VERTEBRATE ZOOLOGY

70 (3): 291 – 304
2020

SENCKENBERG

Constrictores Oppel, 1811 – the available name for the taxonomic group uniting boas and pythons

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Submitted April 25, 2020.
Accepted June 17, 2020.
Published online at www.senckenberg.de/vertebrate-zoology on June 26, 2020.
Published in print Q3/2020.

Editor in charge: Uwe Fritz

Abstract

Recent advances in the phylogenetic relationships of snakes using both molecular and morphological data have generally demonstrated a close relationship between boas and pythons but also induced nomenclatural changes that rob the least inclusive clade to which both belong of a name. This name would be tremendously useful, because it is the least inclusive group to which a large number of fossil boa-like or python-like taxa can be assigned. Accordingly, an update of higher-level nomenclature is desirable. We herein provide an overview of all the names that have historically been applied to boas and pythons. We show that the earliest name for the supra-familial group encompassing boas and pythons is Constrictores Oppel, 1811. We herein revalidate it as an order-group name below Alethinophidia Nopcsa, 1923 and provide a phylogenetic definition of it to encompass the modern concepts of Booidea and Pythonoidea. We provide emended diagnoses for Constrictores, Booidea, and Pythonoidea based on recent morphological data-sets.

Key words

Booidea, nomenclature, Pythonoidea, Serpentes.

Introduction

Boas and pythons are among the most well known snakes. They comprise the largest forms, both extinct and extant (Murphy & Henderson, 1997; Head *et al*., 2009), and have fascinated humans at least since Antiquity (Schneider, 1821). They have a broad geographic distribution, covering almost all continents except Antarctica, being found even in remote oceanic islands (Wallach *et al*., 2014). Although many species are widely distributed, the range of other species is rather confined geographically. Especially the latter species are increasingly in need of conservation efforts (e.g., Reynolds & Henderson, 2018); one of them, *Bolyeria multocarinata* (Boié in Boié, 1827) went extinct in historical times, as recently as the 1980s (Day, 1989; Wallach *et al*., 2014). They have an extensive fossil record, dominating snake assemblages throughout the Paleogene in North America and Europe, and achieved a considerable species richness and diversity, with a variety of sizes and habits (Rage, 1984; Szyndlar, 1991; Head *et al*., 2009; Georgalis & Scheyer, 2019). Their fossil record comprises primarily vertebrae and, more rarely, isolated skull bones (e.g., Gilmore, 1938; Rage, 1984; Holman, 2000; Szyndlar & Rage, 2003; Smith, 2013; Georgalis & Scheyer, 2019), although complete, articulated skeletons have been found in certain *Konservat-Lagerstätten*, and even rare mummified specimens with scales have been recovered (Filhol, 1877; Rochebrune, 1884; Smith & Scanferla, 2016; Smith *et al*., 2018; Scanferla & Smith, 2020).

Recent advances in snake systematics based on DNA sequence data, coupled with novel interpretations of

morphology and skeletal anatomy, have lead to the recognition of boas and pythons as distinct superfamily-level taxa (e.g., Vidal *et al*., 2007; Vidal & Hedges, 2009; Burbrink & Crother, 2011; Reynolds *et al*., 2014). Divergence dates among boas and pythons are estimated to have occurred as early as the Paleocene or the Late Cretaceous (Head, 2015; Hsiang *et al*., 2015; Zheng & Wiens, 2016). The content of Booidea as a superfamily has been restricted (Pyron *et al*., 2014) to Neotropical boas (Boidae), American dwarf boas (Ungaliophiinae), the Rainbow Boa and rubber boas (Charininae), the Calabar Burrowing Python (*Calabaria reinhardtii*), the Malagasy boas (Sanziniidae), the Old World sand boas (*Eryx* [including *Gongylophis*]), and the Pacific Island boas (*Candoia*). Pythonoidea, in turn, encompasses Old World pythons (Pythonidae), sunbeam snakes (*Xenopeltis*) and the Mexican Burrowing Python (*Loxocemus bicolor*). Boa- and python-like fossils, the majority of which are known exclusively from vertebrae, frequently cannot be assigned with confidence to the boa or python clades, and a term is now lacking for that higher-level clade (Burbrink *et al*., 2020) comprising both (e.g., Georgalis & Scheyer, 2019). The question thus arises, what should be the name for the clade uniting boas and pythons? We demonstrate that there is in fact an available name for this group and we accordingly revalidate and redefine it here.

Taxonomic history

Several available names in the old literature have been established to denote the taxonomic entity comprising boas and pythons. Many early workers simply assigned all boas to the genus *Boa* Linnaeus, 1758 (e.g., Linnaeus, 1758; Boddaert, 1783; Gmelin, 1789; Seetzen, 1796; Link, 1807); pythons were instead referred to "couleuvres" (e.g., Lacépède, 1789) or even formally to the genus *Coluber* Linnaeus, 1758 (e.g., Linnaeus, 1758; Gmelin, 1789; Bonnaterre, 1790; Shaw, 1802). Others assigned the then-known species only to the genera *Boa*, *Python* Daudin, 1803b, and *Eryx* Daudin, 1803d, but did not provide any higher group name (e.g., Daudin, 1803b, d). Schneider (1801) placed several boas and pythons in the genus *Boa*, but still kept *Python molurus* (Linnaeus, 1758) in *Coluber*, and he treated "erycine" species as members of *Anguis* Linnaeus, 1758 (note that in this paper we use the term "erycine" in quotes, because molecular and combined phylogenetic analyses have universally held the taxon Erycinae sensu Rage [1984] to be polyphyletic). In a similar vein, Latreille (1804), although he distinguished boas and pythons, included both in Coluberini, along with the majority of snake genera. Duméril (1805) used the (apparently informal) name "boas" (with lower-case "b") to include *Boa*, *Coralle* (i.e., *Corallus* Daudin, 1803b), and *Python*, but also the homalopsid *Hurria* Daudin, 1803b (misspelled as *Hurriah*; currently *Cerberus* Cuvier, 1829) and the elapid *Acanthophis* Daudin, 1803b. Duméril (1805), however, did not place *Eryx* (misspelled by him as *Erix*) into "boas" but rather treated it as distinct. The same author, nevertheless, included "boas" and *Erix* in a higher, formal, group, which he named Hétérodermes, that also included a number of other snake groups (Duméril, 1805).

Oppel (1811a, b) applied the name Constrictores, in two different publications during the same year, to encompass only the genera *Boa* and *Eryx*. Although the genera *Python* Daudin, 1803b, and *Eryx* Daudin, 1803d, had been already established prior to Oppel's (1811a, b) works, the latter author mentioned *Eryx* but not *Python*. In Oppel's (1811a:383; 1811b:58) concept of *Boa*, however, besides the mentioned species in his text, he also inserted "etc.", thus making clear that he did not intend to list all known taxa. Notably, he also listed the species *Boa regia* Shaw, 1802 (currently *Python regius*; Wallach *et al*., 2014). It thus appears that Oppel (1811a, b) intended his Constrictores to encompass all large taxa recognized as booids and pythonoids today; furthermore, he specifically excluded aniliids (which he placed in *Tortrix* Oppel, 1811b) from his Constrictores. The name Constrictores was subsequently used by Fischer von Waldheim (1813), who, however, expanded the denoted group to include the hydrophiine elapids *Platurus* Latreille in Sonnini and Latreille, 1801 (i.e., *Laticauda* Laurenti, 1768) and *Hydrophis* Latreille in Sonnini and Latreille, 1801.

Rafinesque (1815) applied the name Aplepia to encompass *Boa*, *Python*, *Eryx*, and *Corallus*, as well as the peculiar homalopsid genus *Erpeton* Lacépède, 1801. Rafinesque (1815:77) united these genera into Aplepia on the basis of their shared presence of "[u]n seul rang de plaques sous la queue ou le corps" [a single row of plates underneath the body]; according to his taxonomic scheme, Aplepia was the counterpart of Diplepia (including *Coluber* and certain other colubrids, but also the elapid *Acanthophis*) and both of them together constituted the family Colubrinia, which in turn belonged to the suborder Heterodermia.

Cuvier (1817) placed boas in their own group, termed Boas, subdivided into "Boas propres", Erix (sic), and Erpetons (including *Erpeton*), whereas he placed pythons (his Pythons) along with colubrids in a different group, Couleuvres. The same author subsequently kept practically the same taxonomic arrangement, with his Boas being distinct from his Pythons, the latter still pertaining to Couleuvres (Cuvier, 1829).

Mayer (1824) created the name Phaenopoda, denoting the presence of "spur-like" hind-limb rudiments in these snakes, to encompass *Boa*, *Python*, and *Eryx*, as well as *Tortrix* (i.e., aniliids). That name was later discussed by Duméril & Bibron (1844; as "Phénopodes"), but curiously the name Phaenopoda was not mentioned at all in the detailed catalog of Boulenger (1893).

Gray (1825) established Boidæ to include both boas and pythons, an arrangement that the same author continued to follow (e.g., Gray, 1842, 1849, 1858). This arrangement met wide acceptance among prominent ophidian researchers from the second half of the 19th through

the 20th centuries, who all placed these snakes together into a single family, Boidae (e.g., Cantor, 1847; Boæidæ of Jan, 1863; Boulenger, 1890, 1893, 1913; Sclater, 1891; Zacharias, 1898; Zenneck, 1898). In this scheme, until recently, boas and pythons were usually distinguished at the subfamily level, as Boinae and Pythoninae respectively (Gadow, 1909; Fraser, 1937; Hoffstetter, 1939, 1955; Kuhn, 1946, 1963; Romer, 1956; Frazzetta, 1959, 1966; Roux-Estève, 1965; Rage, 1984; Underwood & Stimson, 1990; Szyndlar, 1991; Holman, 2000; Ivanov, 2000; Szyndlar & Rage, 2003).

Haworth (1825) placed *Boa*, *Eryx*, and *Python*, as well as a number of other non-venomous snakes in a group termed Innocua, this being the counterpart of all venomous snakes, which were forming the group Venenata. A similar arrangement of snakes on the basis of venomousness continued to appear in the 19th century literature (e.g., Serpenti Innocui and Serpenti Velenosi of Filippi, 1840).

Fitzinger (1826) also placed both boas and pythons in a single group, which he called Pythonoidea. He later included them in Saurophidia, which comprised Gongylophes (*Eryx* and allied forms), Centrophes (boas), and Pythophes (pythons), along with scolecophidians and aniliids (Fitzinger, 1843). Still later, he emended the spelling of Pythophes to Pythonophes (Fitzinger, 1861). The names Centrophes (for boas) and Pythophes (for pythons) were subsequently adopted by Diesing (1851), who in his taxonomic scheme, however, omitted *Eryx*. The name Pythonoidea for both boas and pythons was used by Leuckart (1841), whereas Eichwald (1831) and Schinz (1833–1835) used the spellings Pythonoidei and Pythonoideae respectively for the same group.

Ritgen (1826) used the name Onychophori to denote the group encompassing the genera *Eryx*, *Python*, and *Boa*, but also *Tortrix* (i.e., aniliids).

Curiously, Boié (1826, 1827) placed *Boa*, *Python*, and *Eryx* into Colubrini. Bonaparte (1831) used the name Boidæ to encompass the subgroups Boina (including both *Boa* and *Python*) and Erycina but also Typhlopodina (i.e., scolecophidians). The same author subsequently modified his taxonomic scheme, removed scolecophidians from snakes, but still treated *Eryx* as distinct from boas and pythons, thus recognizing the families Erycidae (including Erycina but also Calamarina [i.e., the caenophidian *Calamaria* Boié H. in Boié F., 1827]) and Boidae (including Boina and Pythonina).

Müller (1831) used the name Macrostomata to differentiate large-gaped snakes from their counterpart Microstomata (which included scolecophidians, aniliids, but also amphisbaenians). The concept of Macrostomata includes, in addition to boas and pythons, an array of other snake taxa; indeed, under modern phylogenetic concepts, this taxonomic entity is now used to encompass all alethinophidians to the exclusion of *Anilius*, cylindrophiids, and uropeltids (e.g., Lee & Scanlon, 2002; Wilcox *et al*., 2002; Hsiang *et al*., 2015; but see Burbrink *et al*., 2020). Note also, however, that contrary to the widespread misconception that Müller (1831) created that name, Macrostomata was first used by Ritgen (1826). Within Macrostomata Müller (1831) distinguished Holodonta (for pythons) and Isodonta or Aproterodonta (for boas).

The name Peropodes appeared first in Wiegmann (1832) to denote the group encompassing all boas, erycines, and pythons and quickly became among the most widely used in the 19th century literature (Fedorovich Gorianinow, 1834; Burmeister, 1837; Schubert, 1837; Gorski, 1852; Troschel, 1861; Meyer, 1874; Schreiber, 1875; Müller, 1878, 1880; Peters, 1882; Hoffman, 1890; Girard, 1895). It was later emended as Peropodae (Brehm, 1878; Bedriaga, 1882) or Peropoda (Lichtenstein & Mertens, 1856; Cope, 1862, 1886, 1893, 1894, 1895, 1898), and this name was even, although sporadically, also used during the 20th century (e.g., Kiritzescu, 1902; Noguchi, 1909; Leblanc, 1920; Gilmore, 1938). Indeed, the name Peropodes seems to have been so widespread that even Fitzinger (1867) adopted it over names he had previously used for the group encompassing boas and pythons as well as *Uropeltis* Cuvier, 1829, *Xenopeltis* Reinwardt in Boié, 1827, and (the currently much distantly related) *Calamaria*.

Schlegel (1837) included a group termed Boas the genera *Boa* and *Python* as well as the caenophidian *Acrochordus* Hornstedt, 1787.

Swainson (1839) placed *Boa*, *Python*, and *Eryx* in Coluberidæ, along with a large array of other, non-venomous, snake genera, mainly Colubriformes (sensu Zaher *et al*., 2009).

In their monumental work, Duméril & Bibron (1844) introduced the name Azémiophides to encompass all boas (Boæides and Érycides), pythons (Pythonides), and ungaliophiines as well as aniliids (Tortricides). A few years later, they redefined the concept of Azémiophides, proposing also the alternative name Aglyphodontes, which encompassed the aforementioned taxa plus acrochordids, uropeltids, and certain Colubriformes (Duméril, 1853; Duméril *et al*., 1854a, b). They still, nevertheless, treated boas and erycines as a group (Aprotérodontes) distinct from that of pythons (Holodontes or Holodontiens) (Duméril & Bibron, 1844; Duméril, 1853, 1859; Duméril *et al*., 1854a, b) and this arrangement continued even later (Rochebrune, 1880).

The name Asinea was used by Cope (1864) to denote the group encompassing *Xenopeltis*, pythons, boas as well as *Acrochordus*, which he all, nevertheless, still treated as distinct families (Xenopeltidæ, Pythonidæ, Boidæ, and Acrochordidæ respectively). This distinction of Pythonidae from Boidae was subsequently followed by the same author (Cope, 1893) and some other prominent workers (Günther, 1864; Zittel, 1887–1890; Lydekker, 1888; Hoffmann, 1890). The name Asinea was subsequently also used by Gilmore (1938).

Jan (1865) called the group as Boidiens, and further divided it into Erycides, Boaeides, and Pythonides. The same author excluded from that group *Xenopeltis*, which he placed instead with "anilioids" (his Tortriciens).

The name Boaeformes has also appeared in the literature (Heilprin, 1907; Haas, 1952), being also circulated

under the alternative spelling Boaeformia (Ihering, 1911; Stromer, 1912; Kuhn, 1946).

Hoffstetter (1939) introduced the term Henophidia for a group uniting boas, pythons, and "anilioids", and this arrangement was followed more or less consistently in the next decades (e.g., Hoffstetter, 1955; Romer, 1956; Underwood, 1967; Gasc, 1974; Rieppel, 1977, 1988; Groombridge, 1979; Harding & Holman, 1981; Cundall *et al*., 1993; Reynolds *et al*., 2014). However, Henophidia has now also been used for the clade comprising both boas, pythons, and caenophidians, i.e., alethinophidians to the exclusion of "anilioids", and sometimes *Xenopeltis* and *Loxocemus* Cope, 1861 (e.g., Burbrink & Crother, 2011; Gauthier *et al*., 2012; Figueroa *et al*., 2016; Pethermann & Gauthier, 2018).

Current taxonomies

Recent rank-based taxonomies, relying on molecular and/or morphology-based phylogenies, currently treat Boidae and Pythonidae as distinct families, and a number of smaller groups are also separated as different families (Dowling *et al*., 1996; Slowinski & Lawson, 2002; Wilcox *et al*., 2002; Lawson *et al*., 2004; Noonan & Chippindale, 2006; Vidal *et al*., 2007, 2009; Vidal & Hedges, 2009; Wiens *et al*., 2012; Pyron *et al*., 2013; Reynolds *et al*., 2014; Hsiang *et al*., 2015; Figueroa *et al*., 2016; Streicher & Wiens, 2016; Zheng & Wiens, 2016; Harrington & Reeder, 2017; Burbrink *et al*., 2020). The relatives of Boidae and Pythonidae are united as superfamilies, i.e., Booidea and Pythonoidea (e.g., Scanlon & Lee, 2011; Pyron *et al*., 2014; Wallach *et al*., 2014). In particular, the family "Boidae" sensu Pyron *et al*. (2013) and Reynolds *et al*. (2014) has been elevated to the supefamily Booidea, containing the families Boidae, Calabariidae, Candoiidae, Charinidae (comprising Charininae and Ungaliophiinae), Erycidae, and Sanziniidae (Pyron *et al*., 2014), whereas Pythonoidea is conceived as containing Pythonidae, Loxocemidae, and Xenopeltidae (Wallach *et al*., 2014). Bolyeriidae (Round Island boas) and Xenophidiidae (comprising only *Xenophidion*) are thought to be closely related to Booidea or Pythonoidea based on molecular analyses (e.g., Wallach *et al*., 2014).

Some recent phylogenetic analyses using DNA sequence or combined data have suggested that Pythonoidea may be more closely related to Uropeltidae and/or Cylindrophiidae than to Booidea (Lawson *et al*., 2004; Oguiura *et al*., 2010; Reynolds *et al*., 2014; Tonini *et al*., 2016), or even Booidea more closely related to Cylindrophiidae than Pythonoidea (Li *et al*., 2020), but Booidea and Pythonoidea are otherwise found to be monophyletic with respect to those and other major clades (e.g., Slowinski & Lawson, 2002; Lee *et al*., 2007; Pyron *et al*., 2013; Streicher & Wiens, 2016). Most recently, Burbrink *et al*. (2020), considered 394 loci. In their maximum likelihood tree based on analysis of the partitioned, concatenated dataset, they found bootstrap support of 99.7% (ultrafast bootstrap approximation) and Shimodaira-Hasegawa approximate likelihood ratio test value of 100% for a clade comprising Pythonoidea, Bolyeriidae, and Booidea as defined above (Burbrink *et al*., 2020:Supplementary Data S7); such values comprise unambiguous support in Zaher *et al*.'s (2019) classification. Fossil-calibrated species-tree methods applied to the same dataset recovered the same topology with less strong support (Burbrink *et al*., 2020). Thus, the analyses with the broadest taxon sampling (Pyron *et al*., 2013) and the most in-depth gene sampling (Burbrink *et al*., 2020) have come to the same conclusion.

Furthermore, phylogenetic analyses of morphology have also strongly supported a sister-group relationship between boas and pythons (e.g., Lee & Scanlon, 2002; Gauthier *et al*., 2012; Zaher & Scanferla, 2012; Scanferla & Smith, 2020), although the position of minor lineages (*Xenopeltis*, *Loxocemus*, Bolyeriidae, *Calabaria*) relative to this clade has vacillated.

Thus, in contrast to the taxon name Iguanidae (= Pleurodonta; Torres-Carvajal *et al*., in press), there has been no single name referring to a group of similar composition throughout the previous century. In addition to repeated alterations to the extant members of Boidae, we also note that some fossil taxa were previously placed in this taxon (Simpson, 1933; Gilmore, 1938; Hoffstetter, 1955; Rage, 1984; Holman, 2000), which are now universally accepted to pertain to other groups, such as the extinct Palaeophiidae and Madtsoiidae (Rage *et al*., 2003; Wallach *et al*., 2014; Georgalis *et al*., 2020).

Availability and a phylogenetic definition of Constrictores Oppel, 1811

Taking into consideration the survey of literature presented above, it is evident that the oldest available name for the least inclusive group uniting boas and pythons is Constrictores Oppel, 1811a. As mentioned above, Oppel (1811a, b) published his squamate classification in two different works: the first (Oppel, 1811a was published in the 16th volume of *Annales du Museum d'histoire Naturelle* – this volume is dated on its cover page as "1810", however, it has been subsequently demonstrated by Sherborn (1914) that the volume was in fact published in early 1811 (pages 328 – 428 of the volume were published between January and March of that year). The second work (Oppel, 1811b), which is by far the most popular and remains a key publication for reptile systematics, was a book published in Munich around December 1811 and dealt with all extant reptile and amphibian groups. It is thus clear that Oppel (1811a) was published before Oppel (1811b) and therefore, the name Constrictores first appeared in Oppel (1811a). Be that as it may, the relevant text about Constrictores (and the inclusive genera *Eryx* and *Boa*) in both Oppel's (1811a, b) works was almost identical, with only minor wording differences (e.g., "corpus cylindraceum" in

Oppel [1811a:382] vs. "corpus cylindricum" in Oppel [1811b:56]). Another difference between Oppel (1811a) and (1811b) is that in the latter he used the Latin word "Familia" prior to the word Constrictores (Oppel, 1811b) but he did not use any such denomination or rank in his earlier (1811a) work.

Note that the name Constrictores is a formal Latin name and not a vernacular of German, French or some other modern language. The word "constrictor" is derived from the Latin verb "constringere" (constrict, strangle). It is masculine substantive of the third declension. Accordingly, the nominative plural carries the suffix -es, viz. "constrictores" (Pr. Patrick Smith, pers. comm., 2019). "Constrictor" is not a French word (Robert French Dictionary). Moreover, the name Constrictores does not originate from the genus name *Constrictor*, as Oppel (1811a, b) does not mention this genus at all (see also Etymology below). Many other formal Latin names appear in the same Oppel's (1811a, b) paper (e.g., Squamata [spelled as "Squammata" in the 1811a paper], Testudinata, Saurii, Ophidii, Colubrini, etc). Almost the whole text of both papers is written in Latin, with only the title and few paragraphs being in French in the first paper (Oppel, 1811a) and only the title and a few pages being in German in the second paper (Oppel, 1811b). The fact that the word Constrictores is Latin is further supported by the fact that the immediately succeeding words of its "diagnosis" are also in Latin ("Cauda attenuata, rotundata; tela venenifera nulla; calcaria ad anum" [Oppel, 1811a:377; Oppel, 1811b:49]).

Oppel (1811a) did not provide any rank denomination for Constrictores in his earlier work, though he later used the term "Familia" for that grouping (Oppel, 1811b). In the modern taxonomic scheme we propose for Constrictores that encompasses both boas and pythons, this grouping is not a family-level one. Therefore it does not necessitate an amendment of the name or its ending, as has been the case with family-level names introduced in Oppel's (1811a, b) works (such as Viperini, emended to Viperidae, and Colubrini, emended to Colubridae). The fact that the name was not originally proposed as a family group name helps to avoid one potential complication that would ensue. Namely, even though Oppel (1811a) did not mention the genus *Constrictor* Laurenti, 1768, one could hypothesize that it could be the type genus of the family Constrictoridae. The ICZN (1999: Article 11.7.1.1) dictates: "a family-group name when first published must be a noun in the nominative plural formed from the stem of an available generic name [Art. 29] (indicated either by express reference to the generic name or by inference from its stem); the generic name must be a name then used as valid in the new family-group taxon [Arts. 63, 64] (use of the stem alone in forming the name is accepted as evidence that the author used the generic name as valid in the new family-group taxon unless there is evidence to the contrary)" and later clarifies that "[the family group name must] be clearly used as a scientific name to denote a suprageneric taxon and not merely as a plural noun or adjective referring to the members of a genus" (ICZN, 1999: Article 11.7.1.2). In summary, whereas Oppel (1811a) did clearly use Constrictores as a scientific name, it was not as a family-group name, so there would be no reason to emend it to Constrictoridae.

Most importantly, *Constrictor* is a junior synonym of *Boa* Linnaeus, 1758, with the latter genus mentioned by Oppel (1811a). The ICZN (1999:Article 40.1) dictates that "when the name of a type genus of a nominal family-group taxon is considered to be a junior synonym of the name of another nominal genus, the family-group name is not to be replaced on that account alone", so Boidae would still have priority over the hypothetical family level Constrictoridae.

We therefore regard Constrictores Oppel, 1811a as a valid name at the supra-familial level (order-group name). From the point of view of hierarchy, Constrictores is ranked below the level of Alethinophidia Nopcsa, 1923, and above the level of the superfamilies Booidea and Pythonoidea.

The fact that the name Constrictores had virtually no usage or mentions during the 19th and 20th centuries does not invalidate it or render it obsolete, as would certainly be the case with names at the family, genus, or species level: the latter would eventually be rendered nomina oblita (ICZN, 1999). As such, there is no criterion of prevailing usage in the case of names above the family level, which could possibly lead to the revalidation of the name Peropodes, which appeared extensively in the 19th century literature and also occasionally appeared even in 20th century. Thus, we resurrect the name Constrictores Oppel, 1811a as an ordinal-group name encompassing Booidea, Pythonoidea and Bolyerioidea.

Furthermore, we define the name phylogenetically following the PhyloCode (Cantino & de Queiroz, 2014).

Constrictores Oppel, 1811a [Georgalis & Smith, this paper], converted clade name

Registration number. 309 [www.phyloregnum.org]

Definition. The crown clade originating in the last common ancestor of *Boa constrictor* Linnaeus, 1758, and *Python* (originally *Boa*) *regius* (Shaw, 1802), provided that neither internal specifier is more closely related to any of the following species than to each other: *Typhlops lumbricalis* (Linnaeus, 1758), *Leptotyphlops nigricans* (Schlegel, 1837 – 1844), *Anomalepis mexicanus* Jan, 1860, *Anilius scytale* (Linnaeus, 1758), *Uropeltis ceylanicus* Cuvier, 1829, *Cylindrophis ruffus* (Laurenti, 1768), and *Coluber constrictor* Linnaeus, 1758. Abbreviated definition: *Constrictores* = < ∇ *Boa constrictor* Linnaeus, 1758 & *Python regius* (Shaw, 1802), provided that neither internal specifier is more closely related to any of the following species than to each other: *Typhlops lumbricalis* (Linnaeus, 1758), *Leptotyphlops nigricans* (Schlegel, 1837 – 1844), *Anomalepis mexicanus* Jan, 1860, *Anilius scytale* (Linnaeus, 1758), *Uropeltis ceylanicus* Cuvier,

1829, *Cylindrophis ruffus* (Laurenti, 1768), and *Coluber constrictor* Linnaeus, 1758.

Note that in this definition we chose to exclude not only the first-named scolecophidian (i.e., the typhlopid *Typhlops lumbricallis*) but also the types of the eponymous Linnaean families Leptotyphlopidae and Anomalepididae, taking into consideration that many phylogenetic analyses indicate that Scolecophidia is paraphyletic (e.g., Zheng & Wiens, 2016; Harrington & Reeder, 2017; Miralles *et al*., 2018; Burbrink *et al*., 2020; but see Streicher & Wiens, 2016). Further note that the eponymous type species of Leptotyphlopidae is *Leptotyphlops nigricans* (Schlegel, 1837–1844) and not *Leptotyphlops albifrons*, i.e., *Stenostoma albifrons* Wagler in Spix and Wagler, 1824 (currently *Epictia albifrons*) as stated by Lee *et al*. (2007).

Etymology. As was mentioned above, the word "Constrictores" originates from the Latin verb "constringere" (constrict, strangle). The name of the type species of Boidae, *Boa constrictor*, obviously refers to the snake's method of killing prey (e.g., Boback *et al*., 2015). Note that the genus names *Constrictor* Laurenti, 1768 and *Constrictor* Wagler, 1830, were independently established to accommodate species of *Boa* and *Python* respectively (as was also mentioned above, Oppel [1811a, b] made no single mention of the genus name *Constrictor* in his works). Neither should *Constrictores* be confused with the type species of Colubridae, *Coluber constrictor* Linnaeus, 1758. Constriction appears to be a widespread killing method across the different lineages within *Constrictores* (e.g., Cundall & Irish, 1986). Of course, the killing of prey by constriction is a widespread habit among members of other snake clades (e.g., Hsiang *et al*., 2015). We propose to use the informal term "constrictors" to refer to members of the clade *Constrictores*.

Primary reference phylogeny. Burbrink *et al*. (2020), fig. S7; this paper, Fig. 1.

Composition. Apart from the taxa subsuming the internal specifiers, i.e., Boidae Gray, 1825, sensu Pyron *et al*. (2014) and Pythonidae Fitzinger, 1826, sensu Wallach *et al*. (2014), the taxonomic content of Constrictores following the reference phylogeny and most other molecular and combined analyses is clear: *Eryx*, *Candoia*, Sanziniidae, Charinidae, *Calabaria*, *Loxocemus*, *Xenopeltis*, Bolyeriidae, and *Xenophidion*.

On the booid side, *Eryx* was for long time treated as a distinct family, Erycidae (e.g., Érycides of Duméril & Bibron, 1844, and Duméril *et al*., 1854c; Jan, 1862; Günther, 1864; Carus, 1868; Cope, 1883; Boettger, 1884; Hoffmann, 1890; Počta, 1905; Stromer, 1910); since the mid-20th century, Erycidae was usually treated as a subfamily of Boidae, as Erycinae (e.g., Hecht, 1959; Hoffstetter & Rage, 1972; Rage, 1977, 1984; Szyndlar, 1991; Kluge, 1993; Szyndlar & Schleich, 1994; Szyndlar & Rage, 2003; Baszio, 2004; Smith, 2013; Wallach *et al*., 2014). Recent taxonomic schemes place *Eryx* in a distinct family close to Boidae (e.g., Pyron *et al*., 2014; Figueroa *et al*., 2016; Burbrink *et al*., 2020). Other clear members of Constrictores on the booid side are Charinidae Gray, 1849 (sensu Pyron *et al*., 2014) (comprising Charininae Gray, 1849, and Ungaliophiinae McDowell, 1987), *Candoia* Gray, 1842 (for which the monotypic family Candoiidae Pyron, Reynolds, & Burbrink, 2014 was established), *Calabaria* Gray, 1858 (for which the monotypic family Calabariidae Gray, 1858, was established), and Sanziniidae Romer, 1956 (including *Acrantophis* Jan, 1860, and *Sanzinia* Gray, 1849).

On the pythonoid side, *Xenopeltis* Reinwardt in Boié, 1827 (for which the monotypic family Xenopeltidae Bonaparte, 1845, was established) and *Loxocemus* Cope, 1861 (for which the monotypic family Loxocemidae Cope, 1861, was established) are inferred to be successive sister taxa of Pythonidae in molecular analyses (e.g., Slowinski & Lawson, 2002; Pyron *et al*., 2013; Reynolds *et al*., 2014; Figueroa *et al*., 2016; Streicher & Wiens, 2016; Zheng & Wiens, 2016; Harrington & Reeder, 2017; Burbrink *et al*., 2020), which makes them members of Constrictores. Note, however, that in many morphology-only analyses these two lineages fall outside of the clade comprising boas, pythons, and caenophidians (e.g., Lee & Scanlon, 2002; Hsiang *et al*., 2015). More recent studies have concluded that the Asian *Xenophidion* Günther and Manthey, 1995 (for which the monotypic family Xenophidiidae Wallach & Günther, 1998, was established) and/or the Mascarene Bolyeriidae Hoffstetter, 1946, are related to boas (Streicher & Wiens, 2016; Zheng & Wiens, 2016; Harrington & Reeder, 2017; Burbrink *et al*., 2020), which would also make them members of Constrictores; this conclusion is unchanged if they are more closely related to pythons instead (Lawson *et al*., 2004; species-tree analysis of Burbrink *et al*., 2020). There is considerably molecular evidence that *Xenophidion* and Bolyeriidae are sister-taxa, starting with Lawson *et al*. (2004), and they share a synapomorphy that is unique among tetrapods: a jointed maxilla. However, *Xenophidion* was not included in the reference phylogeny of Burbrink *et al*. (2020), so further work is desirable to test its membership.

The case of Tropidophiidae (i.e., extant *Tropidophis* Bibron in Ramón de la Sagra, 1838–1843, and *Trachyboa* Peters, 1860) bears elaboration. They were long lumped into boids (e.g., Romer, 1956; Rage, 1984; Szyndlar & Böhme, 1996), including also ungaliophiines (e.g., Szyndlar & Rage, 2003). However, formal phylogenetic analyses of morphology (e.g., Lee & Scanlon, 2002; Gauthier *et al*., 2012; Zaher & Scanferla, 2012; Hsiang *et al*., 2015; Scanferla *et al*., 2016; Scanferla & Smith, 2020) have generally supported the hypothesis of Zaher (1994), based on external and muscular morphology, that Tropidophiidae is more closely related to Caenophidia than to Ungaliophiinae, and the latter related to boas. Molecular studies, on the other hand, have suggested a radically different topology, with Tropidophiidae being the sister taxon to *Anilius* (Wilcox *et al*., 2002; Lawson *et al*., 2004; Gower *et al*., 2005; Vidal *et al*., 2007, 2009;

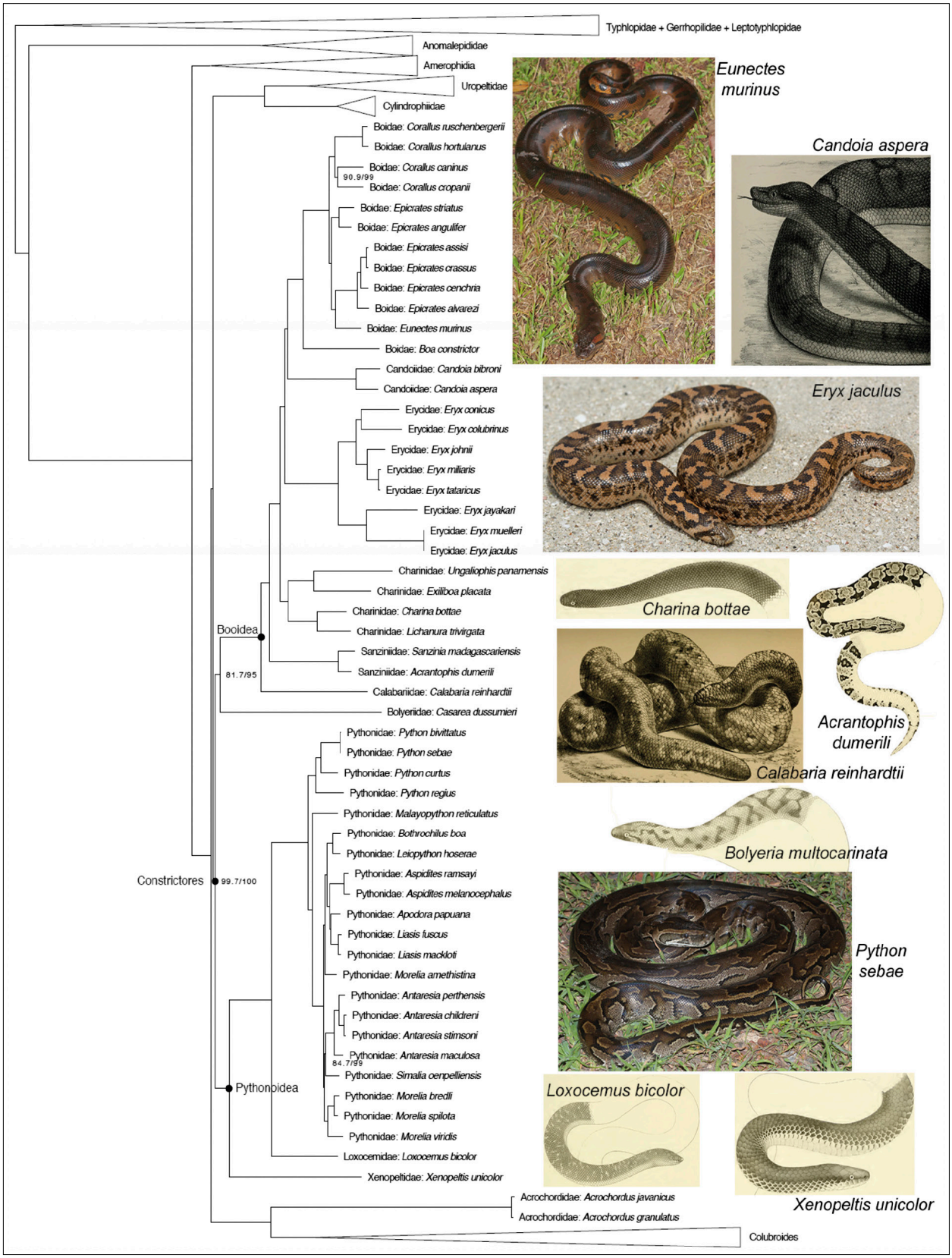

Fig. 1. Reference phylogeny (after Burbrink *et al*., 2020: Data File S7). Lizard outgroups were removed and snake outgroups to Constrictores were collapsed. Support values are BS/SH and are 100/100 for all ingroup taxa except where noted. The nodes corresponding to Booidea, Pythonoidea and Constrictores are labeled. Note also that the Xenophidiidae is not included herein, althouth it could pertain as well to Constrictores, as it was not included in the analysis of Burbrink *et al*. (2020). Abbreviations: SH, the Shimodaira-Hasegawa likelihood ratio; BS, bootstrap. Photograph of *Eryx jaculus* by Ilias Strachinis; photographs of *Eunectes murinus* and *Python sebae* by Alberto Sanchez Vialas. Images of *Acrantophis dumerili*, *Bolyeria multocarinata*, *Charina bottae*, *Loxocemus bicolor*, and *Xenopeltis unicolor* reproduced from Jan & Sordelli (1860–1866), *Calabaria reinhardtii* from Gray (1858), and *Candoia aspera* from Günther (1877).

Burbrink & Crother, 2011; Reynolds *et al*., 2014; Streicher & Wiens, 2016; Miralles *et al*., 2018; Burbrink *et al*., 2020). The distinctiveness of Tropidophiidae and Ungaliophiinae is further corroborated by their cranial (Bogert, 1968a) and vertebral anatomy (Bogert, 1968a, b; Szyndlar & Rage, 2003; Smith, 2013). In summary, there is neither morphological nor molecular support for the inclusion of Tropidophiidae in Constrictores.

Synonyms. Aplepia of Rafinesque (1815), partial (also others)

Phaenopoda of Mayer (1824), partial (also "anilioids")

Boidæ of Gray (1825), approximate

Innocua of Haworth (1825), partial

Pythonoidea of Fitzinger (1826), approximate

Onychophori of Ritgen (1826), partial (also "anilioids")

Macrostomata of Müller (1831), partial (also others)

Peropodes of Wiegmann (1832), approximate

Boas of Schlegel (1837), partial (also acrochordids)

Saurophidia of Fitzinger (1843), partial (also scolecophidians and "anilioids")

Azémiophides of Duméril & Bibron (1844), partial (also "anilioids")

Aglyphodontes of Duméril (1853), partial (also "anilioids" and others)

Asinea of Cope (1864), approximate

Boidiens of Jan (1865), approximate

Boaeformes of Heilprin (1907), approximate

Henophidia of Hoffstetter (1939), partial (also "anilioids" and others)

Booidea of Gauthier *et al*. (2012), approximate

Henophidia of Wallach *et al*. (2014), approximate

Diagnoses of Constrictores, Pythonoidea, and Booidea

A number of features have previously been listed as capable of differentiating "pythons" (Pythonidae sensu Wallach *et al*., 2014) and "boas" (Booidea sensu Pyron *et al*., 2014). Whereas many of these features are serviceable in the sense of a dichotomous key, in many cases either the characters have not been included, or character polarity is ambiguous when evaluated in, broad-scale studies of snake phylogeny (e.g., Gauthier *et al*., 2012). The most important features lie in the cranial anatomy, and some of them were already recognized in the 19th century. Pythonids (as well as *Loxocemus bicolor* Cope, 1861) possess premaxillary teeth (with the exception of the Australian genus *Aspidites* Peters, 1877), in constrast to boids, where the premaxilla is always toothless (Frazzetta, 1975; Szyndlar & Rage, 2003). Furthermore, in pythonids, a foramen is present in the palatine for the infraorbital nerve of maxillary division of the trigeminal, a feature that is absent in booids (Szyndlar & Rage, 2003). Also, pythonids (as well as *Loxocemus bicolor*) possess a supraorbital bone, in contrast to booids (except *Calabaria reinhardtii* [Schlegel, 1851]), which lack it (Romer, 1956; Frazzetta, 1975). On the basis of vertebral anatomy, boids share strong resemblance with pythonids; both have the massively built vertebrae, with a generally low ratio of their centrum length / neural arch width (<1.1), the high neural spines, and a thick zygosphene (Ivanov, 2000; Szyndlar & Rage, 2003; Georgalis & Scheyer, 2019). Nevertheless, Boidae (sensu Pyron *et al*., 2014) usually have paracotylar foramina on their vertebrae, whereas pythonids and the majority of non-boid booids almost always lack them (Kluge, 1993; Szyndlar & Schleich, 1993; Szyndlar & Rage, 2003; Georgalis, 2019; pers. observ.). However, this character can be variable and indeed its taxonomic utility has been questioned (Rage, 2001). Furthermore, in pythonids, the shape of the haemal keel is defined by grooves or depressions beginning at the cotylar rim, but projecting below the centrum only in the posterior part of each vertebra (Scanlon & Mackness, 2002; Szyndlar & Rage, 2003). Pythonids usually possess a higher number of vertebrae in comparison with booids (Schaal, 2004), but Scanferla & Smith (2020) recently showed that some extinct booids had as many vertebrae as pythonids. Also, it can be stated that large pythonids possess thicker zygosphenes in comparison with similarly sized booids, but this is also subjected to variability (GLG, pers. obs.). Finally, pythonids are usually characterized by a relatively homogeneous intracolumnar vertebral morphology, in contrast to booids (Szyndlar & Rage, 2003).

Modern diagnoses consistent with a current understanding of relationships have not been provided for Constrictores, Booidea or Pythonoidea. To determine morphological apomorphies diagnostic of those clades that are compatible with the reference phylogeny, we took the morphological data matrices of Hsiang *et al*. (2015, hereafter HEA), for osteology, and Reeder *et al*. (2015, hereafter REA), for squamation, and subjected them to maximum parsimony analysis in PAUP, using the phylogenetic tree of Burbrink *et al*. (2020:Data File S7) as a backbone topological constraint. In both matrices, we took all anguimorph taxa as outgroups and deleted Gekkota, Dibamidae, Scinciformata, Laterata, Iguania, and Rhynchocephalia. Because the primary reference phylogeny is based on molecular data and the content of Constrictores in morphological analyses is different (lacking *Xenopeltis*, *Loxocemus*, and Bolyeriidae), as noted above, we refrain from providing diagnoses based on such topologies. For diagnoses of Constrictores, Pythonoidea and Booidea for a tree in which Bolyeriidae and *Xenophidion* fall outside Constrictores, see Scanferla & Smith (2020:Document S1, section 2.3).

Unambiguous synapomorphies (i.e., those character state changes optimized under both acctran and deltran as synapomorphies of the clade in question) are as follows. Note that Bolyeriidae is not considered to belong either to Booidea or to Pythonoidea. In the reference phylogeny

(Burbrink *et al*., 2020) it is the immediate sister-group to Booidea, but if its position were to shift some of these diagnostic features might change.

Constrictores. Maxillary process of premaxilla tapers to a point distally (HEA 5/1); dorsum sellae enclosed in distinct fossa (HEA 404/2); Vidian canal caudal opening within basisphenoid (HEA 430/0); dentary mental foramen position displaced caudally (HEA 470/1). Additionally, we note that anteroposteriorly short vertebrae – that is, those with a low centrum length / neural arch width ratio (< 1.1) are associated with this clade. The ratio is higher in most outgroups and lower in all ingroup taxa (including Bolyeriidae, based on figs. 1–2 in Hecht & LaDuke, 1988) except Ungaliophiinae and *Xenopeltis* (e.g., Smith, 2013). However, the vertebrae of *Xenophidion* have not been described (cf. Wallach & Günther, 1998) and the taxon is not included in the reference phylogeny of Burbrink *et al*. (2020). Moreover, *Xenopeltis* with elongate vertebrae (Smith, 2013) is basal in Pythonoidea. Finally, the character is not unique to Constrictores, as it also occurs in Madtsoiidae and certain other snake taxa like *Acrochordus* (see Hoffstetter & Gayrard, 1964; Zaher *et al*., 2019) and Tropidophiidae (see Bogert, 1968a).

Pythonoidea. Medial frontal pillar suture to subolfactory process (HEA 54/2); ectopterygoid overlap of pterygoid long (HEA 362/1); posterior auditory foramen enclosed entirely in prootic (HEA 393/1); splenial anterior inferior alveolar foramen absent (HEA 491/1); premaxillary teeth absent on midline but present at lateral margins of element (HEA 547/1); elongate postmentals present (REA 650/1).

Booidea. Premaxilla internasal process narrowly clasped between nasals (HEA 15/2); frontal descending process abuts parietal (HEA 56/2); suture between frontal and parietal in medial wall of orbit vertical or only slightly anteriorly inclined (HEA 69/1); frontal suboptic shelf below optic foramen deep (HEA 72/1); quadrate suprastapedial process absent (HEA 219/0); lateral edge of stapedial footplate nearly in same cross-sectional plane as medial edge (HEA 238/1); posterior base of lateral flange of septomaxilla distinctly cranial to vomeronasal organ (HEA 252/1); palatine maxillary process at posterior end of palatine (HEA 297/1); ectopterygoid maxillary process tapering or parallel-sided (HEA 347/0); ectopterygoid abuts pterygoid laterally (HEA 358/2); cranial rim of crista circumfenestralis caudal extent relative to medial margin of stapedial footplate: former roughly on same level as latter in dorsal view at level of shaft (HEA 385/1); maxillary branch of trigeminal nerve passes dorsally between palatine and prefrontal (HEA 401/1); posterior opening of right Vidian canal large (HEA 422/1); angular process of dentary terminates well posterior to splenio-angular joint (HEA 476/2); coronoid eminence composed of both surangular and coronoid (HEA 501/0); retroarticular process (in situ) extends posteriorly (HEA 529/0); dentary teeth conspicuously enlarged anteriorly (HEA 544/1).

Acknowledgments

We thank Pr. Patrick Smith, Thomas Lehmann, Kevin de Queiroz, and Van Wallach for discussion and Nico Cellinese for help with registration. GLG acknowledges support from a postdoctoral grant of the Università degli Studi di Torino and the National Scholarship Program of the Slovak Republic (SAIA). GLG also acknowledges study of comparative material through the grants SYNTHESYS ES-TAF-5910 (MNCN), SYNTHESYS AT-TAF-5911 (NHMW), SYNTHESYS HU-TAF-6145 (HNHM), and SYNTHESYS GB-TAF-6591 (NHMUK), and the respective curators (Marta Calvo-Revuelta, Silke Schweiger, Judit Vörös, and Sandra Chapman) are highly thanked here. For permission to use their photographs of extant Constrictores in Fig. 1, we are grateful to Ilias Strachinis and Alberto Sanchez Vialas. The quality of the manuscript was enhanced by useful comments made by the Editor Uwe Fritz and two anonymous reviewers. We also thank anonymous reviewers of a previous version of this manuscript, who pointed out overlooked literature and useful comments that improved the paper.

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