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## A Taxonomic Revision of Boas (Serpentes: Boidae)

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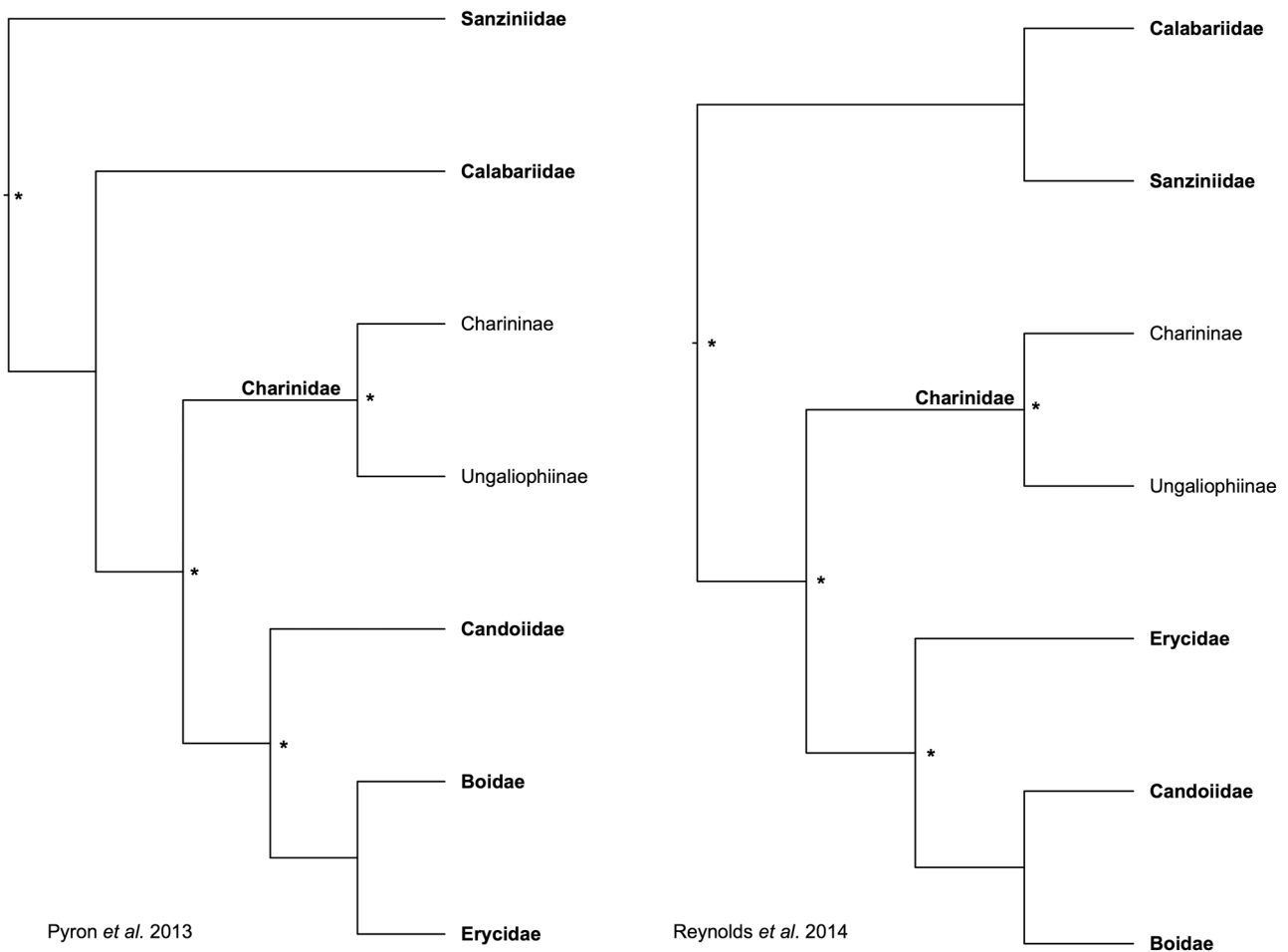
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Large molecular datasets including many species and loci have greatly improved our knowledge of snake phylogeny, particularly within the group including boas (Table 1). Recent taxonomic revisions using molecular phylogenies have clarified some of the previously contentious nomenclature of the group (Wilcox *et al.* 2002; Lawson *et al.* 2004; Burbrink 2005; Noonan & Chippindale 2006), resulting in a robust taxonomy that is mostly concordant with the phylogeny as currently known, which includes ~85% of described, extant species (Pyron *et al.* 2013; Reynolds *et al.* 2014). However, a few unresolved issues remain, related primarily to the rules of the International Code of Zoological Nomenclature (*the Code* hereafter) and the application of Linnaean ranks (International Commission on Zoological Nomenclature 1999).

Two taxonomic changes were made to Boidae in a recent large-scale phylogenetic analysis of Squamata (Pyron *et al.* 2013). The first was to erect a new subfamily of boid snakes (Candoiinae) for the genus *Candoia*, which rendered Boinae paraphyletic with strong support. The second was to move the genera *Charina* and *Lichanura* into the strongly supported subfamily Ungaliophiinae (*Exiliboa* and *Ungaliophis*), as *Charina* and *Lichanura* rendered Erycinae (the subfamily in which they were placed traditionally) paraphyletic. Unfortunately, two unrelated lapses render these actions problematic.

First, the study was published in an online-only open-access journal (*BMC Evolutionary Biology*). Thus, the creation of new, valid taxonomic names in the work is governed by the recent amendment to the Code recognizing electronic publication (see Dubois *et al.* 2013). A key requirement of this amendment is that the work be registered with a Life Sciences ID at the ICZN's official online repository of names (ZooBank.org). Unfortunately, registration to ZooBank did not occur in Pyron *et al.* (2013), and Candoiinae is thus unavailable from that work. In addition, a grammatical ambiguity in the definition gave the impression to some readers that diagnostic characters were not shared by all species in the subfamily (genus *Candoia*). We resolve these issues here by re-describing the taxon with an expanded diagnosis, and provide comments that will produce a clearer and more consistent taxonomy within Booidea.

Second, an older family-group name (Charinina = Charininae) is already associated with the genera *Charina* and *Lichanura* (Gray 1849), and thus has priority over Ungaliophiinae (McDowell 1987), which previously contained only *Exiliboa* and *Ungaliophis*. The name Charinina was mentioned in synonymy by Boulenger (1893), but has rarely been used as a valid name citing Gray (1849), only in passing and without an authority (e.g., Oguiura *et al.* 2009). The family name Charinidae was formalized by Cope (1886a, b) as a new family, since group-name emendations and the Principle of Coordination (see below) had not yet been formalized. This name has also not been widely used, and was overlooked by Pyron *et al.* (2013). Under the Principle of Priority, Charinina (=Charininae) of Gray (1849) has priority over Ungaliophiinae as the family-series name of the taxon comprising *Charina*, *Exiliboa*, *Lichanura*, and *Ungaliophis*. Here, we restrict Charininae to *Charina* and *Lichanura* and Ungaliophiinae to *Exiliboa* and *Ungaliophis*, altering in turn the ranks of the other subfamily-level taxa (see below).



**FIGURE 1.** Comparison of recent phylogenetic topologies for Booidea with nomenclature proposed herein. Asterisks (\*) represent strongly supported nodes using either SHL (Pyron *et al.* 2013) or BS (Reynolds *et al.* 2014) values.

This change causes some additional nomenclatural problems outside of snakes. The amblypygid genus *Charinus* was described by Simon (1892), and the family Charinidae was erected by Quintero (1986) to contain this group. However, Charinidae is preoccupied by Charinina (Gray 1849; =Charinidae, Cope 1886a). As Charininae has been used after 1899 (Cope 1900; Oguiura *et al.* 2009), reversal of precedence for the family-group name is not indicated (Article 23.9). Thus, the Principle of Homonymy applies, and Charinina (Gray 1849) is the valid family-group name for the snake taxon under the Principle of Priority, and a junior homonym for the spider taxon. Presumably, a new family-group name will be needed for the tailless whipscorpions of the genera *Catageus*, *Charinus*, and *Sarax*. The Code recommends avoidance of homonymy in family-group names by the use of the entire generic name as the stem (Article 29.6, Recommendation 29A), such that Charinusiidae would be the preferred name.

Under the Principle of Coordination of the Code (International Commission on Zoological Nomenclature 1999; Louchart *et al.* 2013), the family-series names Candoiinae and Charininae (subfamilies) were also simultaneously established at the family and superfamily level (Candoiidae and Candoidea, Charinidae and Charinoidea) by the original publications. Thus, future revisions using those ranks would cite this work or Gray (1849) as authorities. As the current taxonomy of boid snakes does not actually reflect monophyletic groups in the most recent and well-sampled phylogenetic estimates (Pyron *et al.* 2013; Reynolds *et al.* 2014), we suggest that the application of these ranks needs to be re-considered for the group.

The family Boidae as currently defined comprises five subfamilies: Sanziniinae, Charininae, Erycinae, Candoiinae, and Boinae. These subfamilies are distinct both morphologically and biogeographically (Underwood 1967; Kluge 1991); being restricted to Madagascar (Sanziniinae); North and Central America (Charininae; *U. panamensis* also inhabits a small portion of western Colombia); North Africa, Europe, the Middle East, and South

and Central Asia (Erycinae); Oceania (Candoiinae); and the Neotropics (Boinae). However, this group is rendered paraphyletic in recent molecular phylogenetic analyses by the African family Calabariidae (*Calabaria*), which forms the sister-group to Sanziniinae (Reynolds *et al.* 2014), or all boids to the exclusion of Sanziniinae (Pyron *et al.* 2013). Therefore, current taxonomy does not reflect monophyletic groups in the analyses sampling the most characters and taxa.

Thus, we are presented with a number of biogeographically distinct subfamilies, all of which are strongly supported as monophyletic in essentially all recent molecular phylogenetic analyses and by available morphological data. Relationships among these subfamilies are variable, and in some analyses another family-level taxon renders the family paraphyletic. We suggest that the most straightforward action is therefore to change the rank of the boid subfamilies to families, for which family-series names are already available under the Principle of Coordination. This resolves all nomenclatural problems revealed by phylogenetic analyses, as all groups are monophyletic, and relationships among them do not then affect their rank.

The taxon comprising the current Boidae + Calabariidae now forms the superfamily Booidea (Table 1), containing the families Calabariidae (*Calabaria*), Sanziniidae (*Sanzinia* and *Acrantophis*), Charinidae (subfamilies Charininae [*Charina* and *Lichanura*] and Ungaliophiinae [*Exiliboa* and *Ungaliophis*]), Erycidae (*Eryx*), Candoiidae fam. nov. (*Candoia*), and Boidae (*Boa*, *Corallus*, *Eunectes*, *Epicrates*, and *Chilabothrus*). Conceivably, Ungaliophiidae could be recognized as a family distinct from Charinidae, but this seems unnecessary given their geographic proximity and morphological similarity. Instead, we retain them as subfamilies of Charinidae. Following are taxonomic accounts for the group as re-delimited here (see Table 1 for species content of genera and original descriptions):

**TABLE 1.** Classification of 58 species of booid snake and original descriptions. Type species of genera are indicated with an asterisk (\*). Synonymies after McDiarmid *et al.* (1999) and Wallach *et al.* (2014).

Taxon	Original Name	Reference
<b>Superfamily Booidea</b>		Gray 1825
<b>Family Boidae</b>		Gray 1825
Genus <i>Boa</i>		Linnaeus 1758
<i>Boa constrictor</i> *	<i>Boa constrictor</i>	Linnaeus 1758
Genus <i>Chilabothrus</i>		Duméril & Bibron 1844
<i>Chilabothrus angulifer</i>	<i>Epicrates angulifer</i>	Bibron 1840 <i>in de la Sagra</i> 1838–1843
<i>Chilabothrus chrysogaster</i>	<i>Homalochilus chrysogaster</i>	Cope 1871
<i>Chilabothrus exsul</i>	<i>Epicrates exsul</i>	Netting & Goin 1944
<i>Chilabothrus fordii</i>	<i>Pelophilus fordii</i>	Günther 1861
<i>Chilabothrus gracilis</i>	<i>Chilabothrus gracilis</i>	Fischer 1888
<i>Chilabothrus inornatus</i> *	<i>Boa inornata</i>	Reinhardt 1843
<i>Chilabothrus monensis</i>	<i>Epicrates monensis</i>	Zenneck 1898
<i>Chilabothrus striatus</i>	<i>Homalochilus striatus</i>	Fischer 1856
<i>Chilabothrus strigilatus</i>	<i>Homalochilus strigilatus</i>	Cope 1862
<i>Chilabothrus subflavus</i>	<i>Epicrates subflavus</i>	Stejneger 1901
Genus <i>Corallus</i>		Daudin 1803
<i>Corallus annulatus</i>	<i>Xiphosoma annulatum</i>	Cope 1875
<i>Corallus batesii</i>	<i>Chrysenis batesii</i>	Gray 1860
<i>Corallus blombergi</i>	<i>Boa annulata blombergi</i>	Rendahl & Vestergren 1941
<i>Corallus caninus</i>	<i>Boa canina</i>	Linnaeus 1758
<i>Corallus cookii</i>	<i>Corallus cookii</i>	Gray 1842
<i>Corallus cropanii</i>	<i>Xenoboa cropanii</i>	Hoge 1954

.....continued on the next page

**TABLE 1.** (Continued)

<b>Taxon</b>	<b>Original Name</b>	<b>Reference</b>
<i>Corallus grenadensis</i>	<i>Boa grenadensis</i>	Barbour 1914
<i>Corallus hortulanus*</i>	<i>Boa hortulana</i>	Linnaeus 1758
<i>Corallus ruschenbergerii</i>	<i>Xiphosoma ruschenbergerii</i>	Cope 1875
Genus <i>Epicrates</i>		Wagler 1830
<i>Epicrates alvarezi</i>	<i>Epicrates cenchria alvarezi</i>	Abalos <i>et al.</i> 1964
<i>Epicrates assisi</i>	<i>Epicrates cenchria assisi</i>	Machado 1944
<i>Epicrates cenchria*</i>	<i>Boa cenchria</i>	Linnaeus 1758
<i>Epicrates crassus</i>	<i>Epicrates crassus</i>	Cope 1862
<i>Epicrates maurus</i>	<i>Epicrates maurus</i>	Gray 1849
Genus <i>Eunectes</i>		Wagler 1830
<i>Eunectes beniensis</i>	<i>Eunectes beniensis</i>	Dirksen 2002
<i>Eunectes deschauenseei</i>	<i>Eunectes deschauenseei</i>	Dunn & Conant 1936
<i>Eunectes murinus*</i>	<i>Boa murina</i>	Linnaeus 1758
<i>Eunectes notaeus</i>	<i>Eunectes notaeus</i>	Cope 1862
<b>Family Calabariidae</b>		Gray 1858
Genus <i>Calabaria</i>		Gray 1858
<i>Calabaria reinhardtii*</i>	<i>Eryx reinhardtii</i>	Schlegel 1848
<b>Family Candoiidae</b>		This work
Genus <i>Candoia</i>		Gray 1842
<i>Candoia aspera</i>	<i>Erebophis asper</i>	Günther 1877
<i>Candoia bibroni</i>	<i>Enygrus bibroni</i>	Duméril & Bibron 1844
<i>Candoia carinata*</i>	<i>Boa carinata</i>	Schneider 1801
<i>Candoia paulsoni</i>	<i>Enygrus carinatus paulsoni</i>	Stull 1956
<i>Candoia superciliosa</i>	<i>Enygrus superciliosus</i>	Günther 1863
<b>Family Charinidae</b>		Gray 1849
Subfamily Charininae		Gray 1849
Genus <i>Charina</i>		Gray 1849
<i>Charina bottae*</i>	<i>Tortrix bottae</i>	Blainville 1835
<i>Charina umbratica</i>	<i>Charina bottae umbratica</i>	Klauber 1943
Genus <i>Lichanura</i>		Cope 1861
<i>Lichanura orcutti</i>	<i>Lichanura orcutti</i>	Stejneger 1889
<i>Lichanura trivirgata*</i>	<i>Lichanura trivirgata</i>	Cope 1861
Subfamily Ungaliophiinae		McDowell 1987
Genus <i>Exiliboa</i>		Bogert 1968
<i>Exiliboa placata*</i>	<i>Exiliboa placata</i>	Bogert 1968
Genus <i>Ungaliophis</i>		Müller 1880

.....continued on the next page

TABLE 1. (Continued)

Taxon	Original Name	Reference
<i>Ungaliophis continentalis</i> *	<i>Ungaliophis continentalis</i>	Müller 1880
<i>Ungaliophis panamensis</i>	<i>Ungaliophis panamensis</i>	Schmidt 1933
<b>Family Erycidae</b>		Bonaparte 1831
Genus <i>Eryx</i>		Daudin 1803
<i>Eryx borrii</i>	<i>Eryx borrii</i>	Lanza & Nistri 2005
<i>Eryx colubrinus</i>	<i>Anguis colubrina</i>	Linnaeus 1758
<i>Eryx conicus</i>	<i>Boa conica</i>	Schneider 1801
<i>Eryx elegans</i>	<i>Cusoria elegans</i>	Gray 1849
<i>Eryx jaculus</i> *	<i>Anguis jaculus</i>	Linnaeus 1758
<i>Eryx jayakari</i>	<i>Eryx jayakari</i>	Boulenger 1888
<i>Eryx johnii</i>	<i>Boa johnii</i>	Russell 1802
<i>Eryx miliaris</i>	<i>Anguis miliaris</i>	Pallas 1773
<i>Eryx muelleri</i>	<i>Gongylophis muelleri</i>	Boulenger 1892
<i>Eryx somalicus</i>	<i>Eryx somalicus</i>	Scortecci 1939
<i>Eryx tataricus</i>	<i>Boa tatarica</i>	Lichtenstein 1823
<i>Eryx vittatus</i>	<i>Eryx vittatus</i>	Chernov 1959
<i>Eryx whitakeri</i>	<i>Eryx whitakeri</i>	Das 1991
<b>Family Sanziniidae</b>		Romer 1956
Genus <i>Acrantophis</i>		Jan 1860 in Jan & Sordelli 1860–1866
<i>Acrantophis dumerili</i> *	<i>Acrantophis dumerili</i>	Jan 1860 in Jan & Sordelli, 1860–1866
<i>Acrantophis madagascariensis</i>	<i>Pelophilus madagascariensis</i>	Duméril & Bibron 1844
Genus <i>Sanzinia</i>		Gray 1849
<i>Sanzinia madagascariensis</i> *	<i>Xiphosoma madagascariense</i>	Duméril & Bibron 1844

## Superfamily Booidea Gray 1825

### Family Calabariidae Gray 1858

**Type genus.** *Calabaria* Gray 1858

**Genus content.** *Calabaria*

**Diagnosis.** Calabariids can be distinguished from all other similar or related taxa by the following combination of characters: lack of palatine teeth, presence of premaxillary teeth, supraorbital bone lacking a dorsal lobe, enlarged head shields, and oviparous reproduction (see Frazzetta 1959; Kluge 1993).

**Phylogenetic definition.** Currently monotypic; would include any newly discovered species more closely related to *Calabaria reinhardtii* than any other species.

**Etymology.** Refers to type locality of Old Calabar (Akwa Akpa; “Duke Town”), the Portuguese name (of unknown derivation) for a 19<sup>th</sup> century city-state on the river of the same name in southeastern Nigeria.

**Distribution.** Rainforests of western Africa, from Sierra Leone to northern Congo and western Central African Republic.

**Remarks.** This group has a confusing taxonomic history, having long been considered a pythonoid, as well being synonymized with *Charina* (see Kluge 1993). Molecular phylogenetic analyses clearly show booid affinities, as well as distinctiveness from all other booid genera (Noonan and Chippindale 2006; Wiens *et al.* 2008; Burbrink & Pyron 2012; Pyron *et al.* 2013; Reynolds *et al.* 2014).

## Family Sanziniidae Romer 1956

**Type genus.** *Sanzinia* Gray 1849

**Genus content.** *Acrantophis*, *Sanzinia*

**Diagnosis.** Sanziniids can be distinguished from all other similar or related taxa by the following combination of characters: mineralized internarial septum presenting only a small fenestra, postorbital and frontal broadly separated by the parietal, distal border of the optic foramen formed mostly by the parietal with anterior margin formed by the frontal, apex of the coronoid extends well above the surangular, lateroventral ledge of the surangular restricted to the anterior region, posterior trunk intercostal arteries supply one body segment each, hemipenis with longitudinal flounce, and sulcus terminating below the tips of the arms (see Kluge 1993).

**Phylogenetic definition.** Includes the most recent common ancestor (MRCA) of included *Acrantophis* and *Sanzinia* and all descendants thereof, and all species more closely related to *S. madagascariensis* than *Calabaria reinhardtii*.

**Etymology.** Unclear. Many names erected by J.E. Gray were apparently chosen for euphony but lack any substantial etymology (A.M. Bauer, pers. comm.).

**Distribution.** Madagascar.

**Remarks.** This group was originally described to include the Mauritian taxa *Bolyeria* and *Casarea* (Romer 1956; see Frazzetta 1959), which are only distantly related (Wiens *et al.* 2008; Burbrink & Pyron 2012; Pyron *et al.* 2013; Reynolds *et al.* 2014). Potential homonymy issues exist with the specific epithet *madagascariensis* (Table 1), and the name “*Boa*” *manditra* is available for *S. madagascariensis* if any such problems arise in the future (see Kluge 1993; Vences *et al.* 2001).

## Family Charinidae Gray 1849

**Type genus.** *Charina* Gray 1849

**Genus content.** Subfamily Charininae Gray 1849 (*Charina*, *Lichanura*), subfamily Ungaliophiinae McDowell 1987 (*Exiliboa*, *Ungaliophis*)

**Diagnosis.** Charinids can be distinguished from all other similar or related taxa by the following combination of characters: in all species, a distinct lateral muscular bundle (M.) in the jaw known as the *adductor mandibulae externus medialis pars anterior* (M. *aem1* of Zaher 1994), with loss of the left lung and presence of a tracheal lung in *Exiliboa* and *Ungaliophis* (Ungaliophiinae), and in *Charina* and *Lichanura* (Charininae), an M. *aem1* comprised of elongated and undifferentiated fibers, as well as lack of a postorbital, anterior end of ectopterygoid narrow and pointed, crista circumfenestris small or absent between the fenestra pseudorotunda and foramen of the vagus cranial nerve, and coronoid absent on the prearticular portion of the compound bone (see Kluge 1993; Zaher 1994).

**Phylogenetic definition.** Includes the MRCA of included *Charina* and *Lichanura* (Charininae) and *Exiliboa* and *Ungaliophis* (Ungaliophiinae) and all descendants thereof, and all species more closely related to *Cha. bottae* than to *Boa constrictor* (stem of Charinidae), all species more closely related to *Cha. bottae* than to *U. continentalis* (stem of Charininae), and all species more closely related to *U. continentalis* than to *Cha. bottae* (stem of Ungaliophiinae).

**Etymology.** From the Greek *charieis* for ‘graceful’ or ‘delightful.’

**Distribution.** North and Central America, including southern Canada, the western United States and northwestern Mexico for Charininae, and southwestern Mexico, Central America, and extreme northwestern South America for Ungaliophiinae.

**Remarks.** This group has had a turbulent taxonomic history, as many morphological characters are poorly known and apparently exhibit strong convergence (see Kluge 1991; Zaher 1994; Wilcox *et al.* 2002). However, recent molecular results are unambiguous in supporting the monophyly of this group and uniting it with Booidea (Wilcox *et al.* 2002; Noonan and Chippindale 2006; Wiens *et al.* 2008; Pyron *et al.* 2013; Reynolds *et al.* 2014).

## Family Erycidae Bonaparte 1831

**Type genus.** *Eryx* Daudin 1803

**Genus content.** *Eryx*

**Diagnosis.** Erycids can be distinguished from all other similar or related taxa by the following combination of characters: transverse process of the premaxilla long, internarial septum of the premaxilla absent, vomerine process of the premaxilla long and narrow, anterior one-third to one-half of the ventral lamina of the nasal decreases anteriorly or is absent, anterior end of the horizontal lamina of the nasal expands slightly to markedly viewed dorsally, anterolateral edge of the horizontal lamina of the nasal bulges outward viewed dorsolaterally, lateroposterior margin of the horizontal lamina of the nasal adjacent to the prefrontal oriented vertically as a large wall, dorsal lappet of the prefrontal approximately straight on the dorsolateral margin contacting the frontal and nasal, anterolateral and medial laminae of the prefrontal form a gradually rounded corner, frontonasal facet where ventral lamina of the nasal contacts the frontal lies between and below the olfactory canal with long horizontal-ventral portion, facet present on the preorbital process of the frontal, anterolateral corner of the frontal projects anteriorly and partially exposes the preorbital process, floor of the optic foramen formed by the parietal, postorbital process of the parietal large, midsagittal crest markedly developed on the anterior portion of the parietal, choanal process of the palatine tiny and discontinuous, maxillary process of the palatine narrow, medioventral margin of the posterior third of the pterygoid folded into deep groove, parasphenoid shallow anteriorly deepening posteriorly with groove absent anteriorly and present posteriorly, interparietal area of the parasphenoid of modest width with parallel sides, anteriorly projecting process present on the neural spine, distal tip of the posterior diapophysis of caudal vertebrae oriented nearly vertically into a thin and occasionally convoluted blade, distal tip of anterior diapophysis of caudal vertebrae elaborated into a horizontal blade originating from centrum, transverse process of caudal vertebrae forms a large and rounded anteroposteriorly oriented blade, caudal haemopophysis flattened terminally and curved towards opposite-side counterpart but widely separated therefrom, first infralabial scale small and separated from counterpart by one or more scales, dorsal head scales small and usually asymmetrically arranged, and 34 diploid chromosomes (see Kluge 1993).

**Phylogenetic definition.** Includes the MRCA of the included *Eryx* species and all descendants thereof, and all species more closely related to *E. jaculus* than to *Boa constrictor*.

**Etymology.** Named, apparently without special significance, after a son of Aphrodite, king of the mountain city Eryx in Sicily, who was defeated by Heracles in a boxing match.

**Distribution.** Southeastern Europe, northern Africa, Middle East, and southwestern Asia.

**Remarks.** This taxon has been recognized as a distinct family in the past, as well as by some current authors (see Wallach *et al.* 2014).

## Candoiidae fam. nov.

**Type genus.** *Candoia* Gray 1842

**Genus content.** *Candoia*

**Diagnosis.** Candoiids can be distinguished from all other related or similar species by the following combination of characters: low distinct posterior hypapophyseal keel on trunk vertebrae, lack of labial pits, lack of paired common carotid arteries, flattened rostrum leading to an angular snout, dorsal margin of the transverse process of the premaxilla adjacent to the nasal process forms a thin high wall noticeably curved posteriorly, wide pre-maxillary floor, vomerine processes projecting posteriorly from the floor of the premaxilla short or absent, lateral edge of the maxilla beneath the orbit is markedly inflected laterally, paracotylar foramina are present in mid-trunk vertebrae, body distinctly compressed laterally with head much larger than neck, small head scales with little evidence of bilateral symmetry, body scales keeled, hemipenis with well-defined longitudinal flounce and sulcus terminating below the tips of the arms (see Underwood 1967; McDowell 1979; Kluge 1991).

**Phylogenetic definition.** Includes MRCA of included *Candoia* and all descendants thereof (Pyron *et al.* 2013; Reynolds *et al.* 2014), and all species more closely related to *Can. carinata* than to *Boa constrictor* or *Eryx jaculus* (Fig. 1, Table 1).

**Etymology.** Unclear. Many names erected by J.E. Gray were apparently chosen for euphony but lack any substantial etymology (A.M. Bauer, pers. comm.).

**Distribution.** Candoiidae is restricted to the Pacific islands of New Guinea and Melanesia, and the eastern Indonesian archipelago (Noonan & Chippindale 2006; Zug 2013). One species occurs in the Palauan archipelago of western Micronesia.

**Remarks.** This group renders Boinae paraphyletic in some analyses (Noonan & Chippindale 2006; Pyron *et al.* 2013) but not others (Reynolds *et al.* 2014), though support is often equivocal. A sister-group relationship with *Sanzinia* and *Acrantophis* (Sanziniidae) was found in past studies, though with much less taxon and character sampling (Austin 2000; Vidal & Hedges 2002; Lawson *et al.* 2004; Burbrink 2005). Divergence-time estimates support a vicariant origin of Candoiidae with intermediate extinction from other Gondwanan landmasses, as early divergences in Boidae pre-date the final breakup of Gondwana (Noonan & Sites 2010).

Family-group names for *Candoia* have been used before, but not validly. A previous description of a subfamily (Candoiinae) was unavailable due to not meeting the requirements of publication under Article 8 of the Code (Pyron *et al.* 2013), which is thus made available here. The tribe name Candoiini was used informally by Hoffstetter (1968), but was unaccompanied by a diagnosis and is thus a *nomen nudum* under Article 13 of the Code. This name has been referenced sporadically (Underwood 1976; Rage 1984; Holman 2000), but as per Article 11.5.2, this does not confer validity, and a valid description is thus still needed.

## Family Boidae

**Type genus.** *Boa* Linnaeus 1758

**Genus content.** *Boa*, *Chilabothrus*, *Corallus*, *Epicrates*, *Eunectes*

**Diagnosis.** Boids can be distinguished from all other similar or related taxa by the following combination of characters: internarial septum with large fenestra, anterior margin of the ventral lamina of the nasal indented in lateral view, anterolateral margin of horizontal lamina of nasal noticeably indented viewed dorsally, horizontal lamina of the nasal does not overlap dorsal surface of frontal, most of palatine process of maxilla occurs posteriorly within the orbit, anterior end of ectopterygoid consists of indistinct lateral and medial heads, supratemporal inclined slightly in lateral view, posterior end of supratemporal rounded but not dilated, parasphenoid wing large and without pedicellate ventral surface, dorsal margin of prearticular noticeably curved upward near attachment of adductor posterior muscle, cornua of hyobranchium discontinuous anteriorly, and shallow labial pits (see Kluge 1991).

**Phylogenetic definition.** Includes the MRCA of included *Boa*, *Chilabothrus*, *Corallus*, *Epicrates*, and *Eunectes* species and all descendants thereof, and all species more closely related to *Boa constrictor* than to *Candoia carinata* or *Eryx jaculus*.

**Etymology.** From the Latin *boa* for 'large snake,' after an animal mentioned in the *Natural History* of Pliny the Elder.

**Distribution.** New World tropics, from northern Mexico to Argentina, and the West Indies.

**Remarks.** Several species in this group contain significant intra-specific genetic variation (Colston *et al.* 2013; Reynolds *et al.* 2014), and more species may be recognized in the future.

This arrangement (family-level rank of the former boid subfamilies) provides a robust taxonomy for booid snakes. All families are strongly supported as monophyletic by both molecular and morphological data, and their nomenclature is thus unlikely to be affected in the future by the sampling of additional taxa or characters in phylogenetic analyses. The recognition of these ecomorphologically and biogeographically distinct groups as families mirrors other squamate and amphibian taxa such as Iguania (Frost & Etheridge 1989; Frost *et al.* 2001) and Ranoidea (Frost *et al.* 2006; Pyron & Wiens 2011), where large cosmopolitan families (Iguanidae and Ranidae) have been broken up into more manageable and geographically localized units. This classification should provide a stable basis for future revision and description of new species, and other comparative analyses.

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