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Ghost in the forest: additional notes on the search of the mysterious São Tomé Green Mamba (Elapidae: *Dendroaspis*)

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The putative existence of a population of Green Mambas, genus *Dendroaspis* Schlegel, 1848, in São Tomé Island in the Gulf of Guinea (West Africa) has attracted the attention and curiosity of many herpetologists since the second half of the 19th century. Ceríaco et al. (2018, 2022) presented an historical review of this taxonomic mystery, only to conclude that no definitive answer regarding its existence on this island could yet be reached. Is this population real or the byproduct of a series of mislabeled specimens and misspelled localities? Three well respected herpetologists –the Italian Giorgio Jan (1791–1866), the German Johann Gustav Fischer (1819–1889) and the Russian Jacques von Bedriaga (1854–1906) – all studied and referred to *Dendroaspis* from São Tomé, providing credibility to its taxonomic allocation. The references to São Tomé *Dendroaspis* on three independent/different occasions argue against the possibility that the referred locality may reflect a mislabeling or misspelling of localities. Yet, the mystery remains.

The elusive nature of the "São Tomé Green Mamba" is remarkable. No specimens have been collected or observed in the field since the mid-1880s and all the historical museum specimens studied by Jan in the Museo Civico di Storia Naturale of Milan (Jan 1857, 1858, 1859, 1863), by Fischer in the Naturhistorisches Museum of Hamburg (Fischer 1855, 1856a, 1856b) and by Bedriaga from his private collections (Bedriaga 1892 [1893]) were respectively destroyed by the Allied bombings in Italy and Germany during World War II, or vanished into oblivion (see Böhme 1995, Hallermann 1998, 2006, Ceríaco et al. 2018, 2022). However, and despite the interest that this topic has raised in different generations of herpetologist dedicated to the study of São Tomé & Príncipe herpetofauna, this elusiveness extends to its bibliographic history.

Most of the authors who have dealt in more detail with the case of the São Tomé Green Mamba have referred to Fischer's (1856b) illustration (Fig. 1; see Bocage 1888, 1892, 1905, Bedriaga 1893, Schätti & Loumont 1992, Nill 1993, Ceríaco et al. 2018, 2022). The illustration was published in volume 3 of the journal "Abhandlungen und Verhandlungen des Naturwissenschaftlichen Vereins in Hamburg", in a paper entitled "Neue Schlangen des Hamburgischen Naturhistorischen Museums" [Translation: New snakes of the natural history museum of Hamburg] (Fischer 1856b). In this paper, Fischer described several new species of snakes from various regions of the world (including *Boaedon nigrum*, supposedly from São Tomé Island, but see Ceríaco et al. 2021) and presented both colour full-body illustrations and schematic representations of different parts/characters of the snakes. None of the de-

scriptions presented in the paper referred to the São Tomé Green Mamba, but Fischer decided to include its full-body colour illustration in the paper. The explanation for this inclusion is presented in a footnote on the figures list page of the paper (Figure 2).

In the footnote (see translation in the caption of Fig. 2), Fischer justified its inclusion in the paper noting that no good illustration of the species was available at the time, but also notes that he had already described the species in the previous year under the name *Dendroëchis reticulata* (Fischer 1855). Despite being stated in the footnote, the name and the original description have apparently been neglected by all the authors that have wrote on the São Tomé Green Mamba case (Jan 1857, 1858, 1859, 1863, Bocage 1888, 1892, 1905, Bedriaga 1893, Schätti & Loumont 1992, Nill 1993, Ceríaco et al. 2018, 2022). As a mea culpa, this includes some of the authors of the present manuscript (LMPC, MPM, AMB), who, despite being dedicated to the study of São Tomé herpetofauna for more than a decade and having spent some time studying the case of the elusive Green Mamba, have completely overlooked the information in this footnote. One of the reasons that may explain the neglect of this description is the fact that it originally appeared in a monograph dedicated to sea-snakes (Fischer 1856a) and in its precursor, which appeared in a publication of the Akademisches Gymnasium Johanneum (also known and mentioned by Fischer (1856b) as "der Hamb[urgischen]. Realschule"), a school in Hamburg where Fischer studied and later taught (Fischer 1855). Adler (2007) had already noted that some of Fischer's publications had been issued twice, as is the case of the monograph on sea snakes, causing confusion. Regarding this specific case, Adler (2007) notes the difference on the number of pages between the two versions of the 'Die Familie der Seeschlangen, systematisch beschrieben', noting that the 1855 version had priority. Wallach et al. (2014) cited *Dendroëchis reticulata* Fischer, 1855 in the synonym list of *Dendroaspis viridis* but never mentioned that it referred to a São Tomé population.

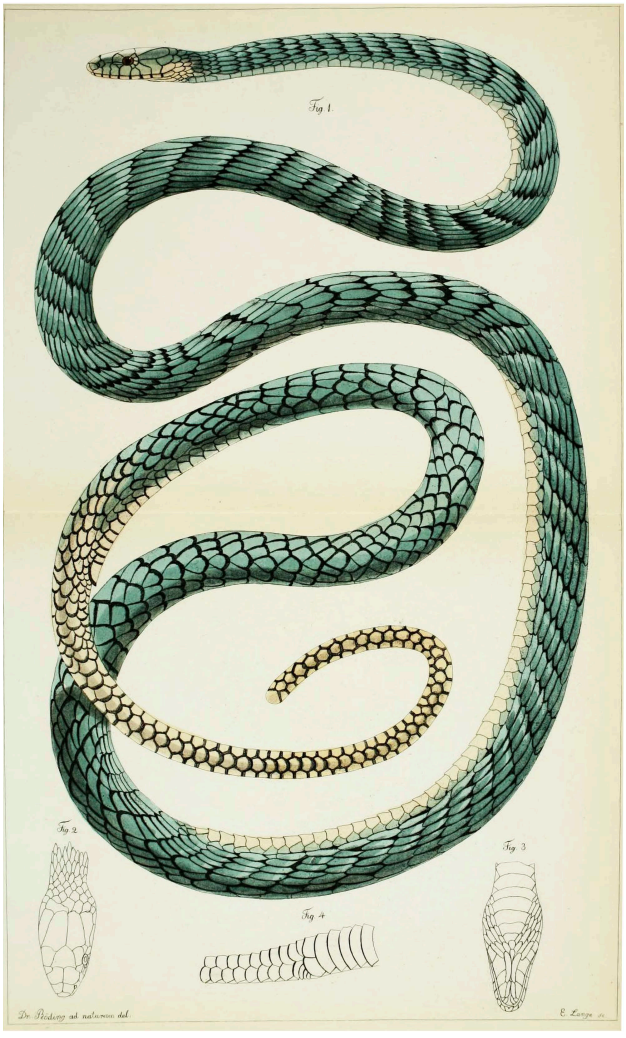
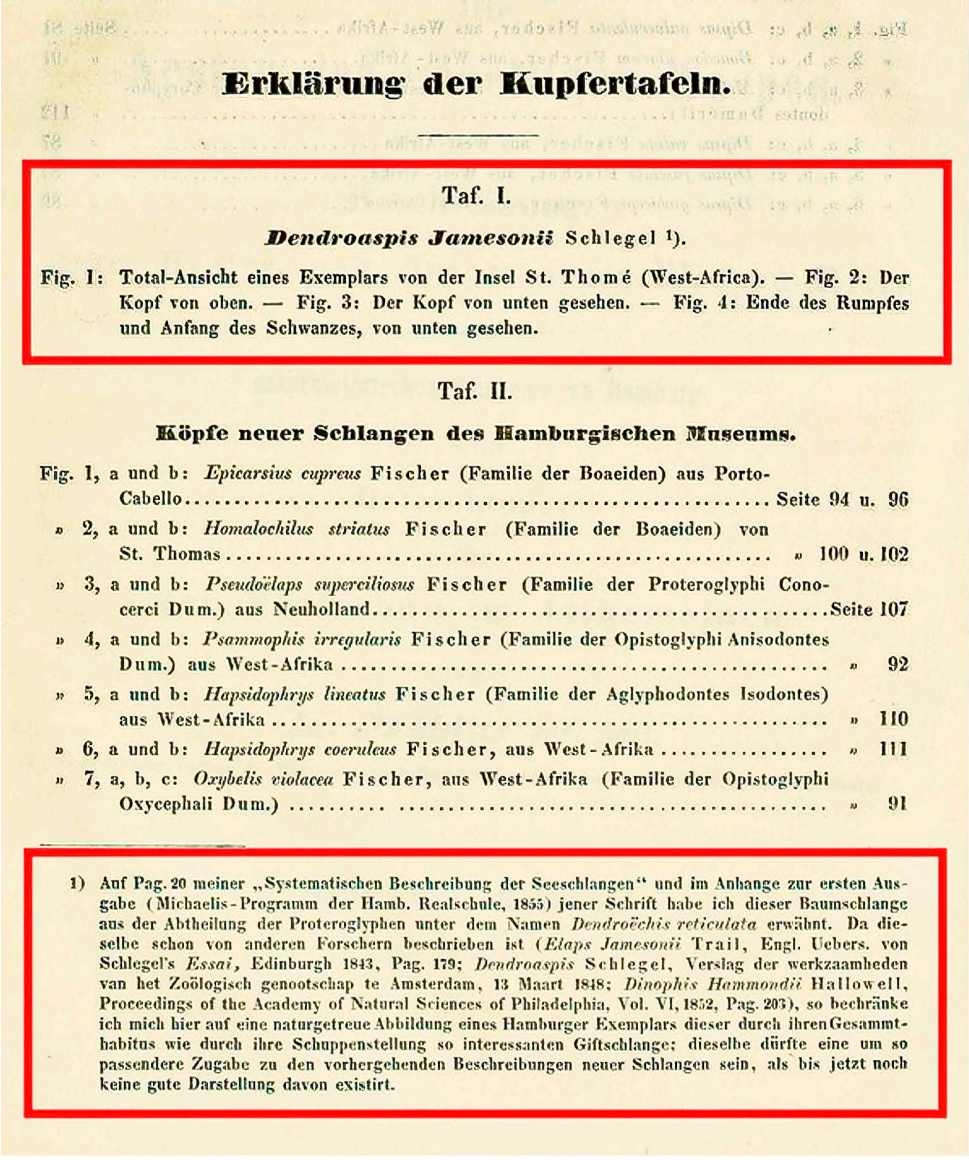


Figure 1. Fischer's (1856b) plate depicting a "*Dendroaspis Jamesonii*" from São Tomé Island.

In the "Die Familie der Seeschlangen, systematisch beschrieben" (Fischer 1855), the name first appears in a footnote initiated in page 19, where Fischer explains how he confirmed the presence of the inner poison canal in the fangs of several elapids, "*Dendroëchis reticulata* nov. spec." included. In the same footnote, and immediately after citing the name, Fischer notes that its description is in the appendix. On page 25, while discussing the systematic position of proteroglyphs, Fischer mentions the species as an example. In the appendix of the work, Fischer presented the formal description of the taxon. He particularly noted that "the genus *Dendroëchis*, as the first example of an arboreal snake found to date from the Proteroglyphic division" would "likely attract the attention of herpetologists", and more detailed descriptions of these two snake species would be presented in the forthcoming work that would describe several new snakes from the Hamburg Museum collections [the "Neue Schlangen des Hamburgischen Naturhistorischen Museums" (Fischer 1856b)]. Regarding *Dendroëchis reticulata*, Fischer (1855) clearly noted that the species was from "der Insel St. Thomé (West-Afrika)" [= São Tomé Island, West Africa], and provided a brief description of what he considered a new genus, *Dendroëchis*, and the new species *reticulata* (Fig. 3). According to the description, the new genus was defined by the following characters: "No small solid teeth behind the fang of the upper jaw; Body elongated, very slender, similar to that of tree snakes; Scales smooth, very long, those of the midline of the back much larger; Tail plates double", while the species diagnosis referred that the species had "anal scales divided; Prefrontal shields abutting the fourth upper lip shield; colour green ; every scale, including the head shields, is edged in black". The general characters that Fischer used to diagnose *Dendroechis reticulata* partly overlap with those used by Trail (1843) to describe *Dendroaspis jamesoni*, and that is surely the reason why he then decided to use the latter name in his 1856 illustration of the specimen (Fi-

scher 1856b). In the 1856 version of the "Die Familie der Seeschlangen, systematisch beschrieben" (Fischer 1856a), the description of *Dendroëchis reticulata* is absent, but the name appears in the same footnotes as in the 1855 version (Fischer 1855).

The reevaluation of Fischer's (1855) description brings additional layers of data to the case of the "São Tomé Green Mamba", namely the fact that there is an available name for the population, if it is confirmed to be a valid taxon. Given the description (1855 version) and illustration (1856 version) provided by Fischer (1855, 1856b) but also the opinions of Jan (1857, 1858, 1859, 1863), Bocage (1888, 1892, 1905) and Bedriaga (1893), there are no reasons to question that the snake indeed belongs to the genus *Dendroaspis*. However, its specific nature needs to be properly reviewed, especially in the light of our current understanding of the speciation



Erklärung der Kupfertafeln.

Taf. I.

Dendroaspis Jamesonii Schlegel [1]).

Fig. 1: Total-Ansicht eines Exemplars von der Insel St. Thomé (West-Africa). — Fig. 2: Der Kopf von oben. — Fig. 3: Der Kopf von unten gesehen. — Fig. 4: Ende des Rumpfes und Anfang des Schwanzes, von unten gesehen.

Taf. II.

Köpfe neuer Schlangen des Hamburgischen Museums.

Fig. 1, a und b: *Epicarsius cupreus* Fischer (Familie der Boaeiden) aus Porto-Cabello ..... Seite 94 u. 96

» 2, a und b: *Homalochilus striatus* Fischer (Familie der Boaeiden) von St. Thomas ..... » 100 u. 102

» 3, a und b: *Pseudoëlaps superciliosus* Fischer (Familie der Proteroglyphi Conocerci Dum.) aus Neuholland ..... Seite 107

» 4, a und b: *Psammophis irregularis* Fischer (Familie der Opistoglyphi Anisodontes Dum.) aus West-Afrika ..... » 92

» 5, a und b: *Hapsidophrys lineatus* Fischer (Familie der Aglyphodontes Isodontes) aus West-Afrika ..... » 110

» 6, a und b: *Hapsidophrys coeruleus* Fischer, aus West-Afrika ..... » 111

» 7, a, b, c: *Oxybelis violacea* Fischer, aus West-Afrika (Familie der Opistoglyphi Oxycephali Dum.) ..... » 91

1) Auf Pag. 20 meiner „Systematischen Beschreibung der Seeschlangen" und im Anhange zur ersten Ausgabe (Michaelis-Programm der Hamb. Realschule, 1855) jener Schrift habe ich dieser Baumschlange aus der Abtheilung der Proteroglyphen unter dem Namen *Dendroëchis reticulata* erwähnt. Da dieselbe schon von anderen Forschern beschrieben ist (*Elaps Jamesonii* Trail, Engl. Uebers. von Schlegel's *Essai*, Edinburgh 1843, Pag. 179; *Dendroaspis* Schlegel, Verslag der werkzaamheden van het Zoölogisch genootschap te Amsterdam, 13 Maart 1848; *Dinophis Hammondii* Hallowell, Proceedings of the Academy of Natural Sciences of Philadelphia, Vol. VI, 1852, Pag. 203), so beschränke ich mich hier auf eine naturgetreue Abbildung eines Hamburger Exemplars dieser durch ihren Gesammthabitus wie durch ihre Schuppenstellung so interessanten Giftschlange; dieselbe dürfte eine um so passendere Zugabe zu den vorhergehenden Beschreibungen neuer Schlangen sein, als bis jetzt noch keine gute Darstellung davon existirt.

Figure 2. Figure list page from Fischer (1856b). Red brackets indicate the parts referring to the São Tomé Green Mamba. Translation of the footnote: On p. 20 of my "Systematischen Beschreibung der Seeschlangen" and in the appendix to the first version (Michaelis – Programm der Hamb. Realschule, 1855) of that work, I have mentioned this tree snake from the division of Proteroglyphs under the name *Dendroëchis reticulata*. Since it has already been described by other researchers (*Elaps Jamesonii* Trail, English translation of Schlegel's *Essai*, Edinburgh 1843, p. 179; *Dendroaspis* Schlegel, Verslag der werkzaamheden van het Zoologisch genootschap te Amsterdam, 13 Maart 1848; *Dinophis Hammondii* Hallowell, Proceedings of the Academy of Natural Sciences of Philadelphia, Vol. VI, 1852, p. 203), I refer here to a lifelike illustration of the Hamburg specimen of this poisonous snake, which is so interesting for its overall habitus as well as for its scale position; This may be a more fitting addition to the preceding descriptions of new snakes, as no good account of them has yet existed.

processes in the Gulf of Guinea Oceanic Islands and the recent taxonomic updates of São Tomé and Príncipe herpetofauna (Ceríaco et al. 2022). The recent recognition of the São Tomé Cobra Preta, *Naja* (*Boulengerina*) *peroescobari* Ceríaco, Marques, Schmitz & Bauer, 2017, as an endemic species and not as an insular population of the African Forest Cobra, *Naja* (*Boulengerina*) *melanoleuca* Hallowell, 1857 (Ceríaco et al. 2017), is a compelling precedent for the revalidation of Fischer's (1855) *Dendroëchis* [= *Dendroaspis*] *reticulata* as a valid species, most likely endemic to the island.

But besides the existence of another endemic elapid in the island and the biogeographic and endemism patterns of the Gulf of Guinea Oceanic Islands in general, and São Tomé in particular, is there any data that would support such taxonomic decision? As the specimens originally studied by Fischer, Jan and Bedriaga seem to have been lost and no additional specimens have been collected until now, the only available sources of data regarding these animals are the brief description by Fischer (1855), its illustration (Fischer 1856b) and the detailed description provided by Bedriaga (1893) from a specimen collected in Roça Ubo-Budo in the eastern part of the island by Adolfo F. Möller (1842–1920) in 1885 (fide Bocage 1905). The source(s)/collector(s) of the specimens used by Jan and Fischer is not known. Fischer's works do not provide much data, but Bedriaga (1893) presents a considerably more detailed description of the studied specimen. The recorded total body length of the specimen was 1284 mm, the length of the "trunk" around 1013 mm, while the length of the tail was 235 mm. The examined specimen had 219 ventral scales, 62 subcaudal scales and 13 midbody scale rows.

Nachtrag.

Zu Pag. 19 und 20. Da mit den vorstehenden Seiten die dieser Schrift gesteckten Grenzen ausgefüllt sind, so beschränke ich mich hier auf eine kurze Diagnose der Pag. 19 und 20 erwähnten zwei neuen Schlangen, von denen namentlich die Gattung *Dendroëchis*, als das erste bis jetzt aufgefundene Beispiel einer Baumschlange aus der Abtheilung der Proteroglyphen, das Interesse der Herpetologen auf sich ziehen dürfte. Eine ausführliche Beschreibung derselben wird zugleich mit der Beschreibung mehrer anderer neuer Schlangen des hamburgischen Museums noch in diesem Jahre als besondere Abhandlung erscheinen.

I. *Dendroëchis reticulata* Fischer,

von der Insel St. Thomé (West-Afrika).

Gattung: *Dendroëchis* Fischer. Hinter dem Giftzahn des Oberkiefers keine kleinen soliden Zähne; Körper langgestreckt, sehr schlank, dem der Baumschlangen ähnlich; Schuppen glatt, sehr lang, die der Mittellinie des Rückens viel grösser; Schwanzschilder doppelt.

Art: *Dendroëchis reticulata* Fischer. Analschuppe getheilt; Praefrontalschilder auf das vierte Oberlippenschild stossend; Farbe grün; jede Schuppe, auch die Kopfschilder, schwarz eingefasst.

II. *Pseudoëlaps superciliosus* Fischer,

aus Neu-Holland (Sidney).

Gattung: *Pseudoëlaps* Fitzinger. Eine bis zum Mundwinkel reichende Reihe kleiner, theilweise gefurchter Zähne hinter dem Giftzahn. Die Schuppen der Mittellinie des Rückens nicht grösser als die benachbarten; Bedeckungen des Halses keiner Erweiterung fähig; Schwanzschilder sämmtlich doppelt.

Art: *Pseudoëlaps superciliosus* Fischer. Körper robust; Analschuppe getheilt; ein Praeocular-, zwei Postocular-Schilder; zweites Nasalschild dreieckig mit nach hinten an das Praeocularschild stossender Spitze; Schuppen gross, glatt, rhombisch, mit freier Spitze; Farbe einfach schmutzig-braun ohne alle Abzeichen.

Figure 3. Appendix of the "Die Familie der Seeschlangen, systematisch beschrieben", where Fischer provides the description of his new genus and species, *Dendroechis reticulata* (highlighted in the red box). From Fischer (1855).

Bedriaga (1893) identified this specimen as *Dendroaspis angusticeps*, but Bocage (1892) reidentified it as a *Dendroaspis jamesoni*. However, Bocage's (1888, 1892) interpretation of *D. jamesoni* was at the time erroneous, as he considered the species with 13 midbody scale rows as *D. jamesoni* (in fact this is *Dendroaspis viridis*), identifying the species with 15 midbody scale rows (the true *D. jamesoni*) as *Dendroaspis neglectus*, a name he coined (Bocage 1888). Only in 1905 did Bocage reidentify the São Tomé animals as *D. viridis* (Bocage 1905).

While most of the characters presented by Bedriaga are concordant with those of the nominotypical *D. viridis*, the number of subcaudals is notably low for all known species of the genus *Dendroaspis*. The low number reported by Bedriaga was noted by Bocage (1892) as an "anomaly". Another "anomaly" reported by Bocage (1892) in Bedriaga's description was the presence of seven supralabials instead of eight. *Dendroaspis jamesoni* has between 94 and 122 subcaudals (103 to 122 in *D. jamesoni jamesoni*, 94 to 107 in *D. jamesoni kaimosae*; see Loveridge 1936), *D. viridis* has between 111 and 125, while *D. angusticeps* has between 99 and 126 (Trape 2023, Loveridge 1950). The Black-mamba, *Dendroaspis polylepis*, has between 105 and 131 (Chippaux 2006, Chippaux & Jackson 2019, Trape 2023). It could be argued that the considerably lower number of subcaudals presented by Bedriaga (1893) is due the tail being incomplete. However, caudal pseudoautotomy (sensu Slowinski & Savage 1995) remains unexamined in species of the genus *Dendroaspis* and is rare among most African elapids. Consequently, if a specimen exhibits an incomplete tail, it is likely the result of a predatory encounter. This would be the most parsimonious explanation to justify the lower number of subcaudals in this specimen. However, the meticulous and detailed description provided by Bedriaga, in which he refers that there is "a double anal and a scale enveloping the tip of the tail; the edge of this terminal scale is visible below", excludes the scenario of the tail being incomplete. The difference between the number of supralabials is also of interest, as Bedriaga reported only seven, while *D. viridis* usually has between 9 to 10 (Chippaux 2006). Although not mentioned by Fischer (1855), the illustration of the specimen depicted in Fischer (1856b) seems to also have between 7 and 8 supralabials.

Such a discrepancy in the number of subcaudals and supralabials may be taxonomically relevant. Despite its medical importance and being one of the most iconic groups of African snakes, the genus *Dendroaspis* hasn't been the subject of a modern taxonomic review. The most recent and authoritative field guides on African snakes recognize five valid taxa: *Dendroaspis jamesoni jamesoni*, *D. jamesoni kaimosae*, *D. viridis*, *D. angusticeps* and *D. polylepis* (Loveridge 1936, 1950, Chippaux 2006, Spawls et al. 2018, 2020, Chippaux & Jackson 2019, Trape 2023). All these guides differentiate the five taxa based on few morphological characters, such as the number of scales around midbody, number of subcaudals, and coloration of both body and tail (see Key to genus below).

Key to the genus *Dendroaspis*
(including the putative São Tomé Green Mamba, "*Dendroaspis reticulata*")

1) Midbody scales rows 13 ..... 2)
1') Midbody scales rows ≥ 15 ..... 3)
2) 62 subcaudals, 7 to 8 supralabials ..... "***D. reticulata***"
2') 111 to 125 subcaudals, 9 to 10 supralabials ... ***D. viridis***
3) Overall body coloration from olive to grey, midbody scales rows 23 to 24 ..... ***D. polylepis***
3') Overall body coloration green, midbody scales rows 15 to 19 ..... 4)
4) Midbody scale rows 17 to 21, distributed in eastern Africa ..... ***D. angusticeps***
4') Midbody scale rows 15 to 17, distributed in central and western Africa ..... 5)
5) Tail uniformly black, 94 to 107 subcaudals ..... ***D. jamesoni kaimosae***
5') Tail uniformly green, 103 to 122 subcaudals ..... ***D. jamesoni jamesoni***

The lower number of subcaudals rapidly separates the São Tomé specimen not only from its morphologically closer congener, *D. viridis*, but from all the remaining species of *Dendroaspis*. The different number of supralabials is an additional argument. Such a major morphological difference in a morphologically conservative genus is good indication of taxonomic separation of the São Tomé population. Such taxonomic separation is further plausible given the insular nature of the population and indeed by the existence of an otherwise entirely endemic snake fauna in the islands, including other elapids. For example, the São Tomé Cobra Preta, *N. (B.) peroescobari* differs from the continental forms by much more modest morphological differences (see Ceríaco et al. 2017), but its taxonomic status and systematic position have been independently confirmed by two molecular datasets (Ceríaco et al. 2017, Wüster et al. 2018). Following this argumentation and de Queiroz (1999) general lineage species concept, the obvious outcome would be to recognize the São Tomé population of *Dendroaspis* as an island endemic species, differing from all its congeners by its lower number of subcaudal scales, and named *D. reticulata* (Fischer, 1855).

Such recognition would raise a set of different questions. No molecular data exists for the taxon, thus its systematic position among the other members of the genus can only be indirectly inferred. Its morphological similarity with *D. viridis* and the geographic distribution of the latter suggest some phylogenetic proximity, as observed in other herpetological groups occurring on the island (*Ptychadena*, Measey et al. 2007; *Hyperolius*, Bell et al. 2015; *Trachylepis*, Ceríaco et al. 2016; *Naja*, Ceríaco et al. 2017; *Panaspis*, Soares et al. 2018; *Boaedon*, Ceríaco et al. 2021). As no specimens have been collected nor observed since the late nineteenth century, can the species be already

extinct? Or has its presumed arboreal behavior, as in other members of the genus, allowed it to go unnoticed in the dense canopy of São Tomé forests? Is the reduced number of subcaudal vertebrae attributable to an ecomorphological constraint or specialization?

However, a more cautious approach is needed before we accept the existence (or past existence) of an endemic species of *Dendroaspis* on São Tomé. Despite all the arguments above, the fact is that no specimens are currently available for our examination. The disappearance of Bedriaga's specimen precludes the confirmation of his observations through the reexamination of the specimen, and thus the intactness of the tail can't be confirmed. As neither Jan (1857, 1858, 1859, 1863) or Fischer (1855, 1856a, 1856b) provided any data regarding the number of subcaudals, we rely on a single specimen. A sample size of one raises the possibility that the specimen examined by Bedriaga could indeed be "anomalous" as suggested by Bocage, i.e. an individual presenting some kind of malformation or mutation and therefore not a good representative of the population.

The mystery of the São Tomé Green Mamba continues. Further research is needed, both in museums and in São Tomé's forests, in order to find this elusive animal.

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