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Redescription, taxonomy and phylogenetic relationships of *Boavus* Marsh, 1871 (Serpentes: Booidea) from the early–middle Eocene of the United States

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Supplementary Table 1: Details about the specimens of *Boavus* and comparative material examined in this study. Asterisks denote holotypes italics denote CT scanned.

Taxon	Specimen's catalogue	Notes
	number	
Acrantophis dumerili	USNM 497683	Dry
Acrantophis madagascariensis	MNHN 1887-53; MNHN 1889- 341; MNHN 1900-121; MNHN 1910-186; MNHN 1963-199; MNHN 2002-10; USNM 22552; ZFMK 21670; ZFMK 86469	Dry
Acrochordus granulatus	SAMA R6708	CT scanned
Acrochordus javanicus	AMNH R-46251; AMNH R- 89839; AMNH R-140814	Dry
Anilius scytale	MCZ 19537, RBINS 411; SAMA R36774; USNM 204078	Dry, CT scanned
Antaresia childreni	AMNH R92764	Dry
Antaresia maculosa	AMNH R69278	Dry
Antaresia stimsoni	SAMA 45396; SAMA R54580	CT scanned
Aspidites melanocephalus	AMNH R-76200; AMNH R- 69302	Dry
Bitis gabonica	AMNH R-57799; AMNH R- 64518; AMNH R-137177; SAMA <i>R-unreg</i> ; ZFMK 5186; ZFMK 21716; ZFMK 21718	Dry, CT scanned
Boa constrictor	AMNH 131475; <i>FMNH 31182</i> ; MNHN 1876-618; RBINS 3397; RBINS 3404; RBINS3405; RBINS3406; RBINS 3407; RBINS 8444997; RBINS 2809; USNM 220300; USNM 291912	Dry, CT scanned
Boa imperator	AMNH R 155261; AMNH R 155257; AMNH R 77590; AMNH R 74737; AMNH R 57472; USNM 59047; USNM 90885	Dry
Boavus affinis	LACM 5119	Fossil material
Boavus agilis	YPM PV 467*; YPM PV 2765; YPM PV 2766	Fossil material
Boavus brevis	USNM 427732; YPM PV 468*; YPM PV 58331; YPM PV PU 17210; YPM PV unnumbered material (labelled 474)	Fossil material
Boavus cf. occidentalis	USNM 427693; USNM 427694.	Fossil material
Boavus idelmani	AMNH 3850; USNM 537817	Casts of the holotypes
Boavus occidentalis	USNM 427732; USNM V 12980; YPM VP 511*; YPM VP 2706; YPM VP 2717; YPM VP 2770; YPM VP 3752; YPM VP 59190; YPM VP 59191	Fossil material
Bothrochilus boa	AMNH R44002; ZFMK 5203	Dry
Calabaria reinhardtii	AMNH R10092; <i>FMNH 117833</i> ; MNHN 1941-328; MNHN 1967-	Dry, CT scanned

	360; USNM 523576; ZFMK	
	89190	
Candoia aspera	AMNH R-95137	Dry
Candoia bibroni	AMNH R-81601; RBINS 414	Dry
Candoia carinata	AMNH R-36404; AMNH R- 73942; AMNH R-103632; AMNH R-107138; <i>SAMA R5267D</i> ; USNM 3485503	Dry, CT scanned
Candoia paulsoni	AMNH R-92068; AMNH R92068	Dry
Candoia superciliosa	USNM 507558; USNM 509342	Dry
Casarea dussumieri	MCZ 49135; NHMUK 1992.995; UMMZ 190285	Dry, CT scanned
Charina bottae	AMNH R-63487; FMNH 22348; FMNH 31300; USNM 9255; USNM 52377; USNM 523578; USNM 523579	Dry
Chilabothrus angulifer	AMNH R77596; AMNH R114497; MNHN 1892-89	Dry
Chilabothrus exsul	AMNH R73005	Dry
Chilabothrus fordii	AMNH R40116	Dry
Chilabothrus gracilis	AMNH R42977	Dry
Chilabothrus monensis	USNM 306210	Dry
Chilabothrus striatus	AMNH R140542; USNM 59918	Dry, CT scanned
Chilabothrus strigilatus	AMNH R70263; AMNH R77057; AMNH R77633	Dry
Chilabothrus subflavus	USNM 292500	Dry
Coniophis precedens	UCMP 53935, UCMP 49999, AMNH 26999, USNM 2143*, AMNH 26833, YPM 16845	Fossil material, data from Longrich et al. (2012)
Coluber constrictor	FMNH 135284	CT scanned
Corallus annulatus	AMNH R73252; AMNH R114496	Dry
Corallus caninus	AMNH R155265; AMNH R57816; AMNH R139338; AMNH R155260; AMNH R155265; AMNH R57788; AMNH R73347; AMNH R169154; AMNH R155260; AMNH R73347; AMNH R155264; AMNH R155263; AMNH R57816 RBINS 415; RBINS 13693	Dry
Corallus cookii	AMNH R57812; AMNH R118702; AMNH R141098; AMNH R74832; AMNH R7812; AMNH R75740; AMNH R57809	Dry
Corallus cropanii	AMNH R92997	Dry
Corallus hortulanus	AMNH R57786; AMNH R104528; MCN-PV DR 0001; RBINS 416; UFTM 02389; USNM 348598	Dry
Cylindrophis ruffus	AMNH R85647; <i>FMNH 60958</i> ; <i>SAMA R12956</i> ; USNM 297456	Dry, CT scanned
Dinilysia patagonica	MLP 26-410*, MACN RN976, MACN RN1013, MACN	Fossil material, additional data from Caldwell and Calvo (2008),

	RN1014, MACN RN1016, MACN PV116	Zaher and Scanferla (2011), and Garberoglio et al. (2019a)
Eoconstrictor fischeri	SMF-ME 929	Fossil material, additional data from Scanferla and Smith (2020) and Georgalis et al. (2021)
Epicrates cenchria	AMNH R62577; AMNH R114716; AMNH R57473; AMNH R71153; AMNH R75796; AMNH R75795; MCN-PV DR 0002; MNHN 1869-792; USNM 523572; ZFMK 5168; ZFMK 21665; ZFMK 21666; ZFMK 86470	Dry
Eryx colubrinus	AMNH R61633; <i>FMNH 63117</i> ; FMNH 223196; ZFMK 50246	Dry, CT scanned
Eryx conicus	MNHN 1907-138; RBINS 412	Dry
Eryx jaculus	MNHN 1889-409; RBINS 2833	Dry
Eryx johnii	AMNH R102155; AMNH R102155; AMNH R102222; NHMUK 1930.5.8.34; NHMUK 1964.1240; RBINS 413; ZFMK 21660	Dry
Eunectes murinus	AMNH R57474; AMNH R29349; AMNH R43308; AMNH R62559; AMNH R62560; MCN.D 306; MCN.D 316; MCN.D 319; MCN.D 342; MNHN 1869-782; MNHN 1883-494; MNHN 1940- 353; RBINS 3114; <i>SAMA R69321</i> ; USNM 523575	Dry, CT scanned
Eunectes notaeus	MNHN 1869-778; USNM 135453; USNM 135454; USNM 523575	Dry
Eupodophis descouensi	MSNM V4014; MSNM V3661; Rh-E.F. 9001-9002-9003*	Fossil material, additional data from Rage and Escuillie (2000), Rieppel and Head (2004), Houssaye et al. (2011), and Palci et al. (2013a).
Exiliboa placata	AMNH R-102892; FMNH 207669	Dry, CT scanned
Haasiophis terrasanctus	HUJ-Pal. EJ 695*	Fossil material, additional data from Rieppel et al. (2003)
Heloderma suspectum	SAM R55982; SAM R66657	Dry
Lichanura trivirgata	AMNH R73360; USNM 558335; USNM 558336; USNM 558341; USNM 558342; USNM 558344; <i>YPM 12869</i>	Dry, CT Scanned
Liotyphlops albirostris	FMNH 216257	<i>CT scanned</i> , additional data from List (1966)
Liotyphlops beui	SAMA R40142	CT scanned
Loxocemus bicolor	AMNH R-110151; FMNH 104800	Dry, CT Scanned
Malayopython reticulatus	FMNH 15678; FMNH 51631; MNHN 1931-70; MNHN 1912- 429; RBINS 275; RBINS 12433; RBINS 12433b; RBINS 13692; ZFMK 21671; ZFMK 70207	Dry

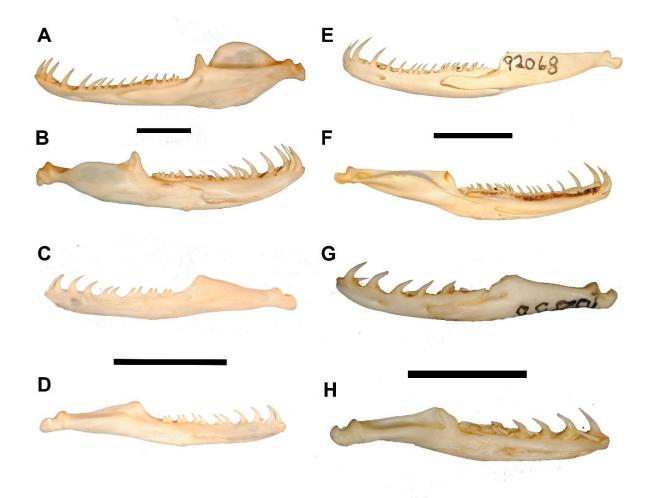
Messelophis variatus	SMF ME 1828 a+b	Fossil material, data from Scanferla et al. (2016)
Messelopython freyi	SMK-PAL 461	Fossil material from Zaher & Smith (2020)
Micrurus fulvius	FMNH 34282; FMNH 229600; FMNH 39479	Dry, CT scanned
Montypythonoides riversleighensis	QM F12926	Fossil material
Morelia viridis	MNHN 1969-125; <i>SAMA R69719</i> ; USNM 297395	Dry, CT scanned
Najash rionegrina	MPCA 389*, MPCA 391–397*, MPCA 400*, MPCA 500	Fossil material, additional data from Zaher et al. (2009), Palci et al. (2013b), and Garberoglio et al. (2019a,b).
Pachyrhachis problematicus	HUJ-Pal 3659*; HUJ-Pal 3775	Fossil material, additional data from Caldwell and Lee (1997), Polcyn et al. (2005), and Palci et al. (2013a).
Paleryx rhombifer	NHMUK PV OR 25259	Data of fossil material from Georgalis et al. (2021)
Pontosaurus kornhuberi	MSNM V3662*	Fossil material from Caldwell (2006)
Pontosaurus lesinensis	GBA 1873/4/2*	Fossil material from Pierce & Caldwell (2004)
Python molurus	<i>TMM</i> 62769; MNHN 1886-690; MNHN 1931-71; MNHN A5313; RBINS 417; USNM 220305; USNM 220306	Dry, CT scanned
Python sebae	MNHN 1951-265; MNHN 1953- 155; ZFMK 5200; ZFMK 21678	Dry
Rageryx schmidi	HLMD-Me 9723	Fossil material, data from Smith & Scanferla (2021)
Rieppelophis ermannorum	SMF ME 1812	Fossil material, data from Scanferla et al. (2016)
Sanzinia madagascariensis	AMNH R160190; MNHN 1900- 122A; MNHN 1953-232; MNHN 1889-365; MNHN 1900-122; USNM 220313; ZFMK 61722; ZFMK 70428	Dry
Simalia amethistina	RBINS 2743; USNM 523582	Dry
Trilepida dimidiata	SAMA 40143	CT scanned
Tropidophis haetianus	TMM 64040; TMM unreg.	CT scanned
Typhlops jamaicensis	AMNH R 160154; USNM 12378	Dry, CT scanned
Ungaliophis continentalis	UTA 50569	CT scanned
Ungaliophis panamensis	AMNH R-58845; AMNH R- 62639; AMNH R-76305	Dry
Uropeltis woodmasoni	TMM 10006	CT scanned
Uropeltis pulneyensis	MCZ 3870	Dry
Uropeltis rubrolineatus	MCZ 47101	Dry
Varanus varius	SAM R40022; SAM R27033; SAM R40023; SAM V543	Dry
Xenodermus javanicus	FMNH 67427; FMNH 158613	Dry, CT Scanned
Xenopeltis unicolor	FMNH 148900; USNM 287277	Dry, CT Scanned
Yurlunggur sp.	<i>QM F45391, QM F45111</i> , QM F- unreg.	Fossil material, CT Scanned

Wonambi naracoortensis	SAMA P30178A, SAMA P30178B,	Fossil material, CT Scanned	
	SAMA P27777, SAMA P48706	1 ossii materiat, C1 Scannea	

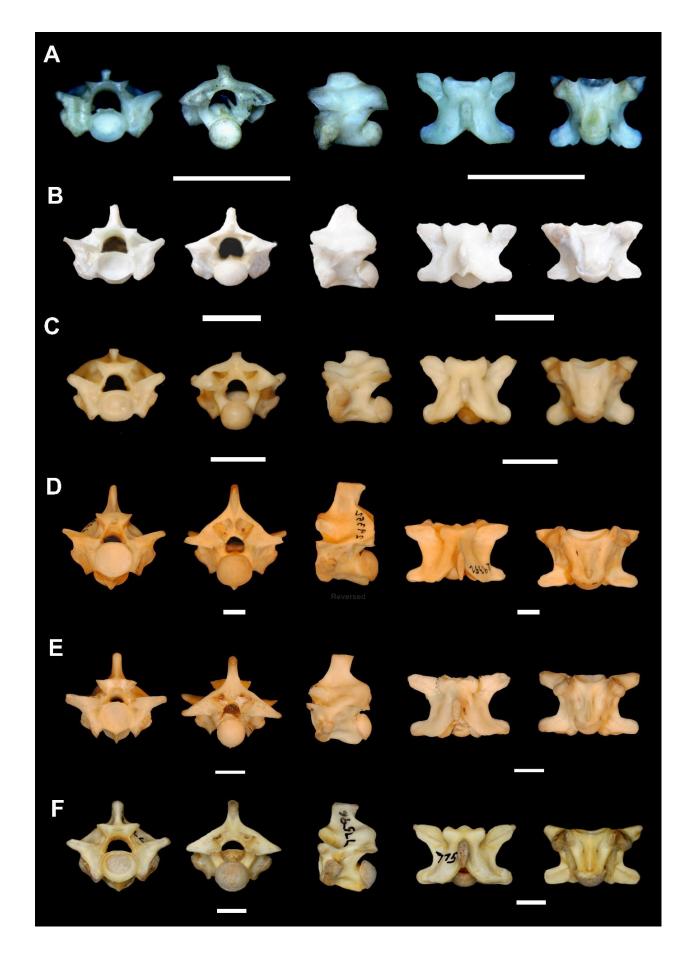
Institutional abbreviations

AMNH: American Museum of Natural History, New York, USA; FMNH: Field Museum of Natural History, Chicago, USA; GBA, Austrian Geological Survey, Wien, Austria; HLMD-Me: Messel collection, Hessisches Landesmuseum, Darmstadt, Germany; HUJ-Pal: Hebrew University of Jerusalem Paleontology Collections, Jerusalem, Israel; LACM: Natural History Museum, Los Angeles County, USA; MACN: Museo de Ciencias Naturales Bernardino Rivadavia, Buenos Aires, Argentina; MCN.D: Museu de Ciências Naturais da Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre, Brazil; MCN-PV DR: Seção de Paleontologia do Museu de Ciências Naturais da Fundação Zoobotânica do Rio Grande do Sul, Coleção de Paleontologia de Vertebrados, Coleção Didática de Répteis, Porto Alegre, Brazil; MCZ, Museum of Comparative Zoology, Cambridge, Massachusetts, USA; MLP, Museo de La Plata, La Plata, Argentina; MNHN: Muséum National d'Histoire Naturelle, Paris, France; MPCA: Museo Paleontológico 'Carlos Ameghino', Cipolletti, Rió Negro, Argentina; MSNM, Museo di Storia Naturale di Milano, Milano, Italy; NHMUK: Natural History Museum, London, United Kingdom; QM: Queensland Museum, Brisbane, Queensland, Australia; RBINS: Royal Belgian Institute of Natural Sciences, Brussels, Belgium; Rh-E.F.: Museum of Gannat, Gannat, France; SAMA: South Australian Museum, Adelaide, Australia; SMF: Forschungsintitutes Senckenberg in Frankfurt, Frankfurt, Germany; TMM: Texas Memorial Museum, Austin, Texas, USA; UCMP: University of California Museum of Paleontology, Berkeley, California, USA; UFMT: Coleção da Universidade Federal do Mato Grosso, Mato Grosso, Brazil; UMMZ, University of Michigan Museum of Zoology, Ann Arbor, Michigan, USA; USNM: National Museum of Natural History,

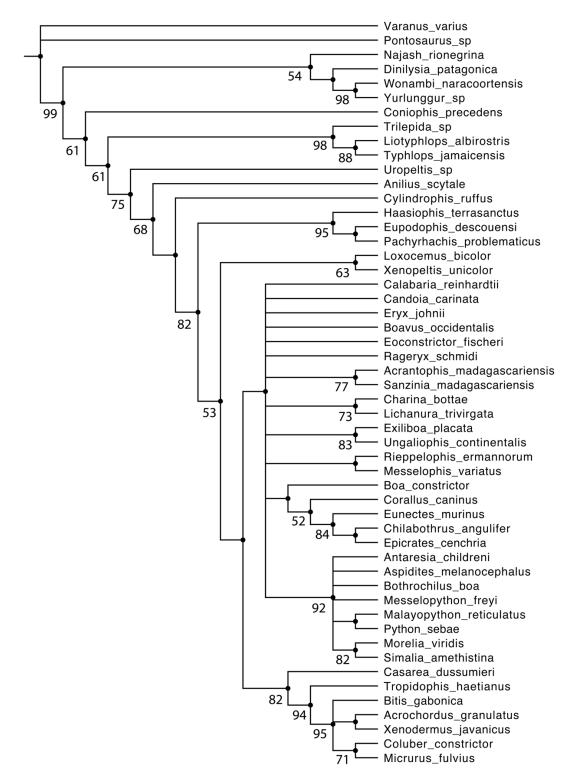
Washington, DC, USA; **UTA**: University of Texas at Arlington, Texas, USA; **YPM**: Yale Peabody Museum of Natural History, New Haven, USA; **ZFMK**: Zoological Research Museum Alexander Koenig, Bonn, Germany.



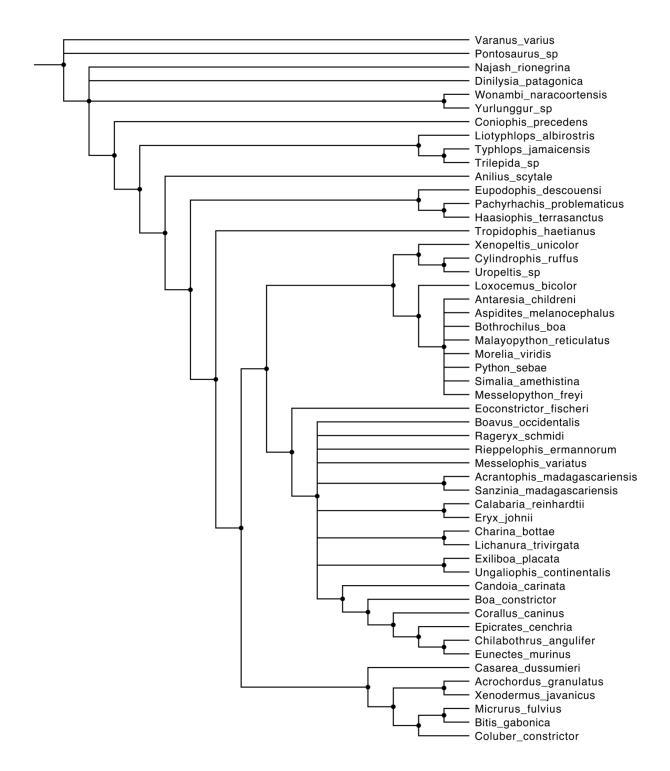
Supplementary Figure S1: Selection of lower jaws from extant booids used for comparisons. **A**, **B** *Sanzinia madagascariensis* USNM 220313 in labial and lingual view; **C**, D *Calabaria reinhardtii* USNM 523576 in labial and lingual view; **E**, **F**, *Candoia paulsoni* AMNH R92068 in labial and lingual view; **G**, **H**, *Eryx johnii* AMNH R-102155 in labial and lingual view. Scale bar: 5 mm.



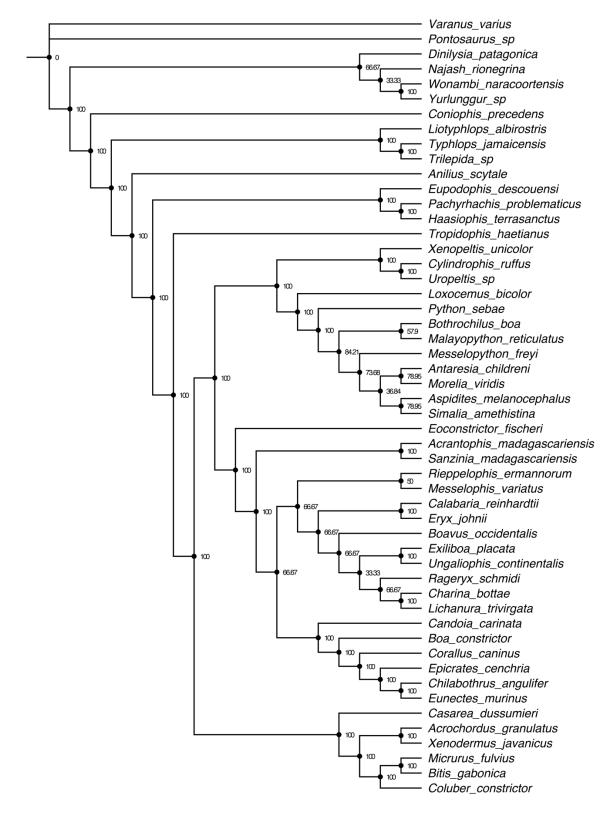
Supplementary Figure S2: Selection of comparative vertebral material used in the study; all midtrunk vertebrae in anterior, posterior, lateral, dorsal, and ventral view. **A**, *Charina bottae* (Charinidae) (USNM 523577); **B**, *Calabaria reinhardtii* (Calabaridae) (MNHN 1967-360); **C**, *Eryx johnii* (Erycidae) (AMNH R-102155); **D**, *Python molurus* (Pythonidae) (USNM 220305); **E**, *Sanzinia madagascariensis* (Sanzinidae) (USNM 220313); and **F**, *Chilabothrus angulifer* (Boidae) (AMNH R-77596). Note that (D) *Python molurus* lateral view was reversed for comparison. Scale bar: 5 mm.



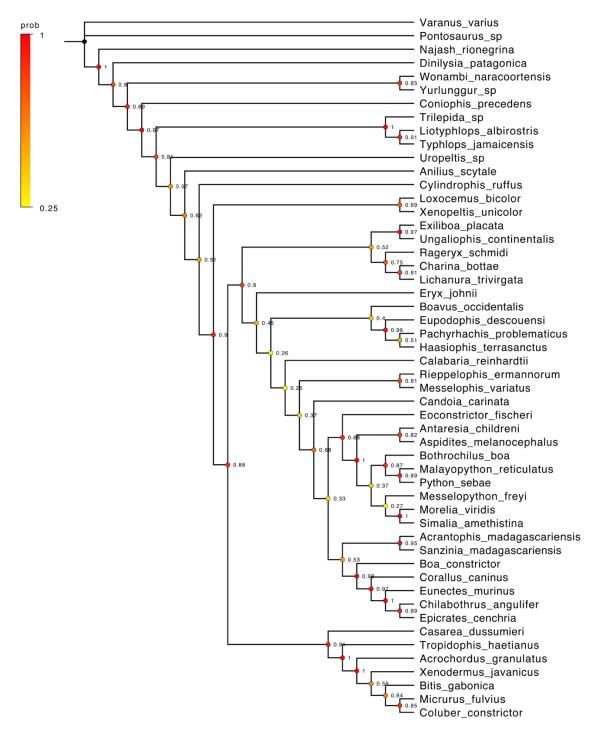
Supplementary Figure S3: Phylogenetic position of *Boavus* within snakes using the morphology dataset (dataset 1) obtained under parsimony optimality criterion. Strict consensus tree derived from 287 most-parsimonious trees of 887 steps (consistency index 0.38. retention index 0.72). Numbers below the branches denote bootstrap support.



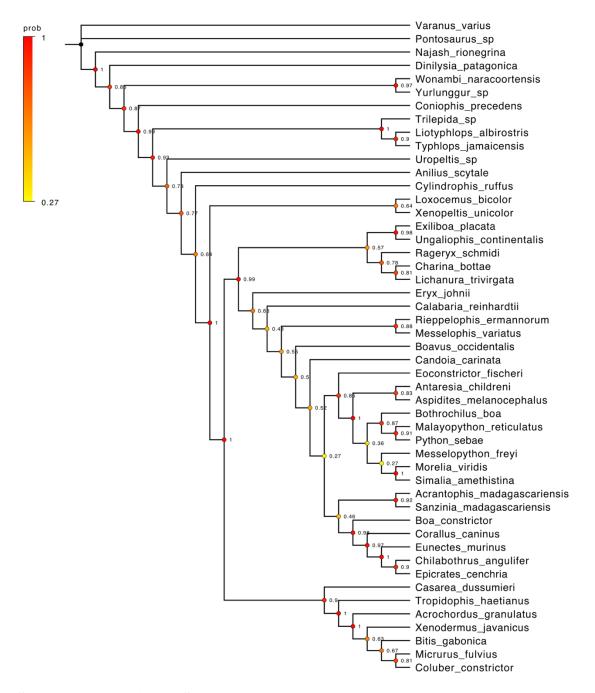
Supplementary Figure S4: Phylogenetic position of *Boavus* within snakes using the morphology + molecules dataset (dataset 2) obtained under parsimony optimality criterion. strict consensus tree derived from 342 most-parsimonious trees of 21516 steps (consistency index 0.51. retention index 0.38).



Supplementary Figure S5: Majority-rule consensus tree derived from the parsimony analysis using dataset 2 (morphology + molecules). Numbers at nodes denote the percentage of most parsimonious trees containing the node. See also Figure 6 in the main text.



Supplementary Figure S6: Phylogenetic position of *Boavus* within snakes estimated under undated Bayesian inference using all 52 OTUs. Tree topology obtained from the analysis using morphological dataset only (dataset 1). Scale bar denotes the range of posterior probability (PP); numbers at nodes are posterior probabilities. The position of similiophiids (*Eupodophis, Pachyrhachis, Haasiophis*) is highly unstable and they can be considered wildcard taxa; deleting them from the analysis does not greatly change relationships among other taxa (see next figure).



Supplementary Figure S7: Phylogenetic position of *Boavus* within snakes estimated under undated Bayesian inference excluding the simoliophiids. Resultant tree topology obtained from the analysis using morphological dataset only (dataset 1). Scale bar denotes the range of posterior probability (PP). Note the increase of support in the nodes.

Phylogenetic analyses Supplementary text

Taxonomic sampling strategy and modifications from Garberoglio et al. (2019)

Most of the data (i.e. scorings and character list) used in this study derives from the study of Garberoglio et al. (2019) with some minor modifications. The taxonomic sampling consists of 52 terminal taxa including one lizard (*Varanus varius*) and one dolichosaurid (*Pontosaurus* sp.) and 50 species of snakes (36 extant species and 14 extinct fossil taxa). The following changes to the OTUs were made to the data matrix in Garberoglio et al. (2019):

- The following OTUS previously scored in Garberoglio et al., (2019) were not included in this work due to their fragmentary nature, and phylogenetic distance from the focal taxon *Boavus: Xiaophis, Nanowana, Anomochilus, Madtsoia camposi, Menarana nosymena, Aff. Parviraptor estesi, Parviraptor estesi, Eophis woodwardia, Diablophis gilmorei, Portugalophis lignites*, and *Sanajeh*;
- 2. The outgroup taxon Varanus was scored based on the exemplar species Varanus varius;
- 3. The outgroup taxon *Pontosaurus* sp. was added, and scored based on the ytype specimens of *P. kornhuberi* and *P. lesinensis*.
- The following exemplar species were scored as terminal taxa representing the scolecophidian families: Typhlopidae: *Typhlops jamaicensis*; Anomalepididae: *Liotyphlops albirostris*; and Leptotyphlopidae: *Trilepida dimidiata*;
- 5. The suprageneric group "*Uropeltidae*" was scored in this study based on the exemplar species *Uropeltis woodmasoni*.

- 6. The terminal Tropidophiidae was scored based on the exemplar species *Tropidophis haetianus*;
- 7. The terminal Bolyeriidae was scored based on the exemplar species Casarea dussumieri;
- 8. The terminal Acrochordidae was scored based on the exemplar species *Acrochordus granulatus*;
- The group Colubroidea (i.e. basal colubroides in Garberoglio et al. [2019]) was split in the following exemplar species: *Xenodermus javanicus* (Xenodermatidae); *Bitis gabonica* (Viperidae); *Micrurus fulvius* (Elapidae); and *Coluber constrictor* (Colubridae) in order to represent the group;
- 10. The subfamily "Pythoninae" from Garberoglio et al. (2019) was split into these exemplar species: *Python sebae*; *Malayopython reticulatus*; *Aspidites melanocephalus*; *Bothrochilus boa*; *Simalia amethistina*; *Antaresia childreni*; *Morelia viridis*; and the recently described fossil python *Messelopython freyi*;
- 11. Concerning the ingroup Booidea, the terminals "Ungaliophiidae", "Erycinae", and "Boinae" were redefined, split, and scored based on the following exemplar species representing the main families: (a) *Calabaria reinhardtii* (Calabariidae); (b) *Exiliboa placata, Ungaliophis continentalis, Charina bottae,* and *Lichanura trivirgata* (Charinaidae); (c) *Eryx johnii* (Erycidae); (d) *Acrantophis madagascariensis* and *Sanzinia madagascariensis* (Sanziniidae); (e) *Candoia carinata* (Candoiidae); and (f) *Boa constrictor, Corallus caninus, Chilabothrus angulifer, Epicrates cenchria and Eunectes murinus* (Boidae).
- 12. The following terminal taxa were scored representing the fossil booid forms: *Rageryx schmidi*; *Rieppelophis ernmanorum*; *Messelophis variatus*; and *Eoconstrictor fischeri*.

List of characters for phylogenetic analysis

The character list comprises a modified rearranged version (i.e. sorted by skeletal region and bone) of the character list of Garberoglio et al. (2019), with the addition of characters from other studies such as Kluge (1991), Vasile et al. (2013), Scanferla & Smith (2020), Smith & Scanferla (2021) as well as five new characters. Twelve characters from the list of Garberoglio et al. (2019) were excluded because redundant with other characters in our selection, or because partially redundant, in which case they were merged with other similar characters. These characters were: 28, 51, 70, 97, 124, 136, 175, 185, 187, 190, 204, 223 (numbers correspond to those in original study by Garberoglio et al. [2019]).

New characters introduced in this study are identified by the specifier "*New character*"; Character that have been modified from their previous version are identified with the specifier "*Modified character*". The abbreviations for previous studies are as follows: *K91* (Kluge, 1991); *V13* (Vasile et al., 2013); *G19* (Garberoglio et al. 2019); *SS20* (Scanferla & Smith, 2020); and *SS21* (Smith & Scanferla, 2021). For example, character 5 from Kluge (1991) is abbreviated *K91/char5*.

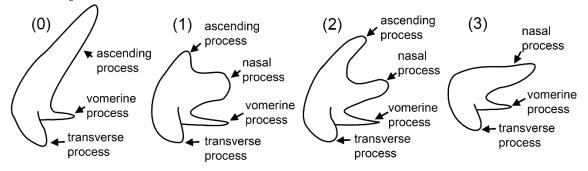
The following 18 characters were considered multistate morphoclines and thus treated as ordered: 21, 39, 66, 69, 71, 85, 131, 158, 160, 174, 196, 214, 224, 239, 241, 247, 249, 258. Note: Numbers denote the characters from the Nexus file and the list below, please note that the TNT file has all character numbers shifted down by 1 because of its numbering system starting from 0. Therefore, in the TNT file the ordered characters are: 20, 38, 65, 68, 70, 84, 130, 157, 159, 173, 195, 213, 223, 238, 240, 246, 248, 257.

DENTITION

- 1. Maxillary and dentary teeth: relatively short conical, upright (0); robust, recurved (1); elongate needle-shaped, distinctly recurved (2). *G19/char1*
- 2. Premaxillary dentition: present (0); absent (1). G19/char2
- 3. Dentition, dentary teeth: present (0); absent (1). G19/char244
- 4. Alveoli and base of teeth: not expanded transversely (0); wider transversely than anteroposteriorly (1). *G19/char3*
- 5. Pterygoid teeth: absent (0); present (1). G19/char4

SKULL

- 6. Premaxilla: broadly articulated with maxilla (0); loosely contacting maxilla (1). G19/char5
- 7. Transverse processes of premaxilla: curved backwards (0); extending straight laterally or anterolaterally (1). *G19/char6*
- 8. Premaxilla: The transverse process of the premaxilla is directed horizontally or downward (0), or upward (1). *K91/char5*
- 9. Nasal process of premaxilla: elongate, approaching or contacting frontals (0); short, divides nasals only at anterior margin or not at all (1). *G19/char7*
- 10. Premaxilla: ascending process transversely expanded, partly roofing external nares (0); ascending process mediolaterally compressed, blade-like or spine-like (1). *G19/char158*
- 11. Premaxilla: premaxilla medial to maxillae (0); located anterior to maxillae (1). G19/char159
- 12. Expanded naris: Weakly developed naris (0) [shown in *Anilius scytale*]; strongly concave anterior margin of prefrontal bordering naris (1) [shown in *Loxocemus bicolor*]. *G19/char162*
- 13. Dorsal (horizontal) lamina of nasal: relatively broad anteriorly, with narrow gap between lateral margin and vertical flange of septomaxilla (0); dorsal lamina of nasal distinctly tapering anteriorly, leaving a wide gap between lateral margin and vertical flange of septomaxilla (1); relatively broad anteriorly, presenting a wide gap between the nasal lateral lamina and the vertical flanges of septomaxilla (3). *Modified character from G19/char8*
- 14. Internarial septum of premaxilla: ascending process present, nasal process absent (0); shallow emargination separating ascending process (directed dorsally/posterodorsally) and nasal process (directed posteriorly) (1); deep emargination separating ascending process (directed dorsally/posterodorsally) and nasal process (directed posteriorly), this condition is typically associated with a fenestration between premaxilla and nasals (2); ascending process absent and posteriorly directed nasal process present (3). Note: the ascending process of the premaxilla is typically near the anterior end of the nasals, while the nasal process typically runs along the ventral edge of the vertical nasal flanges, some lateral overlapping of nasals on premaxilla may occur in both cases. Both processes can vary in relative length from short to very long. *Modified character from K91/char6*



- 15. Medial vertical flanges of nasals: absent (0); present (1). G19/char142
- 16. Medial flanges of nasal, articulation with median frontal pillars: present (0); absent (1). G19/char9
- 17. Contact of the medial nasal flanges with the medial frontal flange (medial frontal pillars): dorsal and ventral contact (0); contact only dorsally (1); contact only ventrally (2); absent (3). *New character*.
- 18. Anterior margin of nasals: restricted to posteromedial margins of nares (0); extend anteriorly toward tip of rostrum (1). *G19/char10*
- 19. Lateral flanges of nasals: articulate with anterior margin of frontals (0); separated from frontals (1). *G19/char11*
- 20. Posterolateral margin of nasal: contacts posteromedian margin of prefrontal (0); elements in contact along most of their length (1); contact between elements with interfingering of nasal and prefrontal margins (2); nasals do not contact prefrontals (3). *G19/char12*
- 21. Septomaxilla posterior dorsal process of lateral vertical flange: absent (0); short (1); long (2). Ordered. *Varanus* was rescored as inapplicable (not 0). *G19/char13*
- 22. Septomaxilla: The lateroventral edge of the septomaxilla projects modestly, at all, posterior to the fenestra vomeronasalis externa the opening for the duct of Jacobson's organ, (0) or the edge forms a large blade posterior to the fenestra (1). *K91/char49*
- 23. Septomaxilla articulation with median frontal pillars: absent (0); present (1). G19/char14
- 24. Ventral portion of posterior edge of lateral flange of septomaxilla and opening of Jacobsen's organ: located at level of posterior edge or behind (0); distinctly in front (1). *G19/char15*
- 25. Vomeronasal cupola: fenestrated medially (0); closed medially by a sutural contact of septomaxilla and vomer (1). *G19/char16*
- 26. Septomaxilla: forms lateral margin of opening of Jacobson's organ (0); vomer extends into posterior part of lateral margin, restricting septomaxilla to anterolateral part of lateral margin of opening of Jacobson's organ (1). *G19/char17*
- 27. Vomeronasal nerve: does not pierce vomer (0); exits vomer through single large foramen (1); through cluster of small foramina (2). *G19/char18*
- 28. Posterior ventral (horizontal) lamina of vomer: long, parallel edged (0); short, tapering to a distinct pointed tip (1). *G19/char19*
- 29. Posterior dorsal (vertical) lamina of vomer: well developed (0); reduced or absent (1). G19/char20
- 30. Preorbital ridge: dorsally exposed (0); overlapped by prefrontal (1). G19/char143
- 31. Sclerotic ring: present (0); absent (1). G19/char198
- 32. Prefrontal: articulates with frontal laterally (0); anterolaterally (1). G19/char21
- 33. Posterior margin of prefrontal (in lateral view) slanting anteroventrally (0); positioned almost vertically or slanting posteroventrally (1). *Modified character from G19/char22*. *Varanus* was rescored with state 1 (not 0).
- 34. Prefrontal: prefrontal socket for dorsal peg of maxilla absent (0); present (1). G19/char160
- 35. Prefrontal extends medially across frontal for more than 75% of width of frontal: absent (0); present (1). *G19/char161*
- 36. Lacrimal foramen on prefrontal: not completely enclosed (0); enclosed by prefrontal (1); prefrontal lacking foramen (2). *G19/char23*
- 37. Lateral foot process of prefrontal: absent (0); contacts maxilla only (1); maxilla and palatine (2); palatine only (3). *G19/char24*
- 38. Lateral foot process of prefrontal: articulates with lateral edge of maxilla via thin anteroposteriorly directed lamina (0); articulates with maxilla via large contact that runs from lateral to medial dorsal surface of maxilla (1). *G19/char144*
- 39. Medial foot process of prefrontal: absent (0); present, low (1); present, high (2). Ordered. *G19/char25*

- 40. Anterior/lateral flange of prefrontal covering nasal gland and roofing auditus conchae: absent (0); present (1). *G19/char26*
- 41. Ventral margin of lateral surface of prefrontal: articulates with dorsal surface of maxilla (0); retains only posterior contact (1). *G19/char27*
- 42. Medial frontal pillars: absent (0), present (1). G19/char29
- 43. Transverse horizontal shelf of frontal: developed and broadly overlapped by nasals (0); poorly developed and never broadly overlapped by nasals (1); absent (2). *G19/char30*
- 44. Frontal: nasal processes of frontal project between nasals (0); nasal processes absent (1). G19/char163
- 45. Frontals: frontals taper anteriorly, distinct interorbital constriction (0); frontals broad anteriorly, interorbital region broad (1). *G19/char164*
- 46. Frontal: subolfactory process abuts prefrontal in immobile articulation (0); subolfactory process articulates with prefrontal in mobile joint (1); subolfactory process with distinct lateral peg or process that clasped dorsally and ventrally by prefrontal (2). *G19/char165*
- 47. Frontals and parietals: do not contact ventrally (0); descending wings of frontals and parietals contact ventrally to enclose optic foramen (1). *G19/char166*
- 48. Frontal subolfactory process: absent or present as simple horizontal lamina (0); present and closing tractus olfactorius medially (1). *G19/char148*
- 49. Lacrimal: present (0); absent (1). G19/char31
- 50. Postfrontal: present (0); absent (1). *G19/char32*
- 51. Postfrontal: anterior and posterior processes clasping frontals and parietals (0); anterior and posterior processes present, but postfrontal abuts frontals and parietals (1); anterior and posterior processes absent (2). *G19/char186*
- 52. Jugal: present (0); fused or absent (1). G19/char33
- 53. Jugal, ventral tip: Contact or approaches prefrontal (or lacrimal), forming or contributing to ventral margin of orbit (0); contacts or closely approaches ectopterygoid/maxilla, forming almost complete posterior margin of orbit (1); remains separated by wide gap from ectopterygoid (2). *G19/char34*
- 54. Jugal, distinct posterior process for quadratomaxillary ligament: present (0); absent (1). G19/char239
- 55. Jugal, dorsal head: Contacts with postorbital (0); Contacts with parietal (1); fuses articulates with only the posterodorsal surface of postfrontal (2); Lack of dorsal contact (3). *G19/char35*
- 56. Parietals: single (0); remain paired in adult skull (1). G19/char245
- 57. Parietal: without lateral wings meeting postorbital bones (0); with lateral wings meeting postorbital bones (1). *G19/char36*
- 58. Distinct lateral ridge of parietal: extending posteriorly from anterior lateral wing up to prootic: absent (0); present (1). *G19/char37*
- 59. Frontoparietal suture: relatively straight (0); frontoparietal suture U-shaped (1). G19/char38
- 60. Optic foramen, posterior margin: posteriorly located, straight parietal margin (0), posteriorly located, concave parietal margin (1); anteriorly located, posterior border within frontal (2). *G19/char39*
- 61. Optic Foramen: The dorsal border of the optic foramen is formed nearly equally by the frontal and parietal (0) it consists mostly of the parietal, the frontal forming only the anterior margin (1); Consists mostly of the frontal forming the margin (2); optic enclosed in frontals (3). *K91/char30*
- 62. Lateral margins of braincase open anterior to prootic (0); descending lateral processes of parietal enclose braincase (1). *G19/char40*
- 63. Supratemporal processes of parietal: distinctly developed (0); not distinctly developed (1).

G19/char41

- 64. Parietal enters anterior aspect of base of basipterygoid process: absent (0); present (1). G19/char42
- 65. Contact between parietal and supraoccipital: V-shaped with apex pointing anteriorly (0); straight transverse line (1); V-shaped with apex pointing posteriorly (2). *G19/char43*
- 66. Parietal, sagittal crest: absent (0); present posteriorly but not anteriorly, and extending for no more than 50% of parietal midline length (1); present anteriorly and posteriorly, and extending more than 50% of parietal midline length (2). Ordered. *G19/char167*
- 67. Parietal: mediolaterally narrow (0); expanded mediolaterally (1). *Modified character from* G19/char168
- 68. Parietal. Posteriorly broad parietal (0) [shown in *Loxocemus bicolor*] (1); posteriorly narrow parietal (1) [shown in *Tropidophis haetianus*]. *G19/char169*
- 69. Ascending process of maxilla: tall, extending to dorsal margin of prefrontal (0); short (1); absent (2). Ordered.
- 70. Ascending/facial process of maxilla, posterior notch on medial surface for prefrontal: present (0); absent (1). *G19/char44*
- 71. Number of maxillary labial foramina: 5 or more (0); 4 to 2 (1), one (2) and zero (3). *Modified character from SS20/char74*
- 72. Maxilla: palatine process short, weakly developed (0); palatine process long, strongly projecting medially (1). *G19/char173*
- 73. Maxilla, premaxillary process: medial projection articulating with vomers present (0); premaxillary process does not contact vomers (1). *G19/char174*
- 74. Maxilla, supradental shelf development: extending full length of maxilla (0); reduced anterior to palatine process (1). *G19/char176*
- 75. Maxilla: medial surface of facial process with distinct naso-lacrimal recess demarcated dorsally by anteroventrally trending ridge: (0) present; (1) absent. *G19/char177*
- 76. Maxilla: medial surface of facial process with well-defined fossa for lateral recess of nasal capsule: present (0); reduced and present as small fossa on back of facial process (1); absent, fossa for lateral recess developed entirely on prefrontal (2). *G19/char178*
- 77. Maxilla: extensive contact of dorsal margin of maxilla with nasal (0); nasal-maxilla contact lost (1). *G19/char179*
- 78. Maxilla: maxilla overlaps prefrontal laterally in tight sutural connection (0); overlap reduced, mobile articulation (1). *G19/char180*
- 79. Maxilla: palatine process of maxilla projects medially (0); palatine process of maxilla downturned (1). *G19/char181*
- 80. Maxilla: superior alveolar foramen: positioned near middle of palatine process, opening posterodorsally (0); positioned near anterior margin of palatine process, opening medially (1). G19/char182
- 81. Maxilla, accessory foramen posterior to palatine process: absent (0); present (1). G19/char183
- 82. Maxilla, ectopterygoid process: absent (0); present (1). G19/char184
- 83. Maxilla: 15 or more maxillary teeth (0); fewer than 15 maxillary teeth (1); maxilla without teeth (2). *G19/char185*
- 84. Small horizontal shelf on medial surface of anterior end of maxilla: present (0); absent (1). G19/char45
- 85. Posterior end of maxilla: does not project beyond posterior margin of orbit (0); projects moderately beyond posterior margin of orbit (1); projects distinctly beyond posterior margin of orbit, with broad flat surface (2). Ordered. *G19/char46*
- 86. Medial (palatine) process of maxilla: located in front of orbit (0); located below orbit (1). *G19/char47*

- 87. Medial (palatine) process of maxilla: pierced (0); not pierced (1). G19/char48
- 88. Anterior end of supratemporal: located behind or above posterior border of trigeminal foramen (0); anterior to posterior border of trigeminal foramen (1). *G19/char49*
- 89. Supratemporal facet on opisthotic-exoccipital: flat (0); sculptured and delineated with projecting posterior rim that overhangs exoccipital (1). *G19/char50*
- 90. Supratemporal: present (0); absent (1). *G19/char52*
- 91. Supratemporal: The supratemporal is rounded and noticeably enlarged (0), the supratemporal is elongated (rod like) possessing a rounded posterior region (1) or the supratemporal is elongated (rod like) possessing a markedly hooked posteroventrally directed posterior end (2). *K91/char46*
- 92. Supratemporal: supratemporal short, does not extend posterior to paroccipital process (0); elongate, extending well beyond paroccipital process (1). *G19/char177*
- 93. Anterior dentigerous process of palatine: absent (0); present (1). G19/char53
- 94. Medial (choanal) process of palatine: forms extensive concave surface dorsal to ductus nasopharingeus (0); narrows abruptly to form curved finger-like process (1); forms short horizontal lamina that does not reach vomer (2). *G19/char54*
- 95. Choanal process of palatine: without expanded anterior flange articulating with vomer (0); with anterior flange (1). *G19/char55*
- 96. Pterygoid contacts palatine: complex and finger-like articulations (0); tongue-in-groove joint (1); reduced to flap-overlap (2). *G19/char56*
- 97. Palatine contact with ectopterygoid: present (0); absent (1). G19/char57
- 98. Maxillary process of palatine: main element bridging contact with maxilla and palatine in ventral view (0); covered ventrally by expanded palatine process of maxilla (1). *G19/char149*
- 99. Dentigerous process of palatine contact with vomer and/or septomaxilla posterolateral to opening for Jacobson's organ: present (0); absent (1). *G19/char58*
- 100. Maxillary process of palatine: anterior to posterior end of palatine (0); at posterior end of palatine (1). *G19/char59*
- 101. Lateral (maxillary) process of palatine and maxilla: in well-defined articulation (0); loosely overlapping medial (palatine) process of maxilla, or absent (1). *G19/char60*
- 102. Maxillary branch of trigeminal nerve: pierces lateral (maxillary) process of palatine (0); passes dorsally between palatine and prefrontal (1). *G19/char61*
- 103. Vomerine (choanal) process of palatine: articulates broadly with posterior end of vomer (0); meets vomer in well-defined articular facet (1); touches or abuts vomer without articulation or remains separated from vomer (2). *G19/char62*
- 104. Internal articulation of palatine with pterygoid: short (0); long (1). G19/char63
- 105. Palatine, dentition: teeth small relative to lateral teeth (0); or enlarged, palatine teeth at least half diameter of posterior maxillary teeth (1); palatine lacking dentition (2). *G19/char191*
- 106. Palatine, elongate lateral process projecting to lateral edge of orbit to articulate with caudal margin of prefrontal: absent (0); present (1). *G19/char192*
- 107. Pterygoid tooth row: anterior to basipterygoid joint (0); tooth row reaches or passes level of basipterygoid joint (1). *G19/char64*
- 108. Pterygoid: An anteromedial palatine process on the pterygoid is absent (0) or present (1). *K915/char4*
- 109. Quadrate ramus of pterygoid: robust, rounded or triangular in cross-section, but without groove (0): blade-like and with distinct longitudinal groove for protractor pterygoidei (1). *G19/char65*
- 110. Transverse (lateral) process of pterygoid: forms distinct, well-defined lateral projection (0); gently curved lateral expansion of pterygoid, or absent (1). *G19/char66*
- 111. Ectopterygoid: present (0); highly reduced or absent (1). G19/char248

- 112. Lateral edge of ectopterygoid straight (0); angulated at contact with maxilla (1). G19/char67
- 113. Ectopterygoid: clasps pterygoid anteromedially (0); ectopterygoid overlaps pterygoid (1); ectopterygoid abuts pterygoid medially (2). *G19/char194*
- 114. Ectopterygoid contact with pterygoid: restricted to transverse (lateral) process of pterygoid (0); contact expanded significantly on dorsal surface of pterygoid body (1). *G19/char149*
- 115. Medial finger-like process of ectopterygoid articulating with medial surface of maxilla: present (0); absent (1). *G19/char145*
- 116. Anterior end of ectopterygoid: restricted to posteromedial edge of maxilla (0); invades dorsal surface of maxilla (1). *G19/char68*
- 117. Ectopterygoid: A mid-lateral prominence originates from the entire or dorsal margin of the ectopterygoid (0), or it originates from the ventral margin alone (1); or the prominence is absent (2). *K91/char38*.
- 118. Ectopterygoid: The anterior end of the ectopterygoid (Rieppel, 1979, fig. 6) consists of distinct (0) or indistinct (1) lateral and medial heads, or that end of the ectopterygoid is not indented (2). *K91/char32*.
- 119. Pterygoid attached to basicranium: by strong ligaments at palatobasal articulation (0); pterygoid free from basicranium in dried skulls (1). *G19/char69*
- 120. Quadrate: slanted clearly anteriorly, posterior tip of pterygoid dislocated anteriorly from mandibular condyle of quadrate (0); positioned slight anteriorly or vertically (cephalic condyle positioned behind or at same level of mandibular condyle) (1); slanted posteriorly (cephalic condyle positioned in front of mandibular condyle) (2). *G19/char71*
- 121. Cephalic condyle of quadrate: elaborated into posteriorly projecting suprastapedial process (0); suprastapedial process absent or vestigial (1). *G19/char72*
- 122. Quadrate, lateral conch: present (0); absent (1). G19/char188
- 123. Quadrate, maximum length relative to proximal width: quadrate elongate, maximum length at least 125% of maximum width of quadrate head (0); quadrate short, length less than 125% of width of quadrate head (1). *G19/char189*
- 124. Quadrate, plate-like dorsal end: absent (0); present (1). G19/char190
- 125. Stapedial footplate: broad and massive (0); narrow and thin (1). G19/char73
- 126. Stylohyal: not fused to quadrate (0); fuses to posterior/posteroventral tip of distinct suprastapedial process (1); stylohyal fuses to quadrate shaft (2). *Modified character from* G19/char74
- 127. Stapedial shaft: straight (0); angulated (1). G19/char75
- 128. Stapedial shaft: slender and longer than diameter of stapedial foot-plate (0); thick, and equal to, or shorter than diameter of stapedial foot-plate (1). *G19/char76*
- 129. Epipterygoid: present (0); absent (1). G19/char193
- 130. Paroccipital process of otooccipital: well developed and laterally projected (0); reduced to short projection or absent (1). *G19/char77*
- 131. Juxtastapedial space defined by a crista prootica, crista tuberalis and crista interfenestralis: absent (0), present, but not completely enclosed ("incipient" crista circumfenestralis) (1); present and enclosed (i.e., fully developed crista circumfenestralis) (2). Ordered. *G19/char78*
- 132. Stapedial footplate: mostly exposed laterally (0); Prootic and otoocipital converges upon stapedial footplate (1). *G19/char79*
- 133. Crista interfenestralis: does not form individualized component around the juxtastapedial space (0); does form individualized component around juxtastapedial space (1). Original definition changed in the recognition of the crista interfenestralis independently from the development of the crista circumfenestralis. *G19/char80*
- 134. Jugular foramen: exposed in lateral view by crista tuberalis (0); concealed in lateral view by

crista tuberalis (1). G19/char81

- 135. Otooccipitals: do not contact each other dorsally (0); contact each other dorsally (1). G19/char82
- 136. Otooccipitals, when in contact dorsally: do not project posteriorly to level of occipital condyle (0); project posteriorly to conceal occipital condyle in dorsal view (1). *Varanus* has been rescored as inapplicable (not 0). *G19/char197*
- 137. Otooccipital posterolateral processes: short and narrow, do not extend toward posterior margin of occipital condyle (0); wider than condyle and long, combine with crista tuberalis to extend to approximate posterior margin of occipital condyle (1). *G19/char83*
- 138. Supraoccipitals: single (0); remain paired in adult skull (1). G19/char246
- 139. Supraoccipital: A supraoccipital midsagittal crest is absent or only weakly developed (0) or the crest is tall and occupies most, if not all, of the length of the supraoccipital (1). *K91/char42*.
- 140. Supraoccipital: The supraoccipital is not covered by the parietal (0); or nearly covered by the parietal midsagittal crest (1). *K91/char43*.
- 141. Supraoccipital, shape of dorsal exposure: broad and square (0); wider than longer, with broad edges (rectangular) (1); wider than long, with pointed medial edges (2); diamond-shaped (3); 'M'-shaped (4); absent or fused (5). *G19/char236*
- 142. Supraoccipital, size of dorsal exposure, expressed as ratio of supraoccipital length (measured at the midline) to parietal width (measured at the line delimited by the anterior borders of the prootic): large, ratio of 0.5 or more (0); small, ratio less than 0.5 (1). *G19/char237*
- 143. Supraoccipital contact with prootic: with narrow (0); broad (1). *G19/char84*
- 144. Supraoccipital region of skull: nuchal crests absent (0); present (1). G19/char171
- 145. Skull, postorbital region relative length: short, less than half of rest of skull (0); elongate, half or more of rest of skull (1). *G19/char170*
- 146. Exoccipital-opisthotic: horizontal, wing-like crista tuberalis absent (0); present (1). G19/char196
- 147. Prootic: separated element (0); fused to braincase (1). G19/char247
- 148. Prootic exclusion of parietal from trigeminal foramen: absent (0); present (1). G19/char85
- 149. Laterosphenoid: absent (0): present (1). G19/char86
- 150. Prootic ledge underlap of posterior trigeminal foramen: absent (0); present (1). G19/char87
- 151. Prootic: exposed in dorsal view medial to supratemporal or to supratemporal process of parietal (0); fully concealed by supratemporal or parietal in dorsal view (1). *Haasiophis* was rescored as ? (not 1). *G19/char88*
- 152. Exit hyomandibular branch of facial nerve inside opening for mandibular branch of trigeminal nerve: absent (0); present (1). *G19/char89*
- 153. Vidian canal: does not open intracranially (0); open intracranially (1). G19/char90
- 154. Anterior opening of Vidian canal: single (0); divided (1). *G19/char91*
- 155. Vidian canals: posterior openings symmetrical (0); asymmetrical (1). G19/char195
- 156. Sella turcica: bordered posteriorly by well-developed dorsum sellae (0); dorsum sellae low (1); dorsum sellae not developed, sella turcica with shallow posterior margin (2). *G19/char92*
- 157. 'Lateral wings of basisphenoid': absent (0); present (1). G19/char93
- 158. Ventral surface of basisphenoid: smooth (0); with weakly developed sagittal crest from which protractor pterygoidei originates (1); with strongly projecting sagittal crest (2). Ordered. *G19/char94*
- 159. Posterolateral corners of basisphenoid: strongly ventrolaterally projected (0); not projected (1). *G19/char146*

- 160. Basisphenoid: The parasphenoid wing (the basipterygoid process of Frazzetta [1959:470]) is absent or only weakly developed (0) or large and without (1) or with (2) a distinctly flattened (pedicellate) ventral surface. *K91/char56*.Ordered.
- 161. Basioccipital: contributes to ventral margin of foramen magnum (0); basioccipital excluded by medial contact of otooccipitals (1). *G19/char95*
- 162. Basioccipital: expanded laterally to form floor of recessus scalae tympani (0); excluded from floor of recessus scalae tympani by otooccipital (1). *G19/char147*
- 163. Basisphenoid-basioccipital suture: smooth (0); transversely crested (1). *Varanus* has been rescored with state 0 (not -). *G19/char96*
- 164. Crista trabeculares: short and or indistinct (0); elongate and distinct in lateral view (1). G19/char98
- 165. Cultriform process of parabasisphenoid: does not extend anteriorly to approach posterior margin of choanae (0); approaches posterior margin of vomer (1). *G19/char99*
- 166. Parabasisphenoidal rostrum behind optic foramen: narrow (0); broad (1). G19/char100
- 167. Parabasisphenoid rostroventral surface: flat or broadly convex (0); concave (1). G19/char101
- 168. Basioccipital meets parabasisphenoid: suture located at level of fenestra ovalis (0); located at or behind trigeminal foramen (1); basioccipital and parabasisphenoid fused (2). *G19/char102*
- 169. Parasphenoid rostrum interchoanal process: absent (0); broad (1); narrow (2). G19/char103

MANDIBLE

- 170. Anteromedial margin of dentaries: symphyseal articular facet (0); no symphyseal facet (1). *G19/char104*
- 171. Posterior dentigerous process of dentary: absent (0); present, short (1); present, long (2). G19/char105
- 172. Medial margin of adductor fossa: relatively low and smoothly rounded (0); forms distinct dorsally projecting crest (1). *G19/char106*
- 173. Mental foramina on lateral surface of dentary: two or more (0); one (1). *Eupodophis* was rescored as ? (not 1) *G19/char107*
- 174. Coronoid process of coronoid bone: high, tapering distally (0); high, with rectangular shape(1); low, not exceeding significantly coronoid process of compound bone (2). Ordered. *G19/char108*
- 175. Coronoid bone: present (0); absent (1). G19/char109
- 176. Coronoid: The coronoid contacts the angular (0) or the two bones are separated (1). *K91/char61*.
- 177. Coronoid bone contributes to anterior margin of adductor fossa: present (0); absent (1). G19/char151
- 178. Coronoid bone: sits mostly on dorsal and dorsomedial surfaces of compound bone, being exposed in both lateral and medial views of mandible (0); applied to medial surface of compound bone (1). *G19/char152*
- 179. Posteroventral process of coronoid: present (0); absent (1). G19/char110
- 180. Coronoid process on lower jaw: formed by coronoid bone only (0); or by coronoid and compound bone (1); or by compound bone only (2) (i.e. coronoid absent). *G19/char111*
- 181. Coronoid, lateral overlap of coronoid onto dentary: absent (0); present (1). G19/char211
- 182. Postdentary elements: presence of separate elements (0); fusion of surangular /articular into compound bone (1). *G19/char112*
- 183. Dentary, enlarged mental foramen: absent (0); present (1). G19/char199
- 184. Dentary, depth of Meckelian groove anteriorly: deep slot (0); shallow sulcus (1). G19/char200

- 185. Dentary, angular process shape: posteroventral margin of dentary angular process weakly wrapped around underside of jaw (0); dentary angular process projects more nearly horizontally to wrap beneath jaw (1). *G19/char201*
- 186. Dentary, angular process length relative to coronoid process: angular process distinctly shorter than coronoid process, former terminating well anterior to latter (0); subequal in length posteriorly (1). *G19/char202*
- 187. Dentary, medial flange at anterior end: weakly projecting medially (0); hooked inward and strongly projecting medially (1). *G19/char203*
- 188. Dentary, coronoid process: wraps around surangular laterally and medially (0); broad and sits atop surangular (1). *G19/char205*
- 189. Dentary, coronoid process with slot for medial tab of surangular: absent (0) or present (1). *G19/char206*
- 190. Dentary, subdental shelf: present along entire tooth row (0); present only along posterior portion of tooth row (1); absent (2). *G19/char207*
- 191. Surangular, dentary process with distinct triradiate cross-section: absent (0); present (1). G19/char208
- 192. Surangular, adductor fossa: small or absent (0); extended caudally towards jaw articulation (1). *G19/char209*
- 193. Surangular: ventrolateral surface of surangular bearing distinct crest for attachment of adductor muscles: absent (0); present (1). *G19/char210*
- 194. Surangular, enlarged anterior surangular foramen: absent (0); or present (1). G19/char218
- 195. Coronoid eminence of surangular: (0) well-developed; (1) weakly developed or absent. G19/char218
- 196. Splenial attachment to dentary above Meckel's canal: close throughout length (0); loose, with dorsal dentary suture confined to posterodorsal corner of splenial (1); contact with subdental shelf reduced to small spur of bone or contact lost entirely (2). Ordered. *G19/char212*
- 197. Splenial angular articulation: splenial overlaps angular (0); splenial abuts against angular to form hinge joint (1). *G19/char213*
- 198. Splenial, size: splenial elongate, extends more than half distance from angular to dentary symphysis (0); splenial short, extends less than half distance from angular to symphysis (1). *G19/char214*
- 199. Splenial, anterior mylohyoid foramen: present (0); absent (1). G19/char215
- 200. Splenial: The anterior edge of the splenial (Frazzetta, 1959) exhibits a noticeable indentation, a hooked condition, at the level of Meckel's groove (0) or the edge gradually tapers anteroventrally (1). *K91/char59*
- 201. Angular, lateral exposure (with coronoid region pointing dorsally): angular broadly exposed laterally along length (0); angular narrowly exposed laterally (1). *G19/char216*
- 202. Angular, length posteriorly relative to glenoid (quadrate articulation): relatively long, extends more than half distance from anterior end of angular to glenoid; (0) relatively short, half or less of distance to glenoid (1); very short, one third or less of distance to glenoid (2). *Haasiophis* was rescored as 0 (not ?); *Wonambi* was rescored as state 0 (not 1). *G19/char217*
- 203. Glenoid, shape: quadrate cotyle shallow (0), anteroposteriorly concave and transversely arched, 'saddle shaped' (1). *G19/char220*
- 204. Retroarticular process: retroarticular process elongate (0) or shortened (1). G19/char221

TEETH

- 205. Teeth, implantation: interdental ridges absent (0): interdental ridges present (1). G19/char153
- 206. Teeth, replacement: replacement teeth lie vertically (0); lie horizontally in jaws (1).

G19/char154

- 207. Teeth, replacement: single replacement tooth per tooth position (0); two or more replacement teeth per tooth position (1). *G19/char155*
- 208. Teeth, attachment: ankylosed to jaws (0) teeth loosely attached by connective tissue (1). *G19/char156*
- 209. Teeth, size: crowns enlarged at middle of tooth row (0); crowns large anteriorly and decrease in size posteriorly (1). *Modified character from G19/char157*

VERTEBRAE

- 210. Chevrons: present (0); absent (1). G19/char113
- 211. Hemapophyses on caudal vertebrae: absent (0); present, short (1); present, long (2); merged into a single median process (3). *Varanus* has been rescored with state 0 (not 1); *Acrantophis* was rescored with state 0 (not 2); *Anilius* was rescored with state 0 (not 1); *Cylindrophis* was rescored with state 0 (not 1); *Trilepida* was rescored with state 0 (not 1). *Exiliboa* and *Ungaliophis* now have state 3. *Modified character from G19/char114*
- 212. Hypapophyses: restricted to anterior-most precloacal vertebrae (0); present throughout precloacal skeleton (1). *G19/char115*
- 213. Para-diapophysis: confluent (0); separated into dorsal and ventral facet (1). G19/char116
- 214. Prezygapophyseal accessory processes: absent (0); present as a short projection or small pointed protrusion (1); well develop long processes (2). *Modified character from G19/char117* Ordered.
- 215. Subcentral paralymphatic fossae on posterior precloacal vertebrae: absent (0); present (1). *G19/char118*
- 216. Subcentral foramina: absent (0); present, consistently small (1); present, of variable size (2). *G19/char119*
- 217. Well-developed, consistently distributed paracotylar foramina: absent (0); present (1). G19/char120
- 218. Ventral margin of centra: smooth (0); median prominence from cotyle to condyle (1). *G19/char121*
- 219. Axis intercentrum: not fused to anterior region of axis centrum (0); fused (1). G19/char122
- 220. Neural spine height on mid-trunk vertebrae: well-developed process (0); low ridge or absent (1). *G19/char123*
- 221. Cotyle shape of precloacal vertebrae: oval (0); circular (1). G19/char125
- 222. Parazygantral foramen: absent (0); present (1). G19/char126
- 223. Lymphapophyses: absent (0); present (1). *Varanus* was rescored as 0 (not ?); *Eupodophis* was rescored as ? (not 0).
- 224. Lymphapophyses: three or fewer (0); three lymphapophyses and one forked rib (1); more than three lymphapophyses and one forked rib (2). *Varanus* was rescored as (not 0); *Pachyrhachis* was rescored as ? (not 2); *Anilius* was rescored as 2 (not 1); *Cylindrophis* was rescored as 2 (not 1); *Exiliboa* was rescored as 1 (not 2); *Ungaliophis* was rescored as 1 (not 2); *Uropeltis* was rescored as 1 (not 2); *Trilepida* was rescored as 0 (not 2). Ordered. *G19/char128*
- 225. Sacral vertebrae: present (0); absent (1). G19/char129
- 226. Position of synapophyses in relation to lateral edge of prezygapophyses: at same level or slightly more projected laterally (0); clearly medial to edge of prezygapophyses (1). *G19/char130*
- 227. Pachyostotic vertebrae: absent (0); present (1). G19/char131
- 228. Precloacal vertebrae number: fewer than 100 (0); more than 100 (1). *G19/char132*
- 229. Caudal vertebrae number: greater than 50% of precloacal number (0); approximately 10% or

less than precloacal number (1). G19/char133

- 230. Tuber costae absent from ribs (0), tuber costae present (1). G19/char134
- 231. Hypapophyses of anterior precloacals: short, about 50% length of centrum (0); long, subequal to or longer than centrum (1). *G19/char222*
- 232. Vertebrae, dorsolateral ridges of neural arch: absent (0); present (1). G19/char224
- 233. Vertebrae, vertebral centrum: narrow in ventral view (0); broad and subtriangular in shape (1); broad and square (2). *G19/char225*
- 234. Vertebrae, arterial grooves: absent in neural arch (0); present (1). G19/char226
- 235. Vertebrae, posterior condyle: confluent with centrum ventrally (0); distinctly separated from centrum by groove/constriction between centrum and condyle (1). *G19/char227*
- 236. Vertebrae: narrow, width across zygapophyses not significantly greater than distance from prezygapophyses to postzygapophyses (0); vertebrae wide, width across zygapophyses 150% of length or more (1). *G19/char228*
- 237. Well-developed paired foramen on the neural arch: absent (0); present (1). New character.
- 238. Median tubercle on anterior border of zygosphene: absent (0); present (1). New character.
- 239. Vertebrae, zygosphene anterior margin: deeply concave anterior edge (0); shallowly concave anterior edge (1); straight or slightly sinuous anterior edge (2). *G19/char229*. Ordered.
- 240. Vertebrae, zygosphene width, expressed as ratio of zygosphene width to cotyle width, in anterior view: wide, ratio close to or more than 1 (0); narrow, ratio significantly less than 1 (1). *G19/char231*
- 241. Vertebrae, posteromedial notch of neural arch, expressed as ratio of postzygapophyses width to posterior embayment depth: slight embayment, ratio more than 12 (0); medium embayment, ratio between 12 and 6.5 (1); marked embayment, exposing largest part of condyle, ratio less than 6.5 (2). *From G19*. Ordered.
- 242. Vertebrae, constriction index, expressed as neural arch minimal width to total width, measured at the level of the prezygapophyseal lateral edge: slight constriction, ratio equal to or more than 0.67 (0); marked constriction, ratio less than 0.67 (1). *From G19. Eupodophis* was rescored as 0 (not 1). *G19/char232*
- 243. Vertebrae, narrow and sharp haemal keel: absent (0); present (1). G19/char233
- 244. Vertebrae, cotyle size, expressed as ratio of cotyle width to total width (measured as the interdiapophyseal width): large cotyle, ratio more than 0.5 (0); middle-sized cotyle, ratio between 0.5 and 0.3 (1); small cotyle, ratio less than 0.3 (2). *G19/char234*
- 245. Vertebrae, small lateral ridge on precloacal vertebrae extending from the parapophyses, below lateral foramen: absent (0); present (1). *G19/char235*
- 246. Vertebrae: unfused intercentra in precloacal vertebrae posterior to the axis: present (0); absent (1). *From G19. Pachyrhachis* has been rescored with state 0 (not ?). *G19/char238*
- 247. Orientation of zygapophyses of mid-trunk vertebrae: (0) steeply inclined medially, 26° or more from the horizontal; (1) moderately inclined medially, between 15–26° from the horizontal; (2) not inclined medially, <15° from horizontal. *Modified from V13.*. Ordered.
- 248. Vertebrae, arqual ridges on middle precloacals: absent (0); present (1) (Garberoglio 241). *G19/char241*
- 249. In dorsal view, neural spine originates from: the anterior edge of the zygosphene roof (0); from the middle of the zygosphene roof (1); in the neural arch posterior to the zygosphene roof (2). *New character*. Ordered.
- 250. Neural spine in distal caudal vertebrae unitary (0), bifurcated (1). SS2/char192
- 251. Postzygapophyseal wings in distal caudal vertebrae absent (0), present (1). SS21/char193
- 252. Posterior extensions of prezygapophyses in distal caudal vertebrae absent (0), present (1).

SS21/char194

- 253. Tubercular prominences in distal caudal vertebrae absent (0), present (1). SS21/char195
- 254. Pterapophyses in postcloacal vertebrae absent (0), or present (1). SS2/char197
- 255. Distal tip of prezygapophyses in postcloacal vertebrae undifferentiated (0), or elaborated into a horizontal blade (1). *SS21/char198*
- 256. Distal caudal vertebrae longer than tall, or height = length (0), much taller than long (1). *SS21/char199*

LIMBS AND GIRDLES

- 257. Pectoral girdle and forelimbs: present (0); absent (1). G19/char135
- 258. Hindlimbs: autopodium, zeugopodium, and stylopodium present (0); autopodium absent (1); autopodium and zeugopodium absent (2); autopodium, zeugopodium, and stylopodium absent (3). Ordered. *New character*
- 259. Trochanter externus: present (0); absent (1). Uropeltis was rescored as (not 1); Liotyphlops was rescored as (not ?). G19/char137
- 260. Pelvis: external to sacral-cloacal ribs (0); internal to sacral-cloacal ribs (1). This and the following 3 characters are inapplicable in taxa where the relevant pelvic elements are absent. *Uropeltis* was rescored as (not 1). *Liotyphlops* was rescored as 1 (not ?). *G19/char138*
- 261. Ilium and pubis length: ilium longer than pubis (0); ilium and pubis about the same size (1); pubis much longer than ilium (2). *Anilius* was rescored as 2 (not 1); *Calabaria* was rescored as (not 2); *Liotyphlops* was rescored as (not 1); *Cylindrophis* was rescored as 2 (not 1); *Ungaliophis* was rescored as (not 2); *Uropeltis* was rescored as (not 1); *Trilepida* was rescored as (not 1); *Eupodophis* was rescored as 1 (not ?); *Wonambi* was rescored as 1 (not ?); *Morelia* was rescored as (not 2). *G19/char139*
- 262. Pubis, obturator foramen: present (0); absent (1). *Uropeltis* was rescored as (not 1); *Liotyphlops* was rescored as (not 1); *Coluber* was rescored as (not 1). *G19/char242*
- 263. Pelvic elements: three elements strongly sutured or fused together (0); three or fewer elements with weak (cartilaginous) contacts (1). *Modified character from G19/char140*
- 264. Pelvic elements: present (0); absent (1). Uropeltis was rescored as 1 (not 0). G19/char141.

References

Caldwell, M. W. 2006. A new species of *Pontosaurus* (Squamata, Pythonomorpha) from the Upper Cretaceous of Lebanon and a phylogenetic analysis of Pythonomorpha. *Memorie della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano*, **34**, 1–42.

Caldwell, M. W., & Calvo, J. 2008. Details of a new skull and articulated cervical column of Dinilysia patagonica Woodward, 1901. *Journal of Vertebrate Paleontology*, **28**, 349–362.

Caldwell, M. W., & Lee, M. S. 1997. A snake with legs from the marine Cretaceous of the Middle East. *Nature*, **386**, 705–709.

Garberoglio, F. F., Gómez, R. O., Simões, T. R., Caldwell, M. W., & Apesteguía, S. 2019a. The evolution of the axial skeleton intercentrum system in snakes revealed by new data from the Cretaceous snakes *Dinilysia* and *Najash*. *Scientific Reports*, **9**, 1–10.

Garberoglio, F. F., Apesteguía, S., Simões, T. R., Palci, A., Gómez, R. O., Nydam, R. L., Larsson, H. C., Lee, M. S. Y. & Caldwell, M.W. 2019b. New skulls and skeletons of the Cretaceous legged snake *Najash*, and the evolution of the modern snake body plan. *Science Adances*, **5**, eaax5833. doi: 10.1126/sciadv.aax5833

Georgalis, G. L., Rabi, M., & Smith, K. T. 2021. Taxonomic revision of the snakes of the genera *Palaeopython* and *Paleryx* (Serpentes, Constrictores) from the Paleogene of Europe. *Swiss Journal of Palaeontology*, **140**, 1–140.

Houssaye, A., F. Xu, L. Helfen, V. De Buffrénil, T. Baumbach, and P. Tafforeau. 2011. Three-dimensional pelvis and limb anatomy of the Cenomanian hind-limbed snake *Eupodophis descouensi* (Squamata, Ophidia) revealed by synchrotron-radiation computed laminography. *Journal of Vertebrate Paleontology*, **31**, 2–7.

Kluge, A.G. 1991. Boine snake phylogeny and research cycles. *Miscellaneous Publications Museum of Zoology, University of Michigan*, **178**, 1–58.

Longrich, N.R., Bhullar, B.A.S, & Gauthier, J.A. 2012. A transitional snake from the Late Cretaceous period of North America. *Nature*, **488**, 205–208.

Palci, A., Caldwell, M. W., & Nydam, R. L. 2013a. Reevaluation of the anatomy of the Cenomanian (Upper Cretaceous) hind-limbed marine fossil snakes *Pachyrhachis, Haasiophis*, and *Eupodophis. Journal of Vertebrate Paleontology*, **33**, 1328–1342.

Palci, A., Caldwell, M. W., & Albino, A. M. 2013. Emended diagnosis and phylogenetic relationships of the Upper Cretaceous fossil snake *Najash rionegrina* Apesteguía and Zaher, 2006. *Journal of Vertebrate Paleontology*, **33**, 131–140.

Pierce, S. E., & Caldwell, M. W. 2004. Redescription and phylogenetic position of the Adriatic (Upper Cretaceous; Cenomanian) dolichosaur *Pontosaurus lesinensis* (Kornhuber, 1873). *Journal of Vertebrate Paleontology*, **24**, 373–386.

Polcyn, M. J., Jacobs, L. L., & Haber, A. 2005. A morphological model and CT assessment of the skull of *Pachyrhachis problematicus* (Squamata, Serpentes), a 98 million year old snake with legs from the Middle East. *Palaeontologia Electronica*, **8**, 1–24.

Rage, J. C., & Escuillié, F. 2000. Un nouveau serpent bipède du Cénomanien (Crétacé). Implications phylétiques. *Comptes Rendus de l'Académie des Sciences-Series IIA-Earth and Planetary Science*, **330**, 513–520.

Rieppel, O., and J. J. Head. 2004. New specimens of the fossil snake genus *Eupodophis* Rage and Escuillié, from Cenomanian (Late Cretaceous) of Lebanon. *Memorie della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano*, 32, 1–26.

Rieppel, O., Zaher, H., Tchernov, E., & Polcyn, M. J. 2003. The anatomy and relationships of *Haasiophis terrasanctus*, a fossil snake by well-developed hind limbs from the Mid-Cretaceous of the Middle East. *Journal of Paleontology*, **77**, 536–558.

Scanferla, A. & Smith, K.T. 2020. Exquisitely Preserved Fossil Snakes of Messel: Insight into the Evolution, Biogeography, Habitat Preferences and Sensory Ecology of Early Boas. *Diversity*, 12. doi:10.3390/d12030100

Scanferla, A., Smith, K. T., & Schaal, S. F. 2016. Revision of the cranial anatomy and phylogenetic relationships of the Eocene minute boas *Messelophis variatus* and *Messelophis ermannorum* (Serpentes, Booidea). *Zoological Journal of the Linnean Society*, **176**, 182–206.

Smith, K.T. & Scanferla, A. 2021. A nearly complete skeleton of the oldest definitive erycine boid (Messel, Germany) in Steyer J.-S., Augé M. L. & Métais G. (eds), Memorial Jean-Claude Rage: A life of paleo-herpetologist. *Geodiversitas* **43** (1): 1–24. https://doi.org/10.5252/geodiversitas2021v43a1. http://geodiversitas.com/43/1

Vasile, S., Csiki-Sava, Z., & Venczel, M. 2013. A new madtsoiid snake from the Upper Cretaceous of the Hateg Basin, western Romania. *Journal of Vertebrate Paleontology*, **33**, 1100–1119.

Zaher, H., & Scanferla, C. A. 2012. The skull of the Upper Cretaceous snake *Dinilysia* patagonica Smith-Woodward, 1901, and its phylogenetic position revisited. *Zoological Journal of the Linnean Society*, **164**, 194–238.

Zaher, H., Apesteguia, S., & Scanferla, C. A. (2009). The anatomy of the upper cretaceous snake *Najash rionegrina* Apesteguía & Zaher, 2006, and the evolution of limblessness in snakes. *Zoological Journal of the Linnean Society*, **156**, 801–826.