boulenger, 1915, Proc. Zool. Soc. London, p. 219 (partim), (Kassai, Belgian Congo).—Boulenger, 1919, Rev. Zool. Africaine, VII, p. 27 (Avakubi).—WITTE, 1920, Rev. Zool. Africaine, VIII, p. 276.—Schmidt, 1923, Bull. Amer. Mus. Nat. Hist., XLIX, p. 130 (Poko and Akenge, Belgian Congo).—Werner, 1925, Sitzber. Akad. Wiss. Wien, CXXXIV, p. 64 (Yaunde, Cameroon).—Ferreira, 1930, Bull. Antivenin Inst. Amer., IV, pp. 55, 56.—?DIT-MARS, 1931, "Snakes of the World," p. 171.-WITTE, 1933, Ann. Mus. Congo Belge, (1) III, p. 97 (Macaco, Eala, Makaia N'Tete, Temvo, Koteli and Medje, Belgian Congo).—Angel, 1933, "Les Serpents de l'Afrique Occidentale Française," p. 188, fig. 70 (partim).—Parker, 1936, Novit. Zool., XL, p. 126 (Quirimbo, Angola).—Loveridge, 1936, Zool. Ser. Field Mus. Nat. Hist., XXII, p. 42 (Irumu, Belgian Congo).—Pitman, 1938, "A Guide to the Snakes of Uganda," Part X, pp. 227–229, 316, Pl. xvII, fig. 4, and colored Pl. (W), fig. 1 (Mabira Forest, Uganda).—Bogert, 1940, Bull. Amer. Mus. Nat. Hist., LXXVII, p. 90 (Lukolela, Belgian Congo).—Loveridge, 1940, Sci. Monthly, L, p. 505 (Bundibugyo, Uganda). Naia yakomae Mocquard, 1895 (1896), C. R. Congr. Int. Zool., III, p. 233 (type locality, "Yakoma, pays de Abiras," Belgian Congo).

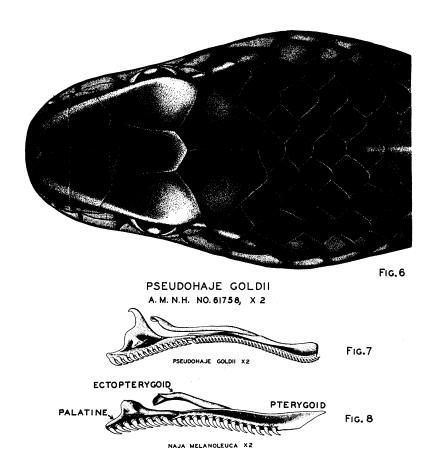
MATERIAL EXAMINED.—Thirteen specimens in museums in the United States have been examined. These include six males, four females and two skins (with skulls separate) as follows: Cameroon, Lolodorf (CM No. 15212), Metet (CM No. 4144, MCZ No. 9388), Kribi (MCZ No. 7853), Sakbayeme (MCZ No. 18950); Belgian Congo, Poko (AMNH No. 12362), Akenge (AMNH No. 12363), Lukolela (AMNH 61758), Irumu (FMNH No. 6977), Niapu (AMNH Nos. 12389–90); Uganda, Bundibugyo, Bwamba (MCZ No. 48473); and

Lepidosis.—Cephalic scalation as depicted in figures 5 and 6 with the following variations noted, including those reported in the literature cited above. Supralabials 7, and the third and fourth entering the orbit (Boulenger, 1896, reports the

"Central Africa" (CM No. 7236).



Fig. 5



Figs. 5, 6. Lateral and dorsal views of Pseudohaje goldii, showing characteristic pattern and pro-

Figs. 7, 8. Palatine, estepheri.

Figs. 7, 8. Palatine, estepherigoid and pterygoid of *Pseudohaje goldii* contrasted with the same skeletal elements of *Naja melanoleuca*. Note the more numerous teeth in *Pseudohaje* and their presence on the posterior end of the pterygoid.

fourth only in the type). Infralabials 8, the first four touching the anterior chinshields. Preoculars normally 1, rarely 2; a loreal separated from preocular on both sides of two specimens. Sixty-six per cent of the specimens examined had the second and third labials in contact with the preocular (or loreal, when present), whereas fourty-four per cent had the second labial excluded from contact. Postoculars 3 on all specimens examined although Boulenger (1896 and 1919) reports extremes of 2 and 4. Temporals normally 1 + 2, rarely 1 + 3or 2 + 2. Scale row formula 15–15–13–11. On material examined the reduction to thirteen scale rows, brought about by the loss of the third row on either side, occurs between ventrals 114 and 138, mean for ninteeen sides tabulated 122. The reduction to eleven scale rows, again by the loss of what has become the third row after the previous reduction, occurs between ventrals 128 and 141, mean for seventeen sides Thus, thirteen scale rows occur posterior to midbody for an average distance of twelve ventrals.

Ventrals 194 to 205 for males, 192 to 205 for females, without any evidence of sexual or geographical difference. The average number of ventrals for thirteen specimens examined, including skins, the sex of which unknown, is 198.07. Ten ventral counts reported in the literature added to those recorded on the basis of material examined provide a mean of 197.8 for twentythree specimens. Caudals 78 to 94, the minimum being that recorded by Parker (supra cit.) for an Angolan female, whereas the maximum occurs on a male (CM No. 15212) from the Cameroon. Some evidence of sexual dimorphism in the number of caudals is suggested, four females averaging 83.7, whereas six males average Including all specimens with complete tails examined, plus nine counts recorded by other workers, data for seventeen specimens provide a mean of 87 caudals for the species. Tails, when complete, terminate in a stout but pointed spine.

DIMENSIONS.—The largest specimen examined is represented by a complete skin (in alcohol) measuring 2,565 mm. This specimen (AMNH No. 12390) was one of

two taken by Herbert Lang and Dr. James P. Chapin (erroneously listed under Naja melanoleuca by Schmidt, 1923) at Niapu, Belgian Congo, and Lang's notes indicate that the specimen was 2,410 mm. (tail 557 mm.) over all when measured prior to skinning and preservation. Thus, this specimen in life closely approached a length of 8 feet and several specimens reported are over 2 meters long. A second specimen from Niapu (AMNH No. 12389) was measured when freshly killed as 2,315 mm. Sternfeld (1908) reports the largest of three Cameroon specimens as 2,300 mm. The specimen in Carnegie Museum (CM) 7236) from "Central Africa" is 2,365 mm. in length. Nine specimens from which suitable data are recorded indicate that the ratio of tail to total length varies only from .22 to .24, averaging closer to .23, with no difference between the sexes.

Dentition.—Twenty-one maxillae examined show that the number of small, recurved teeth behind the paired fangs present in each maxilla varies from 2 to 4; sixteen maxillae contained 3 teeth, four contained 4 teeth, and only one contained 2 teeth. The other teeth were examined on three specimens and found to be as follows: palatine teeth, 14 to 17; pterygoid teeth, 37 to 41; mandibular teeth, 24 to 25.

Hemipenis.—The everted hemipenis described (Bogert, 1940) for the Lukolela specimen is obviously similar in most respects to the organ of *P. guentheri* described above from a dissection. On the everted organ, however, reticulated calyces with denticulated edges are present, whereas the calyces are not apparent in the dissected organ of *P. guentheri*.

Coloration.—All adult specimens examined have been nearly alike, black above, and yellow on the anterior half of the venter, with black margins on the ventrals becoming progressively broader on the posterior fourth of the body until the venter and the underside of the tail are entirely black. Sides of the head and end of snout whitish, with black borders on the scales as depicted in figure 5. The "transverse series of small whitish spots" on the dorsum which Boulenger (1895) ascribes to the type, and the extent of white on the

snout which he depicts in his plate (xx) in the "Catalogue" have not been observed on any specimens examined. Young specimens have what may be described as vestigial, whitish cross-bars on the neck as Pitman (1938) depicts for the juvenile from the Mabira Forest.

STOMACH CONTENTS.—The digestive tract of all but one specimen examined contained nothing except a few nematodes or linguatulids. The exception, MCZ No.

7853, from Kribi, Cameroon, contained the slender hind limbs of a large arboreal frog, plus insect remains doubtlessly contained in the frog which was too well digested anteriorly for ready identification.

RANGE.—Twenty-six records for the species, as now redefined, indicate that the range of *P. goldii* is confined to the west and central African forests, from Nigeria on the northwest, eastward through the Cameroon and Belgian Congo to Uganda, and southward to northern Angola.

DIFFERENCES BETWEEN SPECIES

Despite Schmidt's (1923) comment that the pattern of the two forms as synonymized by Boulenger was very characteristic, and his further statement, "The fact that it appears in the specimen referred quentheri by Sternfeld (1910 p. 220) is additional evidence that guentheri cannot be distinguished from goldii," several real differences exist. Although some characters overlap, several dichotomous differences, as well as apparent geographic isolation, point to specific status for each of the two forms in the genus. The several contrasting differences described above may be summarized in tabular form, with extremes given in parentheses.

ably co-extensive with that of the Western Forest Province. Also the ranges of the two species of Pseudohaje correspond to a distributional pattern that is characteristic of several ophidian genera having representatives in the Congo Basin as well as in the forest region west of the Niger. Several species, as well as subspecies, are endemic to the Forest Province west of the Niger. Among the species endemic to this region are Thrasops occidentalis Dendroaspis viridis, two species with arboreal habits that probably closely parallel those of P. nigra. The hiatus in the Rain Forest proper that exists (fide Schmidt, 1919, p. 399, map, after Engler)

Midbody scale rows Ventrals, average Caudals, average Maxillary teeth

Palatine teeth
Pterygoid teeth
Mandibular teeth
Ratio of tail to total length, mean
Pattern and coloration

P. GUENTHERI
13
184.0 (180–189)
77.6 (74–82)
$^{1}\text{II} + 2 \text{ (rarely II} + 3)$
10–12
24-29
21-22

.22 (.21-22)

Venter whitish, with narrow black margins on ventrals and anterior caudals. Tail blackish beneath on posterior portion only. Dorsum brownish or grayish, with darker margins on scales, and lower row distinctly lighter.

P. GOLDII

15 197.7 (192-205) 87.0 (78-94) II + 3 (rarely II + 4 or II + 2) 14-17 37-41 24-25

.23 (.22-.24)

Venter yellow, anterior ventrals with broad black margins which increase in width posterioriy until the posterior fourth of the venter and the underside of the tail are uniformly black. Dorsum nearly jet black.

REMARKS.—The locality records for known specimens of the genus *Pseudohaje* indicate that the range of the genus is prob-

in the general region of southern Dahomey may be an isolating barrier to some forms, or more fundamental factors causing the gap in the forest may be the cause of an isolation resulting in the endemism in the

¹ Roman numerals are used to indicate fangs in contrast to non-canaliculate teeth.

extreme western portion of the Forest Province. Some species are represented in both regions, and the exact nature of the supposed barrier that seemingly exists remains to be determined.

Ditmars (1931, pp. 171–172) mentions both species of *Pseudohaje* (as *Naja goldii* and *Naja guentheri*), listing an erroneous range for *goldii*. His remarks concerning the habits of *goldii*, furthermore, probably are based upon captive specimens of *P. guentheri*, inasmuch as all specimens received from the New York Zoological Park have been the latter form. Furthermore, it is known that nearly all the west African reptiles received from commercial dealers come from within the range of *P. guentheri*. It is doubtful whether *P. goldii* has ever been exhibited alive in any zoological garden.

Ditmars mentions Naja anchietae (= Naja haje anchietae) as a "hoodless form" and states, "Goldii [= guentheri] likewise is a nearly hoodless form. From specimens of both examined by the author these appear to be astonishingly quick and highly dangerous cobras, inclined to bite from a short rush, rather than a strike. Whether or not these 'hoodless' cobras will long remain in the genus Naia depends upon the future deductions of technical workers." N. h. anchietae is definitely referable to the genus Naja, as noted below, but Ditmars' conjecture concerning what must now be known as P. guentheri proves to be a valid one.

The statement has appeared in print that "Naja goldii" "undoubtedly ejects its venom to a distance like Naja haje, Naja nigricollis, etc." Already this statement has been quoted in at least three accounts, although I have been unable to substantiate it. Dr. R. L. Ditmars assures me that he has never observed any Pseudohaje in the zoological park collections eject its venom, nor does an examination of the comparatively short fangs of Pseudohaje warrant the belief. The largest specimen of P.

goldii, the specimen in life 2,410 mm. long, possessed fangs only 4 mm. in length, and the shape of the fang is obviously not adapted for forward projection of the venom, as is true of the "spitters" N. nigricollis and Hemachatus. The species N. haje is not a spitter either, to judge from the shape of the fang, although this species has been reported as one, probably on the basis of a color phase of Naja nigricollis.

The Validity of Pseudohaje.—The assemblage of species placed by Boulenger in the genus Naja has never been subjected to any critical review. A more extended study of the cranial and penial characters of this assemblage, as well as of related genera, has been undertaken by the writer. While more data are to be assembled, sufficient species and specimens have been examined to warrant a few generalizations at this time.

Pseudohaje possesses more teeth in every bone, except the maxilla, than any true Naja. In dental characters, as well as in skull proportions, Pseudohaje differs from Naja in more respects than either Boulengerina or Hemachatus, although both of the latter genera can be retained. The African forms nivea, nigricollis, melanoleuca and haje are full species (with recognizable races of nigricollis and haje) and unquestionably can be retained as congeners of the Asiatic Naja naja (Coluber naja Linneaus), type species of the genus. The king cobra, Naja hannah of Boulenger, differs in numerous skull, as well as penial, characters from all species of Naja and should, as Pope (1935, p. 347) stated, be assigned to the genus *Hamadryas*. Details of the relationships and the anatomical characters will be presented in a paper now in prepa-

Finally, it may be noted that the eyes of the snakes in the arboreal genus *Pseudohaje* are proportionately larger than those of the terrestrial *Naja*, whereas *Naja* possesses eyes that are proportionately smaller than those of the aquatic genus *Boulengerina*.

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