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

GEORGIOS L. GEORGALIS1,2, * & KRISTER T. SMITH3,4

1 Dipartimento di Scienze della Terra, Università di Torino, Via Valperga Caluso 35, Torino, 10125, Italy — 2 Department of Ecology, Laboratory of Evolutionary Biology, Faculty of Natural Sciences, Comenius University in Bratislava, Mlynská dolina, Bratislava, 84215, Slovakia — 3 Department of Messel Research and Mammalogy, Senckenberg Research Institute and Natural History Museum, Senckenberganlage 25, Frankfurt am Main, 60325, Germany — 4 Faculty of Biological Sciences, Institute for Ecology, Diversity and Evolution, Max-von-Laue-Straße 13, University of Frankfurt, 60438 Frankfurt am Main, Germany — * Corresponding author; dimetrodon82@gmail.com

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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 cladethat 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 (Boie in Boie, 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 mumified 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
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. Duménil (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 Hurria; currently Cerberus Cuvier, 1829) and the elapid Acanthophis Daudin, 1803b. Duménil (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 Hétérodernes, that also included a number of other snake groups (Duménil, 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 anilids (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 Phaeonopoda, denoting the presence of “spur-like” hind-limb rudiments in these snakes, to encompass Boa, Python, and Eryx, as well as Tortrix (i.e., anilids). That name was later discussed by Duménil & Bibron (1844; as “Phénopodes”), but curiously the name Phaeonopoda was not mentioned at all in the detailed catalog of Boulenger (1893).

Gray (1825) established Boide 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; Boeide 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; FRANZETTA, 1959, 1966; ROUX-ESTÈVE, 1965; RAGE, 1984; UNDERWOOD & STIMSON, 1990; SZYNDLAR, 1991; HOLMAN, 2000; IVANOVA, 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 Venerata. 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 Gonylophes (Eryx and allied forms), Centropes (boas), and Pythophes (pythons), along with scalecophidians and anilids (FITZINGER, 1843). Still later, he emended the spelling of Pythophes to Pythonophes (FITZINGER, 1861). The names Centropes (for boas) and Pythophes (for pythons) were subsequently adopted by DRESING (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 Pythonoidea 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., anilids).

Curiously, BOÉ (1826, 1827) placed Boa, Python, and Eryx into Colubridae. BONAPARTE (1831) used the name Boidae to encompass the subgroups Boina (including both Boa and Python) and Erycina but also Typhlopidae (i.e., scalecophidians). The same author subsequently modified his taxonomic scheme, removed scalecophidians from snakes, but still treated Eryx as distinct from boas and pythons, thus recognizing the families Erycidae (including Erycina but also Calamaria [i.e., the caenophidian Calamaria Boië H. in Boië F., 1827]) and Boiidae (including Boina and Pythonina).

MÜLLER (1831) used the name Macrostomata to differentiate large-gaped snakes from their counterpart Microstomata (which included scalecophidians, anilids, but also amphibiaenans). 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 Anilina, cynthiophidiids, and urlopeltids (e.g., LEE & SCANLON, 2002; WILCOX et al., 2002; HSANG 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 Fitzen (1826). Within Macrostomata MÜLLER (1831) distinguished Holodonta (for pythons) and Isodonta or Aproterodonta (for boas).

The name Peropodiaceae 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 (FEDOROVIČ GORANIĆ, 1834; BURMEISTER, 1837; SCHRÜBES, 1837; GORSKI, 1852; TROSCHEL, 1861; MEYER, 1874; SCHREIBER, 1875; MÜLLER, 1878, 1880; PETERS, 1882; HOFFMAN, 1890; GIRARD, 1895). It was later emended as Peropodidae (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., KIRITZESCUL, 1902; NOGUCHI, 1909; LEBLANC, 1920; GILMORE, 1938).

Indeed, the name Peropodidæ 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, Xenopeltes Reinwardt in Boë, 1827, and (the currently much distantly related) Calamaria.

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

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

In their monumental work, DUMÉRIL & BIBRON (1844) introduced the name Azémiphioides to encompass all boas (Boaæides and Érycides), pythons (Pythonides), and ungaliophines as well as anilids (Tortricides). A few years later, they redefined the concept of Azémiphioides, proposing also the alternative name Aglyphodontes, which encompassed the aforementioned taxa plus acrochordids, uropeltids, and certain Colubridae (DUMÉRIL, 1853; DUMÉRIL et al., 1854a, b). They still, nevertheless, treated boas and erycines as a group (Apropoëdides) distinct from that of pythons (Holodontes or Holodontiæns) (DUMÉRIL & BIBRON, 1844; DUMÉRIL, 1853, 1859; DUMÉRIL et al., 1854a, b) and this arrangement continued even later (ROCHBRUNE, 1880).

The name Asinea was used by COPE (1864) to denote the group encompassing Xenopeltes, pythons, boas as well as Acrochordus, which he all, nevertheless, still treated as distinct families (Xenopeltidæ, Pythonidæ, Boïidae, and Acrochordidæ respectively). This distinction of Pythonidæ from Boïidae was subsequently followed by the same author (COPE, 1893) and some other prominent workers (GÜTHER, 1864; ZITTEL, 1887–1890; LÝDEKKER, 1888; HOFFMAN, 1890). The name Asinea was subsequently also used by GILMORE (1938).

JAN (1865) called the group as Boidiæns, and further divided it into Erycides, Boæides, and Pythoniæs. The same author excluded from that group Xenopeltes, which he placed instead with “anilids” (his Tortriciæns).

The name Boaæides has also appeared in the literature (HEILPRIN, 1907; HAAS, 1952), being also circulated...
under the alternative spelling Boaeformia (Hering, 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 caenopodians, i.e., alethinophidians to the exclusion of “anilioids”; and sometimes Xenopelitis and Loxocemus Cope, 1861 (e.g., Burbrrink & Crotther, 2011; Gautier et al., 2012; Figueroa et al., 2016; Petermann & Gautier, 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; Harrison & Reeder, 2017; Burbrrink 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 superfamily Booidea, containing the families Boidae, Calabarianidae, Candoiidae, Charinidae (comprising Charinae and Ungaliophiinae), Erycidae, and Sanzniaidae (Pyron et al., 2014), whereas Pythonoidea is conceived as containing Pythonidae, Loxocemidae, and Xenopeltidae (Wallach et al., 2014). Boileriidae (Round Island boas) and Xenophilidae (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; Ogura 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 often 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, Burbrrink 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, Bopyriidae, and Booidea as defined above (Burbrrink 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 (Burbrrink et al., 2020). Thus, the analyses with the broadest taxon sampling (Pyron et al., 2013) and the most in-depth gene sampling (Burbrrink 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; Gautier et al., 2012; Zaher & Scanferla, 2012; Scanferla & Smith, 2020), although the position of minor lineages (Xenopelitis, Loxocemus, Bopyriidae, Calabaria) relative to this clade has vacillated.

Thus, in contrast to the taxon name Iguaniidae (= 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 Musuem 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 Constrictoridae (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 “Squammates” 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; calcarea 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 oblitera (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 lumbraclis (Linnaeus, 1758), Leptotyphlops nigricans (Schlegel, 1837–1844), Anomalepis mexicanus Jan, 1860, Anilius scytale (Linnaeus, 1758), Uropeltis ceylanicus Cuvier, 1829, Cylindrophis raffles (Laurenti, 1768), and Coluber constrictor Linnaeus, 1758. Abbreviated definition: Constrictores = < V 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 lumbraclis (Linnaeus, 1758), Leptotyphlops nigricans (Schlegel, 1837–1844), Anomalepis mexicanus Jan, 1860, Anilius scytale (Linnaeus, 1758), Uropeltis ceylanicus Cuvier,
1829, *Cylindrophis rufus* (Laurenti, 1768), and *Coluber constrictor* Linnaeus, 1758.

Note that in this definition we chose to exclude not only the first-named scolecoephidian (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 Scolecocephalia is paraphyletic (e.g., Zheng & Wiens, 2016; Harrington & Reeder, 2017; Miraîles 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*, 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 species, 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, Sanzinidae, Charinidae, Calabaria, Loxocemus, Xenopeltis, Bolyeriidae, and Xenophidion.

On the boid side, *Eryx* was for long time treated as a distinct family, Erycidae (e.g., Érycines of Dumêril & Bibron, 1844, and Dumêril et al., 1854c; Jan, 1862; Günther, 1864; Carus, 1868;COPE, 1883; Boettger, 1884; Hoffmann, 1890; Pocta, 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 boid 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 Sanzinidae Romer, 1956 (including Acrantophis Jan, 1860, and Sanzinia Gray, 1849).

On the pythonoid side, *Xenopeltis* Reinwardt in Boïé, 1827 (for which the monotypic family Xenopeltididae Bonaparte, 1845, was established) and *Loxocemus* Cope, 1861 (for which the monotypic family Loxocemididae Cope, 1861, was established) are inferred to be successive sister taxa of Pythonidae in molecular analyses (e.g., Slowinski & Lawton, 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 Xenopeltid Günther and Manthey, 1995 (for which the monotypic family Xenophidionidae 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 Xenopeltid and Bolyeriidae are sister-taxon, 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 ungaliophines (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, although 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 fromGRAY (1858), and Candoia aspera fromGÜNTHER (1877).
Bogert & Schaal, 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 (Klug, 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, Booiidea 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, Dibamid, Scinciforma, 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 Bolyeridae), as noted above, we refrain from providing diagnoses based on such topologies. For diagnoses of Constrictores, Pythonoidea and Booiidea for a tree in which Bolyeridae and Xenopeltidion 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 Bolyeridae is not considered to belong either to Booiidea or to Pythonoidea. In the reference phylogeny of maxillary division of the trigeminal, a feature that is absent in booids (SzynDlar & Rage, 2003). Also, pythonids (as well as Loxocemus bicolor Cope, 1861) possess premaxillary teeth (with the exception of the Australian genus Aspidites Peters, 1877), in contrast 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.

Diagnoses of Constrictores, Pythonoidea, and Booiidea

A number of features have previously been listed as capable of differentiating “pythons” (Pythonidae sensu Wallach et al., 2014) and “boas” (Booiidea 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 contrast 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.
(Burbrik 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); dorsal 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 centroid 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 Burbrik 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 Madtsaoidae and certain other snake taxa like Acrochordus (see Hoffstetter & Gayraud, 1964; Zacher 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 474/1); 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); supraorbital process present (HEA 219/0); median edge of supraorbital process 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).

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**References**


