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## Monograph

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# A time relic: a new species of dwarf boa, *Tropidophis* Bibron, 1840 (Serpentes: Amerophidia), from the Upper Amazon Basin

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**Abstract.** The amerophidian snake radiation is a Late Cretaceous superfamily that encompasses two families: Aniliidae, pipe snakes, and Tropidophiidae, dwarf boas. We describe a new dwarf boa snake species, from the Tropidophiidae family, from the cloud forest in northeastern Ecuador. *Tropidophis cacuangoae* sp. nov. can be diagnosed from its congeners based on external and osteological morphology. The new species inhabits eastern tropical piedmont and lower evergreen montane forests, in the Amazon Tropical Rainforest biome, and is likely to be an Ecuadorian endemic. We also discuss the relationships of the new species with South American tropidophiids and provide a key to the identification of mainland South American dwarf boas.

**Keywords.** Taxonomy, osteology, systematics, Serpentes.

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## Introduction

The Alethinophidia Nopcsa, 1923 (Ancient Greek: ‘*Alethin*’ = ‘true’; ‘*-ophidia*’ = ‘snakes’) is an infraorder that encompasses all ‘advanced’ snake species (3511 species), that is, other than Scolecophidia Cope, 1864, a paraphyletic assemblage of blind snakes (462 species) (Miralles *et al.* 2018; Uetz *et al.* 2022). As for the ‘advanced’ snakes, two major lineages diverged approximately 93 million years ago, during the Upper Cretaceous: Amerophidia Vidal, Delmas & Hedges, 2007 (hypothesized to have an ‘American’ origin) and Afrophidia Vidal, Delmas & Hedges, 2007 (hypothesized to have an African origin) (Vidal *et al.* 2007; Head 2015). From these, Afrophidia is the most speciose, encompassing two clades (Henophidia Hoffstetter, 1939 and Caenophidia Hoffstetter, 1939) that are widely distributed and correspond to the majority of extant snakes, while Amerophidia is geographically restricted to the Neotropical region, with two living families, Aniliidae Stejneger, 1907 and Tropicodphiidae Brongersma, 1951 (Vidal *et al.* 2007).

Visually and ecologically, a sister clade relationship among Aniliidae and Tropicodphiidae seems unlikely. Aniliids, also known as pipe snakes or false-coral snakes, are a monotypic family of aposematic and brightly colored fossorial snakes, with red and black colored body bands, medium body size, that have reduced eyes under a scale, with loss of all visual opsins other than *RHI*, and a small mouth gape (Vidal *et al.* 2007; Simões *et al.* 2015; O’Shea 2018). In their external appearance, Aniliidae most closely resemble snakes from the Asian pipe snake families Cylindrophiiidae Fitzinger, 1843, Uropeltidae Müller, 1832 and Anomochilidae Cundall, Wallach & Rossman, 1993, which were once thought to comprise a monophyletic assemblage, the Anilioidea (Vidal *et al.* 2007). On the other hand, tropicodphiids, also known as dwarf boas, are small-sized, stout bodied, arboreal or terrestrial snakes, with well-developed eyes and a large mouth gape that closely resemble Boidae Gray, 1825, particularly Ungaliophiinae McDowell, 1987, in their external morphology (Coborn 1991; O’Shea 2018). Surprisingly, molecular inferences have repeatedly recovered a clade comprised of Aniliidae and Tropicodphiidae, which also share a morphological synapomorphy, an oviduct connecting to the cloacal diverticuli, instead of directly with the cloaca (Vidal *et al.* 2007; Siegel *et al.* 2011; Pyron *et al.* 2013).

The family Tropicodphiidae encompasses two genera, *Trachyboa* Peters, 1860, with two species that occur in the South American Andes mountains, and *Tropidophis* Bibron, 1840, with 29 species that occur in the West Indies and four in mainland South America (Uetz *et al.* 2022). Both *Trachyboa* and *Tropidophis* share a lateral position of the lateral head vein to the muscle adductor mandibulae externus profundus, reduced coronoid process, a present paracotilar foramen, dorsal vertebral hypapophysis, a smooth kidney, and a strongly bilobed hemipenis (Ferrarezzi 1994). These genera also share a similar form and position of the kidney, and only a right and a tracheal lung (Brongersma 1951). Until now, the most comprehensive phylogeny of extant amerophids contained only 10 terminals out of the 36 known species of *Tropidophis*, *Trachyboa*, and *Anilius* Oken, 1816, and recovered a paraphyletic relationship between *Tropidophis* and *Trachyboa* (Reynolds *et al.* 2014). Furthermore, there is no unambiguous diagnosis separating *Tropidophis* and *Trachyboa*, other than *Tropidophis* seemingly lacking the supraocular ‘eyelash’ scale projections, the preocular and postocular fragmented into a single circular row, rugous and keeled dorsals, absent or fragmented rostral, and other traits of unique head pholidosis in *Trachyboa* (Peters 1860; Bogert 1968).

While examining amerophid snake specimens from Ecuador, we encountered a series of specimens, with unique coloration, morphology and genetic characterization, that could not be assigned to any known species. In this work, we provide a detailed comparison of mainland tropicodphiid taxa and genera, describing a new species of snake for the Andes of Ecuador.

## Material and methods

We examined 32 preserved specimens of amerophidian snakes (Appendix 1) from the following collections: Coleção de Herpetologia, Museu de Ciências e Tecnologia da Pontifícia Universidade Católica do Rio

Grande do Sul (MCP), Brazil; División de Herpetología del Museo Ecuatoriano de Ciencias Naturales (DHMECN), Ecuador; Field Museum of Natural History (FMNH), United States; Museu Nacional, Universidade Federal do Rio de Janeiro (MNRJ), Brazil; Kentucky University, Herpetological Collection (KUH), United States; Naturhistorisches Museum Wien (NMW), Austria; Royal Belgian Institute of Natural Sciences (RBINS), Belgium; Smithsonian National Museum of Natural History (USNM); Museo de Zoología de la Pontificia Universidad Católica del Ecuador (QCAZ-R), Ecuador; Leibniz Institute for the Analysis of Biodiversity Change, Museum Koenig (ZFMK), Germany. Specimens and tissue samples were collected under permits MAE-DNB-CM-2016-0045, 2017-0062, and 2019-0120 from Ministerio del Ambiente de Ecuador.

For our molecular analyses, we generated new sequences for a total of three tropidophiid specimens of Ecuador. We pooled the new sequences with GenBank data of Alethinophidia taxa, avoiding combining sequences from different vouchers of the same species. Our final dataset comprises 17 samples, representing six described species of Tropidophiidae and 18 outgroup taxa (Supp. file 1). Total genomic DNA was extracted from liver tissue using the Isolation of Genomic DNA protocol from the Wizard Genomic DNA Purification Kit (PROMEGA). Tissue samples were first prepared by crushing to lyse nuclei. Next, the lysis and protein precipitation solutions were added, and DNA precipitation and rehydration solutions were used to preserve the DNA extracted.

We generated sequences of one nuclear gene (*Neurotrophin-3* [NTF3]). Primers and protocols follow Wiens *et al.* (2008). Each PCR reaction per sample was composed of a 25 µl reaction mix containing: 12.5 µl GoTaq Green Master Mix, 4.5 µl H<sub>2</sub>O, 1.5 µl of 10 µM Forward and Reverse primers, and 5 µl of purified DNA. Amplification was performed on an Applied Biosystems GeneAmp PCR System 9700 thermal cycler. The amplification program was set with an initial denaturation of 94°C (3 min) followed by 25 cycles of 95°C (30 sec), 60°C (30 sec), and 72°C (15 sec), with a final extension temperature of 72°C (40 sec) and 4°C for an unlimited period of time. Amplified DNA products were visualized by electrophoresis on a 2.5% agarose gel and post-staining with Tris/Borate/EDTA buffer (TBE) under blue light. PCR-amplified sequences were purified using illustra™ ExoProStar™ Enzymatic PCR and Sequencing Clean-Up Kit. Sequencing was performed in both DNA strain directions, and the procedure was undertaken by MacroGen Services, Seoul, South Korea (<http://www.macrogen.com>). Chromatograms were quality checked and trimmed with Geneious Prime® 2022.0.2 (Biomatters, Ltd., Auckland, New Zealand). All sequences will be deposited in GenBank.

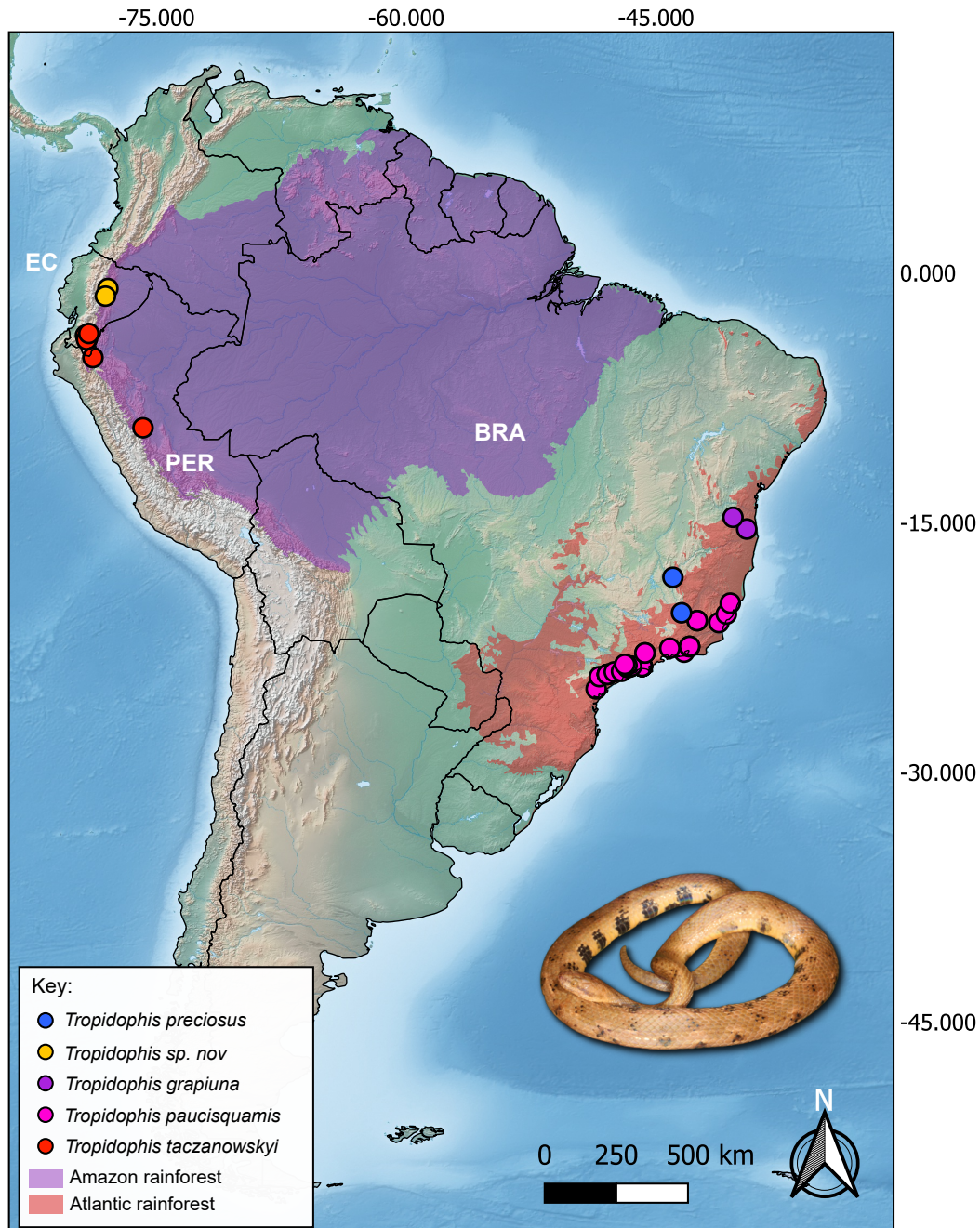
We aligned gene fragments with the MAFFT Alignment plugin (Kato *et al.* 2017), in Geneious Prime 2022.0.2 (Biomatters Ltd.) software, with default settings (Supp. file 2). We employed an inference of Maximum Likelihood (ML) analysis in RAXML ver. 8.3.2 (Stamatakis *et al.* 2014), using a GTR+GAMMA model, setting the rapid bootstrap analysis algorithm (command *-fa*), in order to account for the best scoring ML tree in the same run, while also setting 1000 bootstrap iterations for branch support estimation.

Uncorrected genetic distances (*p*-distances) were calculated using MEGA software ver. 11 (Tamura *et al.* 2021), using a d parameter (Transitions + Transversions), while assuming uniform rates among sites and a homogeneous pattern among lineages. The *p*-distance calculation was made based on the proportional (*p*) differences among nucleotide sites in which two compared sequences differ, as inferred through the division of nucleotide differences by the total nucleotides (Tamura *et al.* 2021). The ML topology was used to infer branch lengths and patristic distances (absolute time and mutation rate, to which patristic distances represent the sum of branch lengths used to link the terminal nodes of two species in a tree) as reinforcement proxies of genetic distance, following Montingelli *et al.* (2020) and Entiauspe-Neto *et al.* (2021), inferred with Geneious ver. 5.4 (Drummond *et al.* 2011). We performed analyses of species delimitation on the alignment using Bayesian Poisson Tree Process (bPTP) and Poisson Tree Process (bPTP) models (Zhang *et al.* 2013), which infers speciations or branching events as analogous to the number of mutations over a tree topology.

In order to evaluate for topological congruence among methods, given that analysis based on single-locus, short gene fragments were recently shown to yield poor and erratic results in phylogenetic estimation and species delimitation (e.g., Chan *et al.* 2022), we generated a matrix of morphological characters, stating ‘0’ for qualitative characters generally corresponds to the presumed ancestral condition for Lepidosauria, and ‘1–4’ to derived conditions, based on its presence among ingroup species as well as a succession of late Paleozoic and early Mesozoic outgroups, modified from Gauthier *et al.* (2012). Our final dataset contains 610 characters that were evaluated on 196 squamate taxa (Appendix 2). A morphological phylogeny was inferred under Maximum Parsimony criteria with TNT ver. 1 (Goloboff *et al.* 2012), using 100 000 iterations using traditional search and a tree bisection reconnection swapping algorithm. Resulting trees were then pruned to a Majority-Rule consensus, with a cut-off value of 50. Within Tropidophiidae, we generated a list of putative morphological synapomorphic characters, which is given in Appendix 2, and were evaluated over the morphological phylogeny with YBYRÁ (Machado 2015) software, using TNT script applications in Python language. YBARÁ categorizes character transformation events from any source of a data given all possible optimization schemes in a set of trees. It proceeds by spawning trees and data matrix to TNT to compile synapomorphies using TNT’s ‘apo’ command. Character-state transformations of a node were considered synapomorphies if they (i) were optimized unambiguously (without arbitrary selection of accelerated, ACCTRAN, or delayed optimization, DELTRAN) and (ii) were shared by all dichotomized most parsimonious trees. YBYRÁ generates color-coded boxes to indicate if a synapomorphic character-state occurs only in the clade in question (non homoplastic) or also occurs in other clades (homoplastic), and if it is shared by all terminals of the clade (unique) or is subsequently transformed into one or more different states within the clade (non-unique) (Machado 2015).

We obtained information on skeletal morphology from both specimens of the new species of *Tropidophis* (DHMECN 15893, DHMECN 16725) by use of an X-ray in 2D (Faxitron X-ray LX60), available at ZFMK. Description of the cranial morphology is mainly based on a high-resolution micro-CT scan of the paratype (DHMECN 15893), performed with a Bruker SkyScan 1173 at ZFMK, with the following settings: an X-ray beam with 35 kV source voltage and 150  $\mu$ A current, no filter, 0.3° rotation steps, frame averaging of 5, recorded over a 180° rotation, resulting in 800 projections of 280 ms exposure time each and a total scan duration of 30:06 min. This magnification setup generated data with an isotropic voxel size of 17.75  $\mu$ m. The CT-dataset was reconstructed with N-Recon software ver. 1.7.1.6 (Bruker MicroCT) and rendered in three dimensions using Amira visualization software (FEI, Thermo Fisher Scientific). Segmentation to separate and coloring of the bones was also carried out using Amira. The cranial description is supplemented by some information on intraspecific variations derived from a CT scan of the skull of the holotype (DHMECN 16725), using the same CT scanner and scanning parameters as for the paratype. However, some images from the image stack of this scan have been lost, so information on the posterior part of this skull in particular is missing. For comparison with closely related taxa we further CT-scanned a specimen of *Tropidophis melanurus* (Schlegel, 1837) (ZFMK 65041) and of *Trachyboa boulengeri* Peracca, 1910 (ZFMK 98727) at ZFMK, and obtained a CT-scan of the lectotype of *Tropidophis taczanowskyi* (Steindachner, 1880) (NMW 14858) from NMW and of the holotype of *Tropidophis battersbyi* Laurent, 1949 (RBINS 3701) from RBINS. *Tropidophis melanurus* and *Tra. boulengeri* were scanned with a Bruker SkyScan 1173 at an X-ray beam of 43 kV source voltage and 116  $\mu$ A current, without a filter, with 0.25° (*Tra. boulengeri*) or 0.3° (*Tro. melanurus*) rotation steps, frame averaging of 5, recorded over a 180° rotation, resulting in 800 (*Tro. melanurus*) or 960 (*Tra. boulengeri*) projections of 500 ms exposure time each and a total scan duration of 47:03 min (*Tro. melanurus*) or 56:50 min (*Tra. boulengeri*). These magnification setups generated data with an isotropic voxel size of 8.87  $\mu$ m (*Tra. boulengeri*) and 13.84  $\mu$ m (*Tro. melanurus*). The datasets were reconstructed with N-Recon. *Tropidophis battersbyi* was scanned with a UniTom (XRE, <https://xre.be/product/unitom/>) at an X-ray beam of 75 kV source voltage and 125  $\mu$ A current, without a filter, frame averaging of 1, recorded over a 360° rotation, generating 1800 projections of 300 ms exposure time each and a total scan duration of 10 min, resulting in a magnification setup with an isotropic voxel size of 14.52  $\mu$ m. *Tropidophis*

*taczanowskyi* was scanned with an YXLON FF35 CT (YXLON International GmbH) at an X-ray beam of 120 kV source voltage and 140  $\mu$ A current, recorded over a 360° rotation, generating 2070 projections of 2000 ms exposure time each and a total scan duration of 1:09:04 h, resulting in a magnification setup with an isotropic voxel size of 13.6  $\mu$ m. All specimens, except *Tro. battersbyi*, were rendered and segmented using Amira. Osteological terminology follows Cundall & Irish (2008).



**Fig. 1.** Geographic distribution of mainland species of *Tropidophis* Bibron, 1840 in South America. Note the disjunct distribution pattern, with two allopatric groups: Andes mountain range (*Tropidophis cacuangoae* sp. nov, *T. taczanowskyi* (Steindachner, 1880)) and Atlantic Forest range (*T. grapiuna* Curcio *et al.*, 2012, *T. preciosus* Curcio *et al.*, 2012, *T. paucisquamis* (Müller in Schenkel, 1901)). Inset photograph: *T. cacuangoae* sp. nov. (not to scale).

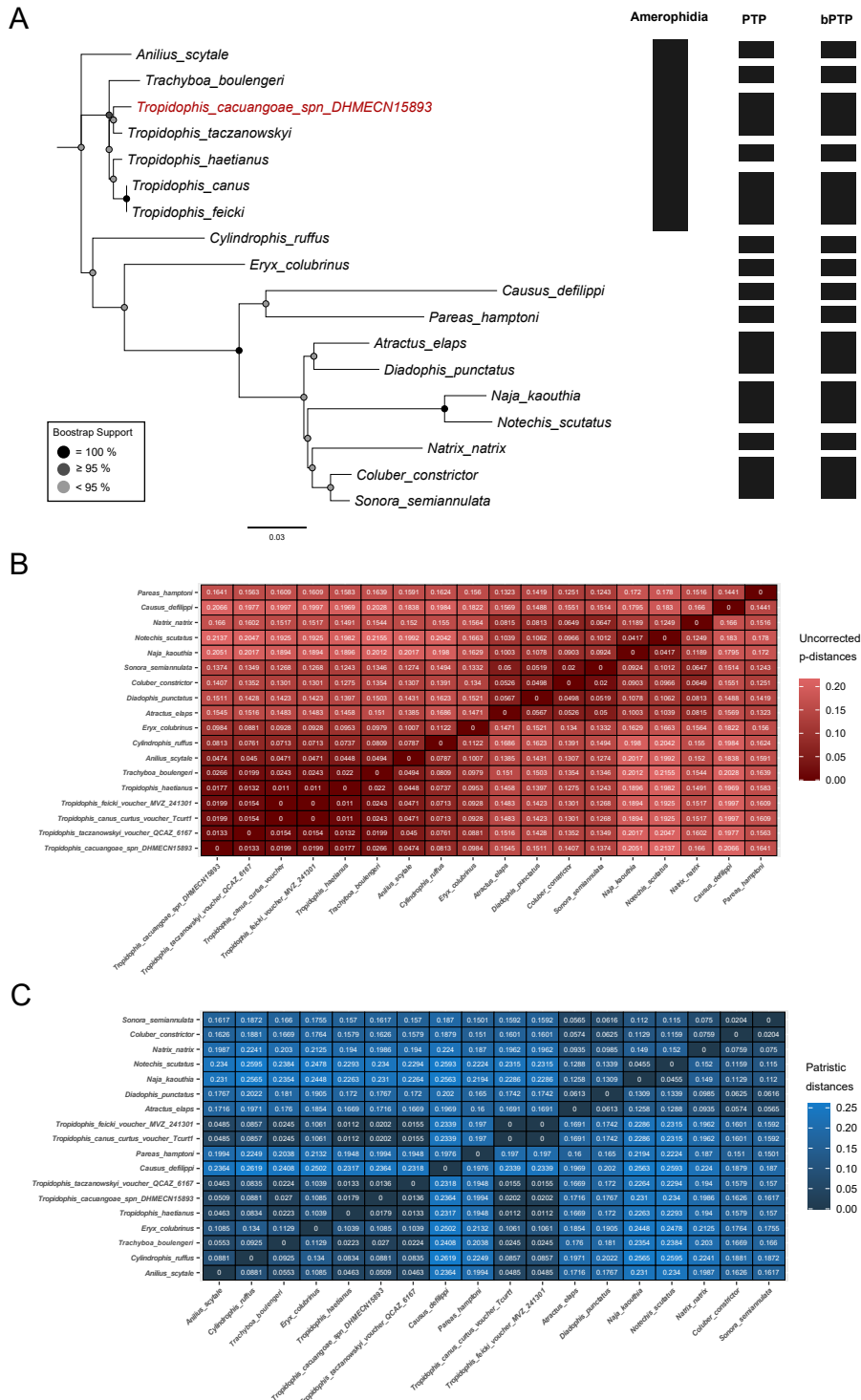
Comparative external morphological data was obtained from Peters & Orejas-Miranda (1970), Zaher (1994), and Curcio *et al.* (2012). We follow standard terminology for describing scalation and coloration (Peters 1963, Peters & Orejas-Miranda 1970, Savage & Slowinski 1992, Curcio *et al.* 2012). Measurements of snout-vent length (SVL) and tail length were taken with a flexible ruler (to the nearest 1 mm), while measurements of head, eye and scales were taken with a dial caliper (to the nearest 0.05 mm). Sex was determined either by subcaudal incision or through visual inspection of everted hemipenes. A ratio of ventral per subcaudal scales was calculated by dividing a ventral scale count by its subcaudal scale count. Measurements and meristic counts were not considered for damaged or incomplete specimens. Abbreviation: n = number of specimens. Voucher numbers for the specimens used for the geographic distribution map (Fig. 1) can be found in [Supp. file 3](#).

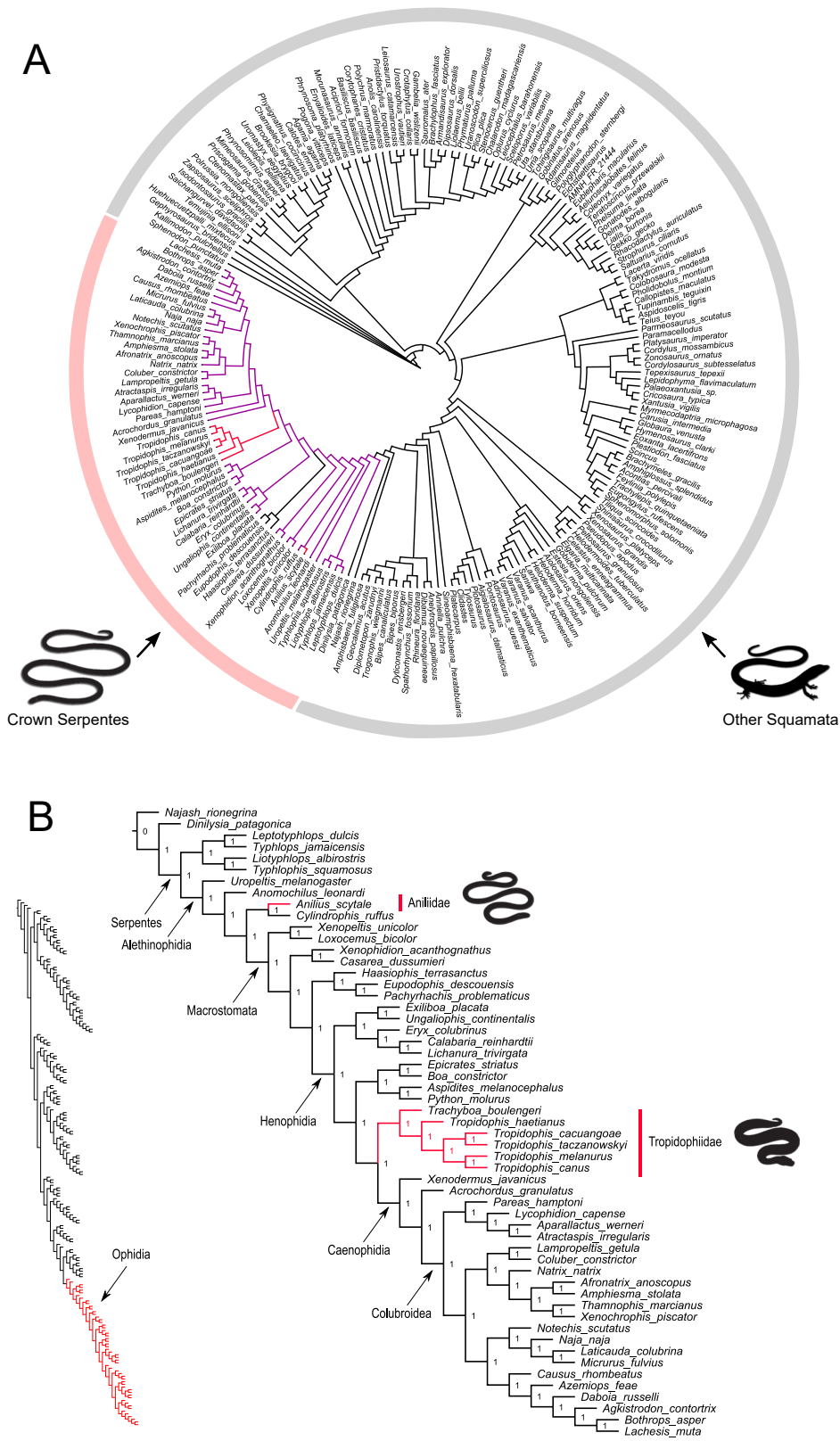
## Results

### *Molecular analyses and systematics*

Our final alignment consists of 18 terminal taxa, for which 464 base pairs are available. Our Maximum Likelihood inference over these nuclear gene fragments recovers a poorly supported clade of *Anilius*, *Trachyboa* and *Tropidophis*, supporting the hypothesis of a monophyletic Amerophidia. Interspecific genetic p-distances range from 0.01 to 0.04 for the *Neurotrophin-3* [NTF3] locus within amerophid taxa. The intraspecific uncorrected p-distance between *T. cacuangoae* sp. nov. and *T. taczanowskyi* is 0.0133, and range from 0.0133 to 0.0199% within *Tropidophis* taxa. The largest recovered distance between the new species and *Tropidophis* terminals is of *Tropidophis feicki* Schwartz, 1957 (0.0192), an extralimital species from western Cuba, an island in the Greater Antilles. However, it should be noted that no sequences from other mainland *Tropidophis* were available for this analysis, to which this species very likely bears ancestral commonality ([Supp. files 4, 5](#)). Patristic distances, as inferred for the maximum likelihood topology, range from 0.01 to 0.04 for amerophid terminals (Fig. 2). The phylogenetic inference of the Maximum Likelihood tree (lnL = -2175.559394), based on nuclear DNA, recovered *Tropidophis cacuangoae* sp. nov. in a sister-clade with *T. taczanowskyi*, in a poorly supported node. Considering the small number of available sequenced taxa for *Neurotrophin-3* locus, this phylogenetic arrangement should be seen as provisional. *Trachyboa* is recovered as a sister group to *Tropidophis*. However, it should also be noted that *Trachyboa* was recovered as paraphyletic regarding *Tropidophis* by previous inferences (e.g., Reynolds *et al.* 2014), although also poorly supported (SH-aLRT support [72.8%] / ultrafast bootstrap support [68%]). Further studies, incorporating more taxa and loci, are needed in order to evaluate whether this paraphyletic relationship is a result of poorly informative gene sites, incomplete lineage sorting, or rather a different generic arrangement is required for the group.

Our morphology-based Maximum Parsimony inference of squamate taxa recovers a monophyletic clade of Serpentes (Bremer support = 1), a paraphyletic Amerophidia, with Aniliidae nested with Cyliodrophiidae in a basal Alethinophidia clade (Bremer support = 1), and a monophyletic Tropidophiidae (Bremer support = 1), as a sister-clade to Caenophidia (Fig. 3A). The morphological phylogeny significantly differs from our molecular phylogeny in having *Trachyboa* as a sister group to a monophyletic *Tropidophis* (Bremer support = 1; Fig. 3B), and from other recent molecular phylogenetic studies for recovering Aniliidae outside of Macrostromata (e.g., Reynolds *et al.* 2014). These deviations are possibly explained by our small sample of tropidophiid terminals (n = 6), which corresponds to a small fraction of the known species (n = 35). Furthermore, considering our morphological analyses rely heavily on skull osteology, it is likely that a relationship between Aniliidae and Cyliodrophiidae was only recovered due to the similar ecological habits of these groups and subsequent convergent evolution of osteological phenotype, subjected to the same pressures caused by fossoriality and ophiophagous diet. While *T. taczanowskyi* could not be assessed in our molecular phylogeny, it is recovered as a sister-species to *T. cacuangoae* sp. nov.





**Fig. 3.** Morphological phylogeny of Squamata, inferred under Maximum Parsimony. **A.** Overview of full topology (Amerophidia, red; Extant Serpentes, purple; Other Squamates, black). **B.** Ophidia topology (Amerophidia, red; node support is Bremer Support).



Some putative synapomorphies of Tropidophiidae and of the clade composed by Tropidophiidae and Caenophidia, as outlined by Gauthier *et al.* (2014), are also reinterpreted here by our morphological evidence. As for the putative synapomorphies of Tropidophiidae, the posterior extension of the maxilla suborbital ramus is recovered in the posterior quarter of the orbit in *T. canus* (Cope, 1868), and posteriorly to the edge of the orbit in the other tropidophiid terminals. The posterior extent of maxillary teeth rows is recovered as posterior to the orbit in *T. taczanowskyi* and *T. cacuangoae* sp. nov., being in the posterior third of the orbit for all other tropidophiid terminals. The dentary teeth count is recovered as 10–20 in *T. melanurus* and *T. canus*, being 21–35 for other tropidophiid terminals. As for the clade composed by Tropidophiidae and Caenophidia, the nasal dorsal lamina can be seen in a narrow contact with the frontal in *T. canus*, while this contact is absent in other tropidophiid terminals. The dorsomedial head of the postorbital is undivided in *T. taczanowskyi*, being divided into two heads for other tropidophiid terminals. As for the parietal-supraoccipital contact, the parietal overlaps the supraoccipital on the midline for *T. melanurus*, and it abuts the supraoccipital on the midline for other tropidophiid terminals.

### ***Taxonomic account***

Phylum Chordata Haeckel, 1874  
 Class Reptilia Laurenti, 1768  
 Order Squamata Oppel, 1811  
 Suborder Serpentes Linnaeus, 1758  
 Superfamily Amerophidia Vidal, Delmas & Hedges, 2007  
 Family Tropidophiidae Brongersma, 1951  
 Genus *Tropidophis* Bibron, 1840

***Tropidophis cacuangoae* sp. nov.**

[urn:lsid:zoobank.org:act:BF8BCF5A-B93E-4C89-A9C5-EAE47B662863](https://zoobank.org/act:BF8BCF5A-B93E-4C89-A9C5-EAE47B662863)

Figs 1, 4–13, 16

### **Diagnosis**

*Tropidophis cacuangoae* sp. nov. can be distinguished from all its congeners based on the following combination of characters: (1) slightly keeled dorsal scales with no apical pits, 23/22/17 or 22/23/17 rows; (2) postoculars three; (3) loreal absent, possibly fused with nasal plate; (4) temporal formula 3 + 4 + 3 or 2 + 3 + 3; (5) supralabials 8–10, with 4<sup>th</sup> and 5<sup>th</sup> in contact with eye orbit; (6) infralabials 10–11, with first two pairs in contact with anterior chinshields; (7) ventrals 162 in single male, 156 in single female; (8) subcaudals single, 33 in single male, 30 in single female, male with cloacal spines; (9) in life, dorsal background coloration light brown, with diffuse dorsolateral black blotches, gray vertebral coloration, dark brown postocular stripe and diffuse dark brown pigmentation on labials; (10) in life, ventral background coloration light orange, with large ocellar black blotches, ranging from 16–20, covering up to four ventrals each; (11) maximum SVL 271 mm in single male, and 255 mm in single female; (12) maximum tail length 49 mm in single male, 40 mm in single female; (13) vertebral scale rows 161–162 on body, 32–35 on tail; (14) nasal contacting rostral, first and second supralabials, preocular, anterior prefrontal, and internasal; (15) two pairs of prefrontals; (16) maxillary teeth 18–21; (17) prefrontal and maxilla bones in contact; (18) dentary and angular bones in contact; (19) medial contact of exoccipitals loose; (20) small ventral ethmoidal foramen in premaxilla body; (21) cervical vertebrae two or less; (22) vomer further expanded laterally to completely encapsulate vomeronasal organ posteriorly; (23) postorbital, dorsomedial head divided in two heads.

### **Etymology**

The specific epithet ‘*cacuangoae*’, is a noun in genitive case, a Latinization honoring Dolores Cacuango, an Ecuadorian benchmark of feminism and human rights of the early twentieth century. She claimed the

identity and rights of the Ecuadorian indigenous people, leading them to defend themselves from abuse and discrimination. Also, she demanded the teaching of Quechua and founded the first bilingual schools in Ecuador and the Ecuadorian Indigenous Federation.

#### Type material

##### Holotype

ECUADOR • adult ♂; Napo Province, San Juan de Muyuna Municipality, Reserva Biológica Colonso Chalupas, Campamento 2; 0.93370 N, 77.92239 W; alt. 1613 m; H.M. Ortega-Andrade leg.; sequence: DHMECN 16725; DHMECN 16725. (Figs 4, 7A–C, 8A, 16).

##### Paratype

ECUADOR • adult ♀; Pastaza Province, Mera County, Sumak Kawsay In Situ reserve; 1.3930470 N, 78.0686059 W; alt. 1481 m; A. Bentley leg.; sequence: HMOA1935\_RBCC; DHMECN 15893. (Figs 5–7, 7D–F, 8B, 9–13).

#### Referred specimen

ECUADOR • adult ♂; Zamora-Chinchi Province, Guayzimi, Nangaritza Municipality; sequence: AB161\_NTF3; DHMECN 16126. Unconfirmed candidate new species (*Tropidophis* cf. *cacuangoae*).



**Fig. 4.** Lateral view of *Tropidophis cacuangoae* sp. nov., ♂, holotype (DHMECN 16725). Scale bar = 10 mm.

**Description of holotype**

Adult male. Total length 320 mm; SVL 271 mm; tail length 49 mm (15.3% of total length, 18.8% of SVL). Head length 8.71 mm (2.72% of total length, 3.21% of SVL); head width 6.78 mm (77% of head length, 2.12% of total length); interorbital distance 3.7 mm (54.5% of head width); rostro-orbital distance 4 mm; nostril-orbital distance 4 mm (45.92% of head length); cervical constriction distinct, with a conspicuously flat vertebral row; head distinct from neck, triangular in dorsal view, narrow anteriorly, arched in lateral view; pupil elliptical, oval shaped; rostral rounded, 2.07 mm wide, projected over lower jaw, length of portion visible in dorsal view slightly smaller than internasal suture; internasals paired, square, 1.45 mm long, 1.32 mm wide; each internasal contacting nasal, rostral, and anterior prefrontal, separated from supralabials; anterior prefrontals paired, square, 1.18 mm long, 1.78 mm wide; each anterior prefrontal contacts internasals, nasal, preocular, and posterior prefrontals; posterior prefrontals paired, square, 0.8 mm long, 1.44 mm wide; each posterior prefrontal contacts frontal, preocular, anterior prefrontals and supraoculars; frontal hexagonal, 3.13 mm long, 1.73 mm wide, contacting posterior prefrontals, supraoculars, and parietals; supraocular trapezoidal, 2.64 mm long, 1.25 mm wide, in contact with preocular, posterior prefrontal, frontal, parietal, and upper postocular; parietals paired, 3.8 mm long, 3 mm at its largest width, broadly in contact, with a single interparietal, contacting parietals, upper postocular, frontal, temporals, and occipitals; occipitals square-shaped, enlarged, in four rows, contacting dorsals; nasal trapezoidal, undivided, 3 mm long, 0.85 mm high, contacting rostral, internasals, 1<sup>st</sup> and 2<sup>nd</sup> supralabials, anterior prefrontal, and preocular; nostril located in anterior third of nasal, not visible



**Fig. 5.** Lateral view of *Tropidophis cauangoae* sp. nov., ♀, paratype (DHMECN 15893). Scale bar = 10 mm.

from above; preocular trapezoidal, 0.97 mm long, 1.61 mm high, contacting nasal, anterior prefrontal, posterior prefrontal, 2<sup>nd</sup> and 3<sup>rd</sup> supralabials, and supraocular; upper postocular 1.03 mm long, 0.98 mm high, contacting supraocular, parietal, middle postocular, and 1<sup>st</sup> row of temporals; middle postocular 0.89 mm long, 0.77 mm high, contacting upper postocular, 1<sup>st</sup> row of temporals, and lower postocular; lower postocular 0.9 mm long, 0.5 mm high, contacting 5<sup>th</sup>, 6<sup>th</sup>, and 7<sup>th</sup> supralabials, and middle postocular; temporals 3 + 4 + 3, first row contacting upper and middle postoculars, parietal, 7<sup>th</sup> and 8<sup>th</sup> supralabials, second row contacting parietals, 8<sup>th</sup> and 9<sup>th</sup> supralabials, third row contacting parietals, occipitals, 9<sup>th</sup> and 10<sup>th</sup> supralabials; supralabials ten, 4–5 entering orbit; first supralabial contacts rostral and nasal, second contacts nasal and preocular, third contacts preocular, fifth and sixth contact lower postocular, seventh contacts first row of temporals, middle and lower postoculars, eighth contacts first and second row of temporals, ninth contacts second and third row of temporals, tenth contacts third row of temporals; mental triangular, 0.75 mm long, 2.28 mm wide; anterior chinshields paired, 1.95 mm long, 0.68 mm wide; infralabials ten, first pair separated by mental and anterior chinshields, 1–2 in contact with anterior chinshields, 2–3 in unilateral (right side) contact with posterior chinshields, second and third largest, equal in size; dorsal scales slightly keeled, in 23/22/17 rows; pre-cloacal scale entire, with spines; ventrals 162; single preventral; subcaudals entire, 33; terminal scale acuminate, curved ventrally; vertebral scale rows 162 on body, 35 on tail.

Two cervical vertebrae; trunk vertebrae 158; caudal vertebrae 39; remnants of pelvic bones present (Fig. 8A).

Head background coloration light brown dorsally and laterally, dark brown pigmentation dispersed through center of head, coalescing outwards from suture of internasals, prefrontals, and frontal; rostral, supralabials, nasals and preocular with light brown background coloration, and diffuse dark pigmentation on scale edges; conspicuous postocular dark brown stripe, covering upper and middle postoculars,

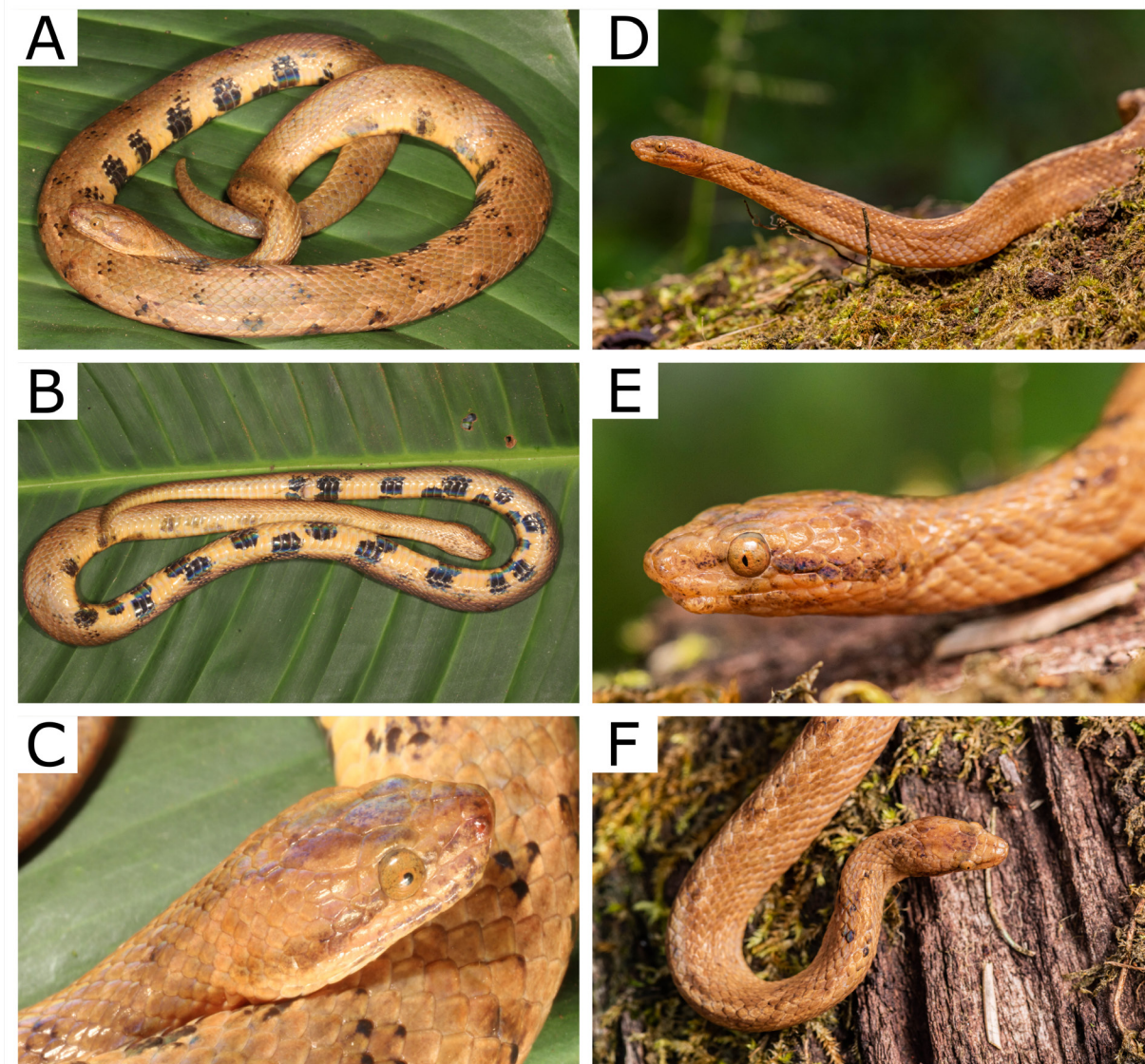


**Fig. 6.** Dorsal view of *Tropidophis cacuangoae* sp. nov., ♀, paratype (DHMECN 15893) in life. Photograph credits: Danilo Medina.

temporals, and dorsals; dark brown pigmentation on edges of infralabials, and into chinshields and gulars; dorsal background coloration light brown, with ocellar black blotches (mostly confined to edges of dorsals), coalescing outwards from dorsoventral region and ventral blotches; ventral background coloration uniformly cream, with 16 ventral ocelli-shaped black blotches.

### Variation

The new species is known solely based on two specimens. Measurements (given in mm) range from: SVL 255–271 (255 in female, 271 in male), tail length 40–49 (40 in female, 49 in male), total length 295–320 (295 in female, 320 in male); head length 8.41–8.71 (8.41 in female, 8.71 in male); head width 5.51–6.78 (5.51 in female, 6.78 in male); rostral length 1.07–1.32 (1.07 in female, 1.32 in male); rostral width 1.53–2.07 (1.53 in female, 2.07 in male); internasal length 1.65–1.83 (1.65 in female, 1.83 in male); nasal length 1.78–3 (1.78 in female, 3 in male); nasal width 0.8–0.85 (0.8 in female, 0.85 in male);



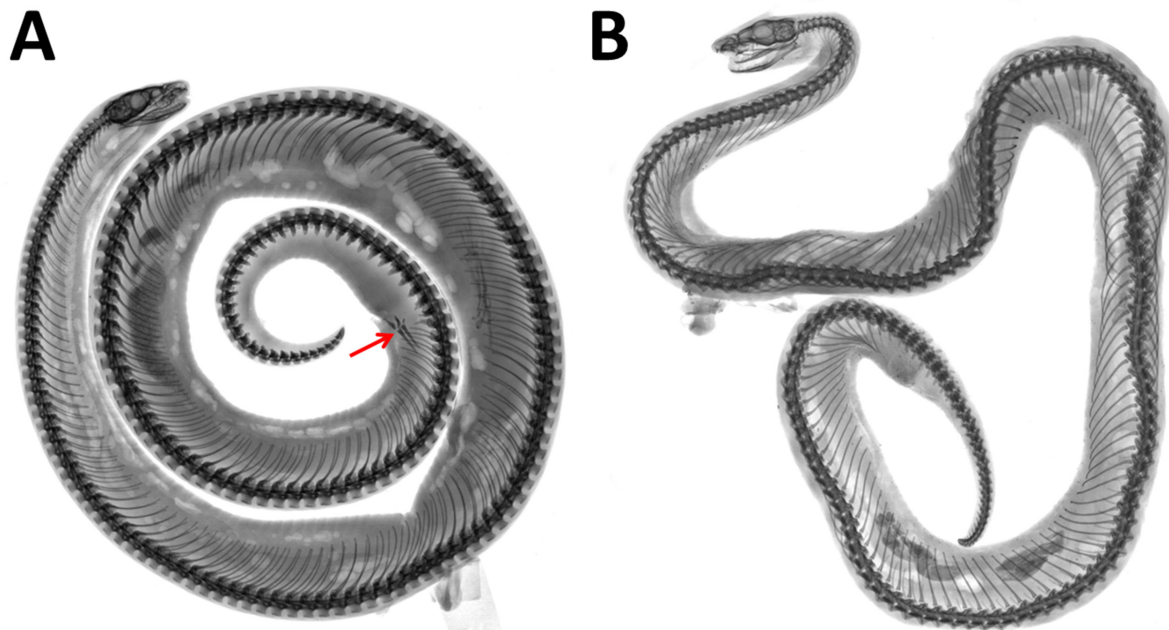
**Fig. 7.** Head views of *Tropidophis cacuangoae* sp. nov. in life. A–C. ♂, holotype (DHMECN 16725). D–F. ♀, paratype (DHMECN 15893). Photograph credits: A–C = H. Mauricio Ortega-Andrade; D–F = Danilo Medina.

anterior prefrontal length 0.92–1.18 (0.92 in female, 1.18 in male); anterior prefrontal width 1.78–2.47 (2.47 in female, 1.78 in male); posterior prefrontal length 0.87–0.9 (0.9 in female, 0.87 in male); posterior prefrontal width 1.13–1.44 (1.13 in female, 1.44 in male); frontal length 3.03–3.13 (3.03 in female, 3.13 in male); frontal width 1.73–1.9 (1.9 in female, 1.73 in male); supraocular length 2.23–2.64 (2.23 in female, 2.64 in male); supraocular width 0.83–1.25 (0.83 in female, 1.25 in male); preocular length 0.74–0.97 (0.74 in female, 0.97 in male); preocular width 1.48–1.61 (1.48 in female, 1.61 in male); upper postocular length 1.03–1.06 (1.06 in female, 1.03 in male); upper postocular width 0.98–1.16 (0.98 in female, 1.16 in male); middle postocular length 0.89–0.91 (0.91 in female, 0.89 in male); middle postocular width 0.77–0.97 (0.97 in female, 0.77 in male); lower postocular length 0.7–0.9 (0.7 in female, 0.9 in male); lower postocular width 0.43–0.54 (0.43 in female, 0.54 in male); mental length 0.66–0.75 (0.66 in female, 0.75 in male); mental width 2.09–2.28 (2.09 in female, 2.28 in male); anterior chinshield length 1.92–1.95 (1.92 in female, 1.95 in male); anterior chinshield width 0.67–0.68 (0.67 in female, 0.68 in male); posterior chinshield length 2.32–2.61 (2.61 in female, 2.32 in male); posterior chinshield width 0.75–0.85 (0.75 in female, 0.85 in male). Scale counts may vary: dorsals 23/22/17 or 22/23/17; temporals 3 + 4 + 3 or 2 + 3 + 3; supralabials 8/8 or 10/9, with 3–5 or 3–4 contacting orbit; infralabials 9/9 or 10/9, with 1–2 contacting anterior chinshields; gular scale rows 7–12; vertebral scales on body 161–162, on tail 32–35; ventrals 156–162 (156 in female, 162 in male); subcaudals single, 30–33 shields (30 in female, 33 in male).

The female paratype has two cervical vertebrae, 155 trunk vertebrae and 30 caudal vertebrae, and lacks pelvic remnants (Fig. 8B).

### Coloration

The two known specimens largely agree in coloration patterns. Head background coloration light brown dorsally and laterally, dark brown pigmentation dispersed through the center of the head, coalescing outwards from suture of internasals, prefrontals, and frontal; rostral, supralabials, nasals and preocular



**Fig. 8.** X-ray images of *Tropidophis cacuangoae* sp. nov. **A.** ♂, holotype (DHMECN 16725). **B.** ♀, paratype (DHMECN 15893). The red arrow shows the pelvic remnants of the male specimen, which are absent in the female.

with light brown background coloration, and diffuse dark pigmentation on scale edges; conspicuous postocular dark brown stripe, covering upper and middle postoculars, temporals, and dorsals; dark brown pigmentation on edges of infralabials, and into chinshields and gulars; dorsal background coloration light brown or light orange, with ocellar black blotches (mostly confined to the edges of dorsals), coalescing outwards from dorsoventral region and ventral blotches; ventral background coloration uniformly cream in preserved specimens, and uniformly orange in life, with 16–20 ventral ocelli-shaped black blotches.

### **Cranial morphology** (Figs 9–13)

An overview of interspecific osteological comparisons can be seen in Table 1. Cranial information is mainly based on CT scan data of the paratype DHMECN 15893, an adult female. The skull shows slight damage. The tooth row of the left palatine is missing, the right ectopterygoid and pterygoid are broken and the right quadrate is dislocated. Some information on intraspecific variation is supplemented from CT scan data of the male holotype (DHMECN 16725). The premaxilla is edentulous, subtriangular in frontal view, 2.5 (DHMECN 15893) to 2.8 (DHMECN 16725) times as broad as high, with a short, dorsally oriented ascending process; ascending process almost contacting anterior end of nasals; transverse processes are laterally oriented, 1.3 (DHMECN 16725) to 1.7 (DHMECN 15893) times as long as ascending process, define widest part of premaxilla, entirely visible in dorsal view, posteriorly contact (DHMECN 15893) or not (DHMECN 16725) anteriormost tips of septomaxillae, laterally approach maxillae but remain distinctly separated from them; in ventral view, the posteriorly oriented vomerine process is bifurcate with slightly posterolaterally diverging arms (DHMECN 16725), or tripartite with parallel arms, laterally longer and wider, with rounded ends, and a short and narrower, thumb-like, median arm (DHMECN 15893), lateral arms of each specimen distinctly overlapping anterior part of vomers; ventral surface of premaxilla pierced by two foramina in anterior region.

Nasals are paired, in contact medially, each with an elongate triangular dorsal lamina, which is 3.4 (DHMECN 15893) to 4 (DHMECN 16725) times as long as wide, with a pointed anterior tip and a broadened caudal end, which is laterally slightly overlapped by medial process of prefrontal; posteroventral process of nasal contacts or not anteroventral part of frontal; vertical lamina of nasal contacts medial edge of septomaxilla; nasals are approximately half as broad as septomaxillae and frontals.

Septomaxillae are paired and slightly separated, 1.6 (DHMECN 16725) to 1.9 (DHMECN 15893) times as long as wide, each with a broad ascending conchal process that extends freely anterolaterally beyond lateral margins of nasals but does not reach level of lateral nasal edge; anterior end of septomaxilla touches (DHMECN 15893) or not (DHMECN 16725) lateral process of premaxilla; posterior end remains distinctly separated from anterior end of frontal; ventrally, septomaxilla is connected to vomer; dorsally, connected to vertical lamina of nasal along its entire length, with caudal end being squared off and fitting into a notch in ventral edge of vertical lamina of nasal.

Vomers are paired, complex structures, about three times as long as wide, medially in contact and with anterior region diverging; body of vomer with globular mesoventral portion with an anteriorly oriented opening; anteriorly broad contact zone with dorsal surface of vomerine process of premaxilla; dorsally connected to septomaxilla in anterior and central region; vertical lamina of caudal end of vomer is unforked and dorsolaterally in firm contact with anterior region of choanal process of palatine.

The braincase accounts for approximately 70% of the total skull length.

Prefrontals form anterior margin of orbits; orbital lamina is slightly concave and divided into two bones (DHMECN 15893) or not divided (DHMECN 16725), with lacrimal duct enclosed (DHMECN 16725) or not being enclosed by prefrontal but framed dorsally, laterally, and medially by the two bones (DHMECN 15893); in lateral view, anterior process is convexly rounded; in contact with nasal dorsomedially, frontal

**Table 1.** Osteological comparisons among selected species of *Tropidophis* Bibron, 1840 and *Trachyboa boulengeri* Peracca, 1910. Diagnostic characters of *Tropidophis cacuangoae* sp. nov. are highlighted in bold. Species with confirmed records from the Andes mountain range are indicated with a dagger (†).

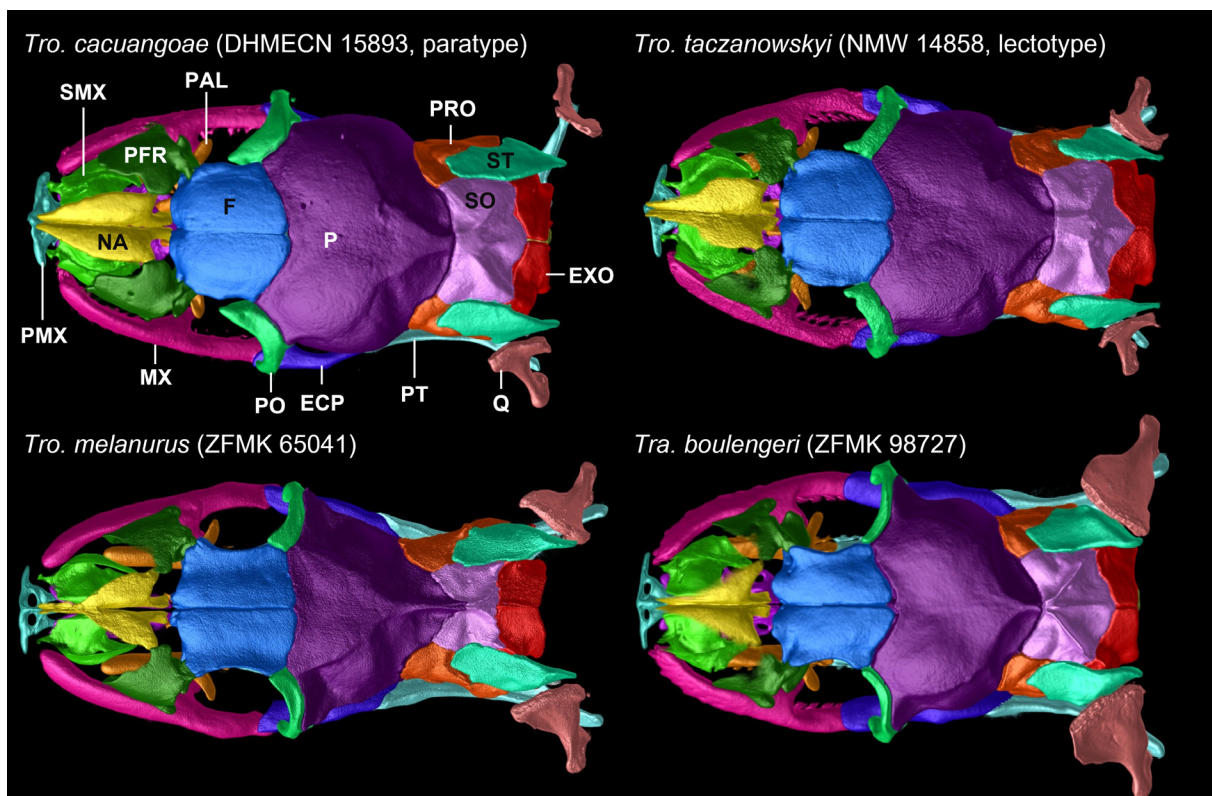
	<i>Tro. cacuangoae</i> sp. nov. † (n = 2); holotype, paratype	<i>Tro.</i> <i>taczanowskyi</i> † (n = 1); lectotype	<i>Tro. melanurus</i> (n = 1)	<i>Tra. boulengeri</i> (n = 1)	<i>Tro. battersbyi</i> (n = 1); holotype
Maxillary teeth	18–21	21–22	17–18	17	13–14
Palatine teeth	7–9	7–8	7	7	7
Pterygoid teeth	11–13	13–14	14	20	10–11
Dentary teeth	22–25	22–23	19	25–27	18–20
Coronoid	present	present	present	absent	absent
Prefrontal-Maxilla contact	<b>present</b>	absent	present	present	present
Lateral borders of frontals in dorsal view	convex	convex	concave	concave	slightly convex
Distance of parietal ridges in posterior region of parietal	distinctly separated	distinctly separated	very close	very close	moderately separated
Suture of parietal and supraoccipital	slightly curved	slightly curved	V-shaped	strongly curved	moderately curved
Suture of supraoccipital and exoccipitals	broadly V-shaped	V-shaped	almost straight	broadly V-shaped	V-shaped
Lateral ridges of supraoccipital	parallel in anterior region, diverging posteriorly, moderately pronounced	parallel in anterior region, diverging posteriorly, moderately pronounced	parallel in anterior region, diverging posteriorly, very pronounced	meet in anterior region with medial ridge and directly diverging posteriorly, very pronounced	parallel in anterior region, diverging posteriorly, moderately pronounced
Medial ridge of supraoccipital	short ( $\frac{1}{3}$ to $\frac{1}{2}$ of supraoccipital length), weakly pronounced	short (about $\frac{1}{2}$ of supraoccipital length), weakly pronounced	absent	as long as supraoccipital, very pronounced	short (about $\frac{1}{2}$ of supraoccipital length), weakly pronounced
Medial contact of exoccipitals	<b>loose</b>	firm	firm	firm	firm
Dorsal ridges of exoccipitals	moderately pronounced	moderately pronounced	long, very pronounced	short, very pronounced	moderately pronounced
Elongate, perpendicular groove at Basisphenoid-Prootic suture	<b>present</b>	absent	absent	absent	present only on prootic
Level of caudal termination of maxilla	at posterior margin of postorbital	at posterior margin of postorbital	at anterior margin of postorbital	at anterior margin of postorbital	distinctly anterior to anterior margin of postorbital
Level of caudal termination of pterygoid	shortly before posterior end of exoccipital	at posterior end of exoccipital	distinctly posterior to posterior end of exoccipital	distinctly posterior to posterior end of exoccipital	shortly behind posterior end of exoccipital
Dentary-Angular contact	absent	present	present	present	present
Splenic-Compound Bone contact	present	present	absent	absent	absent



posterodorsally, maxilla ventrally, and palatine ventromedially; in posterior view, prefrontal exhibits a small process directed medially or slightly anteromedially.

Frontals are paired, in close medial contact with a straight suture, about semicircular in dorsal view, 1.9 (DHMECN 15893) to 2 (DHMECN 16725) times as long as wide; forming dorsal and medial margins of orbits, slightly convex in dorsal view; anterior margin slightly (DHMECN 15893) or strongly (DHMECN 16725) convexly curved; anterolateral edge of frontal forms a short, thumb-like process that fits into a facet of prefrontal; both frontals together form a rounded suture with parietal, which seamlessly adapts shape of parietal; ventral edges of orbital laminae of frontals in medial contact along their entire length; anteromedially, frontal has a vertical lamina that is fused ventrally with lateral lamina to form a short tubular structure in anterior region of each frontal, with vertical laminae of both frontals being in close medial contact; frontal anteriorly in contact with nasal or slightly separated from it, anterolaterally in contact with prefrontal, posteriorly with parietal, posterolaterally with postorbital (DHMECN 15893) or remains slightly separated from it (DHMECN 16725), ventrally with parabasisphenoid rostrum, and approaching but not touching choanal process of palatine.

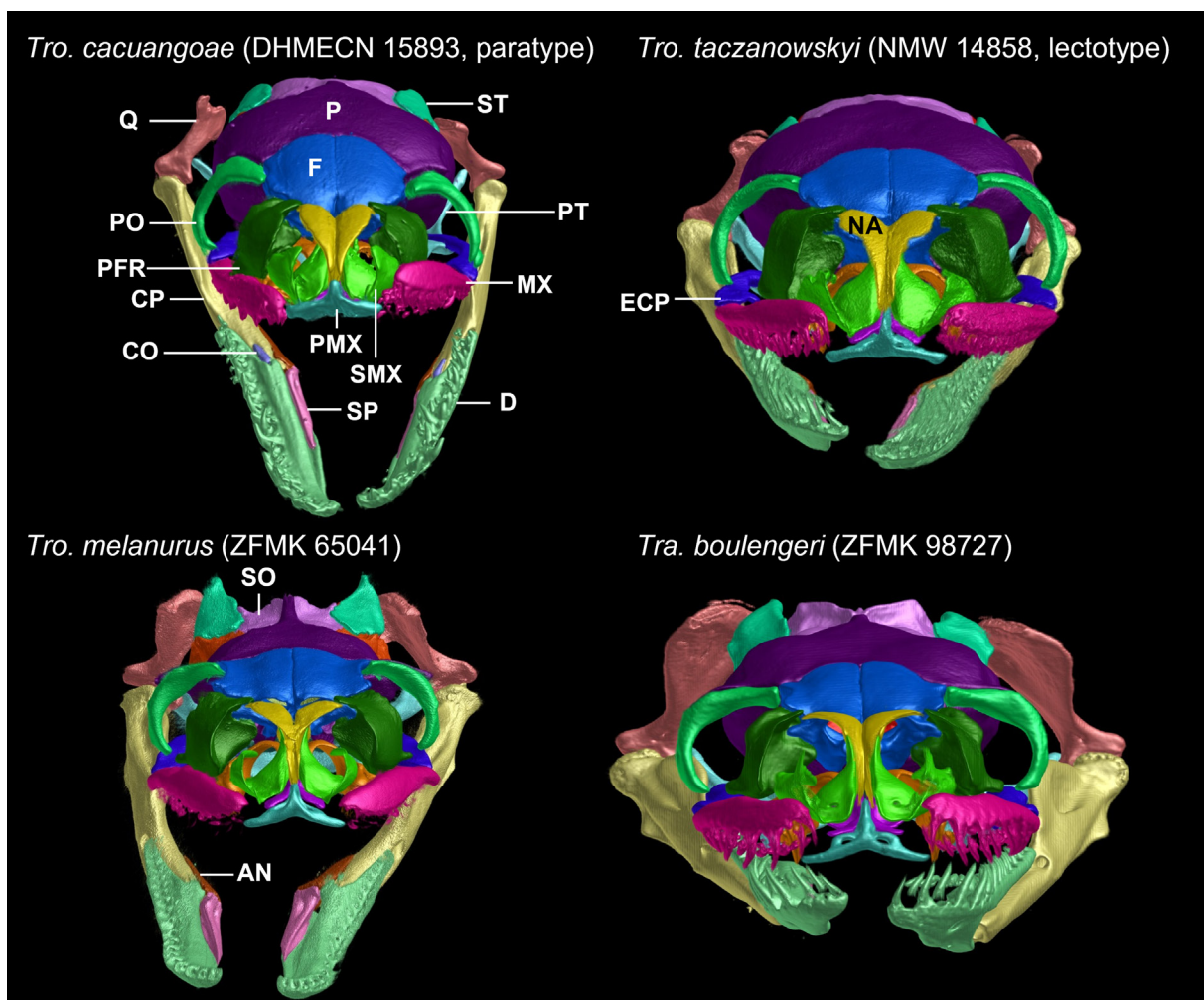
Parietal is single, about 1.2 (DHMECN 16725) to 1.4 (DHMECN 15893) times as wide as long, with concavely rounded anterior and anterolateral edges, and convexly rounded lateral and posterior edges



**Fig. 9.** Micro-CT images of the dorsal view of the skulls of *Tropidophis cacuangoae* sp. nov., ♀ (DHMECN 15893, paratype), *T. taczanowskyi* (Steindachner, 1880) (NMW 14858, lectotype), *T. melanurus* (Schlegel, 1837) (ZFMK 65041), and *Trachyboa boulengeri* Peracca, 1910 (ZFMK 98727). Different skull elements are digitally colored and the mandibulae are removed for better visualization. Abbreviations: ECP = ectopterygoid; EXO = exoccipital; F = frontal; MX = maxilla; NA = nasal; P = parietal; PAL = palatine; PFR = prefrontal; PMX = premaxilla; PO = postorbital; PRO = prootic; PT = pterygoid; Q = quadrate; SMX = septomaxilla; SO = supraoccipital; ST = supratemporal.

in dorsal view; dorsal surface is slightly convex except for a slight longitudinal depression along its midline; not participating in formation of orbit; anterolateral edges in broad and seamless contact with postorbitals; in dorsal view, moderately defined dorsolateral ridges extending posteromedially from posterior point of contact with postorbitals to suture with supraoccipital, approaching but not touching each other; laterally, parietal slopes down forming a strongly convex lateral surface; parietal contacts parabasisphenoid ventrally with an oblique straight suture, frontals anteriorly, prootics posterolaterally with a slightly concave curved suture in dorsal view, and supraoccipital posteriorly with a convex curved suture; parietal does not participate in formation of maxillary branch foramen of trigeminal nerve.

Postorbitals are well developed, elongate, downwardly curved, and meet (DHMECN 15893) or remain slightly separated (DHMECN 16725) from ectopterygoids, in lateral view with a concave anterior margin,

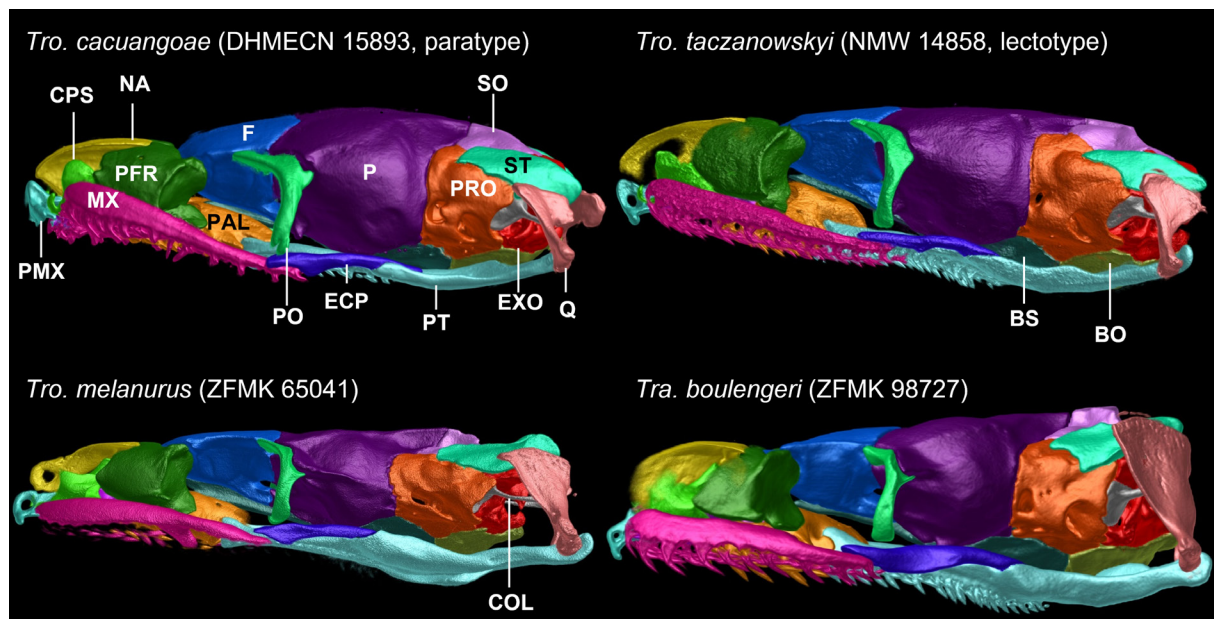


**Fig. 10.** Micro-CT images of the anterior view of the skulls of *Tropidophis cacuangoae* sp. nov., ♀ (DHMECN 15893, paratype), *T. taczanowskyi* (Steindachner, 1880) (NMW 14858, lectotype), *T. melanurus* (Schlegel, 1837) (ZFMK 65041), and *Trachyboa boulengeri* Peracca, 1910 (ZFMK 98727). Different skull elements are digitally colored for better visualization. Abbreviations: AN = angular; CO = coronoid; CP = compound bone; D = dentary; ECP = ectopterygoid; F = frontal; MX = maxilla; NA = nasal; P = parietal; PFR = prefrontal; PMX = premaxilla; PO = postorbital; PT = pterygoid; Q = quadrate; SMX = septomaxilla; SO = supraoccipital; SP = splenial; ST = supratemporal.

forming posterolateral edge of orbit; postorbital contacts parietal posterodorsally, and contacts (DHMECN 15893) or approaches frontal anteromedially without touching (DHMECN 16725).

Supraoccipital is single, subpentagonal, 1.7 (DHMECN 16725) to 1.9 (DHMECN 15893) times as broad as long, with a slightly concave curved anterior suture with parietal, a broadly V-shaped posterior suture with exoccipitals, and an almost straight suture with prootics laterally; lateral edges of supraoccipital are partially overlapped by supratemporals; two lateral ridges originate at anterior margin of supraoccipital lateral to midline, forming a continuation of ridges of parietal, first running parallel to each other for a short distance and then becoming more pronounced and diverging obliquely until they reach posterolateral corner of supraoccipital; in center of supraoccipital there is a medial ridge of about one third (DHMECN 15893) or half (DHMECN 16725) of length of supraoccipital; internally, lateral edges of supraoccipital extend downward and contribute to dorsomedial walls of otic capsules.

Exoccipitals are paired, irregularly shaped, dorsally in loose medial contact along a straight suture; each has a moderately pronounced dorsal ridge that continues corresponding lateral ridge of supraoccipital; each exoccipital contacts supraoccipital anterodorsally, prootic anterolaterally, supratemporal dorsolaterally, and basioccipital ventrally; large fenestra ovalis is located at suture of prootic and exoccipital, the latter forming posterior margin of fenestra; exoccipitals form dorsal, lateral, and lateroventral border of foramen magnum, without preventing basioccipital from its participation in foramen magnum; internally, exoccipital contributes to formation of posteroventral, posteromedial, and posterolateral walls of the otic capsule.

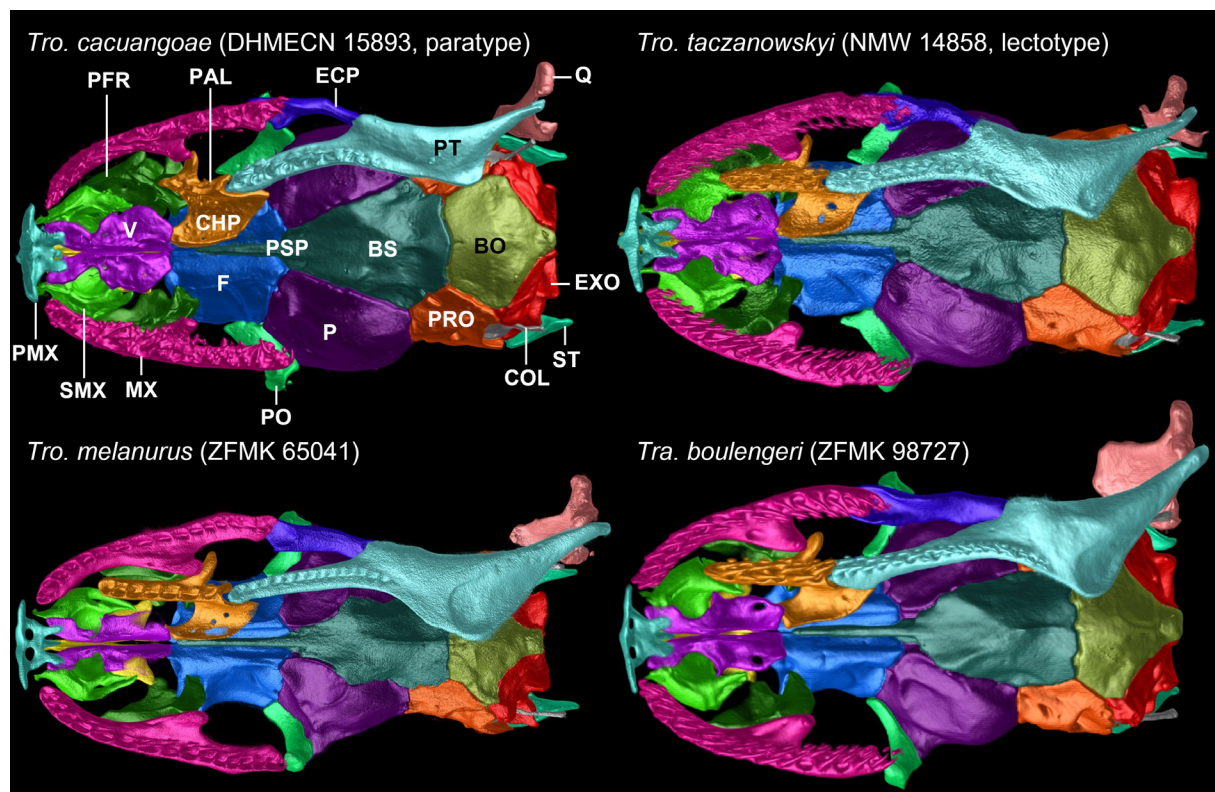


**Fig. 11.** Micro-CT images of the lateral view of the skulls of *Tropidophis cacuangoae* sp. nov., ♀ (DHMECN 15893, paratype), *T. taczanowskyi* (Steindachner, 1880) (NMW 14858, lectotype), *T. melanurus* (Schlegel, 1837) (ZFMK 65041), and *Trachyboa boulengeri* Peracca, 1910 (ZFMK 98727). Different skull elements are digitally colored and the mandibulae are removed for better visualization. Abbreviations: BO = basioccipital; BS = basisphenoid; COL = columella; CPS = conchal process of septomaxilla; ECP = ectopterygoid; EXO = exoccipital; F = frontal; MX = maxilla; NA = nasal; P = parietal; PAL = palatine; PFR = prefrontal; PMX = premaxilla; PO = postorbital; PRO = prootic; PT = pterygoid; Q = quadrate; SO = supraoccipital; ST = supratemporal.

Columella has an enlarged ovaloid footplate inserted into foramen ovalis and firmly in contact with prootic anteriorly and with exoccipital posteriorly; long and thin, posterolaterally oriented stylus extends toward inner surface of quadrate but remains separate from it.

Prootics are ovaloid in lateral view with an uneven surface, 1.2 (DHMECN 16725) to (DHMECN 15893) 1.4 times as high as long; each has a large anterior and posterior trigeminal foramen separated by laterosphenoid, anterior foramen lying entirely within prootic and not at suture with parietal; each prootic contacts parietal anteriorly and dorsoanteriorly, supraoccipital dorsally, exoccipitals posteriorly, parabasisphenoid complex anteroventrally, basioccipital posteroventrally, and is partially overlapped by supratemporal dorsally; posteriorly, prootic forms anterior margin of fenestra ovalis at suture with exoccipital; internally, prootic contributes to formation of anteroventral, anteromedial and anterolateral walls of otic capsule.

Basioccipital is pentagonal and ends posteriorly in a blunt, rounded tip; about 1.2 times as wide as long, with its widest part just posterior to suture of prootic and exoccipital; ventral surface of basioccipital is convex; it contacts parabasisphenoid complex anteriorly with a slightly undulate suture, prootics



**Fig. 12.** Micro-CT images of the ventral view of the skulls of *Tropidophis cacuangoae* sp. nov., ♀ (DHMECN 15893, paratype), *T. taczanowskyi* (Steindachner, 1880) (NMW 14858, lectotype), *T. melanurus* (Schlegel, 1837) (ZFMK 65041), and *Trachyboa boulengeri* Peracca, 1910 (ZFMK 98727). Different skull elements are digitally colored and the mandibulae, and right palatine, pterygoid, ectopterygoid and quadrate are removed for better visualization. Abbreviations: BO = basioccipital; BS = basisphenoid; CHP = choanal process of palatine; COL = columella; ECP = ectopterygoid; EXO = exoccipital; F = frontal; MX = maxilla; P = parietal; PAL = palatine; PFR = prefrontal; PMX = premaxilla; PO = postorbital; PRO = prootic; PSP = parasphenoid rostrum; PT = pterygoid; Q = quadrate; SMX = septomaxilla; ST = supratemporal; V = vomer.

anterolaterally with an oblique straight suture, exoccipitals posterolaterally with an oblique straight suture, and forms ventral border of foramen magnum posteriorly; it is anteroventrally overlapped by pterygoids (DHMECN 16725) or remains slightly separated from them (DHMECN 15893); a short slit-like depression is absent (DHMECN 16725) or located centrally on anterior margin of basioccipital (DHMECN 15893).

Parasphenoid and basisphenoid are fused to form an elongate parabasisphenoid that is about twice as long as wide, with its widest part at contact zone of parietal and prootics; parasphenoid rostrum intervenes ventrally between vertical laminae of frontals and is very narrow and long, with a pointed tip that ends anteriorly well in front of anterior margin of frontals; parasphenoid rostrum laterally contacts (right palatine of DHMECN 15893) or not (DHMECN 16725, left palatine of DHMECN 15893) choanal process of palatine, and does not contact nasals, vomers or septomaxillae; parasphenoid rostrum exhibits a lateral groove at its base on each side; parabasisphenoid contacts parietal laterally, prootics posterolaterally and basioccipital posteriorly; on each side of basisphenoid at about midpoint of suture with prootic, there is a short elongated groove directed perpendicular to suture, which continues approximately with same length on prootic.

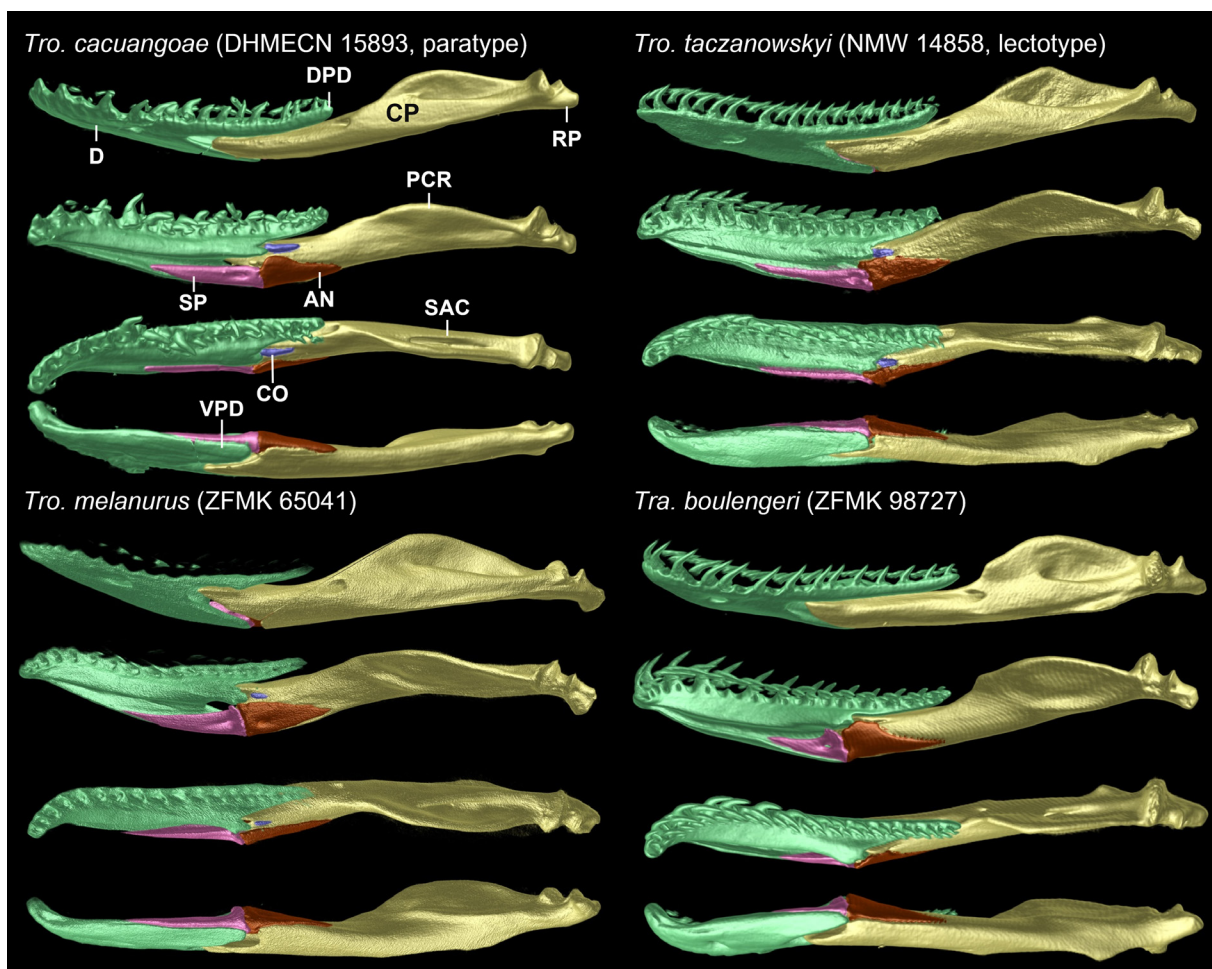
Maxillae are long, account for 45% (DHMECN 16725) to 46% (DHMECN 15893) of skull length, and are about 8 (DHMECN 15893) to 9.8 (DHMECN 16725) times as long as high, with the highest point located at about the level of the fourth tooth; each extending from level of anterior end of vomer to posterior border of postorbital; posterior half forming major part of lower lateral margin of orbit; anteriorly, slightly curved towards premaxilla; ventral surface of maxilla bears 18–21 tooth loci; teeth are slightly higher in anterior region, curved, and rear-facing; a moderately long, subrectangular palatine process is located at about mid-region of maxilla at level between 9<sup>th</sup> and 12<sup>th</sup> tooth, facing posteromedially and slightly curved in ventral direction; a short, knob-like medially oriented ectopterygoid process is located at level of the penultimate and antepenultimate teeth, slightly anterior to anterior tip of medial process of ectopterygoid; each maxilla contacts prefrontal dorsally at two locations both just anterior to and at level of palatine process, maxillary process of palatine dorsomedially by means of palatine process, and lateral process of ectopterygoid posteriorly.

Ectopterygoids are elongate, 5.5 (DHMECN 16725) to 5.6 (DHMECN 15893) times as long as wide, with widest point at level of medial process, approximately axe-shaped in dorsal view; lateral and medial processes are almost indistinguishable, posterior process is long, very narrow, and rod-shaped; in dorsal view, only anterior region of ectopterygoid is visible; each ectopterygoid contacts dorsoposterior end of maxilla with its lateral process, dorsal surface of middle region of pterygoid with posterior half (DHMECN 15893) or one-third (DHMECN 16725) of its posterior process, and it touches (DHMECN 15893) or not (DHMECN 16725) ventral end of postorbital with its lateral process at level of contact point with maxilla.

Palatines are robust, almost straight in ventral view, and account for just under one-third of skull length, each has a moderately long, posterolaterally oriented maxillary process, located about mid-length at level of 5<sup>th</sup> (DHMECN 15893) or 6<sup>th</sup> (DHMECN 16725) tooth, and a very large and broad choanal process, extending from about level of maxillary process to posterior end of palatine; choanal processes of both palatines approach each other to a very short distance; ventral surface with 7–9 tooth loci; teeth about similar in size, curved, and rear-facing; maxillary process contacts (DHMECN 15893) or not (DHMECN 16725) palatine process of maxilla ventrally and touches prefrontal dorsally; choanal process contacts posterior region of vomer medially at its anterior region, and touches (right palatine of DHMECN 15893) or not (DHMECN 16725, left palatine of DHMECN 15893) parasphenoid rostrum dorsally; posteriorly, palatine contacts anterior region of pterygoid; in dorsal view, maxillary processes are the only visible part of palatines.

Pterygoids are elongate, and account for about 60% of skull length; ventral surface bears 11–13 tooth loci; teeth subequal, slightly decreasing in size posteriorly, curved, and rear-facing; each pterygoid is narrowed in anterior part up to level of 8<sup>th</sup> to 11<sup>th</sup> tooth and then broadens abruptly at level of contact zone with ectopterygoid, about last quarter tapers sharply and is posterolaterally oriented; anterior region is dorsally overlain by posterior portion of palatine; pterygoids are slightly (DHMECN 16725) or moderately (DHMECN 15893) curved along tooth line, and have the greatest distance from each other at their posterior ends; posterior end of pterygoid approaches medially ventromedial process of quadrate without touching it; apart from palatine and ectopterygoid, pterygoid touches basioccipital (DHMECN 16725) or remains separated from it (DHMECN 15893); dorsal surface behind tooth line is concavely curved; in dorsal view, pterygoids are hardly visible, being mainly covered by roofing skull bones.

Supratemporals are laminar, elongate, and broad, about 2.3 (DHMECN 15893) to 2.6 (DHMECN 16725) times as long as wide, and exhibit their greatest width at about level of contact zone of prootic and



**Fig. 13.** Micro-CT images of the right mandibula of *Tropidophis cacuangoae* sp. nov., ♀ (DHMECN 15893, paratype), *T. taczanowskyi* (Steindachner, 1880) (NMW 14858, lectotype), *T. melanurus* (Schlegel, 1837) (ZFMK 65041), and *Trachyboa boulengeri* Peracca, 1910 (ZFMK 98727) in lateral, medial, dorsal, and ventral views (from top to bottom). Different bones are digitally colored for better visualization. Abbreviations: AN = angular; CO = coronoid; CP = compound bone; D = dentary; DPD = dorsal process of dentary; PCR = prearticular crest of compound bone; RP = retroarticular process of compound bone; SAC = surangular crest of compound bone; SP = splenial; VPD = ventral process of dentary.

exoccipital; anterior half of each supratemporal overlaps and firmly attaches to prootic, ending well before suture of prootic with parietal; anterior portion of posterior half overlies anterolateral portion of exoccipital, while most of posterior half extends freely and surpasses exoccipital and quadrate posteriorly, forming caudal margin of skull; supratemporal overlaps supraoccipital medially and approaches quadrate with its posterolateral surface, but remains slightly separated from it.

Quadrates are flattened and broad dorsally, about 1.4 times as high as long, oriented vertically and obliquely from anterodorsal to posteroventral, and tapering dorsoventrally in lateral view; no short process is visible in medial part; ventral part is slightly bifurcated and spans glenoid cavity of retroarticular process of compound bone; quadrate does not exceed posterior limit of skull roof.

Each mandible consists of dentary, splenial, angular, compound bone, and a tiny coronoid; in dorsal view, it is almost completely straight, except for anterior third of dentary, which is curved medially (Fig. 13).

Dentaries are elongate, account for about 55% of lengths of mandibula; dorsal surface of each dentary bears 22–25 tooth loci; teeth are subequal, curved, rear-facing, and slightly decreasing in size posteriorly; elongate mental foramen is located at about level of 9<sup>th</sup> or 10<sup>th</sup> tooth; at about level of 13<sup>th</sup> (DHMECN 15893) or 15<sup>th</sup> (DHMECN 16725) tooth, dentary branches into a long, slender, toothed dorsal process that overlies compound bone and contacts or not coronoid medially, and a ventromedial process about half as long or even shorter that is in contact with splenial for almost its entire length, and loosely connected to anterior portion of compound bone; at level of 16<sup>th</sup> (DHMECN 15893) or 19<sup>th</sup> (DHMECN 16725) tooth, dorsal process branches again into a tiny knob-like medial process and a much longer tooth-bearing dorsal process; inner surface bears a long groove in extension to depression for splenial, which extends anteriorly to level of 2<sup>nd</sup> tooth.

Coronoids are tiny, elongate, about 4.5 times as long as high, and by far the smallest bones of the mandibles; each contacts dentary anteriorly and dorsolaterally or remains slightly separated from dentary, compound bone laterally, and angular ventrally (DHMECN 16725) or remains slightly separated from it (DHMECN 15893).

Splenials are elongate, triangular, tapering anteriorly to a sharp tip, 1.6 (DHMECN 16725; due to posterior dorsal extension) or 5.5 (DHMECN 15893) times as long as high, with (DHMECN 16725) or without (DHMECN 15893) a dorsal extension at posterior end; anterior mylohyoid foramen is present in posterior region; each extends medially along dentary between 10<sup>th</sup> and 17<sup>th</sup> tooth (DHMECN 15893) or between 13<sup>th</sup> and 20<sup>th</sup> tooth (DHMECN 16725), and posteriorly contacts anterior region of angular, and has a minimal contact point with compound bone.

Angulars are elongate, triangular, tapering posteriorly to a blunt (DHMECN 15893) or pointed (DHMECN 16725) tip, and about twice (DHMECN 16725) or 3 times (DHMECN 15893) as long as high, accounting for 77% (DHMECN 15893) to 80% (DHMECN 16725) of length of splenial; each angular contacts compound bone laterally and dorsally, splenial anteriorly, and touches (DHMECN 16725) or not (DHMECN 15893) coronoid anterodorsally; a posterior mylohyoid foramen is absent (DHMECN 15893) or slightly indicated (DHMECN 16725).

Compound bones are elongate, about 6.4 times as long as high, and account for about two-thirds of length of mandible; each attaches to dentary at level of 14<sup>th</sup> (DHMECN 15893) or 16<sup>th</sup> (DHMECN 16725) tooth, and in lateral view its anteriorly tapering rostral end extends between dorsal and ventromedial processes of dentary; medial prearticular crest is prominent, completely visible in lateral view, much higher than surangular crest, the latter not visible in medial view; anteriorly oriented foramen is located at or just behind point where posterior tip of toothed dorsal process of dentary meets compound bone; mandibular fossa is deep, elongate, narrow, dorsolaterally oriented and visible in lateral view; articular part, where

**Table 2.** Morphological comparisons among mainland *Tropidophis* Bibron, 1840 of South America. Diagnostic characters of *Tropidophis cacuangoae* sp. nov. are highlighted in bold. Supporting data from Curcio *et al.* 2012 are indicated with an asterisk (\*). Species with confirmed records from the Andes mountain range are indicated with a dagger (†).

	<i>Tro. cacuangoae</i> sp. nov. †	<i>Tro. battersbyi</i>	<i>Tro. taczanowksyi</i> * †	<i>Tro. grapiuna</i> *	<i>Tro. paucisquamis</i> *	<i>Tro. preciosus</i> *
Dorsals	<b>23/22/17</b> (n = 1) or <b>22/23/17</b> (n = 1)	21/23/17 (n = 1)	23/23/21 (n = 7), 25/23/21 (n = 4), or 23/23/19 (n = 2)	23/23/19 (n = 1)	16/21/15 (n = 1), 21/21/15 (n = 12), 21/21/16 (n = 3), 21/21/17 (n = 2), 21/23/17 (n = 2), 23/23/16 (n = 2), 23/23/17 (n = 14), 23/23/18 (n = 1), 23/23/19 (n = 3)	23/23/17 (n = 1)
Keels	<b>present, small or indistinct</b>	absent	present, conspicuous	present	absent or indistinct	absent
Ventrals	162 (♂) (n = 1); 156 (♀) (n = 1)	200 (♂) (n = 1)	148–160 (♂) (n = 4); 146–156 (♀) (n = 9)	154–155 (♀) (n = 2)	164–178 (♂) (n = 20); 167–183 (♀) (n = 30)	196–203 (♀) (n = 2)
Rostral scale	present, entire	present, entire	present, entire	present, entire	present, entire	present, entire
Temporals	<b>3 + 4 + 3</b> (n = 1) or <b>2 + 3 + 3</b> (n = 1)	3 + 4 (n = 1)	2 + 3 (n = 13)	2 + 3 (n = 2)	2 + 3 (n = 8)	2 + 3 (n = 2)
Subcaudals	33 (♂) (n = 1); 30 (♀) (n = 1)	41 (♂) (n = 1)	25–33 (♂) (n = 9); 23–27 (♀) (n = 4)	26–30 (♀) (n = 2)	29–38 (♂) (n = 19); 30–37 (♀) (n = 29)	27 (♀) (n = 1)
Supralabials	8–10 (n = 2)	11 (n = 1)	8–11 (n = 13)	10–11 (n = 2)	8–10 (n = 12)	9–10 (n = 1)
Infralabials	9–10 (n = 2)	11 (n = 1)	9–11 (n = 13)	11–12 (n = 2)	8–11 (n = 12)	11–12 (n = 2)
Dorsal pattern	<b>uniformly light brown,</b> <b>small diffuse brown spots</b>	large dark brown spots over a light gray background	striped-spotted, lateral orange stripes over a dark brown background	small dark brown spots over a dark brown background	small dark brown spots over a dark brown background, vertebral light brown stripe	irregular dark brown blotches over a dark brown background
Ventral pattern	<b>large black blotches on an orange background</b>	alternating black elliptical blotches	alternating black squares on a white background	alternating black elliptical blotches	large black elliptical blotches on an orange background	alternating large black squares
Eyelashes	absent	absent	absent	absent	absent	absent
Parietal contact	<b>in contact</b>	separated	usually separated	separated	in contact	in contact
Interparietals	<b>absent or small</b>	present, conspicuous	present, conspicuous	present, conspicuous	usually absent	absent
Maximum SVL (mm)	320 (♂), 255 (♀)	299 (♂)	335 (♂), 348 (♀)	289 (♀)	336 (♂), 357 (♀)	449 (♀)
Geographic distribution	Northeastern Ecuador	Ecuador, but likely from Greater Antilles	Southeastern Ecuador and Northeastern Peru.	Northeastern Brazil	Southeastern Brazil	Southeastern Brazil



it is joined to quadrate, has a deep, saddle-shaped notch; retroarticular process is short, slightly directed medially, and does not extend beyond posterior end of exoccipital in dorsal view.

### Comparisons

Characteristics from other species are presented in parentheses in this section. Comparisons are restricted to mainland tropidophiid species (*sensu* Curcio *et al.* 2012). An overview of morphological comparisons can be seen in Table 2. In its geographic range, *Tropidophis cacuangoae* sp. nov. might only be confused with another andine amerophid, *Tropidophis taczanowskyi* (Steindachner, 1880) (Figs 14–16), which occurs in Ecuador and Peru. Both species share a small-sized and stout body, and similar counts of ventrals, subcaudals, supralabials, and infralabials. However, there are striking differences between these species. The dorsal scales of *Tro. cacuangoae* sp. nov. have lower counts for the anterior and posterior rows, ranging from 22/23/17 to 23/22/17 (23/23/21, 23/23/19, 25/23/21 in *Tro. taczanowskyi*), and are also mostly smooth, with small or indistinct keels (conspicuously keeled in *Tro. taczanowskyi*). The new species also has different temporal scale formulae, ranging from 2 + 3 + 3 to 3 + 4 + 3 (2 + 3 in *Tro. taczanowskyi*), and absent or small interparietals (present in *Tro. taczanowskyi*), vertebral row enlarged (not enlarged in *Tro. taczanowskyi*), retaining contact between both parietals (usually absent in *Tro. taczanowskyi*). Furthermore, these two species also have significant differences in coloration and pattern, as *Tro. cacuangoae* sp. nov. has a dorsal pattern uniformly light brown, with small diffuse



**Fig. 14.** Dorsal view of *Tropidophis taczanowskyi* (Steindachner, 1880) from Ecuador. Notice its conspicuously keeled dorsal scales and dorsolateral stripes. Photograph credit: Alejandro Arteaga.

brown spots (striped-spotted, lateral orange stripes over a dark brown background in *Tro. taczanowskyi*), a prefrontal and maxilla bone contact present (absent in *Tro. taczanowskyi*), a dentary and angular bone contact present (absent in *Tro. taczanowskyi*), medial contact of exoccipitals loose (firm in *Tro. taczanowskyi*), a small premaxilla body ventral ethmoidal foramen (large in *Tro. taczanowskyi*), postorbital dorsomedial head divided in two heads (undivided in *Tro. taczanowskyi*), vomer further expanded laterally to completely encapsulate vomeronasal organ posteriorly (with margins enclosing posterior wall sloping ventrolaterally in *Tro. taczanowskyi*), fenestra ovalis oriented posterolaterally (fenestra ovalis opens ventrolaterally in *Tro. taczanowskyi*), frontal descending process abuts parietal (parietal overlaps frontal laterally in *Tro. taczanowskyi*), and ventral pattern with large black blotches on an orange background (alternating black squares on a white background in *Tro. taczanowskyi*).

Another tropidophiid species reported from the Andes range is *Tropidophis battersbyi* Laurent, 1949. This species was described based on a specimen received by The Royal Museum of Natural History in Brussels in 1874–1875, from an unknown locality in Ecuador. The species is known solely based on its holotype,



**Fig. 15.** Lectotype of *Tropidophis taczanowskyi* (Steindachner, 1880) (NMW 14858) from Tambillo, Peru. Note its conspicuous keeled dorsal scales and striped dorsolateral pattern. Photograph credit: Georg Gassner.

and no other available information has surfaced. Díaz & Cádiz (2020) highlight that *Tro. battersbyi* likely represents a labeling error, and could not be diagnosed from two Antillean taxa, *Tropidophis spiritus* Hedges & Garrido, 1999 and *Tropidophis morenoi* Hedges, Garrido & Diaz, 2001. Nonetheless, *Tro. cacuangoae* sp. nov. can be readily distinguished from *Tro. battersbyi* based on its uniformly light brown coloration pattern (large dark brown spots over a light gray background in *Tro. battersbyi*), its lower ventral scale counts, which range from 156 to 162 (200 in *Tro. battersbyi*), and lower subcaudal counts, which range from 30 to 33 (41 in *Tro. battersbyi*).



**Fig. 16.** Distinction in dorsal keel character states, well developed in *Tropidophis taczanowskyi* (Steindachner, 1880) (top, DHMECN 16391), and inconspicuous or absent in *Tropidophis cacuangoae* sp. nov. (bottom, DHMECN 16725).

The genus *Trachyboa* contains two species, *Trachyboa gularis* Peters, 1860 and *Trachyboa boulengeri* Peracca, 1910, that also occur in Ecuador, and might be confused with the new species. These are also stout bodied, brown colored, small-sized snakes. However, *Tropidophis cacuangoae* sp. nov. is readily distinguished from these species in having mostly smooth or weakly keeled dorsal scales (rugous and keeled in *Tra. gularis* and *Tra. boulengeri*), a large and entire rostral plate (absent or fragmented into small scales in *Tra. gularis* and *Tra. boulengeri*), a single preocular (fragmented in a circular row of up to 14 ocular scales in *Tra. gularis* and *Tra. boulengeri*), and for lacking horn-like supraocular projections (present in *Tra. boulengeri*). However, both species of *Trachyboa* occur west of the Andes, while *Tropidophis cacuangoae* occurs east of the Andes.

Within mainland South America, there are three other extralimital species of *Tropidophis*: *Tropidophis paucisquamis* (Müller in Schenkel, 1901) (Fig. 17), *Tropidophis grapiuna* Curcio, Nunes, Argôlo, Skuk & Rodrigues, 2012, and *Tropidophis preciosus* Curcio, Nunes, Argôlo, Skuk & Rodrigues, 2012. These three species are largely allopatric between each other, and restricted to the Atlantic Forest highlands in southern, southeastern, and northeastern Brazil. The dorsal coloration of *Tro. cacuangoae* sp. nov. resembles that of *Tro. paucisquamis*, differing in having a uniformly colored dorsum (small dark brown spots over a dark brown background, vertebral light brown stripe in *Tro. paucisquamis*), and this species is furthermore distinguished by its lower ventral counts, which range from 156 to 162 (164–178 in males, 167–183 in females of *Tro. paucisquamis*). The new species can be readily distinguished from *Tro. grapiuna* and *Tro. preciosus* based on its distinct, uniformly colored dorsal pattern (dark brown with black spots in both species), lower ventral counts, which range from 156 to 162 (196–203 in females of *Tro. preciosus*), and lower infralabial counts, which range from 8 to 10 (11–12 in *Tro. preciosus* and *Tro. grapiuna*).

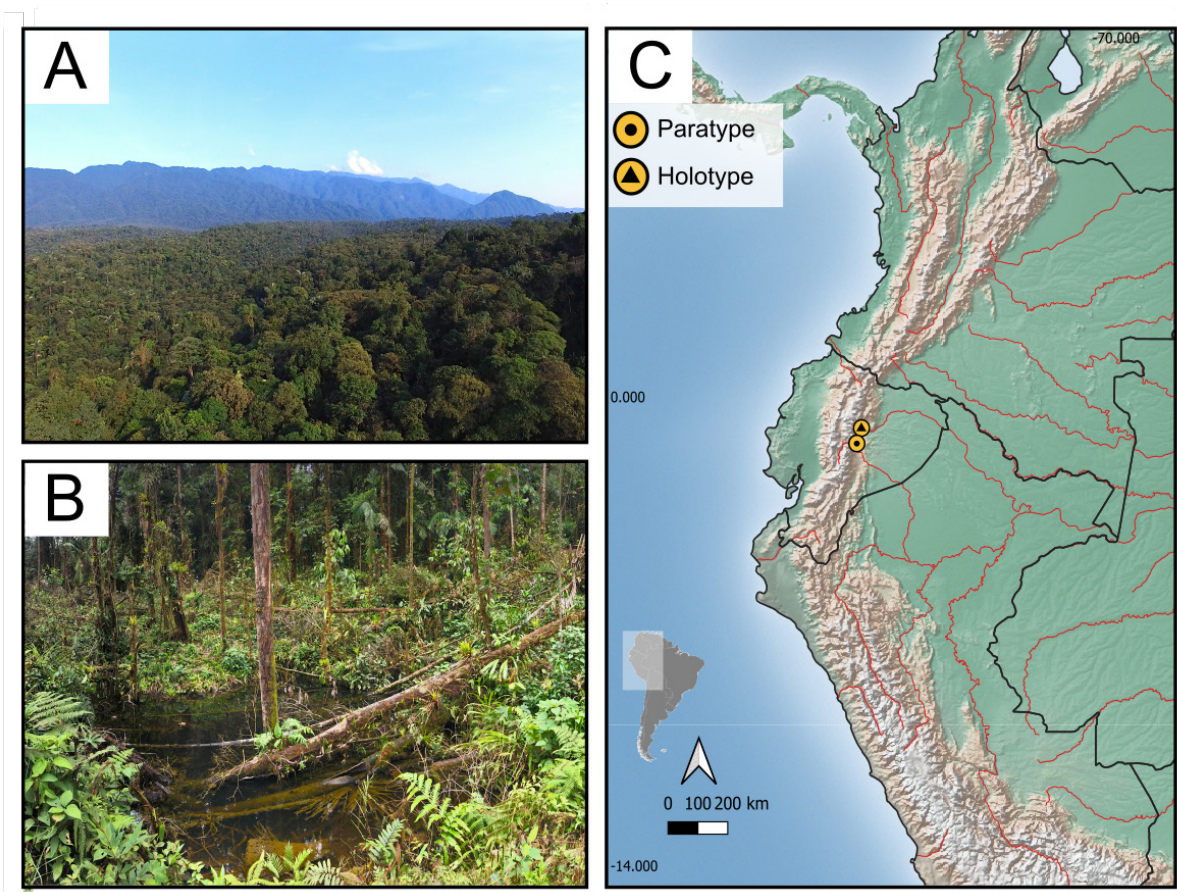


**Fig. 17.** An extralimital tropidophiid from mainland South America, *Tropidophis paucisquamis* (Müller in Schenkel, 1901), from Ubatuba, São Paulo, Brazil. Photograph credit: Edelcio Muscat.

### Geographic distribution and natural history

Currently, two verified specimens of *T. cacuangoae* sp. nov. are known from Ecuador, one (DHMECN 16725) from Reserva Biológica Colonso Chalupas, Campamento 2 (0.93370° N, 77.92239° W), San Juan de Muyuna Municipality, 1613 m altitude, Napo Province, and the other (DHMECN 15893) from Sumak Kawsay In Situ reserve (1.3930470° N, 78.0686059° W), Mera County, 1481 m altitude, Pastaza Province (Fig. 18). Another specimen is similar to *T. cacuangoae* sp. nov. (DHMECN 16126), from Guayzimi, Nangaritza Municipality, in Zamora-Chinchipe Province, Ecuador, and recognized herein as ‘Unconfirmed Candidate Species 1’ (*Tropidophis cf. cacuangoae*). The new species inhabits primary Eastern Piedmont Evergreen and Evergreen Low Montane forests, under the Amazon Rainforest biome, in Napo and Pastaza provinces, at an altitude range of 1481–1613 m above sea level.

The holotype was collected active during the night (23:36 hours), found in the leaf litter, in Evergreen Low Montane Forest. The paratype was collected during the morning (10:00 hours), found coiled between two wooden boards, on the edge of primary Eastern Piedmont Evergreen Forest. Upon being handled, the specimen did not attempt to bite, and engaged in ‘balling’ behavior, cloacal discharges and hiding head between body coils. After being handled, the paratype specimen also engaged in autohemorrhaging of the eyes.



**Fig. 18.** Habitat and geographic range of *Tropidophis cacuangoae* sp. nov. **A.** Overview of Eastern Piedmont Evergreen Forest habitat. **B.** Collection site of *T. cacuangoae* sp. nov. paratype (DHMECN 15893). **C.** Geographic distribution of *T. cacuangoae* sp. nov. in Ecuador.

### Dichotomous key for *Tropidophis* on mainland South America

(\* = Species likely not from mainland South America) († = Species with confirmed records from the Andes mountain range)

1. Dorsal rows conspicuously keeled, interparietals present, lateral stripes present .....  
.....*T. taczanowskyi* (Steindachner, 1880) †  
– Not as above ..... 2
2. Dorsal pattern with large spots, > 40 subcaudals, > 200 ventrals ..... *T. battersbyi* Laurent, 1949\*  
– Dorsal pattern with small spots, < 40 subcaudals, usually < 200 ventrals ..... 3
3. Contact between parietals present ..... 4  
– Contact between parietals absent ..... *T. grapiuna* Curcio *et al.*, 2012
4. Subcaudals fewer than 30 ..... *T. preciosus* Curcio *et al.*, 2012  
– Subcaudals higher than 30 ..... 5
5. Ventrals in males 164–178, in females 167–183, body spots in six rows, bright colored tail .....  
..... *T. paucisquamis* (Müller in Schenkel, 1901)  
– Ventrals in the single male 162, in the single female 156, body spots not in rows, tail uniformly colored ..... *T. cacuangoae* sp. nov. †

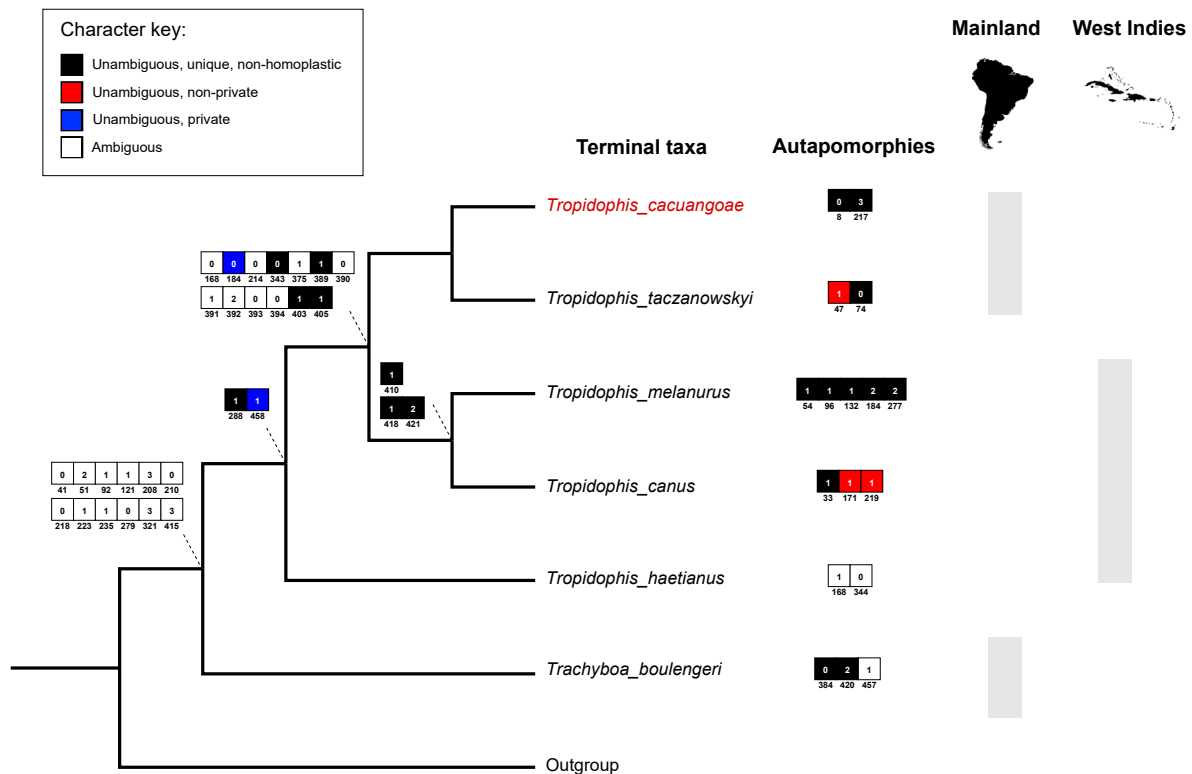
### Discussion

The description of *Tropidophis cacuangoae* sp. nov. raises the number of valid tropidophiid species to 34, and that of mainland species of *Tropidophis* in South America to six. Mainland species of *Tropidophis* have a particularly interesting disjunct distribution pattern, in which three species (*T. grapiuna*, *T. paucisquamis*, and *T. preciosus*) occur in the tropical Atlantic Rainforest highlands of Brazil, while another three (*T. battersbyi*, *T. cacuangoae* sp. nov., and *T. taczanowskyi*) occur in the Andes mountain range, in tropical montane Amazon Rainforests of Ecuador and Peru, separated by approximately 4000 km in a straight line (Fig. 1). Likewise, both groups appear to be associated with moderately cold tropical climates at high altitudes. Although the Amazon and Atlantic rainforests are currently separated by a wide Dry Diagonal of open biomes, there is growing evidence, based on comparative animal phylogeography, geological, and paleontological data, that these two biomes were historically connected (Wang *et al.* 2004; Batalha-Filho *et al.* 2013; Ledo & Colli 2017). However, since sequences of Brazilian species of *Tropidophis* are still unavailable, it is not possible to infer an estimation of divergence time between these two allopatric groups.

The new species appears to be most morphologically similar to *T. taczanowskyi*, which is known from five localities that range from southern Ecuador to eastern Peru (Curcio *et al.* 2012). Both species share similarities in external morphology, such as a small body size and overlapping scale counts of ventrals and subcaudals. In the morphological phylogeny, these species are also recovered in a clade, supported by a present retroarticular process, with lateral notch forming waist proximally, and a 7–15 maxillary teeth count. Notably, the distinctive dorsal scale keels of *T. taczanowskyi* appear to be an unique feature of this species and of *T. grapiuna*, seemingly absent or feeble in all other mainland congeners. However, both species also have differential autapomorphic characters (Fig. 19). Both *T. taczanowskyi* and *T. cacuangoae* sp. nov. are significantly different from their other congener, *T. battersbyi*, which is known based on a single specimen, putatively from Ecuador. Recently, Díaz & Cádiz (2020) argued that this was likely a labeling error based on an old specimen of uncertain provenance, and that *T. battersbyi* should rather be an Antillean specimen. The high counts of ventrals and subcaudals of *T. battersbyi*, added to its dorsal pattern that is remarkably similar to that of other Antillean species (e.g., *T. spiritus* and *T. morenoi*), and

the lack of records with a verified location on the mainland since its collection in the early 19<sup>th</sup> century, are growing evidence that this species needs to have its taxonomic status reassessed.

Notably, the phylogenetic relationships of amerophid genera remain uncertain. The multi-locus phylogenetic inference of Reynolds *et al.* (2014) recovered a paraphyletic relationship between *Trachyboa* and *Tropidophis*, with *T. taczanowskyi* as a sister-group to a stem *Trachyboa* and a crown of remaining *Tropidophis* terminals. Those authors also recovered a poorly supported relationship between Aniliidae and Tropidophiidae. Nonetheless, the small sampling of *Tropidophis* species (eight taxa) and small support for the terminals in this topology (bootstrap support > 50%, posterior probability > 0.95) in the work of Reynolds *et al.* (2014) precludes any further changes to the higher-level relationships of these species. Furthermore, this issue is also complicated by the absence of generic diagnoses for *Tropidophis* and *Trachyboa*; while these two groups have mostly been separated by characters associated with the unique head pholidosis of *Trachyboa*, which has the preocular and postocular fragmented into a single circular row, rugous and keeled dorsals, and an absent or fragmented rostral, these characters might be reinterpreted considering a possibly paraphyletic relationship between these two genera. However, our molecular and morphological phylogenies recover *Trachyboa* as a sister group to other *Tropidophis* terminals (*T. cacuangoae* sp. nov., *T. canus*, *T. haetianus*, *T. melanurus*, *T. taczanowskyi*) and Aniliidae nested outside Macrostromata. The putative morphological synapomorphy between Aniliidae and Tropidophiidae, namely, the oviduct connecting to the cloacal diverticuli instead of directly with the cloaca, could not



**Fig. 19.** Parsimony-based morphological character optimization over molecular phylogenetic tree of sampled species of Tropidophiidae Brongersma, 1951, as inferred with YBYRÁ software, and occurrence of species in South America and the West Indies. Left: Nodes are labeled with unambiguously optimized morphological synapomorphic characters (black square = unique, non-homoplasic; red square = non-unique, homoplasic; blue square = unique, homoplasic; character number = value below or above squares; derived character-states = value inside squares). Right: Geographic distribution of sampled terminals of Tropidophiidae.

be directly assessed for all other species in our morphological matrix and is therefore not included. The position of *T. haetianus*, as a sister species to other Antillean and Mainland *Tropidophis*, is also doubtful and likely to be changed upon the addition of more terminals; it is also not supported by the molecular topology. It should be noted that these conflicting relationships are expected considering both the small sample of molecular data and of morphological terminals; in light of this, these relationships should only be seen as provisional, and should be further evaluated with the integration of more terminals and phylogenomic data. It should also be noted that small uncorrected p-distances, patristic distances, and the grouping of different species in the coalescent-based species delimitation analyses are possibly related to the use of a slow-evolving nuclear marker. Further studies using concatenated datasets of mitochondrial and nuclear gene fragments are needed in order to verify gene flow and reciprocal monophyly of these species.

Some putative synapomorphies of Tropidophiidae and of the clade composed by Tropidophiidae and Caenophidia, as outlined by Gauthier *et al.* (2014), are also reinterpreted here by the inclusion of more terminals. Our morphological evidence provides support against the recognition of the posterior extension of the maxilla suborbital ramus, posterior extent of maxillary teeth rows, and dentary teeth count as synapomorphic characters of Tropidophiidae. As for the clade composed by Tropidophiidae and Caenophidia, we uncovered variation for the narrow contact of the nasal dorsal lamina with the frontal, division of dorsomedial head of the postorbital, and parietal-supraoccipital contact.

The new species is known solely based on two verified specimens, and both localities are approximately 50 km apart, which makes it likely to be endemic to Ecuador. Taking in consideration its small geographic range and records restricted to primary rainforests, we argue that *T. cacuangoae* sp. nov. should be considered as a candidate for threatened species status, and further assessments of its conservation and population trends are necessary. Additional data are needed to test the taxonomic status of the specimen from Zamora province, which might represent another undescribed species, or rather the southernmost range limit for *T. cacuangoae* sp. nov. Our unconfirmed candidate species (DHMECN 16726) also likely represents an undescribed species, known from a single specimen collected in the Andes of southern Ecuador; based on morphology, this specimen cannot be assigned with certainty to *T. cacuangoae* (considering the specimen has a uniformly dark dorsum) or *T. taczanowskyi* (considering the specimen lacks dorsal keels), and its identity is currently being evaluated by the authors of this paper. However, its small sample size precludes us from determining its taxonomic identity at the moment, as it could possibly represent a hybrid or aberrant specimen. Furthermore, we also highlight the need for a wide taxonomic and systematic revision of amorphid genera in order to solve potential nomenclatural issues raised by the paraphyletic nature of its genera. The discovery of this new species highlights an important need to accelerate research in remote areas where information gaps remain, but are suspected to harbor high biodiversity and are severely threatened by human impacts as currently occurs in the Llanganates-Sangay Ecological Corridor and the Reserva Biológica Colonso Chalupas (Simpson *et al.* 2013; Bentley *et al.* 2021; Ortega-Andrade *et al.* 2021). The discovery of *T. cacuangoae* demonstrates that small and cryptic vertebrates can undergo large periods of time without being detected and formally described by science, and as shown by our unconfirmed candidate new species of *Tropidophis*, there is still much to be uncovered.

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### Supplementary files

**Supp. file 1.** Accession number for gene fragments used in the molecular analysis (.xls).

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**Supp. file 2.** Alignment of *Neurotrophin-3* [NTF3] gene fragments for selected snake species (.nexus).

<https://doi.org/10.5852/ejt.2022.854.2021.8303>

**Supp. file 3.** Verified point records of *Tropidophis* from Mainland South America (.xls).

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**Supp. file 4.** RAxML Maximum Likelihood analysis output (.zip).

<https://doi.org/10.5852/ejt.2022.854.2021.8307>

**Supp. file 5.** Maximum Likelihood inference topology (.pdf).

<https://doi.org/10.5852/ejt.2022.854.2021.8309>

**Appendix 1.** Additional material examined

*Anilius scytale* (Linnaeus, 1758) (n = 2)

BRAZIL – **PARÁ** • Santarém; MCP 8890 • Itaituba; MCP 4454.

*Trachyboa boulengeri* Peracca, 1910 (n = 1)

ECUADOR • Santo Domingo De Los Tsáchilas, La Florida, 5 km E; ZFMK 98727.

*Tropidophis battersbyi* Laurent, 1949 (n = 1)

ECUADOR • holotype; Unknown locality (likely in error); RBINS 3701.

*Tropidophis grapiuna* Curcio *et al.*, 2012 (n = 1)

BRAZIL – **Bahia** • holotype; Pedra Lascada range, Barro Preto Municipality; MNRJ 19593.

*Tropidophis melanurus* (Schlegel, 1837) (n = 1)

CUBA • Pinar Del Río, Viñales; ZFMK 65041.

*Tropidophis paucisquamis* (Müller in Schenkel, 1901) (n = 7)

SOUTH AMERICA • holotype of *Ungalia paucisquamis*; unknown locality; NMBA 426.

BRAZIL – **Espírito Santo** • Santa Teresa; USNM 208281. – **Rio De Janeiro** • Teresópolis, Alto do Soberbo; USNM 208666, 166429. – **São Paulo** • Salesópolis, Estação Ecológica Boracéia; USNM 209360, 247873, 243717.

*Tropidophis taczanowskyi* (Steindachner, 1880) (n = 19)

ECUADOR – **Azuay** • Tres Chorreras; QCAZ-R 6224. – **Loja** • unknown locality; DHMECN 16391, 1622 • Unknown locality; QCAZ-R 10039 • San Lucas; KUH 121274 • Yangana; QCAZ-R 6236. – **Morona-Santiago** • Reserva Biológica El Quimi; QCAZ-R 15848. – **Zamora-Chinchipe** • Carretera de Loja a Zamora; QCAZ-R 10868, 10873, 14657 • Fundacion Jocotoco; QCAZ-R 6168–6171, 6198 • Estacion Ecologica San Francisco; QCAZ-R 6832, 6837, 6843.

PERU – **Huamanga** • lectotype of *Ungalia taczanowskyi*; Tambillo; NMW 14858.

## Appendix 2. Morphological Phylogenetic Analysis and NEXUS input file.

State ‘0’ for qualitative characters corresponds to the presumed ancestral condition for Lepidosauria based on its presence among ingroup species as well as a succession of late Paleozoic and early Mesozoic outgroups (e.g. Kuehneosauridae Romer, 1966, *Paliguana whitei* (Broom, 1903), *Saurosternon bainii* (Huxley, 1868), *Prolacerta broomi* Parrington, 1935, *Youngina capensis* Broom, 1914, and *Claudiosaurus germaini* Carroll, 1981). Authorship for characters reflects the first explicit use of a character (or state) as a synapomorphy and matrix follow Gauthier *et al.* (2012). Putative synapomorphies of Tropidophiidae are: 41(0), 51(2), 92(1), 208(3), 210(0), 219(0), 223(1), 235(1), 279(0), 321(3), 337(1), 414(1). Putative synapomorphies of Tropidophiidae + Caenophidia are: 12(3), 91(1), 101(2), 121(1), 189(2), 288(1), 363(2), 389(2), 404(0), 466(1). Ordered characters are indicated in ‘.nexus’ file input below.

1. Premaxilla: (0) paired; (1) fused.
2. Premaxilla palatal shelf: (0) not bifid posteriorly; (1) bifid posteriorly.
3. Premaxilla maxillary process development: (0) normal size; (1) reduced; (2) absent.
4. Premaxilla maxillary process length relative to level of palatine-maxilla suture: (0) premaxilla medial to level of palatinemaxilla suture; (1) premaxilla extends lateral to level of palatine-maxilla suture.
5. Premaxillary-maxillary fenestra: (0) absent; (1) present.
6. Premaxilla body anterior ethmoidal foramina number: (0) two; (1) four or more.
7. Premaxilla body anterior ethmoidal foramina exit via: (0) external naris; (1) premaxilla notch; (2) premaxilla body; (3) between premaxilla and maxilla; (4) in maxilla.
8. Premaxilla body ventral ethmoidal foramen: (0) small; (1) large; (2) absent.
9. Premaxilla-maxilla suture: (0) firm; (1) loose.
10. Premaxilla internasal process length: (0) less than half nasal length; (1) more than half way to frontal between nasals; (2) nearly to, or articulates with, frontal.
11. Premaxilla internasal process shape in cross-section: (0) subtriangular; (1) compressed; (2) depressed.
12. Premaxilla internasal process position relative to nasal descending lamina: (0) premaxilla internasal process lies at level of nasals on skull roof; (1) long internasal process clasped between descending nasal laminae; (2) short overlap between premaxilla and nasal lamina; (3) lamina abuts posteroventral base of premaxilla; (4) loss of nasal descending lamina contact with premaxilla.
13. Premaxilla internasal process shape in anterior view: (0) tapers apically or parallel-sided across nares; (1) widens across nares.
14. Premaxilla internasal process size: (0) well developed; (1) very reduced/absent.
15. Premaxilla internasal process bifid in lateral view, with ancestral dorsal ramus joined by a deeper ventral ramus (premaxillary keel of Lee & Scanlon 2002) extending posteriorly off base of internasal process: (0) absent; (1) present.

16. Premaxilla: (0) without conspicuous vertical margin on maxillary process; (1) with conspicuous vertical margin on maxillary process.
17. Nasals: (0) paired; (1) fused. Species in which the premaxilla internasal process contacts the frontal are scored (?), as nasals bisected by the premaxilla internasal process overprint both of the conditions described in the character and prevent the scoring of either condition.
18. Nasals anterior width: (0) exceeds nasofrontal joint width; (1) is subequal to nasofrontal joint width; (2) less than anterior frontal width. In snakes with kinetic nasofrontal joints, comparison is between the anterior width of the nasals vs the anterior width of the frontals.
19. Nasal-prefrontal suture: (0) present; (1) absent.
20. Nasal-maxilla suture: (0) present; (1) absent.
21. Nasal descending lamina: (0) absent; (1) present, with descending lamina extending below level of nasal-maxilla suture.
22. Nasal supranarial process in dorsal view: (0) well-developed; (1) reduced/absent.
23. Nasal-maxilla suture in cross section anteriorly: (0) maxilla overlaps nasal at roof of nasal chamber; (1) nasal partly overlaps maxilla dorsally; (2) nasal abuts maxilla; (3) nasal underlaps maxilla to floor of narial chamber.
24. Nasals ventral contact beneath premaxillary internasal process: (0) broad contact below; (1) not in contact except near apex.
25. Nasals dorsal contact over premaxilla internasal process: (0) no contact; (1) in contact over apex; (2) broadly in contact.
26. Nasals reduced to narrowly elliptic elements attached to either side of premaxilla internasal process: (0) absent; (1) present.
27. Nasal shape: (0) not small and cruciform; (1) small and cruciform.
28. Nasal length relative to frontal length: (0) nasals shorter than frontals; (1) nasals longer than frontals.
29. Nasal anterior extent toward premaxilla: (0) nasal extends anterior to maxillary tooth row or vomer; (1) nasal terminates posterior to end of maxillary tooth row or vomer tip.
30. Nasofrontal fontanelle: (0) absent, frontal and nasal firmly sutured; (1) present, poorly ossified suture between nasal and frontal on midline. This character, like virtually all others in this analysis, is scored in adult individuals. A 'fontanelle' of sorts in this position may be present in incompletely ossified juveniles.
31. Nasofrontal suture shape: (0) without V-shaped nasal process into frontal midline; (1) with prominent V-shaped nasal process into frontal midline.
32. Nasal-frontal articulation dorsally: (0) nasals suture in two V-shaped recesses of anterodorsal end of frontal; (1) nasals overlap only onto narrow horizontal shelf dorsally on frontals.

33. Nasal dorsal lamina: (0) in broad contact with dorsal frontal lamina; (1) in narrow (medial, point-) contact with frontal; (2) not in contact with frontal.
34. Nasal medial (vertical) flange: (0) in extensive dorsoventral contact with medial frontal flange; (1) in dorsal contact only; (2) in ventral contact only; (3) not in contact with frontal.
35. Nasal medial (vertical) flange, ventral contact with frontal: (0) abutting; (1) reduced to point contact. Character 34(2) correlates with 35(1) in that the ‘point contact’ is always ‘ventral’. However, because ‘ventral contact’ 34(2) can be either ‘abutting’ 35(0) or a ‘point contact’ 35(1), they are treated separately.
36. Frontals: (0) paired; (1) fused.
37. Frontal-maxilla suture: (0) frontal separated from maxilla by nasal-prefrontal contact; (1) frontal contacts maxilla, separating nasal from prefrontal.
38. Frontal subolfactory processes: (0) absent; (1) arch beneath brain but do not contact; (2) arch beneath brain to articulate on ventral midline; (3) arch beneath brain and fuse on the ventral midline.
39. Frontal subolfactory process depth: (0) 25–35%; (1) 42–53%; (2) 58–68%; (3) 75–85%; (4) more than 89%. The ventral depth of frontal subolfactory process is inferred by measured CT cross-sections from the maximum ventral limit of the subolfactory process to the dorsal surface of the palatine, then divided by the distance from the dorsal surface of the frontal (sans any overlying osteoderms) to the dorsal surface of the palatine, with this value subtracted from 100.
40. Frontal subolfactory process-parasphenoid suture: (0) absent; (1) present.
41. Frontal subolfactory process descending lamina-parasphenoid rostrum relationship: (0) absent; (1) descending lamina off frontal subolfactory process (continuation of frontal enclosure of optic nerve) lies dorsolateral to parasphenoid; (2) descending lamina off frontal subolfactory process tightly clasps parasphenoid dorsolaterally.
42. Frontal subolfactory processes delimit a deep narrow canal across most of orbit: (0) absent; (1) present.
43. Frontal subolfactory process prefrontal lamina: (0) absent; (1) knob-like process at anteromedial rim of subolfactory process with prefrontal facet; (2) conspicuous descending lamina off subolfactory process articulating just behind prefrontal; (3) produced into shelf supporting prefrontal ventrally.
44. Frontal subolfactory process: (0) straight; (1) forms thickened anterolaterally projecting flange.
45. Frontal medial pillar: (0) absent; (1) separated anteriorly from subolfactory process by gap; (2) sutured to subolfactory process; (3) fused with subolfactory process.
46. Frontal medial flange separating olfactory tracts: (0) vertically positioned; (1) slants forward (anterior margin of subolfactory process in front of anterior margin of frontal dorsal lamina); (2) slants backwards (anterior margin of subolfactory process behind anterior margin of frontal dorsal lamina).
47. Frontal descending process-parietal contact, in horizontal section: (0) no contact; (1) parietal overlaps frontal laterally; (2) frontal descending process abuts parietal; (3) frontal descending process overlaps parietal laterally, at least in part.



48. Frontal interorbital width/frontoparietal suture width I: (0) 14–19%; (1) 20–22%; (2) 24–26%; (3) 28–34%; (4) 36–40%. Scores for characters 48 and 49 are determined with straight line measurements at the narrowest part of the frontal between the orbits, and between the lateral contact between the frontal and parietal, even if the suture is not straight.
49. Frontal interorbital width/frontoparietal suture width II: (0) less than 44%; (1) 44–47%; (2) 50–53%; (3) 55–58%; (4) 60–63%.
50. Frontal broadly overlaps prefrontal dorsally: (0) absent; (1) present.
51. Frontal supraorbital shelf: (0) absent; (1) present; (2) present and demarcated medially by narrow shallow longitudinal furrow often bearing line of foramina on the dorsal surface of the frontal.
52. Frontal anterior margin shape: (0) mainly trends anteromedially; (1) broadly transverse.
53. Frontal anteroposteriorly narrow, blunt prefrontal process off lateral base of subolfactory process extends into prefrontal socket: (0) absent; (1) present.
54. Frontal posterior margin convex and parietal anterior margin concave, in mid-sagittal section: (0) absent; (1) present.
55. Frontoparietal suture: (0) separate; (1) fused.
56. Frontoparietal suture interdigitation: (0) frontal overlaps parietal dorsally; (1) lightly interdigitate or simple abutment; (2) moderate interdigitation; (3) strong interdigitation; (4) deeply interdigitate.
57. Frontoparietal suture dorsal outline: (0) bowed anteriorly/inverted U; (1) roughly transverse; (2) shallow U or W bowed posteriorly; (3) deeply bowed posteriorly U or W; (4) frontal postero-dorsolateral corner protrudes posterolaterally.
58. Frontal parietal lateral overlap: (0) frontal deeply overlaps parietal; (1) frontal barely overlaps parietal laterally; (2) frontal underlaps parietal laterally.
59. Frontoparietal fontanelle in adults: (0) absent; (1) present.
60. Frontoparietal suture expression in medial wall of orbit: (0) strongly inclined anteriorly; (1) vertical or slightly inclined anteriorly.
61. Frontal suboptic shelves-parietal contact: (0) parasagittal shelves (suboptic shelves) pass from posterior base of frontal subolfactory processes on either side of the dorsal edge of the parasphenoid to near contact, or overlap, parietal medially below optic foramen; (1) frontal suboptic processes widely separated from parietal on either side of the midline at the ventral junction of frontal, parietal and parasphenoid; (2) suboptic shelves absent.
62. Postfrontal: (0) present, not fused to postorbital or frontal; (1) absent; (2) fused to postorbital; (3) fused to frontal.
63. Postfrontal shape: (0) triradiate (notched distally or not), with subequal frontal and parietal processes wrapping around frontoparietal suture; (1) parietal process much shorter than frontal process; (2) parietal process absent, postfrontal subtriangular.

64. Postfrontal distal shape: (0) tapering to point (passing anterior to postorbital); (1) bifid (clasps postorbital).
65. Postfrontal relative to parietal table: (0) ventrolateral; (1) dorsal overlap present; (2) dorsal overlap extensive.
66. Postfrontal-jugal articulation: (0) widely separated; (1) nearly in contact, but still separated; (2) in contact.
67. Postfrontal supratemporal shelf: (0) absent; (1) present as thin shelf extending over anterodorsal corner of supratemporal fenestra; (2) extending posteriorly further than laterally across upper temporal fenestra; (3) extending to (nearly) occlude upper temporal fenestra.
68. Postorbital: (0) present; (1) lost.
69. Postorbital shape: (0) widens anteriorly; (1) narrows anteriorly. Snakes lack a squamosal process, but the postorbital has a conspicuous ventral reach behind the orbit, and they are accordingly regarded as having a ‘wide’ postorbital anteriorly.
70. Postfrontal: (0) not broad and flat; (1) often very broad, always anteroposteriorly extensive and flat, with postorbital process reduced to nub; (2) with a shaft that is club-shaped distally.
71. Postorbital-parietal contact: (0) postorbital entirely distal, separated by postfrontal from parietal; (1) postorbital with discrete process extending toward parietal behind postfrontal; (2) postorbital contacts parietal ventrolaterally at frontoparietal suture; (3) postorbital dorsolaterally behind frontoparietal suture.
72. Postorbital shape at skull roof contact: (0) postorbital abuts parietal dorsolaterally at narrow contact; (1) with a long anterodorsally curving head (that often extends past level of frontoparietal suture midline).
73. Postorbital with small compressed tab at apex passing across frontoparietal suture: (0) absent; (1) present.
74. Postorbital, dorsomedial head: (0) undivided; (1) divided into two heads.
75. Postorbital squamosal process: (0) present; (1) absent.
76. Postorbital restricts upper temporal fenestra (UTF): (0) absent, postorbital tapers to tip; (1) partly occludes UTF, as postorbital expands medially posteriorly; (2) enlarged postorbital completely occludes UTF.
77. Postorbital (nearly) excludes squamosal from upper temporal fenestra: (0) absent; (1) present.
78. Postorbital overlaps squamosal: (0) laterally into V-shaped recess in squamosal; (1) dorsomedially as slender tapering rod attached superficially; (2) dorsally; (3) postorbital in long V-shaped trough dorsally and then rotating dorsolaterally posteriorly; (4) squamosal lies in trough beneath postorbital.
79. Postorbital-squamosal suture: (0) firm, suture no wider than those among surrounding elements; (1) loose, sutural gap wider than that between postorbital and postfrontal, or postorbital and jugal.

80. Postorbital firmly sutured to skull roofing bones (postfrontal or parietal): (0) present; (1) postorbital barely underlaps parietal at frontoparietal suture (equals ‘mobile joint’); (2) postorbital tapers to blunt tip separated from parietal (ordered).
81. Postorbital-ectopterygoid contact: (0) absent; (1) present.
82. Postorbital jugal ramus: (0) extends ventral to quadrate head; (1) level with quadrate head; (2) above quadrate head.
83. Postorbital-jugal suture: (0) long, firm, immobile, tongue-in-groove suture, with jugal largely ventrolateral to postorbital; (1) short abutting suture, with jugal reduced to tab-like dorsal tip that lies distal to postorbital; (2) jugal tapers smoothly to apex, which is loosely joined to lateral face of postorbital via connective tissue; (3) postorbital with process extending lateral to tapering apex of jugal. Note from Gauthier *et al.* (2012): seemingly not visible in dried material.
84. Postorbital contribution to posterior orbital margin: (0) less than 39%; (1) 39–52%; (2) 53–66%; (3) 67–80%; (4) more than 80% (ordered). Postorbital length is measured along the midshaft of the element from the apex of its contact with the skull roof to its ventral tip. The length of the posterior orbital margin is measured from the same point dorsally to the dorsal edge of the maxilla ventrally.
85. Postorbital spreads onto the dorsal surface of postfrontal: (0) absent; (1) present.
86. Postorbital dorsal part, above lateral wing of parietal: (0) uniformly narrow; (1) broadened.
87. Postorbital extent posteriorly: (0) to end of parietal table or less; (1) posterior to parietal table.
88. Parietal fusion: (0) paired; (1) fused.
89. Parietal ventral lappet: (0) poorly developed or absent; (1) prominent V-shaped, flat process.
90. Parietal temporal muscles originate: (0) dorsally on parietal table and supratemporal process of parietal; (1) ventrally on parietal table and dorsally on supratemporal process; (2) ventrally on parietal table and supratemporal process (ordered).
91. Parietal temporal fossa shape: (0) temporal muscles originate dorsally across entire parietal table all the way to frontal anteriorly (at least laterally); (1) anterolateral corner of temporal fossa terminates posteriorly, dorsal and ventral margins of temporal fossa converge behind frontal, so parietal table extends as flat surface toward orbital margin, and temporal muscles are confined laterally. This character tracks an apomorphy arising inside *Serpentes*, and is accordingly considered ‘not applicable’ (?) in other lizards. The apomorphic condition from which it arises in stem snakes, in which the jaw muscles converge on the midline to form a sagittal crest over most of their origin on the parietal table, is tracked by character 93(1).
92. Parietal, middle third: (0) narrow in dorsal view; (1) wide in dorsal view.
93. Parietal sagittal crest: (0) absent; (1) present; (2) projecting dorsally.
94. Parietal nuchal fossa width: (0) narrow; (1) wide; (2) overgrown by parietal (nearly) to midline.
95. Parietal postparietal projection near midline (distally bifid or not; see character 97): (0) absent; (1) present.

96. Parietal-supraoccipital contact: (0) absent; (1) parietal overlaps supraoccipital on midline; (2) abuts supraoccipital on midline; (3) dorsoventral parasagittal abutment; (4) supraoccipital around processus ascendens tectum synoticum forms stout, flat-topped pedicle that abuts parietal posteroventromedially.
97. Parietal bifid supraoccipital process: (0) absent; (1) present; (2) clasping supraoccipital crest.
98. Parietal descending lamina articulates with supraoccipital ascending lamina: (0) absent, parietal descending lamina is anterior to supraoccipital ascending lamina; (1) present, parietal descending lamina is posterior to the supraoccipital ascending lamina.
99. Parietal extent over braincase in dorsal view: (0) does not cover occiput; (1) covers nearly all of occiput; (2) with emarginate lateral fossae.
100. Parietal posterior margin, in dorsal view: (0) does not form an elongate, slender and pointed posterior process; (1) does form an elongate, slender and pointed posterior process.
101. Parietal supratemporal process length: (0) well-developed; (1) reduced, less than 25% of parietal width; (2) absent.
102. Parietal supratemporal process orientation: (0) directed laterally; (1) directed posterolaterally; (2) directed posteriorly.
103. Parietal contribution to back of the upper temporal fenestra: (0) short supratemporal process, parietal only forms about half of the upper temporal fenestra posterior arch, with supratemporal forming distal half; (1) long parietal supratemporal process extends distally to near the quadrate head.
104. Parietal foramen: (0) present; (1) absent.
105. Parietal foramen position: (0) in parietal; (1) at frontoparietal suture; (2) in frontal.
106. Parietal supraorbital process: (0) absent; (1) present; (2) deeply clasping frontal orbital margin.
107. Parietal postorbital process: (0) absent, parietal barely, if at all, laps behind postorbital apex in horizontal section; (1) parietal vertically oriented lappet extends laterally to overlap postorbital to form anteromedial margin of upper temporal fenestra.
108. Parietal epipterygoid process: (0) absent; (1) distinct process; (2) reaches alar process of prootic.
109. Parietal-prootic contact: (0) absent; (1) contact at apex of alar process; (2) extensive conformable contact, with parietal overlapping prootic laterally throughout length; (3) discrete ventral process of parietal overlaps prootic alar process laterally.
110. Parietal ventral triangular downgrowths of temporal muscle origin overlap prootic laterally, with latter abutting former medially, just anterior to supraoccipital: (0) absent; (1) present.
111. Maxilla (post-) premaxillary process contact: (0) not in contact; (1) in contact, or nearly so, but always excluding premaxilla from vomer dorsally; (2) in contact and vertically expanded.
112. Maxilla premaxillary process dorsal surface grooved (often enclosed) for passage of a deeper and more internally placed ramus of the subnarial artery: (0) absent; (1) present.

113. Maxilla and vomer: (0) do not meet at anterior margin of fenestra exochoanalis; (1) meet at anterior margin of fenestra exochoanalis.
114. Maxilla facial process length/maxilla length: (0) 10–15%; (1) 16–23%; (2) 25–36%; (3) 38–55%; (4) more than 56% (ordered). Maxilla length measured just above base of tooth row from premaxillary articulation to posterior terminus of the element. Maxilla facial process length measured from midheight of narial margin to edge of jugal articulation.
115. Maxilla facial process height: (0) tall, to skull roof; (1) reduced; (2) absent; (3) columnar process received in longitudinal concavity on anterior face of prefrontal.
116. Maxilla facial process apical surface faces: (0) laterally; (1) dorsolaterally; (2) anterodorsally; (3) large, triangular, dorsally directed surface sharply set off from nearly vertical external surface of facial process.
117. Maxilla facial process medial face with a posterodorsally trending ridge demarcating the anterior limits of a shallow, oval fossa—the naso-lacrimal fossa—bordered by the lacrimal and infraorbital canals posteriorly: (0) absent; (1) present.
118. Maxilla narial margin rises at: (0) high angle; (1) low angle.
119. Maxilla firmly sutured to palatine: (0) present; (1) prominent palatine process of maxilla; (2) loosely ligamentous connection via projecting palatine process of maxilla and distinct maxillary process of palatine, with the former lying anterior to the latter; (3) maxilla free of palatine, suspended from prefrontal; (4) maxilla rotates to erect fang.
120. Maxilla suborbital ramus extends posteriorly: (0) to roughly midorbit (or anterior); (1) to posterior quarter of orbit; (2) to posterior edge of orbit; (3) posterior to orbit (or frontoparietal suture).
121. Maxilla suborbital process width ventral to ectopterygoid: (0) tapers posteriorly; (1) widens below articulation (i.e., ectopterygoid flange).
122. Jugal depth below orbit: (0) jugal suborbital ramus not much deeper dorsoventrally below mid-orbit than postorbital ramus is wide anteroposteriorly; (1) jugal very deep below orbit. Polyglyphanodontians have a robustly constructed m. pterygoideus insertion reflected in an extensive ectopterygoid-ptyerygoid overlap deep to the maxilla and jugal. The robust construction of the jugal and maxilla lateral to this insertion—reflected particularly in the depth of the jugal suborbital ramus—may represent a correlated response to what must have been a massive jaw adductor.
123. Maxilla suborbital process tip shape at jugal articulation: (0) suborbital margin slopes smoothly to tip; (1) with distinct step or V-shaped notch distally at jugal articulation.
124. Maxilla posterior process shortens: (0) to midorbit or longer; (1) to anterior half of orbit.
125. Maxilla, intramaxillary joint: (0) absent; (1) present.
126. Prefrontal: (0) present; (1) reduced; (2) absent.
127. Prefrontal broadly overlaps frontal posterodorsally: (0) absent; (1) present.
128. Prefrontal orbitonasal margin: (0) slopes ventrolaterally; (1) vertical; (2) slopes ventromedially; (3) extends beneath subolfactory processes; (4) extends to near contact with its opposite on midline.

129. Prefrontal posterior extent along orbital margin: (0) terminates in anterior half of orbit; (1) extends to midorbit; (2) extends posterior to midorbit.
130. Prefrontal boss: (0) absent; (1) present; (2) in projecting canthal crest.
131. Prefrontal nasolacrimal cornu: (0) absent; (1) present.
132. Prefrontal medial extent across anterior margin of frontal: (0) prefrontal extends 50% or less across frontal anterior width; (1) extends 50% to 65% across frontal anterior width; (2) extends 65% to 75% across frontal anterior width; (3) extends 85% or more across frontal to approach midline.
133. Prefrontal-frontal suture in cross-section: (0) prefrontal arcs gently about anterolateral frontal margin along entire anteroposterior length; (1) prefrontal strongly bifid, clasps frontal posteriorly then spreads dorsally and reduced ventrally anteriorly; (2) frontal clasps prefrontal in V-shaped notch.
134. Prefrontal length relative to height: (0) long anteroposteriorly; (1) short anteroposteriorly.
135. Prefrontal-maxilla articulation: (0) prefrontal posteroventromedial corner narrowly (or not at all) in contact with maxilla lateral to palatine; (1) prefrontal broadly contacts maxilla supradental shelf lateral to palatine; (2) prefrontal has mobile contact with maxilla; (3) rod-like prefrontal arched dorsally, bifid at each end, with mobile joints at maxilla and frontal (prefrontal functionally part of upper jaw).
136. Prefrontal arcs about orbitonasal fenestra, with posteroventromedial corner curving inwards toward palatine in cross-section: (0) absent; (1) present.
137. Lacrimal: (0) present; (1) absent.
138. Lacrimal position relative to lacrimal duct: (0) lacrimal with broad exposure laterally, reaching from lateral floor of lacrimal duct up the medial face of the maxilla to contact a lateral process of the prefrontal that roofs the lacrimal duct in cross section; (1) lacrimal arches over the lacrimal duct to replace the prefrontal dorsally, broadly floors the lacrimal duct with a medial process posteriorly passing up the lateral face of the prefrontal; (2) lacrimal reduced to floor of lacrimal duct and lingual surface of maxilla, and barely, if at all, exposed laterally; (3) lacrimal bone reduced ventrally, confined mainly to dorsolateral corner of lacrimal duct.
139. Lacrimal foramen size: (0) small; (1) large.
140. Lacrimal foramen number: (0) one; (1) divided on orbital surface; (2) divided through to olfactory surface.
141. Lacrimal duct position: (0) between prefrontal and lacrimal; (1) enclosed in prefrontal, except ventrally; (2) enclosed entirely in prefrontal (*Xenochrophis piscator*, anterior close-up cutaway view of snout).
142. Jugal: (0) present; (1) absent.
143. Jugal extent anteriorly with respect to tooth row: (0) jugal broadly overlaps level of posterior maxillary tooth row; (1) jugal overlaps the most posterior maxillary tooth; (2) jugal just reaches base of, or stops short of, the most posterior maxillary tooth.
144. Jugal anterior extent: (0) broadly separated from prefrontal; (1) reaches level of prefrontal.

145. Jugal-lacrimal overlap: (0) jugal lateral to lacrimal; (1) jugal medial to lacrimal; (2) jugal ventral to lacrimal.
146. Jugal articulation with maxilla in cross-section: (0) rounded ventral margin of jugal and shallow and more rounded contour of the maxilla supradental shelf; (1) acute ventral margin of jugal lies in narrow longitudinal groove on dorsal surface of maxillary supradental shelf.
147. Jugal lateral extent over maxilla in cross-section: (0) maxilla suborbital border wraps dorsally around jugal external margin; (1) jugal laps over external suborbital margin.
148. Jugal with inverted V-shaped notch clasping suborbital edge of maxilla: (0) absent; (1) present.
149. Jugal lateral exposure below orbit: (0) absent; (1) partly exposed above orbital margin of maxilla; (2) entirely exposed above orbital margin of maxilla.
150. Jugal suborbital ramus: (0) shallow; (1) deep.
151. Jugal suborbital boss: (0) absent; (1) present.
152. Jugal postorbital ramus development: (0) complete bony postorbital bar; (1) incomplete bony postorbital bar; (2) bony postorbital bar absent (ordered).
153. Jugal postorbital ramus shape in lateral outline: (0) narrow; (1) wide.
154. Jugal contacts squamosal: (0) narrow contact; (1) absent; (2) broad contact.
155. Jugal posterior process: (0) complete lower temporal bar; (1) reduced to a discrete bony posterior process; (2) absent.
156. Jugal posterior process orientation: (0) more posterior in orientation; (1) more ventral in orientation.
157. Jugal medial ridge: (0) medial ridge weak, jugal lateral to ectopterygoid at base in dorsal view; (1) medial ridge pronounced, base of medial ridge projects behind ectopterygoid base in dorsal view.
158. Jugal cross-section at level of ectopterygoid: (0) subtriangular; (1) depressed.
159. Squamosal: present (0), absent (1).
160. Squamosal length relative to epipterygoid position: (0) squamosal does not extend anterior to level of epipterygoid; (1) squamosal extends anterior to level of epipterygoid.
161. Squamosal temporal ramus-parietal contact: (0) temporal ramus diverges from parietal supratemporal process; (1) temporal ramus broadly contacts parietal supratemporal process.
162. Squamosal base of temporal ramus: (0) diverges from parietal; (1) base lies against parietal.
163. Squamosal temporal ramus width: (0) slender; (1) widens posteriorly; (2) widens anteriorly with medial shelf along parietal that roofs posterior end of upper temporal fenestra.
164. Squamosal temporal ramus shape: (0) compressed; (1) depressed.
165. Squamosal ascending process: (0) present; (1) absent.

166. Supratemporal: (0) present; (1) absent.
167. Supratemporal shortens: (0) supratemporal longer than squamosal-parietal contact; (1) supratemporal shorter than squamosal-parietal contact; (2) supratemporal very small.
168. Supratemporal lengthens: (0) posterior to level of parietal notch; (1) near to level of parietal notch; (2) anterior to level of parietal notch.
169. Supratemporal anterior suture with parietal: (0) supratemporal lies flat against supratemporal process of parietal; (1) inserts in slot in supratemporal process of parietal.
170. Supratemporal position on parietal: (0) partly ventral; (1) partly ventrolateral; (2) all lateral; (3) dorsolateral (on either parietal or braincase alone).
171. Supratemporal anterior terminus: (0) posterior to level of trigeminal nerve exit; (1) anterior to level of trigeminal nerve exit.
172. Supratemporal anterior extent in snakes without supratemporal process of parietal: (0) supratemporal does not extend anterior of posterior border of parietal table; (1) supratemporal extends anterior of posterior border of parietal table. Not scored in snakes where supratemporal is absent.
173. Supratemporal orientation: (0) anterior to quadrate head; (1) dorsal to quadrate head.
174. Supratemporal free posteriorly: (0) supratemporal ends near attachment to braincase; (1) extends freely posterior to oto-occipital.
175. Supratemporal exposure in dorsal view: (0) supratemporal at least partly exposed dorsally on lateral side of parietal supratemporal process; (1) slender and hidden completely from view by parietal-squamosal contact dorsally.
176. Supratemporal posterior exposure on parietal supratemporal process: (0) narrow or absent; (1) present broadly.
177. Quadrate head attachment: (0) tapering peg-like head loosely attached in socket formed largely by squamosal; (1) quadrate head pivots on slender tapering tip of squamosal; (2) bluntly abuts supratemporal and squamosal. *Sphenodon* retains the ancestral ball and socket suspensorium of Diapsida. In contrast, the quadrate head remains unmodified and firmly attached to the skull in captorhinids and turtles.
178. Quadrate head suspension: (0) supratemporal and squamosal separate quadrate head from braincase (except narrowly beneath tip of supratemporal); (1) quadrate head abuts braincase ventral to supratemporal; (2) quadrate head broadly contacts braincase anteriorly.
179. Quadrate suprastapedial process: (0) absent; (1) present.
180. Quadrate lateral conch: (0) present; (1) absent.
181. Quadratojugal: (0) present; (1) absent.
182. Quadrate-pterygoid overlap: (0) extensive; (1) short overlap or small lappet; (2) very narrow overlap or lappet absent; (3) no overlap, ligamentous connection only.



183. Quadrate accessory process arising off anteromedial edge near quadrate head abuts braincase in region of horizontal semicircular canal: (0) absent; (1) present.
184. Quadrate stylohyal process on medial face of quadrate: (0) absent; (1) present as oval disc; (2) present as narrow cylindrical ridge.
185. Quadrate height to braincase depth ratio (braincase depth measured from near the quadrate head): (0) less than 50%; (1) 50–59%; (2) 60–69%; (3) 70–79%; (4) more than 79%.
186. Quadrate ‘pythonomorph’: (0) bowed more or less, but not in both lateral and posterior views; (1) massive, and strongly bowed anteriorly in lateral view and laterally in posterior view, throughout length, and with prominent ventrally-directed suprastapedial process forming cavum tympani.
187. Quadrate foramen size: (0) large; (1) small; (2) tiny.
188. Quadrate slopes anteroventrally (more than 90° equals anterior slope from quadrate head): (0) vertical to posterior slope; (1) 94–107°; (2) 108–121°; (3) 122–135°; (4) more than or equal to 136°.
189. Quadrate slopes posteroventrally (less than 90° equals posterior slope from quadrate head): (0) vertical to anterior slope (87–93°); (1) 86–68°; (2) 67–49°; (3) 48–31°; (4) less than 30°.
190. Stapes: (0) imperforate; (1) perforate.
191. Stapedial shaft: (0) long and slender; (1) short and thick.
192. Stapedial footplate: (0) small; (1) large.
193. Stapedial footplate: (0) does not fill fenestra ovalis; (1) fills fenestra ovalis.
194. Fenestra ovalis orientation: (0) opens directly laterally; (1) opens anterolaterally; (2) opens ventrolaterally; (3) opens posterolaterally.
195. Extracolumella: (0) present; (1) absent.
196. Septomaxilla: (0) present; (1) absent.
197. Septomaxilla dorsolateral contacts: (0) no contacts; (1) abuts laterally with prefrontal and nasal; (2) abuts laterally with nasal only; (3) abuts laterally with prefrontal only.
198. Anterior end of septomaxilla: (0) meets maxilla in immovable joint; (1) mobile, septomaxilla not contacting maxilla.
199. Septomaxilla position relative to vomeronasal organ: (0) occupies a lateral position, not contributing to nasal cavity or to roofing of vomeronasal organ; (1) occupies a more medial position, contributing to nasal cavity and roofing of vomeronasal organ.
200. Septomaxilla, dorsal expansion: (0) flat or weakly convex, vomeronasal organ small; (1) expanded and convex, reflecting large size of vomeronasal organ.
201. Septomaxilla: (0) does not contact the dorsal surface of the palatal shelf of the maxilla; (1) contacts the dorsal surface of the palatal shelf of the maxilla.

202. Septomaxilla divides vomeronasal organ: (0) absent; (1) present.
203. Septomaxilla medial flange produced into a long, posterodorsally directed, blade-like process: (0) absent; (1) present, but nasal intercedes between septomaxilla and frontal; (2) extends to frontal beneath nasal; (3) develops an expanded faceted articulation with the frontal.
204. Septomaxilla lateral flange: (0) absent; (1) present; (2) reaches well above roof of vomeronasal organ.
205. Septomaxilla medial flange: (0) absent; (1) present.
206. Septomaxilla, posterior extent of medial flange: (0) short, not reaching level of prefrontal; (1) long, extends posteriorly to anteroposterior level of anterior margin of prefrontal. Lee (1998). Short in scolecophidians, but medial to prefrontal: coded (0).
207. Septomaxilla posterior process on laterally ascending flange: (0) short or absent; (1) long, extends posteriorly deep to prefrontals.
208. Nervus ethmoidalis medialis: (0) above septomaxilla; (1) enclosed in septomaxilla anteriorly; (2) in anterior half of septomaxilla; (3) enclosed posteriorly in septomaxilla.
209. Vomeronasal organ, concha: (0) simple diverticulum of nasal capsule; (1) completely separated from nasal capsule, with fungiform body.
210. Vomeronasal organ, cupola: (0) fenestrated medially, even if only narrowly; (1) closed medially.
211. Vomeronasal organ and mushroom body: (0) not fully enclosed by septomaxilla and vomer; (1) fully enclosed by septomaxilla and vomer only.
212. Vomer fusion: (0) absent; (1) partial; (2) fully fused.
213. Vomer size: (0) vomer extends backwards no further than anteriormost contact of palatine with maxilla; (1) vomer extends backwards beyond anteriormost contact of palatine with maxilla.
214. Vomer: (0) main portion plate-like; (1) main portion rod-like.
215. Vomer overlaps (dorsally) the palatal shelf of the maxilla behind the posterior margin of opening of vomeronasal organ: (0) absent; (1) present.
216. Vomer: (0) does not establish any sutural contact with the palatal shelf of the maxilla behind the incisura Jacobsoni; (1) establishes narrow contact with the palatal shelf of the maxilla behind the incisura Jacobsoni; (2) establishes broad contact with the palatal shelf of the maxilla along the entire length of the lateral margin of vomer.
217. Vomer to vomeronasal organ relation: (0) ventral to vomeronasal organ; (1) encapsulates vomeronasal organ posteriorly and medially; (2) with margins enclosing posterior wall sloping ventrolaterally; (3) further expanded laterally to completely encapsulate vomeronasal organ posteriorly.
218. Vomer meets septomaxilla: (0) at posterior margin of opening of vomeronasal organ; (1) at lateral margin of opening of vomeronasal organ.
219. Margin of vomer at opening of vomeronasal organ: (0) flat; (1) curved downwards.

220. Vomeronasal nerve exit: (0) dorsal to vomer; (1) via canals dorsally on vomer; (2) via foramen at back end of vomer; (3) via sieve-like arrangement of foramina through back end of vomer.
221. Vomer degree underlap of palatine: (0) just at tips; (1) extending posteriorly to level of maxilla-ectopterygoid first contact.
222. Vomer ventral longitudinal ridges: (0) absent; (1) long and converge toward midline, well-developed below vomeronasal nerve exit from septomaxilla; (2) short parasagittal ridges anteriorly on vomer at level of vomeronasal duct opening; (3) discrete parasagittal canals anteriorly on vomer delimited by lateral and median ridges.
223. Vomer septum transversely fenestrate: (0) absent; (1) present; (2) at posteroventral corner of vomer septum.
224. Vomer septum (vertical lamina) height: (0) low, not forming septum; (1) partly separating olfactory chambers; (2) nearly completely separating olfactory chambers along with septomaxilla and nasal; (3) only ventral edge of septum remains; (4) V-shaped notch separates dorsal and ventral rami of vomer septum.
225. Vomer, posterodorsal margin forms expanded hollow flange: (0) absent; (1) present.
226. Vomer, transverse flange rises vertically to meet septomaxilla and encloses vomeronasal organ posteriorly: (0) absent; (1) present.
227. Vomer contact with subolfactory process of frontal: (0) absent; (1) present.
228. Vomer, descending tubercle (or ridge) at vomero-palatine junction: (0) absent; (1) tubercle present; (2) ridge/tubercle present on vomer and/or adjacent palatine.
229. Vomer, foramina on palatal surface near midline: (0) paired; (1) single.
230. Vomer, teeth: (0) present; (1) absent.
231. Palatines: (0) separated; (1) anterior contact only; (2) contact extends to midpoint, or beyond.
232. Palatine relative to maxilla-lacrimal-jugal articulation: (0) palatine sits medial to lacrimal and/or jugal and maxilla in cross section; (1) palatine inserts between lacrimal and/or jugal and maxilla in cross section.
233. Palatine dorsal canal: (0) shallow longitudinal sulcus; (1) upturned lateral and medial edges of palatine demarcate deep, narrow canal ending in enclosed fossa.
234. Palatine, vomerine process dorsally on vomer: (0) vomer attaches over entire face of vomerine process of palatine; (1) narrow slender tip of palatine loosely attached to vomer; (2) long slender palatine process clasped in groove on dorsal surface of vomer; (3) ventral edge of vomerine process of palatine attached ligamentously between bifid palatine process of vomer.
235. Palatine, vomerine process buttresses vomer: (0) palatine vomerine process tapers anteromedially; (1) palatine vomerine process splays laterally at tips to buttress vomer posteriorly.
236. Palatine, vomerine process passes vomer: (0) medial to vomer tines; (1) lateral to vomer tines (posteromedial process of vomer).

237. Ventral projections from anterior end of palatine, near palatine-vomer suture: (0) absent; (1) present.
238. Ventromedial extension from maxillary process of palatine (choanal processes of palatine): (0) present but not descending ventromedially; (1) present and descending ventromedially to reach in between (or close to) posterior tips of vomers; (2) absent (ordered).
239. Maxillary process of palatine: (0) situated anterior to the posterior end of palatine; (1) situated at the posterior end of the palatine.
240. Palatine contribution to suborbital fenestra: (0) reduced posteromedially, and pterygoid broadly exposed in suborbital fenestra; (1) palatine extends posteriorly along lateral edge of pterygoid so that pterygoid narrowly enters suborbital fenestra; (2) palatine fully excludes pterygoid from border of suborbital fenestra.
241. Palatine-ptyerygoid overlap: (0) palatine overlaps pterygoid at tip and ectopterygoid near base, otherwise lateral in position; (1) palatine overlaps pterygoid dorsally from lateral to near medial margin of pterygoid, with loose abutment laterally; (2) palatine barely overlaps pterygoid laterally and pterygoid does not extend well anterior to ectopterygoid-jugal-maxilla juncture; (3) palatine barely overlaps pterygoid, joint nearly transverse; (4) complex pattern of clasping projections.
242. Palatine anterior ‘dentigerous’ process: (0) absent; (1) present only as short extension of palatine anterior to maxillary process; (2) present (with teeth).
243. Palatine dentigerous process reduction: (0) long, bearing six or more teeth; (1) short, bearing five or fewer teeth.
244. Infraorbital canal divides anteriorly in palatine: (0) single foramen anteriorly; (1) double anteriorly, with medial palatine ramus small and lateral large.
245. Infraorbital canal position: (0) lateral, between palatine and dorsal surface of supradental shelf of maxilla; (1) medial, entirely in palatine.
246. Palatine foramen: (0) absent; (1) present, enters palatine dorsally toward its anterior end to pass anteroventrolaterally into the infraorbital canal.
247. Palatine, choanal process: (0) curves medially and meets the vomer in a well-defined articular facet; (1) touches or abuts the vomer without articulation, or remains separated from vomer.
248. Palatine, choanal process: (0) forms an extensive concave surface dorsal to the ductus nasopharyngeus; (1) narrows to form a curved finger-like process; (2) forms a short vertical or horizontal lamina that does not reach the vomer.
249. Palatine: (0) simplicipalatinata; (1) incipient duplicipalatinata; (2) intermediate; (3) fully duplicipalatinata.
250. Palatine choanal fossa development: (0) absent; (1) present anteriorly on palatine; (2) extending about half way back on palatine; (3) fully developed to end of element. Snakes that can be scored are given a 3 as they have a well developed choanal fossa, although modification of the palatine precludes application of the state as defined in most snakes.
251. Palatine, subchoanal process medial edge shape in ventral view: (0) present only on anterior one-third of palatine; (1) roughly arcuate; (2) roughly parasagittal. This character assesses the anteroposterior

- extent of character 249, which describes how closely the palatine subchoanal processes approach on the midline.
252. Palatine, posterior emargination of anterodorsal margin of choanal fossa: (0) anterior to anteroposterior midpoint of palatine-maxilla suture; (1) extends posterior to anteroposterior midpoint of palatine-maxilla suture.
253. Posteromedial process of palatine: (0) long, overlaps at least two pterygoid teeth; (1) short, overlaps no more than one pterygoid tooth. *Uropeltis melanogaster*, *Calabaria reinhardtii* and *Anomochilus leonardi* have no pterygoid teeth, but still have a long overlap and are accordingly scored 0.
254. Palatine, shape of posterolateral margin at pterygoid suture: (0) unmodified; (1) palatine with discrete surface set off from choanal fold, extending along lateral margin from maxillary to pterygoid sutures; (2) transversely broad palatine at pterygo-palatine suture strongly restricts suborbital fenestra. This character tracks two separate transformations and is in any case coded incorrectly. State 1 is scored as present in all scincomorphs, but applies only to cordyliforms and scincids. State 2 arises inside gekkotans. These errors will have to be corrected in ensuing versions of this matrix.
255. Palatine teeth: (0) present; (1) absent.
256. Palatine teeth size: (0) small conical denticles; (1) enlarged, but smaller than marginal teeth; (2) highly enlarged, similar in size to marginal teeth.
257. Pterygoids: (0) contacting each other; (1) palatal rami fully separated.
258. Pterygoid separation on midline: (0) pterygoids narrowly separated for most of their length; (1) broad at base, narrow anteriorly; (2) broad at base, but not as narrowly separated anteriorly; (3) broad throughout length.
259. Pterygoid, palatine ramus: (0) contacts vomer; (1) does not contact vomer.
260. Pterygoid-palatine joint, length of complex pattern of projections in snakes: (0) long; (1) medium; (2) short.
261. Pterygoid, palatine ramus clasps pterygoid ramus of palatine: (0) absent; (1) present.
262. Pterygoid transverse process and ectopterygoid (pterygoideus muscle insertion) nearly as deep as mandible (at least 80% mandible depth), and ectopterygoid transversely broad, covering most of transverse process of pterygoid in anterior view: (0) absent; (1) present.
263. Pterygoid posterior extent: (0) pterygoid does not reach level of occipital condyle; (1) pterygoid reaches level of occipital condyle; (2) pterygoid reaches well posterior to level of occipital condyle.
264. Pterygoid, quadrate ramus short and small, tightly wrapping around posteromedial (ventromedial if quadrate horizontally oriented) surface of quadrate: (0) absent; (1) present.
265. Pterygoid, quadrate ramus: (0) robust, rounded or triangular in cross-section, but without groove; (1) blade-like and with distinct longitudinal groove for the insertion of the protractor pterygoidei muscle.
266. Pterygoid, ventral flange ('wing-shaped extension') of quadrate ramus: (0) absent; (1) present.

267. Pterygoid teeth: (0) present; (1) absent.
268. Pterygoid teeth: (0) small conical denticles; (1) enlarged, but smaller than marginal teeth; (2) highly enlarged, similar in size to marginal teeth.
269. Pterygoid teeth: (0) restricted to palatal ramus of pterygoid; (1) extend posteriorly onto quadrate ramus of pterygoid.
270. Ectopterygoid: (0) present; (1) absent.
271. Ectopterygoid size and restriction of suborbital fenestra: (0) ectopterygoid relatively slender, fenestra widely open; (1) ectopterygoid enlarged medially, restricting suborbital fenestra; (2) ectopterygoid highly enlarged medially, closing suborbital fenestra.
272. Ectopterygoid angulation in dorsal view: (0) nearly orthogonal; (1) obtuse angle (including crescentic curve).
273. Ectopterygoid anterior length: (0) well separated from palatine above maxilla; (1) near to or in contact with palatine.
274. Anterior end of ectopterygoid: (0) restricted to posteromedial edge of maxilla; (1) located dorsal to maxilla, invading the dorsal surface of the maxilla to variable degrees.
275. Ectopterygoid-maxilla suture: (0) ectopterygoid lies dorsally along supradental shelf of maxilla; (1) ectopterygoid abuts posteromedial corner of maxilla; (2) ectopterygoid with slot laterally clasping maxilla; (3) ectopterygoid overlapping maxilla more ventrally than dorsally; (4) interdigitating suture, with maxilla at least partly overlapping ectopterygoid dorsally.
276. Ectopterygoid maxillary process shape in dorsal view: (0) tapers or parallel-sided; (1) widens anteriorly; (2) to more than three times as wide as anteriorly relative to ectopterygoid shaft.
277. Ectopterygoid maxillary process anterior notch: (0) tapers forward of maxilla contact; (1) notched anteriorly; (2) with large, rectangular, lateral ramus produced directly laterally.
278. Ectopterygoid-maxilla posterior process suture: (0) ectopterygoid medial and mainly dorsal to maxilla; (1) ectopterygoid abuts maxilla on posteromedial edge only; (2) ectopterygoid contacts jugal only.
279. Lateral edge of maxillary ramus of ectopterygoid: (0) slopes medially; (1) straight.
280. Ectopterygoid, prefrontal and palatine relations: (0) ectopterygoid does not underlap palatine posteriorly below prefrontal; (1) ectopterygoid underlaps palatine below prefrontal.
281. Ectopterygoid-palatine ventral articulation: (0) palatine-maxilla contact excludes ectopterygoid; (1) ectopterygoid anterior process largely separates palatine from maxilla posteriorly.
282. Ectopterygoid hooked posterior process flat and exposed dorsally, ventrally and laterally: (0) absent; (1) present.
283. Ectopterygoid posterior process: (0) prominent; (1) small lateral knob; (2) absent.

284. Ectopterygoid posterior process lengthens: (0) does not extend past coronoid apex; (1) extends past coronoid apex.
285. Ectopterygoid dorsal process height: (0) tall; (1) short; (2) absent (not extending up medial face of jugal).
286. Ectopterygoid: (0) does not contact prefrontal; (1) contacts prefrontal at base of orbit.
287. Ectopterygoid-pterygoid contact: (0) predominantly dorsal; (1) predominantly lateral.
288. Ectopterygoid-pterygoid process length: (0) short; (1) longer, but still anterior to trigeminal foramen; (2) longest, extending posterior to trigeminal foramen.
289. Ectopterygoid overlap of pterygoid: (0) short; (1) long.
290. Epipterygoid: (0) present; (1) absent.
291. Epipterygoid, in resting position: (0) located lateral to prootic (even if only narrowly so); (1) located entirely anterior to prootic.
292. Epipterygoid relative to alar process of prootic: (0) epipterygoid anterolateral to prootic alar process; (1) epipterygoid abuts anteroventral tip of alar process.
293. Epipterygoid length: (0) long (reaches nearly to level of top of braincase, or above quadrate head, or more than half distance between pterygoid and parietal table); (1) short (reaches only to level of quadrate head, barely to semicircular canal, or half or less of distance between pterygoid and parietal table).
294. Epipterygoid-parietal contact: (0) absent; (1) overlaps parietal temporal muscle origin.
295. Epipterygoid: (0) expanded dorsoventrally and ventrally; (1) columelliform.
296. Braincase fusion: (0) unfused in adult; (1) opisthotic and prootic fused in adult; (2) complete braincase fusion in adult.
297. Processus ascendens of synotic tectum: (0) absent; (1) present.
298. Supraoccipital: (0) single; (1) double.
299. Supraoccipital origin of temporal muscles: (0) restricted to parietal; (1) spread onto supraoccipital, contacting nuchal crest in roughly T-shaped outline; (2) spread onto supraoccipital to form Y-shaped crest; (3) temporal muscles spread onto braincase dorsally, but sagittal and nuchal crests join to form roughly anchor-shaped outline.
300. Supraoccipital nuchal crest lateral extent: (0) absent; (1) present on supraoccipital; (2) present on supraoccipital and otoccipital.
301. Supraoccipital crest: (0) absent; (1) present; (2) meets ventral parietal.
302. Supraoccipital relative to oto-occipital on midline: (0) overlaps oto-occipital laterally; (1) laps over oto-occipital on midline as part of sagittal crest; (2) all three bones visible in cross-section, overlapped by parietal.

303. Supraoccipital contribution to internal sidewall of neurocranium: (0) participates in sidewall; (1) absent, only dorsal plate remains; (2) dorsal plate absent.
304. Epiotic foramen: (0) absent; (1) present.
305. Prootic, alar process: (0) small or absent; (1) prominent.
306. Prootic, supratrigeminal process: (0) absent; (1) weakly developed, not projecting beyond cupola anterior; (2) present as a finger-like projection above trigeminal notch, projecting beyond cupola anterior.
307. Crista prootica (ridge on lateral surface of the prootic, overhanging facial foramen): (0) well-developed lateral flange; (1) reduced to weak ridge; (2) absent.
308. Crista prootica: (0) does not extend onto basiptyergoid process; (1) extends onto basiptyergoid process forming open or closed bony canal.
309. Crista prootica aliform in outline in ventral view (extended butterfly shape): (0) absent; (1) present; (2) prominent, extending further laterally.
310. Crista tuberalis and crista prootica: (0) separate; (1) combined to surround stapedial footplate and lateral aperture of recessus scalae tympani.
311. Crista interfenestralis: (0) prominent; (1) reduced; (2) absent (ordered).
312. Crista tuberalis: (0) prominent; (1) reduced; (2) absent.
313. Facial foramen (lateral exit on prootic for the facial or VII cranial nerve): (0) single; (1) double.
314. Prootic participates in medial aperture of the recessus scala tympani (MARST): (0) absent; (1) prootic forms part of MARST.
315. Posterior auditory foramen: (0) bordered by opisthotic (oto-occipital) posteromedially; (1) enclosed entirely in prootic.
316. Orbitosphenoid, calcified/ossified: (0) absent; (1) present; (2) expanded to floor the braincase.
317. Orbitosphenoid: (0) well developed; (1) reduced.
318. Orbitosphenoid: (0) paired; (1) single (fused ventrally).
319. Optic foramen: (0) present; (1) absent.
320. Optic foramen: (0) not fully enclosed by bone; (1) enclosed partly or entirely by frontals; (2) entirely within orbitosphenoid; (3) entirely within parietal.
321. Trigeminal foramen or foramina: (0) anterior margin not enclosed in bone; (1) anterior margin enclosed by descending flange of parietal; (2) anterior margin enclosed by orbitosphenoid; (3) enclosed by prootic.
322. Trigeminal nerve maxillary branch: (0) pierces the lateral (maxillary) process of the palatine; (1) passes dorsally between the palatine and the prefrontal.



323. Ophidiosphenoid (equals ‘laterosphenoid’ or ‘pleurosphenoid’): (0) absent; (1) present.
324. Dorsum sellae shape in longitudinal cross-section: (0) crista sellaris forms posterior wall, usually low and vertically disposed with more or less anterior slope; (1) dorsum sellae poorly differentiated with, at most, shallow fossa with low crista sellaris; (2) enclosed in distinct fossa, a cup-like depression walled laterally and ventrally by the basisphenoid and anteriorly by the parasphenoid rostrum; (3) completely enclosed tube-like dorsum sellae.
325. Dorsum sella fossa roofed posteriorly by crista sellaris (not scored in species with reduced/absent crista sellaris): (0) fossa only modestly roofed by crista sellaris; (1) roofing more extensive over deep fossa.
326. Parabasisphenoidal keel: (0) absent; (1) present below dorsum sellae; (2) deep keel (ordered).
327. Parasphenoid rostrum in cross-section below posterior frontal articulation: (0) somewhat subrectangular; (1) distinctly I-beam shaped, strongly compressed laterally, abruptly narrows at trabeculae; (2) with an arrowhead-shaped apex in cross-section; (3) with prominent ventrolaterally directed alae.
328. Cultriform process: (0) long; (1) short; (2) absent.
329. Vidian canal rostral opening: (0) roofed by parietal; (1) exits via parasphenoid rostrum only.
330. Vidian canal opening on right side: (0) is not larger than that of left Vidian canal; (1) is larger than that of the left Vidian canal.
331. Trabeculae cranii: (0) tropibasic; (1) platybasic.
332. Basipterygoid process (and synovial palatobasal articulation): (0) present, formed by ossified basitrabecular process; (1) present, formed by outgrowth from parabasisphenoid (no basitrabecular process known; synovial palatobasal articulation absent); (2) basipterygoid process absent.
333. Basipterygoid process: (0) long, i.e., projecting far beyond the body of the basisphenoid; (1) short, i.e., not projecting very far beyond the body of the basisphenoid.
334. Basipterygoid process: (0) not expanded at distal end; (1) distal end expanded.
335. Sesamoid bone at basipterygoid-pterygoid articulation: (0) absent; (1) present.
336. Vidian canal formed by the basisphenoid enclosing the internal carotid artery and the base of the palatine artery, as they pass over the basipterygoid process: (0) absent; (1) present.
337. Vidian canal caudal opening: (0) within basisphenoid; (1) anterior margin at basisphenoid-prootic suture; (2) entirely within prootic; (3) the dibamid-amphisbaenian condition.
338. Carotid artery exits rostral end of Vidian canal: (0) at same level (or slightly above) as the remnant of the embryonic neurocranial trabeculae; (1) below the level of the remnant of the embryonic neurocranial trabeculae.
339. Basal tubera position: (0) posterolateral, with apex on lateral edge of basioccipital just behind base of prootic-opisthotic suture; (1) anteromedial, with apex at lateral juncture of sphenoid and basioccipital, anterior and medial to prootic-opisthotic suture.

340. Apophyseal ossification (Element 'X') caps basal tubera: (0) absent; (1) present; (2) large.
341. Occipital condyle: (0) posterior surface of condyle straight in ventral view; (1) posterior surface of condyle concave in ventral view.
342. Basioccipital: (0) contributes to ventral border of foramen magnum; (1) excluded from ventral border of foramen magnum by contact of exoccipitals.
343. Basioccipital ventral keel: (0) absent; (1) crest; (2) keel.
344. Medial aperture of the recessus scala tympani (MARST): (0) between basioccipital and opisthotic; (1) entirely in opisthotic.
345. Cranial nerve IX exits braincase via: (0) MARST internally and lateral aperture of recessus scala tympani (LARST) externally; (1) exits dorsal to MARST then out LARST.
346. Cranial nerve IX exits braincase via: (0) foramen magnum; (1) laterally via LARST; (2) posteriorly via vagus (= jugular) foramen.
347. Medial aperture of the recessus scalae tympani (MARST) subdivided, IX cranial nerve exits posteriorly: (0) absent; (1) large oval MARST undivided, with IX cranial nerve exiting at posterodorsal end; (2) MARST divided into anterior and posterior openings by bony process, with IX cranial nerve exiting via posterodorsal foramen.
348. Vagus foramen ('jugular foramen' in other amniotes) far from MARST: (0) with hypoglossal foramina lying below and between them medially; (1) vagus foramen closer to MARST, with hypoglossal foramina extending posterior to vagus.
349. Hypoglossal (XII) foramina exit(s) relative to vagus (X–XI) foramen on external surface of braincase: (0) hypoglossal foramina separated from vagus (jugular) foramen; (1) at least one hypoglossal foramen emerges from the same fossa as the vagus foramen; (2) only one hypoglossal foramen still exits separately from the vagus foramen fossa; (3) all three hypoglossals emerge from the same fossa as the vagus foramen.
350. LARST (lateral aperture of recessus scalae tympani): (0) open; (1) small; (2) closed.
351. Perilymphatic foramen faces: (0) ventrally; (1) medially; (2) laterally; (3) posteriorly.
352. Opisthotic-exoccipital fusion to form oto-occipital: (0) incompletely fused or separate in adult; (1) completely fused early in post-hatching ontogeny. In extant amniotes generally, dense lamellar bone covers the occipital condyle late in ontogeny, so that one cannot distinguish among the three bones (the exoccipitals dorsolaterally and the basioccipital midventrally) involved in forming the occipital condyle. This event enables determination of (near) adult size in fossil amniotes.
353. Oto-occipitals (exoccipital part) contact above foramen magnum to exclude supraoccipital: (0) absent; (1) present.
354. Metotic fissure: (0) open; (1) subdivided by contact of basal plate and otic capsule.
355. Mandibular symphysis: (0) anterior tips of dentary with distinct flat symphyseal area; (1) anterior tips of dentary smoothly rounded and without distinct symphyseal area.

356. Dentary anterodorsal edge of dental parapet at tip: (0) straight; (1) tipped down (and medially).
357. Dentary bowed ventrally along long axis: (0) straight to slightly bowed; (1) distinctly bowed ventrally. The degree of ventral bowing is nearly continuous and can even be more difficult to parse in cases where dentary shape is markedly transformed (e.g., some scolecophidians). It is most obvious in those cases where both dorsal and ventral margins are bowed ventrally (e.g., *Caserea dussumieri*), though they do not always coincide. Scored as 1 in those snakes with the dentary tipped down (and medially) at its terminus, so long as the dental parapet remains bowed ventrally near the middle of the element. Scored as 0 in those snakes in which the dentary may be bowed ventrally but has a nearly horizontal dental parapet dorsally.
358. Dentary overlaps postdentary bones laterally: (0) extensive; (1) reduced.
359. Dentary suspended from: (0) overlapping parts of coronoid, surangular, prearticular, splenial and angular; (1) surangular; (2) prearticular.
360. Dentary subdental shelf/gutter development in anterior part of dentary: (0) subdental shelf absent; (1) weakly developed subdental shelf; (2) pronounced subdental gutter.
361. Dentary, number of mental foramina on lateral surface: (0) none; (1) one; (2) two; (3) three; (4) four or more.
362. Dentary, size of posteriormost mental foramen: (0) same size as others; (1) enlarged relative to others.
363. Dentary mental foramen position: (0) near tip of dentary; (1) displaced caudally; (2) displaced further caudally.
364. Dentary coronoid process posterior termination: (0) below (or anterior) to level of coronoid apex; (1) just behind level of coronoid apex; (2) well posterior to level of coronoid apex.
365. Dentary subdental shelf hooks around anterior rim of the anterior inferior alveolar foramen: (0) absent; (1) present.
366. Dentary surangular process: (0) lies flat against the dorsolateral face of the surangular below the coronoid; (1) set in a posterodorsally trending groove, open dorsally, that supports it from below on the dorsolateral face of the surangular below the coronoid; (2) set in deep V-shaped, laterally-facing recess on dorsolateral face of surangular behind coronoid.
367. Dentary coronoid process posterodorsal extension: (0) absent or with only small dorsal extension; (1) large, but extending between lateral and medial processes of coronoid; (2) large, but extending dorsally to overlap most of anterolateral surface of coronoid; (3) extremely well developed, covering almost entire lateral surface of coronoid.
368. Dentary angular process reduced; (0) extends to or past coronoid apex; (1) extends anterior to coronoid apex; (2) extends anterior to level of coronoid bone. Regarded as indeterminable in species with an intramandibular joint, which is scored elsewhere.
369. Dentary posterior termination on lateral face of mandible: (0) below (or anterior to) level of coronoid apex; (1) just posterior to coronoid apex; (2) well posterior to level of coronoid apex; (3) nearly to posterior surangular foramen.
370. Dentary angular process prominently bifid: (0) absent; (1) present.

371. Meckel's canal: (0) opens medially for most of length; (1) opens ventrally anterior to anterior inferior alveolar foramen.
372. Dentary restriction of Meckel's canal: (0) does not restrict or enclose Meckelian canal; (1) lower dentary border of Meckel's canal folds up to approach closely upper border to restrict canal; (2) upper and lower borders form sutural contact anterior to splenial; (3) Meckel's canal closed and fused anterior to splenial.
373. Splenial attachment to dentary above Meckel's canal: (0) close throughout length; (1) loose, with dorsal dentary suture confined to posterodorsal corner of splenial.
374. Splenial: (0) present; (1) absent; (2) fused to dentary.
375. Splenial anterior extent: (0) around one-third (or less) length relative to dentary tooth row; (1) about one-half; (2) about two-thirds; (3) three-fourths (or more).
376. Splenial posterior extent: (0) extends posteriorly to or beyond apex of coronoid; (1) does not extend posteriorly to apex of coronoid.
377. Splenial-angular articulation: (0) splenial overlaps angular; (1) with ball on splenial (below level of posterior mylohyoid foramen) fitting into socket on angular; (2) with ball on angular fitting into socket on splenial; (3) flat, abutting joint.
378. Splenial anterior inferior alveolar foramen (aiaf) position relative to dentary: (0) enclosed entirely in splenial; (1) between splenial and dentary. Scored as 'missing' in those species in which the dorsal margin of the splenial, or the entire element, is reduced anterior to the aiaf. Some species, particularly stem acrodontans, but also *Shinisaurus crocodilurus*, have the aiaf in a high position, between the dentary and splenial, as in state 1, but still have the aiaf narrowly enclosed in the splenial as in state 0.
379. Splenial anterior inferior alveolar foramen position relative to anterior mylohyoid foramen: (0) anterodorsal; (1) dorsal to posterodorsal.
380. Angular: (0) present; (1) absent.
381. Angular posterior extent: (0) reaches mandibular condyle; (1) does not reach mandibular condyle.
382. Angular taller anteriorly, closely approaching coronoid (or, if coronoid absent, tooth-bearing margin of dentary above Meckelian canal): (0) absent, angular broadly separated from coronoid; (1) present; (2) with finger-like process over-arching Meckel's canal.
383. Angular medial exposure (relative degree of medial exposure scored with the teeth pointing straight up): (0) broad; (1) reduced; (2) narrow.
384. Posterior mylohyoid foramen position: (0) absent; (1) medial; (2) ventral; (3) lateral.
385. Posterior mylohyoid foramen position relative to coronoid apex: (0) below; (1) posterior; (2) anterior.
386. Coronoid eminence: (0) present; (1) absent.
387. Coronoid eminence composition: (0) formed by both surangular and coronoid; (1) formed exclusively by coronoid; (2) formed exclusively by surangular.

388. Coronoid anteromedial process fits into sulcus beneath tooth-bearing border of the dentary (at or behind end of tooth row): (0) absent; (1) present; (2) present, wrapping around the ventral margin of dentary tooth-bearing border at apex posteriorly.
389. Coronoid bone: (0) present, well developed; (1) present, small and strap-like; (2) absent.
390. Coronoid-surangular articulation: (0) coronoid restricted to medial aspect of mandible; (1) coronoid extends onto dorsal surface of surangular; (2) coronoid arches over dorsal margin of mandible to reach lateral face of surangular.
391. Coronoid, anteromedial process: (0) present; (1) absent.
392. Coronoid, anteromedial ventral margin (at/behind end of tooth row): (0) overlapped by splenial; (1) abuts splenial; (2) does not contact splenial.
393. Coronoid, posteromedial process: (0) absent; (1) present.
394. Coronoid, anterolateral dentary process: (0) absent; (1) present; (2) overlaps dentary past level of tooth row.
395. Coronoid, shape of anterolateral dentary process: (0) extends anteroventrally and smoothly tapers into dentary; (1) extends anteriorly, with dorsal and ventral margins more parallel-sided, terminating in a blunt edge anteriorly.
396. Surangular inserts into dentary lateral to the intramandibular septum, entering the intramandibular canal (which houses the alveolar branch of the inferior alveolar nerve, according to Oelrich 1956): (0) absent; (1) present slightly; (2) present deeply.
397. Surangular, external foramina: (0) two foramina, anterior and posterior; (1) single foramen (anterior surangular foramen).
398. Adductor fossa: (0) faces dorsomedially, medial wall below lateral wall; (1) faces dorsally, medial/lateral walls of same height; (2) no distinct medial wall; (3) faces dorsolaterally, lateral wall below medial wall.
399. Surangular adductor fossa on external face of mandible: (0) shallow and extends ventrally no more than halfway down; (1) deep and extends ventrally more than halfway down (nearly to angular bone).
400. Surangular dorsal margin: (0) nearly horizontal, rising somewhat toward the coronoid, anterodorsal edge set below the level of tooth crowns; (1) rises steeply anterodorsally to the coronoid, with apex reaching above the level of tooth crowns. The character is not scored in species lacking a coronoid eminence to avoid redundancy.
401. Prearticular and surangular fused in adults: (0) absent; (1) present.
402. Prearticular broadly contacts the surangular behind the posteromedial process of coronoid, restricting mandibular adductor fossa anteriorly: (0) absent; (1) present.
403. Prearticular crest: (0) absent; (1) present.
404. Retroarticular process: (0) present; (1) very short or absent.

405. Retroarticular process orientation (scored with teeth pointing straight up): (0) not inflected medially; (1) inflected medially.
406. Retroarticular process orientation in lateral (or posterior) view: (0) extends straight posteriorly; (1) inflected ventrally.
407. Retroarticular process dorsal surface: (0) horizontal; (1) inclined posterodorsally.
408. Retroarticular process emarginate distally: (0) absent; (1) present.
409. Retroarticular process, lateral notch forming waist proximally: (0) absent; (1) present.
410. Retroarticular process breadth (greatest width) relative to mandibular condyle (glenoid): (0) narrower; (1) wider.
411. Prearticular, pterygoideus process (angular process of Oelrich 1956) (i.e., part of retroarticular process): (0) absent; (1) present.
412. Premaxillary teeth (apart from median tooth): (0) of similar size or larger than anterior maxillary teeth; (1) distinctly smaller than anterior maxillary teeth.
413. Median premaxillary tooth: (0) absent; (1) present.
414. Enlarged median tooth on fused premaxilla: (0) median tooth same of size as other premaxillary teeth; (1) slightly enlarged median premaxillary tooth; (2) greatly enlarged median premaxillary tooth.
415. Maxillary tooth row extent posteriorly: (0) to roughly midorbit (or anterior); (1) to posterior third of orbit; (2) posterior to orbit.
416. Maxillary tooth crown height: (0) constant throughout tooth row; (1) length varies, resulting in sinuous occlusal surface; (2) length varies, resulting in convex occlusal surface; (3) length decreases posteriorly; (4) length increases posteriorly.
417. Maxilla, enlarged teeth ('fangs') (relative to adjacent teeth): (0) absent; (1) present on anterior maxilla; (2) present on posterior maxilla. Fangs of uncertain position on the maxilla—i.e., whether they are 'front' or 'rear' fangs—are scored as indeterminable. Unlike elapids, viperids have only fangs, and no other teeth, on the maxilla, so it cannot be determined whether or not those fangs are in the front or rear of the tooth row. *Lycophidion capense*, in which the single fang is neither at the anterior nor posterior end of the maxilla but in the middle of the tooth row, is also scored as indeterminable for this character.
418. Maxilla tooth row length: (0) to or behind midorbit; (1) anterior to midorbit; (2) anterior to orbit. Pregill *et al.* (1986). Unlike character 415, which tracks a lengthening tooth row, this character traces a shortening tooth row. Both start from a condition in which the tooth row extends roughly to the level of the middle of the orbit.
419. Premaxillary tooth count: (0) none; (1) one to three; (2) four to six; (3) seven to nine; (4) 10 or more.
420. Maxillary tooth count: (0) 0; (1) 2–5; (2) 7–15; (3) 16–27; (4) 31 or more.
421. Dentary tooth count: (0) 0; (1) 4–9; (2) 10–20; (3) 21–35; (4) 36 or more.

422. Marginal teeth: (0) all vertical; (1) all recurved; (2) anterior teeth recurved and posterior teeth vertical.
423. Position of marginal teeth relative to tooth-bearing element: (0) on medial side of tooth-bearing element; (1) near/on apical margin of tooth-bearing element.
424. Fusion of marginal teeth: (0) unfused to each other; (1) fused to each other.
425. Bases of marginal teeth: (0) smooth, dentine and enamel not infolded; (1) dentine and enamel infolded into pulp cavity ('plicidentine'), resulting in longitudinal grooves externally at the base of teeth.
426. Bases of marginal teeth expanded: (0) absent; (1) present.
427. Marginal tooth spacing: (0) crowns closely spaced; (1) crowns separated by large gaps.
428. Position of replacement teeth: (0) lingual; (1) posterolingual.
429. Orientation of replacement teeth: (0) erupt upright, growing straight upwards into functional position; (1) erupt horizontally, and then rotate through 90° about the base into functional position.
430. Tooth replacement: (0) present; (1) absent.
431. Resorption pits: (0) present; (1) absent.
432. Development of resorption pits: (0) at base of teeth; (1) on bony tooth pedicel.
433. Palatal teeth: (0) constant in size across palatal tooth row; (1) decrease in size posteriorly.
434. Cusps on posterior teeth: (0) unicuspid; (1) bicuspid; (2) tricuspid.
435. Venom groove on anteromedial surface of teeth: (0) absent; (1) present, unenclosed; (2) present, enclosed tube.
436. V-shaped wear facets of maxillary teeth incised on lateral face of dentary between dentary teeth: (0) absent; (1) present.
437. Teeth swollen, set off from tooth shafts above jaw parapet: (0) absent; (1) present.
438. Basihyal: (0) present; (1) absent.
439. Basihyal, relationship to skull (when mouth is closed): (0) anterior to braincase; (1) ventral to braincase; (2) posterior to braincase.
440. Hyoid, lingual process length: (0) short; (1) medium; (2) long.
441. Hyoid, distal part of lingual process: (0) not detached; (1) detached.
442. Free epibranchials (second epibranchial): (0) absent; (1) present.
443. Free epibranchial: (0) simple (short or sigmoidal); (1) complex (has hooks or processes, and/or doubles back on itself).
444. First epibranchial: (0) shorter than first ceratobranchial; (1) longer than or nearly equal to first ceratobranchial.

445. First ceratobranchial (in lateral view): (0) no dorsolateral angulation; (1) weak dorsolateral angulation (has a distinct bend); (2) strong dorsolateral angulation (90° or more); (3) entire element straight or oriented vertically.
446. Second ceratobranchials: (0) present; (1) absent.
447. Second ceratobranchial: (0) shorter than first ceratobranchial; (1) nearly equal to or longer than first ceratobranchial.
448. Second ceratobranchial apposed on midline: (0) absent; (1) present.
449. Large, wing-like hyoid cornu: (0) absent; (1) present.
450. Hyoid cornu: (0) less than the length of the epihyal; (1) greater than or equal to the length of the epihyal.
451. Epihyal: (0) meets hyoid cornu at (or near) its distal end; (1) meets hyoid cornu along its body.
452. Epihyal: (0) expansion or elaboration at proximal end absent; (1) simple expansion at proximal end present; (2) hook-like elaboration at proximal end present; (3) lateral flange at proximal end present; (4) medial flange at proximal end present.
453. Lateral flange at midpoint of epihyal: (0) absent; (1) present.
454. Presacral vertebrae number reduction: (0) 24 or more presacrals; (1) 23 presacrals; (2) fewer than 23 presacrals.
455. Presacral vertebrae number increase I: (0) 24 or fewer; (1) 25; (2) 26; (3) 27; (4) 28 or more. For characters 455–458, in the absence of a sacral attachment, the last trunk vertebra in here is considered to be the first bearing a distally bifid rib.
456. Presacral vertebrae number increase II: (0) 32 presacrals or fewer; (1) 33–39; (2) 50–55; (3) 61–84; (4) 89 or more (ordered).
457. Presacral vertebrae number increase III: (0) less than 104; (1) 118–132; (2) 144–156; (3) 168–180; (4) 184 or more.
458. Presacral vertebrae number increase IV: (0) less than 193; (1) 197–209; (2) more than 219.
459. Cervical vertebra number reduction: (0) six or more; (1) five; (2) four; (3) three; (4) two. For characters 459–460, ‘cervical’ refers to those anterior vertebrae retaining a primitive rib morphology (short and broad, with pointed cartilaginous apices); the two following ribs between the shoulders that are distinctly longer, narrower, and have blunt, unfinished bony apices, are here considered post-cervical. That yields a primitive count of six for lizards and other amniotes, rather than the usual count of eight based on the first vertebrae whose cartilaginous ventral rib segment contacts the cartilaginous sternum (see character 477).
460. Cervical vertebrae number increase: (0) six or fewer; (1) seven; (2) eight or more.
461. Cervical intercentrum position: (0) intercentral; (1) posterior end of preceding centrum; (2) anterior end of following centrum; (3) absent.



462. Cervical rib ossified portion shape: (0) widens distally, at least in last cervical; (1) tapers distally.
463. Cervical ribs start on vertebra number: (0) two; (1) three; (2) four; (3) five; (4) six.
464. Cervical intercentrum length relative to pedicle length: (0) intercentrum longer than pedicle; (1) intercentrum shorter than pedicle.
465. Cervical pedicle (outgrowth of pleurocentrum to which intercentrum may attach): (0) absent; (1) projecting ventrally with discrete fore and aft margins.
466. Vertebral pedicle ('hypapophysis') posterior extent: (0) in anterior half of vertebral column; (1) throughout vertebral column.
467. Vertebral centrum articulation: (0) amphicoelous (and notochordal); (1) procoelous.
468. Zygosphene-zygantrum accessory intervertebral articulations: (0) absent; (1) dorsolaterally directed facet continuous with prezygapophyseal articulation located just up edge of neural arch; (2) tall, laterally directed facet continuous with prezygapophyseal articulation and extending as high as top as neural canal; (3) separate facet set on distinct pedicle and facing ventrolaterally.
469. Vertebrae (and ribs), mid-dorsals are pachyostotic: (0) absent; (1) present.
470. Caudal autotomic septum position relative to caudal rib: (0) within caudal rib; (1) anterior to caudal rib; (2) posterior to caudal rib; (3) absent. Fracture plane position could be regarded as a continuous variable. Specimens chosen to typify states 0 and 1 indicate the arbitrary distinction used here, i.e., "is any part of the rib traversed by the autotomic septum?"
471. Caudal rib (transverse process) shape: (0) single rib without basal foramen; (1) foramen passing through base of rib; (2) divergent bifid ribs on some caudals.
472. Posterior caudal vertebrae, groove on dorsal surface of neural spines: (0) absent; (1) present.
473. Caudal vertebrae, pterapophysis: (0) absent; (1) present.
474. Caudal vertebrae, distal tip of anterior zygapophyses: (0) undifferentiated; (1) elaborated into a horizontal blade.
475. Caudal haemal arch (intercentrum) position: (0) intercentral, pedicles feeble/absent; (1) contacting mainly condyle but also distinct pedicles beneath preceding centrum; (2) mainly contacting pedicles on preceding centrum but still bordering condyle; (3) well forward of condyle on preceding centrum.
476. Caudal haemal arch pedicle length: (0) short; (1) long.
477. Vertebra whose rib first attaches to sternum: (0) seventh (or more anteriorly); (1) eighth; (2) ninth.
478. Trunk ribs pachyostotic: (0) slender, cancellous ribs; (1) thick, dense ribs.
479. Postcloacal bones: (0) absent; (1) present.
480. Sternum: (0) present; (1) absent.
481. Sternal fontanelle: (0) absent; (1) present.

482. Sternal fontanelle number: (0) single; (1) double.
483. Number of rib attachment points to sternum (including attachment of xiphisternum): (0) five; (1) four; (2) three; (3) two or fewer.
484. Xiphisternum: (0) present; (1) absent.
485. Xiphisternal fontanelle: (0) absent; (1) present.
486. Number of xiphisternal rib attachment points: (0) none; (1) one; (2) two; (3) three; (4) four.
487. Number of postxiphisternal (or poststernal) inscriptional ribs united along the ventral midline to form continuous chevron shaped structures: (0) 0; (1) 1–4; (2) 5–11; (3) 12–30; (4) more than 31.
488. Scapulocoracoid: (0) large; (1) reduced; (2) absent.
489. Scapula: (0) short and wide; (1) elongate and thin.
490. Suprascapular cartilage: (0) present; (1) absent.
491. Suprascapula: (0) large (approximately equal in length to scapula); (1) small.
492. Scapula, emargination on anterodorsal edge (scapular fenestra): (0) absent; (1) present.
493. Scapulocoracoid emargination: (0) absent; (1) present.
494. Scapulocoracoid emargination: (0) closed by cartilage; (1) open; (2) closed by scapula and coracoid.
495. Coracoid, anterior (primary) emargination (fenestra): (0) absent; (1) present.
496. Coracoid, posterior (secondary) emargination (fenestra): (0) absent; (1) present.
497. Coracoid size: (0) enlarged, extending anteriorly to level of clavicles; (1) not enlarged, not extending anteriorly to level of clavicles.
498. Epicoracoid cartilage extent: (0) contacts mesoscapula and suprascapula; (1) does not contact mesoscapula and suprascapula.
499. Clavicle: (0) present; (1) absent.
500. Clavicle: (0) no notch or fenestration present; (1) notch present; (2) fenestration present.
501. Clavicle: (0) rod-like; (1) greatly expanded proximally.
502. Clavicular angulation: (0) simple curved rod, following contour of scapulocoracoid; (1) strongly angulated, curving anteriorly away from scapulocoracoid.
503. Distal clavicle articulation: (0) with scapula; (1) with suprascapula; (2) no distal articulation.
504. Clavicles, medial contact: (0) clavicles do not meet on midline; (1) clavicles meet on midline.
505. Interclavicle: (0) present; (1) absent.

506. Interclavicle lateral process: (0) present; (1) absent.
507. Interclavicle anterior process (extending beyond lateral process): (0) absent; (1) present.
508. Interclavicle anterior process, length (as ratio of interclavicle length): (0) 0.01–0.20; (1) more than 0.20.
509. Interclavicle, anterior end: (0) ventral to clavicles; (1) dorsal to clavicles; (2) abuts clavicles; (3) lies posterior to clavicles.
510. Pubis: (0) present; (1) absent.
511. Pubis, symphyseal process orientation in ventral view: (0) medially directed; (1) anteromedially directed.
512. Pubis, symphyseal process: (0) thick; (1) thin.
513. Pubis, symphyseal process: (0) expanded distally; (1) tapered, not expanded distally.
514. Pectineal (pubic) tubercle: (0) closer to acetabulum than to symphysis; (1) closer to symphysis than to acetabulum (or equal distance).
515. Pubis, tubercle orientation in ventral view: (0) anteriorly directed; (1) ventrally directed.
516. Ischium: (0) present; (1) absent.
517. Ischial tubercle: (0) present; (1) absent, or continuous with hypoischial cartilage.
518. Hypoischium: (0) well developed (expanded at distal end); (1) vestigial (no expansion at distal end); (2) absent (ordered).
519. Hypoischial foramen: (0) absent; (1) present.
520. Ilium: (0) present; (1) absent.
521. Ilium, tubercle: (0) present; (1) absent.
522. Ilium, blade orientation: (0) slopes posterodorsally; (1) oriented vertically; (2) oriented anteriorly.
523. Ilium, dorsal end blades: (0) not compressed laterally, and do not expand or converge dorsomedially; (1) compressed laterally, suprailiac cartilages expanded into triangular plates that converge dorsomedially.
524. Pelvic elements (ilium, ischium, pubis): (0) in close sutural contact throughout postnatal ontogeny and co-ossified into a single pelvic bone late in postnatal ontogeny; (1) distinct elements weakly united in non-sutural contacts.
525. Hyperischium: (0) present; (1) absent.
526. Hyperischial foramen: (0) absent; (1) present.
527. Epiphyses on long bones: (0) present; (1) absent.

528. Proximal forelimb long bones (humerus, radius and ulna): (0) present; (1) absent.
529. Ratio of radius/ulna to humerus: (0) 0.50–0.61; (1) 0.62–0.97; (2) 0.98–1.10.
530. Ectepicondylar foramen: (0) present; (1) absent.
531. Ulnar patella: (0) present; (1) absent.
532. Ulna, olecranon process on proximal epiphysis: (0) prominent; (1) short or absent.
533. Ulna, enlarged distal epiphysis that is nearly hemispherical in profile and fits into a concomitantly enlarged depression on the ulnare: (0) absent; (1) present.
534. Radius, styloid process: (0) absent; (1) present on posterolateral surface of distal epiphysis.
535. Carpal intermedium: (0) large; (1) small; (2) absent.
536. Ball and socket intercarpal joint formed by large central carpal or lateral centrale (ball) and radiale, ulnare and pisiform (socket): (0) absent; (1) present.
537. Lateral centrale in hand: (0) separated from second distal carpal; (1) contacting second distal carpal.
538. Proximal end of first metacarpal: (0) separated from medial centrale; (1) contacting medial centrale.
539. Palmar sesamoid: (0) absent; (1) present.
540. Metacarpals II–IV: (0) longer than proximal phalanges; (1) shorter than proximal phalanges.
541. Metacarpals, sesamoids ventral to distal heads: (0) absent; (1) present.
542. Phalangeal count, reduction in manus digits II–IV: (0) three, four, five; (1) reduced to three digits in III and IV; (2) reduced to four in digit IV; (3) reduced to three in digit III and four in digit IV.
543. Phalangeal count, digit V of manus: (0) three; (1) two; (2) four.
544. Hyperphalangy in manus: (0) absent; (1) present in more than one digit; (2) present only in digit I; (3) present only in digit V.
545. Opposing digits in manus: (0) digits nonopposing; (1) digits I, II and III opposing digits IV and V.
546. Penultimate phalanges in hand: (0) shorter than or equal to antepenultimate; (1) longer than antepenultimate.
547. Sesamoids dorsal to distal heads of penultimate phalanges (manus): (0) present; (1) absent.
548. Femur: (0) present; (1) absent.
550. Femur, internal trochanter: (0) well developed as a prominent, distinct head; (1) poorly developed or absent.
551. Tibial patella: (0) present; (1) absent.
552. Tibial lunula: (0) present; (1) absent.

553. Fibular lunula: (0) present; (1) absent.
554. Dorsal and ventral tibiofemoral lunulae: (0) both present and separate; (1) ventral present, dorsal absent; (2) both absent; (3) both present and fused; (4) dorsal present, ventral absent.
555. Tibia, notching of distal epiphysis: (0) notch not present, epiphysis gently convex for astragalocalcaneal articulation; (1) distinct notch present, fitting onto a ridge on the astragalocalcaneum.
556. Fibulo-astragalar joint: (0) occupies less than half of distal end of fibula; (1) involves most of distal end of fibula.
557. Tibia and fibula: (0) remain widely separated at distal ends; (1) very close or in contact at distal ends.
558. Ball and socket intertarsal joint formed by distal tarsal 4 (ball) and astragalocalcaneum (socket): (0) absent; (1) present.
559. Third distal tarsal: (0) present; (1) absent.
560. Second distal tarsal: (0) present; (1) absent.
561. Astragalus and calcaneum: (0) fused with no suture visible in adult; (1) co-ossified with suture visible; (2) separated.
562. Sesamoid between metatarsal I and astragalocalcaneum (ventrally): (0) present; (1) absent.
563. Metatarsals II–IV: (0) longer than proximal phalanges; (1) shorter than proximal phalanges.
564. Metatarsal V: (0) hooked; (1) broad proximally, but not hooked.
565. Metatarsals, sesamoids ventral to distal heads: (0) absent; (1) present.
566. Phalangeal counts, reduction in pes: (0) two, three, four, five, four; (1) reduced to three phalanges in digits III, IV and V; (2) reduced to four phalanges in digit IV and three phalanges in digit V; (3) reduced to two phalanges in digit V; (4) reduced to three phalanges in digit V.
567. Hyperphalangy in digits of pes: (0) absent; (1) present in more than one digit; (2) present only in digit V.
568. Opposing digits in pes: (0) digits non-opposing; (1) digits I and II opposing digits III, IV and V.
569. Sesamoids dorsal to distal heads of penultimate phalanges: (0) present; (1) absent.
570. Osteoderms on body (and/or tail): (0) not imbricate; (1) imbricate, with gliding surface anteriorly; (2) imbricate anteroposteriorly (with gliding surface), but interdigitate laterally.
571. Osteoderm ornamentation: (0) vermiculate or smooth; (1) tuberculate.
572. Dermal skull bone ornamentation: (0) smooth; (1) lightly rugose about frontoparietal suture; (2) present over dorsum; (3) present on jugal postorbital bar.
573. Palpebral osteoderm below supraorbital scales (and their osteoderms): (0) absent; (1) present.
574. Supracilliary osteoderm (pierced vertically by foramina): (0) absent; (1) present.

575. Osteoderms inside supraorbital scales: (0) absent; (1) single; (2) compound.
576. Supraorbital osteoderms insert into sulcus along frontal supraorbital margin: (0) absent; (1) present.
577. Osteoderms in cheek scales: (0) absent; (1) single; (2) compound.
578. Osteoderms in gular scales: (0) absent; (1) single; (2) compound.
579. Osteoderms in dorsal scales: (0) absent; (1) single; (2) compound.
580. Osteoderms in ventral scales: (0) absent; (1) single; (2) compound.
581. Osteoderms in skull roof scales: (0) single; (1) compound.
582. Osteoderms invest imbricate caudal scales: (0) absent; (1) present.
583. Mineralized cranial scale hinges: (0) absent; (1) present.
584. Scleral ossicle count: (0) 16 or more; (1) 14–15; (2) 12–13; (3) 11 or fewer.
585. Scleral ossicles: (0) complex and irregular in shape; (1) square or rectangular in shape.
586. Interorbital septum: (0) present; (1) absent.
587. Statolith masses: (0) absent; (1) present.
588. Calcified endolymph: (0) absent; (1) present, but confined to occiput; (2) present, extends posteriorly into neck.
589. Foretongue retracts into hind tongue: (0) absent; (1) present; (2) tongue can be retracted entirely into buccal cavity below larynx.
590. Tongue tip notching, as percentage of tongue length: (0) no notch; (1) less than 10%; (2) 10–20%; (3) 20–40%; (4) more than 45%.
591. Tongue papilla crenellated: (0) continuous smooth distal edges of papilla; (1) crenellated distal edge.
592. Tongue papilla shape: (0) long, filamentous, and densely packed papillae; (1) shorter, larger, somewhat compressed and tipped caudally (scale-like papilla); (2) deeply imbricate flat scales.
593. Hindtongue epithelium: (0) discrete papillae (filamentous or scale-like); (1) transverse plicae confined to lateral margins of posterior lobes; (2) transverse plicae extend across hindtongue; (3) and into the anterior half of the tongue.
594. Infralingual folds: (0) absent; (1) present.
595. Papilla on ventrolateral margins of entire tongue: (0) papillose; (1) plicate (transverse scale rows). Plicae passing around dorsolateral margins of posterior lobes formed from broad and/or fused papillae in gekkotans; those running along the entire ventrolateral margins of tongue are composed of fused scale-like papillae in scincomorphs.
596. Tongue papilla arrangement: (0) not in oblique rows; (1) arranged in regular oblique rows.

597. Hypoglossal muscle: (0) paired and smooth ventrally; (1) multiple, and with fine transverse grooves beneath each muscle bundle.
598. Facial tongue wiping (tongue acts as an accessory eyelid): (0) absent; (1) present.
599. Foretongue surface: (0) papillose; (1) smooth.
600. Foretongue filamentous epithelium anterior extent: (0) extends to tongue tip as long filaments; (1) those overlying chemosensory part of tongue are depressed to varying degrees.
601. Arrowhead tongue tip: (0) tongue lateral margins continuous at tip; (1) notched just behind tip.
602. Tongue width across posterior notch/maximum tongue length: (0) 50–60%; (1) 40–44%; (2) 30–35%; (3) 22–25%; (4) less than 12%.
603. Hind tongue papilla: (0) not sharply pointed; (1) sharply pointed.
604. Prey prehension: (0) crickets (or larger animals) taken primarily with tongue; (1) primarily with jaws.
605. Amniote penis: (0) absent; (1) hemipenis present. See character 606(3).
606. Hemipenis mineralizations: (0) absent; (1) comb-like; (2) sleeve-like; (3) spine-like.
607. Rectus abdominis muscles: (0) not attached to belly skin; (1) attached to hinges between ventral transverse scale rows.
608. Ulnar nerve pathway: (0) superficial to limb muscles; (1) deep to limb muscles.
609. Dorsal shank muscle innervation: (0) peroneal nerve; (1) interosseous nerve.
610. Ovipary vs ovovivipary/vivipary: (0) ovipary; (1) ovovivipary to vivipary.

Taxon and Character Matrix, used in Morphological Analysis of Squamate Phylogeny. Nexus file input, also supplied as supplemental material.

#NEXUS

BEGIN DATA;

DIMENSIONS NTAX=196 NCHAR=610;

FORMAT SYMBOLS="0 1 2 3 4" MISSING=? GAP =-;

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 0001010020 0000200000 0000000010 0?00001010 1200102100 0000000010 00000??01? 0000000??0  
 00?0000001 10000?0??0 10?0000001 ?0?01?111? 0000?00000 000?0000?0 000010?0?0 1001121000  
 0000010000 00000100?0 0?0000?0?? 0001010000 0000010000 0101000001 40?10?0110 0200100110  
 1001001202 0110?00000 0000000000 100?000023 2200000?00 0002000001 0100100100 0400000000  
 012?0?1303 0???101000 0?00020000 0111110100 0011000?20 0010000010 0000000010 0011201110  
 0000010000 0010011001 010000000? ?2000?0000 ?001001001 000000?00? 0?00100010

*Gambelia\_wislizenii* 10000?0000 00000?0000 0101000010 000??10010 000?0?0000 000001120?  
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*Enyalioides\_laticeps* 1000002000 20100?0000 0001000011 000??10000 000?0?0200 000001120?  
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 00?0000001 00000?0??0 10?0010001 ?0?11?131? 0000?00000 000?0000?0 000010?0?0 1001121000  
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*Morunasaurus\_annularis* 100000200? 20000?00?0 0101000011 000??11000 000?0?0200 000001120?  
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*Brachylophus\_fasciatus* 1000000000 00000?0000 0001100010 000??10000 000?0?0?10 000001120?  
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 0000000010 0011201110 0000010000 ???011001 1?0000000? ?2000?0000 ?0010010?? ??????????  
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Armandisaurus\_explorator 000001000 000000000 000100010 000010000 000000200 000001120?  
020000000 200000011 000000100 000000000 011020000 111201000 000000001 000001000  
0001000020 000020000 000000000 000011010 120000000 000000010 000000010 000000000?  
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000000000 000000000 000000000 000000000 000000000 000000000 400100000 030000010  
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Dipsosaurus\_dorsalis 100000{12}000 100000000 0001100010 000010000 000000200 000001120?  
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Sauromalus\_ater 100000{12}000 000000000 0001000010 000010000 000000300 000001120?  
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0130001300 2000101000 0000020000 0001010000 0011000020 00100000{01}10 0000000010  
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Liolaemus\_bellii 100000000 000000000 0001100010 000010030 000000100 000001121?  
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Phymaturus\_palluma 1000002000 000000000 0001100010 000010000 000000100 000001121?  
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Chalarodon\_madagascariensis 1000001000 000000000 0001000010 1000010000 000000200  
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*Oplurus cyclurus* 10000?0000 00000?0000 0001000010 100??10000 000?0?0400 000001120?  
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*Petrosaurus mearnsi* 1000001000 00000?0100 0101000011 000??10000 000?0?0000 000001121?  
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*Uta stansburiana* 10000?0000 00000?0000 0001000011 000??10000 000?0?0000 000001121?  
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*Sceloporus variabilis* 10000?0000 00000?0000 0001000011 000??10000 000?0?0100 000001120?  
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*Phrynosoma platyrhinos* 1000001000 00000?0000 0??1100011 000??10000 000?0?0100 000001120?  
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Uma\_scoparia 100000{12}000 00000?0000 0001100011 000??10000 000?0?0000 000001121?  
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Leiocephalus\_barahonensis 10000?0000 00000?0000 0001200010 000??10010 000?0?0200 000001120?  
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Plica\_plica 1010001000 20?00?0000 000?000011 000??10000 000?0?0300 000001120? ?020000000  
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00002?0000 0000000100 0?00001010 120010?100 0000000010 00000??01? 0000000??0 00?0000001  
11000?0??0 10?0000001 ?0?11?121? 0000?00000 000?0000?0 000010?0?0 1000121000 0000010000  
0000?100?0 0?0000?0?? 0001010000 0?01010000 01010000?1 40?2000020 ?3?00?0101 10?2101002  
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Stenocercus\_guentheri 1000001000 00000?0100 0001000010 000??10000 000?0?0300 000001120?  
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Uranoscodon\_superciliosus 10000?0000 00000?0000 0001000011 000??10000 000?0?0300 000001120?  
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Tchingisaurus\_multivagus 10000?0?0? 0??00????? ???????0?0 0?0??0?010 000?0?0?10 0000021?0?  
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00?000???? 0?0??????? 0?0?1?00?? ????????1? ?00?0?00? ?????????? ???????0? ?0?0????00  
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Gobinatus\_arenosus 1000?0?00 00100?00?0 0?1?0000? 000?0?10?0 000?0?0?20 000002110?  
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Adamisaurus\_magnidentatus 10100????? 0?100?00?0 000?000000 000?0?1040 000?0?0?10 0000021?0?  
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Gilmoreteius 10?00????? ?00?0?0000 0?0??00000 ?0?0?000?0 000?0?0?30 0?00021?0? ?001000000  
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Polyglyphanodon\_sternbergi 1000001000 00000?00?0 0001000000 000?0?1040 000?0?0?20 000002110?  
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Sineoamphisbaena\_hexatabularis 10000????? ?00?0?0000 ?00?000000 ?0?0?001?? ??????????  
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Adriosaurus\_suessi 1?100????? ?????????? ?????????? ?0?00????? ?????0??10 0?0?0?1??? ?????0?00??  
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Pontosaurus 10100?0?11 10000?0?11 ?????0000?0 0????10?? ?0????400 000001110? ?2??0?0000  
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2?0??00?? ?0000?0?00 ?0????????? ??????????? ???????????

Aigialosaurus\_dalmaticus ?????????? ??????????11 ??????????0 ?????1????? ???????400 000?0?110?  
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Clidastes 1110012?02 1?000??11 ?????1????? ?????100?0 000??0??1 10000??10? ?2??0?00??  
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0001?2?0?0? 0000000000 0?00001010 1200?1????? ?0?0?????? ??????????? ??????????? ???????????  
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02?11?0?01 ?00?????? 000?000222 2100001110 01?0000??? ??????????? ?0410000 21001013?3  
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Platecarpus 1110012?02 1?000??11 ??????????0 ?????100?0 000??0??1 100?0??10? ?2??0?000?  
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02011?1?00 ?000?????0? 000?000222 3010001?00 0110000??? ??????????? ?0400000 21001013?3  
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Plotosaurus 1?10012?02 10000??11 0????100?0 ?????100?0 000??0?01 10000??10? ?2??0?00??  
0?0?000300 003??11?0 ?0202000? 011000003? 0??010100 0001000?20 0000000000 000100?020  
00012?010? 0000000000 0?0000?010 1200?1?00? ?????00010 ?000??1?? ?0010?0?0? 00?00000??  
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010110?001 ?000100001 000?000223 2210001100 0110000??? ?????????? ???0420000 21?01010?3  
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Tylosaurus 1110012?02 1?000??11 ?????1???0 ?????100?0 000??0?01 100?0??10? ?2??0?00??  
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 00012?0?0? 0000000000 0?00001010 1200?1???? ?????????? ?00?????? ??????0?? ??????????  
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Eichstaettisaurus 0?0?0?0?00 ?000?0100 0?0?000?0 000?001?0 0?0?0?100 00?01?10? ?00?000000  
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 0??????0?? ???????00? ??????????0? ?1?????????0 00??0?0??0 0000?0001? ?0??10????? ?00001?000  
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AMNH\_FR\_21444 ?????????? ??????????0? ??????????0 000?000130 ?00?0?0300 000001010? ?00?000000  
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Delma\_borea 1000001001 00100?0000 0120000000 000??10330 00000?0?20 000101410? ?0000?01?1  
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 ?2??0?011? ?????1?00 ?000??210 1200401300 0000000011 00011??01? 0000000??1 00?0000001  
 00010?1?0 30?0000002 ?0?01?121? 0000?01?0 011?0000?0 ???2?1?0?0 0001120000 0000101000  
 010?0?0??0 0?0000?0?? 0000010000 0?0?012000 01010000?2 30?2000020 030000?001 ???0?01002  
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Lialis\_burtonis 10010?0001 00000?02?0 01100000?0 000??11330 00100?0?0?0 0001011?0? ?0000?01?0  
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 0011000010 1000000000 0010000044 4100001000 00?0000011 0100100000 0000420030 011?0?1002  
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Strophurus\_ciliaris 10000?0000 00000?0000 ?000000010 000??10330 00300?0300 000001020?  
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1001?00020 ?2????01?? ?????????? ???????210 1200401201 0000000011 00010??01? 0000000??0  
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Rhacodactylus\_auriculatus 10000?0000 00100?01?0 0100000000 000??11320 00300?0?11 0000011?0?  
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00?0000001 00010?0??0 30?0000002 ?1?01?131? 0000?01??0 011?1000?0 ??2?21?0?0 0100120000  
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Saltuarius\_cornutus 0000002000 20100?0000 0110000000 000??10330 00300?0301 000001110?  
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1001?00120 ?2????001? ??????00200 0?0000?210 120040?300 0010000011 00010??01? 0000100??0  
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Aeluroscalobates\_felinus 1000002000 00100?00?0 0000000000 000??11310 00100?0300 000001110?  
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0001100??0

Coleonyx\_variegatus 10000?0000 00100000?0 0000000010 000??11310 00000?0300 000001110?  
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002??1102 0??0?1010 0?10020010 0012101002 1011001110 00101002?0 10001?0010 0011201100  
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Eublepharis\_macularius 10000?0000 00100?00?0 0010000000 000??11310 00000?0300 000001110?  
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1003101002 0011000000 ?000000001 0010000144 4000000000 00?0000011 0110100001 0200200000  
002?0?1102 0???0?1010 0?100200{01}0 0010100102 {01}?11001100 0111{01}00100 10001?0010  
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*Teratoscincus\_przewalskii* 10000?0000 10000?0100 0100000000 000??00310 00200?0300 000001110?  
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1000?0?010 ??????011? ??????1???? ???????210 1200?02300 0000000011 000011??1? 0010100??0  
00?0100001 00010?0??0 30?0000002 ?0?21?131? 0000?01??0 010?0000?0 ??2?20?0?0 0100120000  
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002?0?0102 0???0?1000 0?????0000 00101?0?02 1011001110 0011001{01}00 10001?0020 ?011?011?0  
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*Gonatodes\_albogularis* 10000?0001 10000?01?0 0100000000 000??11320 00200?0400 000001110?  
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0000?00010 ?2????011? ?????????? ???????210 120030?301 0000000011 00011??11? 0000000??0  
00?0000001 00010?0??0 30?0000012 01?21?131? 0000?01??0 111?0000?0 ??2?21?0?0 0000120000  
0000100100 0000?1?0?0 3?0000?2?? 0001010000 1?00011000 01010000?2 40?0001020 0300?0?0?1  
1??3101002 001100000? 1000000010 0010000143 3000000000 00?0000011 0110100000 0200200000  
002??0102 0?????1000 0?10020000 0010100000 0011001110 0011{01}002?0 10001?0010 0011201100  
1000010000 000{03}110001 0000100000? ?0000?0000 ?001001201 0010001101 000110?000

*Phelsuma\_lineata* 10000?0000 00000?12?0 0120000000 000??11320 00100?0?10 000001110?  
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1000?00000 ?2????011? ??????00000 0?0000?210 1200302301 0000000011 00011??01? 0000000??0  
00?0100001 00010?0??? 30?0000012 01?21?131? 0000?01??0 011?0000?0 ??2?21?0?0 0000120000  
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002?0?0102 0???0?1000 0?10020000 0011110102 101101??10 1{01}10000100 0000000010 0011201100  
0000001000 0000110001 000000001? ?0000?0000 ?001{01}01001 0010001101 0001100??0

*Gekko\_gecko* 10000?0000 00100?02?0 0100000000 000??11310 00200?0300 000001110? ?0000?01?1  
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0000?0??0 0?0000?2?? 0001010000 1?00012000 01010000?2 40?0000010 030000?001 1??3101002  
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*Lacerta\_viridis* 10000?0000 00100?02?0 0111000000 000??01040 000?0?0?10 000002100? ?00001300?  
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*Takydromus\_ocellatus* 1000001000 00000?02?0 0121000000 000??01010 000?0?0?10 000001400?  
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0201101000

Colobosaura\_modesta 1001101001 20100?00?0 0121000010 000??11020 000?0?0?20 000000?00?  
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Pholidobolus\_montium 1001101001 20100?01?0 0120000000 000??11330 00000?0300 000000?00?  
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0000?00000 0001101000 0100100100 0?00001110 1100102100 0000000011 100110?01? 0010101??1  
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Callopiastes\_maculatus 10000?0000 00000?0000 0101000010 000??10000 000?0?0300 000002110?  
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Tupinambis\_teguixin 10000?0000 00000001?0 0111000010 000??11000 000?0?0300 000002410?  
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0201101110

Aspidoscelis\_tigris 10000?0000 00100?0100 0100000010 000??10000 000?0?0300 000002110?  
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1021001102 0012000010 1010000000 0110000133 3000000000 00?1000011 1110100011 1000200000  
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0000010000 0001110001 010000000? ?2000?0000 ?001001004 0201010001 0301101??0

Teius\_teyou 10000?0000 00100?0000 0100000010 000??10000 000?0?0400 000002110? ?001010000  
0?0?000200 012?0?1110 ??0003000? 0111?00010 0014011000 0000000201 0000000000 0000100020  
00002?1000 0000000000 0?00001110 1100102200 0000000011 100010?01? 0110101??1 02?0000001  
20100?0??0 20?0000003 ?0?11?101? 1000?00100 111?2000?0 101020?0?0 1001121000 0000100000  
0001?100?0 0?0000?0? 0001110000 1?00010100 01010100?1 40?0000100 0000300010 1021001102  
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2??0?1000 1010020000 0011110102 1011001010 00111000{01}0 00000{01}0011 1011{12}01110  
0000010000 000111{01}001 01000?000? ?1000?0000 ?001001004 0201010001 0301101110

Paramacellodus 100?002000 00000?01?0 01?00000?? 000?0?0?010 000?0?0?0?0 0000000?? ???? ??????  
????????? ???????1?2 ??001000?? 011000?0?0 0013011000 0000000100 0000?0??? ?00?000000  
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Parmeosaurus\_scutatus 1000001?00 00000?0?0 0?00000000 000??01010 000?0?0?30 00000?110?  
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Tepexisaurus\_tepexii 10000??0? ????0??0?? ????0??0?? ????0??0?0 ?0??0?0?4? 0??0?1?? ?2??0?000?  
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Cricosaura\_typica 10000?0002 00000??200 012??00010 000??11330 00000?0?30 000001110?  
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00?0000001 10000?0??1 20?1000003 ?0?11?131? 0000?01?? 111?3000?0 010020?0?0 1000121000  
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0?01101001

Palaeoxantusia\_sp. 10000?0?00 10000?01?0 0????00000 000??01030 000?0?0?30 000001110?  
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00?00??1? ?0000??2 20?1000003 ?0?11?1?1? ?000?01??0 111?3000?0 01002??0?0 ??0?12?000  
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Xantusia\_vigilis 10000?0200 1000000100 0121100000 000??01030 000?0?0?20 000001010? ?200000000  
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Platysaurus\_imperator 1000012200 00000?01?0 0100000000 000??01030 000?0?0?300 000001110?  
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00?0000001 00000?0??0 30?1100003 ?0?11?131? 0000?01??0 011?2000?0 001020?0?0 1000121000  
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Cordylus\_mossambicus 1000012000 20000?0200 0120000000 000??10030 000?0?0?400 000001110?  
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Zonosaurus\_ornatus 1000001000 00100?0100 0120000000 000??00030 000?0?0?30 000001110?  
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002?0?1101 0???101000 0?10120000 0011100102 1111001110 1110100110 1000000010 0011{12}01110  
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Cordylosaurus\_subtesselatus 1000001000 00000?01?0 0120000000 000??00030 000?0?0400 000001010?  
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000?101??0

Myrmecodaptia\_microphagosa 0000012?00 00000?0??0 0?00?0000? ??0??11010 010?0?0300  
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Globaura\_venusta 0000002000 00000?01?0 0120000010 000??11010 000?0?0300 0000021?0?  
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?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ??????????  
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Hymenosaurus\_clarki ?????????? ?????????? ??????????0 ?0?0?0?0?0 00?0?0?4? 0?000?????  
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Eoxanta\_lacertifrons 0?000?0?00 00000?01?0 0121000010 000??01110 000?0?0?2? 000002110?  
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?00000000 ?00000000 ?2?0????? ?00000000 ?00000000 ?00000000 ?00000000 ?00000000

Plestiodon\_fasciatus 00000?0000 00000002?0 0120000000 000??01020 000?0?0?20 000001110?  
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Scincus\_ ?02000{12}000 ?0000?02?0 0101000000 000??01020 000?0?0400 000001110? ?20?01201?  
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10000?0??2 20?0100023 00?01?131? 0000?00000 010?1001?0 ?01020?0?0 0000121000 0000100000  
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Brachymeles\_gracilis 00000?0000 00000?02?0 0120000000 000??01030 000?0?0?0?0 000001110?  
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00?0000201 10000?0??1 20?0100023 10?11?131? 0000?01??0 010?1001?0 ??2?20?0?0 0000121000  
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0110000000 0000110001 0100{01}?20001 0210202222 1102001001 120010??01 1?0?100???

Acontias\_percivali 0001001000 00000?01?0 0100000000 000??01230 000?0?0??1 000001110?  
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Amphiglossus\_splendidus 0000001000 00000?02?0 0120000000 000??01030 000?0?0400 000001110?  
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*Feylinia\_polylepis* 1000001000 00000?12?0 0100000100 000??01020 000?0?0??0 0001011?0?  
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*Trachylepis\_quinquetaeniata* 00000?0000 00000?02?0 0100000000 000??11010 000?0?0300 000001110?  
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*Sphenomorphus\_solomonis* 00000?0000 00000?01?0 0120000000 000??11110 000?0?0?30 000001110?  
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*Eugongylus\_rufescens* 10000?0000 00000?02?0 0120000000 000??11010 000?0?0400 000001110?  
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 0011{12}01110 1000010000 0000110001 0100100001 0210202222 1101001001 1200100?01 110?100??0

*Tiliqua\_scincoides* 00010?0000 00000?00?0 0120000000 000??11010 000?0?0400 000001110?  
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 0000?00000 0010101001 1100102002 0?00101110 1200202200 0010000011 100010?21? 0210101??1  
 00?0000201 20000?0??2 20?0100033 20??1?101? 1000?01??0 110?1001?0 ??2020?0?0 0000121000  
 0000100000 0000?110?0 0?0000?1?? 0001010100 1000110020 01010000?2 0??1002020 0300000?00  
 1002101101 0010?00010 1000000000 0010000032 2000000000 00?0000011 0100100000 0300410000  
 202?0?1100 0?????1000 0?10121000 011110010{12} 11110011{12}0 11{01}01002?0 10000?0010  
 0011201110 12000{01}0000 000?110001 0100120001 0200202222 1101001001 1200100001 100110?001

*Shinisaurus\_crocodylurus* 1000002000 00000?0001 0??1100000 000??10010 010?0?0300 000002120?  
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0000200120 0011101000 0100100000 0?00001110 1100102200 0000000011 10001??11? 0000101??1  
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0000101000 00001110?0 0?0000?2?? 0001011001 0001010110 0101001002 40?0001100 0000300000  
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Xenosaurus\_platyceps 1000012002 20000??000 0101000000 000??10020 010?0?0100 000002120?  
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01?0000101 00020?0??0 20?0100002 ?0?01?131? 0000?01??0 010?2000?0 001020?0?0 0000121000  
0000100000 00001110?0 0?0000?0?? 0001010000 0000010000 0101000002 40?0000000 1000300110  
1011101102 0011010000 ?000010000 0010000033 3000000000 00??000001 0??011???? ???04000?0  
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Xenosaurus\_grandis 1000012002 20000??000 0101000000 000??10020 010?0?0200 000002120?  
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Pseudopus\_apodus 10001?0000 0000000000 0110000000 000??00010 000?0?0?40 000002120?  
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213??1003 1???2?000 0?31??0100 001000?000 0010000?3? ?????????? 100{01}??1?? ??????????  
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Peltosaurus\_granulosus 1000002000 20000?01?0 0100000000 000??10040 000?0?0?10 000002120?  
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01?000?001 01020?0??0 20?0100002 ?0?000131? 0000?00000 010?2000?0 001020?0?0 100112?000  
000?100000 00001????? 0?0000?2?? ?00101110? 0000?0?000 0?01000001 40?0010000 1000200100  
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Helodermoides\_tuberculatus 1000??2?00 00100?0000 0101000000 000??00040 000?0?0?40 000002120?  
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?????1??? ????20???? ?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ??????????  
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Anniella\_pulchra 1000001000 00?00000?0 0000000100 000??01240 00000?0?0 000001120?  
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 0001?00020 ?100?001? ???100?01 0?00001111 1100102200 1111000011 100010?21? 0010111??0  
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 1012001002 0011000000 1000010001 0110000112 1100001100 00?0000011 00?001???? ?0430030  
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Celestus\_enneagrammus 1000101100 20100000?0 0100000000 000??01040 000?0?0?20  
 000002120? ?000000000 0?0?001100 012?0?0102 ??0010000? 0110000100 0013011000  
 0000000100 0000000100 0001200020 0001100001 1100101001 0?00001110 1100102300  
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 1000110001 0010000032 2000000100 00?1000011 010011??00 0110410000 202??1001 0??2?1000  
 1110020000 011{01}100100 0111001110 1110100000 1000000010 1011{01}01110 0200010000  
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Elgaria\_multicarinata 1000001000 00000?0000 0100000000 000??10040 000?0?0?10 000002120?  
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Gobiderma\_pulchrum 1000001?00 0000??0000 01?0000010 000??00120 000?0?0?400 000002120?  
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 0??000???? 01020????0 ?0?0100002 ?0?000131? ?000?000?0 011?2000?0 00102??0?0 ??0?12??00  
 00?????000 00???????? 0?001????? ?00101?00? 1?0??0?0?0 ??01001100 40?0000?00 1010110?10  
 10??201002 00111?0000 0000000000 0110000132 2100111??0 1?00000??? ?????????? ??????????  
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Estesia\_mongoliensis 1000001000 00000?0201 01?1?0001? ??0?00120 000?0?0?400 0?002120?  
 ?2??0?000? 0?0?00?1?0 0?2??0?0102 ??010?000? 0111?000?0 001301?100 0001000120 ?000??0100  
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1??????02 0?111?0000 ??00?????? 0110020232 21001111?0 1000000?? ???? ?????? ???? ??????  
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Aiolosaurus\_oriens 110?101000 00000?02?1 01?1000?1? 000?????? ?0?0????? ?????????? ?000010000  
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?0?1?????0? 0100101?00 ?00001100 11?0?0?? ????0??11 ?0??0?2?? ?0?1??1??1 ???0?0???  
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????????? ?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ??????????  
????????? ?????????? ??????????

Heloderma\_horridum 1000000000 0010000201 01?0000000 000?00240 00000?0?? 000002110?  
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0011200020 0001210000 ?1??100210 0?00001110 1100102200 0000000011 100110021? 0011001??1  
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1001201002 0011100000 0000000000 0100020232 1100111000 1??0100011 010011?00 0000410001  
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Heloderma\_suspectum 10000?0000 00100?0201 01?0000000 000?00240 00000?0?? 000002110?  
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Lanthanotus\_borneensis 1100002000 00000?1111 01?1000010 000?00130 000?0?0?? 000001120?  
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1011201002 0111100000 ?000000000 011?020222 2100111100 1?00000011 010011?01 0010410001  
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0200000000 ?00?110001 1100020000 ?010101110 0003?01014 0?0??00?1? 0111101100

Saniwa 1100101000 00000?1111 01??000?10 000?00120 0?0?0?0400 0000021?0? ?20001000?  
0?0?0001?0 0?????01?0 ??0?0?000? 01100000?0 0013010100 00010??10 0000000101 0021200120  
000?2??001 01?010?00? ?000001?10 ??0??0?? ????00011 1?0110?0?? 0001011??1 01?000?001  
01020?0??0 ?0?0100001 ?1?000131? 0000?000?0 ?11?000?1 ?0102????? ?00?121000 0?????1??  
????????? 0?0?0?0?? ?00?????0? 0?0??0?30 ?101?011?0 41?0000?00 1010110?10 ?011201?02  
0?11??000 000?????? 0110000133 2100111?0 1??00000?? ???1????? ???0400001 202?101?03  
0??312000 0??00?0000 00????1?0? ?????????? ?????0??0 0000?0010 10?12011?0 ?000010000  
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Varanus\_salvator 1100101001 1000001211 01?1100010 000?0?220 00000?0?10 000002120? ?2??0?00??  
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010?2?0001 0100100000 0?00001110 1100302200 0000000011 100010?01? 0011011??1 03?0000001  
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 00100110?0 0?0010?0?? 0001011011 0000010130 0101001100 41?0000?00 1010110?10 1011201002  
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 0??312000 0?21??0000 0010111100 00?0000?20 0001001100 0000000010 ?011201110 ?000010000  
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*Varanus\_ acanthurus* 1110002002 10000??211 01?1000010 000??0?220 00000?0300 000001120?  
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*Varanus\_ exanthematicus* 1100002001 100000?211 01?1100010 000??0?220 00000?0400  
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0000?01??0 011?2000?1 101020?0?0 0000121000 0000100000 00101110?0 0?0010?0?? 0001010011  
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 0100000?20 0001001100 0000000010 ?011201110 ?000010000 ?00?110001 1100?4000? ?1100?0100  
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*Anelytropsis\_ papillosus* 1000001200 10000002?0 0121000100 000??01040 000?0?0??0 0001011?0?  
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*Dibamus\_ novaeguineae* 1000002200 10100002?0 0121200100 000??01040 000?0?1??0 0001011?0?  
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*Spathorhynchus\_ fossorium* 1100002002 00000?0?0 0030000000 000??01241 00000????0 000003??0?  
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10?0000001 00000?0??? 20?0000013 00??1?100? 1001?01??0 2?1?22??0 001020?0?1 ?????2??30  
00??102??? 22??12?002 2?0100?0?? ?2??13?02 100????132 3101000002 30?1000011 0300000000  
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Dyticonastis\_rensbergeri 1100012?01 00000?00?0 0030100000 000?01241 00000????0 000003??0?  
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000?102??? 2200?2?002 2?0100?1?? ?010013??2 1001??0?32 3101000002 30?1000021 0300000010  
1011101102 0112010000 100001000? 0112000212 1000001?00 00?0000??? ?????????? ??????????  
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Rhineura\_floridana 1100012000 ?0000?00?0 003?100000 000?01241 00000????0 000003??0?  
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Bipes\_biporus 1001002002 000000?1?0 0001000?00 000??11341 00000????0 00001??0? ?1?????1??  
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?????????1? 0??00000? 0?000??111 1200002400 1112000011 100010?21? 0110011??1 1?00000001  
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0??3??000 1030000110 000?001100 00201????1 ??????012?0 1001??0001 0000201110 0102001011  
????????? ?????????? ?0000?0000 ?00??10004 1200?10001 0?011010?0

Bipes\_caniculatus 1001002002 00000??1?0 0001000?00 000??11341 00000????0 00001??0?  
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01????????? ??????????1? 0??00000? 0?000??111 1200002400 1112000011 100010?21? 0110011??1  
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0112001011 ?????????? ?????????? ?0000?0000 ?00??110?? ?????????? ???10??0

Trogonophis\_wiegmanni 1101002002 00000??1?0 0001000000 000?01241 00000????? 000004??0?  
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Diplometopon\_zarudnyi 1101002002 00000??1?0 0001000000 000??01241 00?00????? 00?004??0?  
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Geocalamus\_acutus 1100002002 00?00??1?0 10?1000000 000??01241 00000????? 000004??0?  
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 0000?00001 0?10?20211 10?1?????? 0012000111 10000?1100 00?0000010 00?0000011 100???????  
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Amphisbaena\_fuliginosa 1000002001 00000?0100 1001100100 000??00241 00000????? 000004??0?  
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 0001000101 0?10?202?1 10?1?????? 0012000221 1000000100 00?0000011 0??01000?? ??0?4200?0  
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Najash\_rionegrina ?????????? ?????????? ?????????? ?????????? ?0????????? ?????0????? ??????????  
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 1?0?0000? ?1??11??0 ?0??????1 ?10101???? 200?????? 00?0????? ?????????? ??????????  
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 ??????????1? ???1????? ?11??01??0 1001??1?? ?????????? ??????????010 ?????????? ??????????  
 ?0??????00 ?????????? ?????????? ??????????

Dinilysia\_patagonica ???????10 ??????0201 1????001?0 ?10??00120 000??1?1?0 1100022?00  
 0000??0000 300010????? 0??40??100 001?010000 0111?00?2? 00?11??113 0000000200 0010201?00  
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 ??????????1 0??20?0?00 20?01000?3 ?0?0011?10 00000?0100 ?100200000 ?0101?1001 ??????0?011  
 010?????? 1?00?0??01 1?01000000 ?1??10?00 0000?0?21 0111??110 2??0000?00 0010?13?10  
 1101202?02 0?10?00?0 1001????? 0??2?00?2 ?110011?? ?0000????? ?????????? ???0?????  
 2??01?130? ???20?0?? ?????????? ?????????? ?????????? ?????????? ?????????? ??????????  
 ?????????? ?????????? ?0?00?0000 ?????????? ?????????? ??????????

Leptotyphlops\_dulcis 100001211? ?010011101 1????00100 1?0??00241 000?0?2??0 0?10012?01  
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 01?0?00001 0?0001010? ?0?0100103 ?0??1?1310 0?000?1??1 ?????????? ??????????1 ??????00100  
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1101201001 2210??0?00 1000000000 0?????000 11000011?0 1??00?0021 00??01???? ???0444040  
311?101303 0000??2001 ??????02?? ?????????1? ???1?1??2? 0?0?1??3? ?0?00??20 ?????3?1???  
?????????? ?????????? ?????????? ?0000?0000 ?00??11024 ???0??001? 04?1101??0

*Typhlops\_jamaicensis* 1000?011?? ?010010101 1????00000 0?0??00241 000?0?2??1 00?0012?0?  
01?????1?? ?????????? ???????100 000??0?00 11?1?1??2? 0?0?1??3? ?0?00??20 ?????3?1???  
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0?000?????1 ???010?201 1?01?00100 12????11??0 000102013? 11111??110 40?0??1?00 02?1?20?20  
1000?01001 0110??0000 1100000000 0?????0?01 0100001100 1??00?0020 ?0??01???? ???04441?0  
311?101303 0000??2001 ??????02?? ??????????1? ???1?1??2? ?????0??2? ??????????1? ???????????  
?????????1? ?????????? ?????????? ?0000?0000 ?00??110?? ?????????? ?????1?1??0

*Liotyphlops\_albirostris* 100??121?? ?0?10011?1 1????00100 1?0??00241 000?0?2??0 1?10012?01  
01?????00? ???10?2?? 0??4??100 000??0?00 2??1?1??2? 0?0?1??3? ?0?00??20 ?????3?1???  
?1????????? ??????????1? ??????1???? ??????????11 130000?40? 1012102111 0002101310 100?002002  
?1?0?00?01 0?0??01?? ?0??0110? ???1?1?131? ?0000?1??0 010?021000 ??2?20?011 ?????10010  
?1100?????1 ???0?0?01 1?01?001?? 12????1??0 0001??012? 01111??110 2??0??0?00 00?1?????0  
1????01000 0110??0?00 1000000000 0?????0?01 1100001100 0??00?0?? ?????????? ???0444130  
311?101303 0000??20?? ??????0?? ?????????? ??????????0 ?????1??2? ??????????1? ???????????  
?????????1? ?????????? ?????????? ?0000?0000 ?00??100?? ?????????? ??????????

*Typhlophis\_squamosus* 100???21?? ?0?10011?1 1????00100 1?0??00241 000?0?2??0 1?10012?01  
01?????00? ???10?2?? 0??4??100 000??0?00 2??1?0??2? 0?0?1??3? ?0?00??20 ?????3?1???  
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??0?00??1 0?0??01?? ?0??0110? ???1?1?131? ?0000?1??0 010?021000 ??2?20?011 ?????10???  
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311??01?0? ?000??0?? ??????0?? ?????????? ?????????? ?????????? ?????????? ??????????  
????????? ?????????? ?0000?0000 ?00??100?? ?????????? ??????????

*Anomochilus\_leonardi* 11000?0110 1100000101 11?1000100 0100000231 1000121??0 1010013?00  
01?????1?? ?????????? ???????100 000?010000 11?1?2??2? 000?1??23 000000?200 0010201?00  
11????????? ??????????1? ??????1???? ?0?0??11 130000220? 1112100011 0002111110 1010002112  
0101?00001 0?00000100 41?0100003 ?00?1?1310 00000?1??0 01??00000 ??2?20?0?1 ?????00011  
01000?????1 1?0000?01 1111?00100 12????11??0 1000020121 2111111110 1?000?0?00 0010?13??0  
1101200010 ?200?21001 1?00000000 0??020001 11000111?0 0??0000?? ?????????? ???0??230  
311??1?0? 0000??0?? ??????0?? ?????????? ??????????0 ?????0??2? 1?????1?? ??????????  
?????????1? ?????????? ?????????? ?0000?0000 ?00??110?? ?????????? ??????????

*Anilius\_scytale* 1100??0110 1100000101 11?1000100 0100000231 1000301??0 1010023?00 01?????1??  
?????????? ???????100 001?010000 01?1?2??2? 000?1??123 000000?200 0010201?00 21?????????  
?????????1? ?????00000 0?0000?111 1300002100 1112100111 0002111310 101?002002 0101?00001  
0?03000100 4200100003 ?00?011310 00000?0100 0100100?10 ??2?200001 ?????00011 01000?????1  
1?0010??01 1111?11000 12????11??0 1000020121 2111101110 1?00?02?10 00?1?????1 ?1?0?00010  
0?00?21101 1?01?????? 010?220022 2100011110 1?1000001? ?0??01???? ???0444230 311?101303  
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????????? ?????????? ?0000?0000 ?00??11024 ??????????1? 0??101??1

*Cylindrophis\_ruffus* 1100??0110 1100000101 1????00100 0100000231 1000121??0 10100?3?00  
01?????00? 31?010?2?? 0??1?0?100 001??10000 01?1?20?2? 000?1??123 000000?200 0110201?00

11????????? ?????????? ?????00201 0?0000??11 1300002010 1?12100111 0002111310 1010002012  
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 01000????1 1?0000??01 1011010?00 12???11?00 0110020121 2111101110 1?000?1?00 0010?11?10  
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 ?????????? ?????????? ?????????? ?0000?0000 ?00??11024 ???????01? 04?110????

*Uropeltis melanogaster* 1000001100 1100000101 11?1100100 0100000231 1000122??0 1010013?00  
 01?????1?? ?????????? ???????100 001??20000 2??1?2??2? 00??1??023 000000??00 0011201?00  
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 0001?000?1 0?0??00100 ?1?0100033 000?1?1310 00000?1??0 0100100000 ???2200001 ?????2001?  
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 311?101303 0000??2001 ??????02?? ?????????1? ???1????? ?????????? ?????????? ??????????  
 ?????????? ?????????? ?????????? ?0000?0000 ?00??110?? ?????????? ???1?????

*Xenopeltis unicolor* 1100??0110 1100000201 1????0010? 0?1000?231 0000221??0 1010013?00  
 01?????10? ?????????? ???????100 001?010000 11?1?2??2? 000?2??23 000000??00 ?2102?1?00  
 11????????? ??????????1? ??????00203 0?010??11 1301202000 1113100111 0012111011 101?002012  
 0?02?00?01 0?030?0100 420010110? ??0?021311 00001?0200 0101011010 ???2201111 ?????00022  
 01000????1 1?0010?01 1012110000 12???10?00 0000020121 011110?110 1?0??0?00 0010?0?0?  
 1000?1??2? ?????2110? 1?0000?000 000?200?44 4110010110 1?1000001? ?0??01???? ???0444030  
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 ???????1?? ?????????? ?????????? ?0000?0000 ?00??11024 ???0??001? 04?110????

*Loxocemus bicolor* 1100??0110 1100000201 1????0010? 010000?231 1000211??0 1010013?00  
 01?????00? 31?110???? 0??3?1?100 001??20000 11?1?20?2? 000?2??23 000000??00 00102?1?00  
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 0?02?00?01 0?030?0100 420010110? ?00?021311 00001?0200 0101011010 ???2200211 ?????00022  
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 1101?02010 0200?21101 1?00000000 010?220013 2110011110 1?100001?? ?0??01???? ???04442?0  
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 ???????0?? ?????????? ?????????? ?0010?0000 ?00??11024 ???????01? 04?110????

*Xenophidion acanthognathus* 1100??001? 1100000201 1????0010? 0101?0?2?1 1000321??0 ?010012?00  
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*Casarea dussumieri* 1100??0010 1100000201 1????0010? 0?2200?231 0000311??0 1010012?01  
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????11?? ?000????01 ??????02?? ???????1? ????1????1 ?????1???? ???????1?? ?????????? ???????1??  
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Haasiophis\_terrasanctus ????0??10 ????00211 1????001?0 010??00??1 ?????????? ???022?0?  
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0????????? 0????????? ?20?????? ????021311 ?0100?0200 ?101??010 0?2?201??1 ?????0?011  
000?????? ????0?0?? ?1??100?? ?1??1??0 ?0?0????? ?0?1?111? 1?0?00?? 0010?1??00  
1?0?0101? 0100?1?? 1?01????? 0?02?00?3 31100111? 1?100?0?? ?????????? ???04420??  
?13?1??13 0??21?101 ?????0?? ????1??1? ????1??0 ?11?01?? 1001??1?? ??????????  
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Eupodophis\_descouensis 11200??10 ?00?0???? 1????????? ?????0?? ?0??1????? ???0?????  
??????000 ?10010??0 ???4?1?? ?0????????? ?????0?? 0??1????? 0??0000?? ???02?????  
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?????0?? ???????1? ????1????? ?????0?? 1001??1?? ?????????? ???????011 ?????1?? ??????????  
????0?0000 00????????? ?????????? ??????????

Pachyrhachis\_problematicus 1?00??1? ???????11 ?????????? ??0?00?? ?????????? ???022?0?  
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????????? 0????????? ?20?????? ????131? ?0200?? ?10101?000 0?2?20??1 ?????0?0?  
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313?1?1?1? ???????101 ?????0?? ????1??1? ????1??0 ?11?01?? 1001??1?? ??????????  
??????011 ?????101? 1????????? ?0000?0000 ?????????? ?????????? ??????????

Exiliboa\_placata 1000?0111? 1300100101 1????0010? 0?11?0?221 0000302?? 1010012?01 01????00?  
31?010???? 0??1?0?100 011??10000 11?1?1??2? 000?2??23 000000?00 00102?1?00 11?????????  
?????????1? ?????00203 0?010??01 1301202010 0113100111 0012111010 100?002012 0?02?00?01  
0?03000110 420010110? ?1?021311 00101?0200 0101001010 ??2?200001 ?????00022 01000??1  
1?0000??01 1112111000 12??10?00 0001020121 0111111110 1?2?0?0?? 0010?11?10 1101?02??  
????21101 1?01????? 0??200003 3110011110 1?10000{01}?? 00??01???? ????0????? 311??1??  
0000??001 ?????02?? ???????1? ????1????? ?????????? ???????1?? ?????????? ??????????  
????????? ?0000?0000 ?00??110?? ?????????? ????1????1

Ungaliophis\_continentalis 1000??011? 1300100201 1????0010? 0101?0?231 0000321?? 1010012?01  
01????00? 31?010???? 0??2?0?100 001??10000 11?1?10?2? 000?2??21 000000?00 01102?1?00  
11????????? ???????1? ?????00203 0?010??01 1301402010 0113100111 0012101010 100?002012  
0?02?00??1 0?03000110 420010110? ?0?021311 00101?0200 0101?01010 ??2?201001 ?????00022  
01000??1 1?0010??01 1112111000 12??11?00 00010?0121 0111111110 1?1?0?0?? 0010?1?00  
1100?02?? ?????21101 1?01????? 0??200002 2110011110 1?10000?? ?0?01???? ????0?????  
311??1?? 0000??001 ?????02?? ???????1? ????1??0 ????0??0 ???????1?? ??????????  
??????0?? ?????????? ?????????? ?0000?0000 ?00??110?? ?????????? ????1????1

Eryx\_colubrinus 1100??01?? 12?1?00201 1????0010? 0?1000?231 1000303?? 1?10012?01 01????00?  
31?010???? 0??4?0?100 001??10001 11?1?10?2? 000?2??23 000000?00 0?02?1?00 11?????????  
?????????1? ?????00203 0?010??01 1301402010 0113100111 0012110010 100?002012 ?02?00?01

0?030?0210 420??????? ?0?021311 00201?0200 0101000000 ??2?201001 ?????000?2 02000????1  
 1?0000?001 1112011001 11???10?00 0000020121 0111101110 1?100?0?00 0010?11?10 1101?00010  
 0100?21101 1?01?????? 0???230002 2110011110 1?100001?? ?0??01???? ???04442?0 311?101303  
 011121?001 ??????02?? ?????????1? ?????1????? ?1???0??? ????1????? ?????????? ???????0??  
 ?????????? ?????????? ?0000?0000 ?00??11024 ???????01? 04?11?1??1

Calabaria\_reinhardtii 1100?0211? ?201?10201 1????0010? 010000?231 1000302??0 1010012?00  
 01?????00? 3??010???? 0??4?0?100 ?10??10000 11?1?00?2? 000?2???23 000000?000 00102?1?00  
 11????????? ??????????1? ??????00203 0?010???01 1301102000 0113100111 0002111010 100?002012  
 ??02?00?01 0?03000110 41?010110? ??0?1?1311 00101?1??0 0101000000 ??2?201001 ?????00022  
 01000????1 1?0010?001 1112111001 11???10?00 1010020121 0111111110 1?100?0?00 0010?13?10  
 1101200010 0200?01101 1?01?????? 0???230003 2110011110 1??00001?? ?0??01???? ???04442?0  
 311?101303 001020?001 ??????02?? ?????????1? ?????1????? ?1???0??? ???????1?? ??????????  
 ???????0?? ?????????? ?????????? ?0010?0000 ?00??11024 ???????01? 04?11?1??0

Lichanura\_trivirgata 1100??011? ?200110201 1????0010? 0?2200?231 1000322??0 1010012?01  
 01?????00? 31?010???? 0??1?0?100 011??10000 11?1?10?2? 000?2???23 000000?000 00102?1?00  
 11????????? ??????????1? ??????00203 0?010???01 1301302000 0113100111 0012110010 100?002012  
 ??02?00?01 0?03000110 421??0110? ??0?021311 00101?0200 0101000000 ??2?200001 ?????0002?  
 00000????1 1?0000?001 1112111000 12???10?00 0000020121 0101101110 1?1?0?0?00 0010?11?10  
 1101?00?2? ?????11101 1?01?????? 0???230003 2110011110 1?100001?? ?0??01???? ???0444230  
 311?101303 011121?001 ??????02?? ?????????1? ?????1????? ?1???0??? ???????1?? ??????????  
 ???????0?? ?????????? ?????????? ?0000?0000 ?00??11024 ???????01? 04?1101??1

Epicrates\_striatus 1100??001? 1300100201 1????0010? 0?2200?221 1000212??0 1010012?00 01?????00?  
 31?010???? 0??3?1?100 001??10001 11?1?00?2? 000?2???23 000000?000 03102?1?00 11?????????  
 ??????????1? ??????00203 0?010???01 1301402010 0113100111 0012111011 100?002012 0?12?00?01  
 0?03000110 421010110? ??1?021311 00201?0200 0101011010 ??2?201001 ?????000?2 02000????1  
 1?0010?001 1112011001 11???10?00 1010020121 0111111110 1?100?0?00 0010?11?10 1101200010  
 0100?21101 1?01?????? 0???230003 2110011110 1?100001?? ?0??01???? ???04442?0 311?101303  
 000021?001 ??????02?? ?????????1? ?????1????? ?1???0??? ?0?0???1?? ?????????? ???????011  
 ?????????? ?????????? ?0000?0000 ?00??11024 ???????01? 0??110????1

Boa\_constrictor 1100??001? 1200100201 1????00100 0?220002?1 1000213??0 1010012?00 01?????00?  
 31?010???? 0??4?1?100 001??10001 11?1?00?2? 000?2???23 000000?000 03102?1?00 11?????????  
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 0?0???0010 42101012?? ??1?021311 00201?0200 0101011010 ??2?201001 ?????000?2 02000????1  
 1?0010?001 1112011001 11???10?00 0110020121 0111110110 1?100?0?00 0010?11?10 1101200010  
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 000021?001 ??????02?? ?????????1? ?????1????? ?1???0??? ?0?0???1?? ?????????? ???????0??  
 ?????????? ?????????? ?0000?0000 ?00??11024 ???????01? 04?11?1??1

Aspidites\_melanocephalus 1100??011? 1100000201 1????0010? 0111?0?231 1000221??0 1010012?00  
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 0?02?00?01 0?0???0010 420010120? ??0?021311 00201?0200 0101011010 ??2?200211 ?????000?2  
 02000????1 1?0010?001 3012001010 11???11?00 10?0020121 0111111110 1?100?0?00 0010?11?00  
 1100?00010 0100?21101 1?01?????? 0???230002 2110011110 1?100001?? ?0??01???? ???04442?0  
 311?101303 0000??001 ??????02?? ?????????1? ?????1????? ?????0??? ????1????? ??????????  
 ???????0?? ?????????? ?????????? ?0010?0000 ?00??11024 ???????01? 04?11????0

Python\_molurus 1100??011? 1100000201 1????0010? 0111?0?221 1000221??0 2010012?00 01?????00?  
31?110???? 0??4?1?100 001??20001 11?1?0??2? 000?2??23 000000??00 03102?1?00 21????????  
?????????1? ??????00203 0?010??01 1301402010 0113100111 0012111010 101?002012 0?02?00?01  
0?0??0010 420010120? ??0?021311 00201?0200 0101011010 ??2?201211 ?????000?2 02000????1  
1?0010??01 3012011010 11??10?00 0010020121 0111111110 1?100?0?00 0010?11??0 1101?00010  
0100?21101 1?01????? 0??230013 2110011110 1?100001?? 0?0?01???? ???04442?0 311?101303  
000021?001 ??????02?? ?????????1? ???1????0 ?1??0??0 ??????1?? ?????????? ???????0??  
????????? ?????????? ?0010?0000 ?00??11024 ???????01? 04?11????0

Trachyboa\_boulengeri 1100??011? 1300100201 1????0010? 0?2200?231 0000222??0 2010012?00  
01?????00? 31?110???? 0??4?1?100 111??20000 2??1?0??2? 000?2??21 100000??00 00102?1?00  
11????????? ?????????1? ??????00203 00010??01 1301402020 0113100111 0012111310 100?002002  
0?12?00?01 0?031?0110 420010100? ??0?021311 00201?0200 0101011000 ??2?200201 ?????00022  
01000????1 1?0000??01 3012111000 12??11?00 0011020121 0111111110 1?2?0?0??0 0010?11?10  
1100?02?? ????2130? 1?00000000 0??130002 3110011110 1?10000?? ?0??01???? ??0441030  
311?111303 0000??001 ??????02?? ?????????1? ???1????0 ???0?0??0 ??????1?? ??????????  
??????0?? ?????????? ?????????? ?0000?0000 ?00??110?? ?????????? ???10????

Tropidophis\_haetianus 1100??011? 1300100201 1????0010? 0?2200?231 0000222??0 2010011?00  
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11????????? ?????????1? ??????00103 00010??01 1301402020 0113100111 0012111310 100?002002  
0?12?00?01 0?031?0110 420010100? ??0?021311 00201?0200 0101011000 ??2?200101 ?????00022  
01000????1 1?0000??01 3012111000 12??11?00 0010020121 0111111110 1?2?0?0??0 0010?11?10  
1101?02?? ????2130? 1?000000?0 0??130003 3110011110 1?10000{01}?? ?0??01???? ??04441?0  
311?111303 000021?001 ??????02?? ?????????1? ???1????0 ?1??0??0 ??????1?? ??????????  
??????0?? ?????????? ?????????? ?0000?0000 ?00??11024 ???????01? 04?1101??1

Xenodermus\_javanicus 1110??011? ?300100111 1????0010? 0?23?0?2?1 1000301??0 1010012?01  
01?????00? 31?110???? 0??4?1?100 101??20000 2??1?00?2? 000?2??23 100000??00 10102?1?00  
21????????? ?????????1? ??????00203 11010??01 1301402020 0113100111 0022111011 101?002113  
0?02?0{01}?01 0?0??0010 42001????? ??0?021312 00201?0210 0101021010 ??2?201211 ?????00022  
01000????1 1?0000??01 10110000?0 12??10??0 1011020121 0111111110 1?2?0?0??0 0010?1??10  
1101?1??2? ?????11301 1?00000000 0??200003 3110011110 1?00000010 00??01???? ??0443030  
312?111303 000021?001 ??????02?? ?????????1? ???1????1 ?????1??1 ??????1?? ??????????  
??????1?? ?????????? ?????????? ?0000?0000 ?00??11024 ???????01? 04?11?1??0

Acrochordus\_granulatus 1000??021? ??1?00211 1????000? ?23?0?2?1 1000322??0 1?100?1?01  
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21????????? ?????????1? ??????00203 11010??01 130?402030 0113100111 0022110011 100?003113  
0?02?00?01 0?0??0000 42001?10?? ??0?021312 00201?0200 0101021000 ??2?200201 ?????00022  
01000????1 1?0?00?03 3112100000 12??10??0 000??20?21 1111110110 1?1?0?0??0 0010?11?10  
1100?1??2? ?????2130? 1?01????? 0??230003 2110011110 1?1000001? ?0??01???? ??0444000  
314?111303 000021?001 ??????02?? ?????????1? ???1????1 ?????1??1 ??????1?? ??????????  
??????1?? ?????????? ?????????? ?0000?0000 ?00??11024 ???????01? 04?11?1??1

Pareas\_hamptoni 1100??001? ?400000111 1????0000? 0?13?0?231 1000302??0 1010011?01 21?????00?  
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?????????1? ??????00103 0?000??01 1302402030 0113100111 0022110011 101?003113 0?22?00?01  
0?0??0000 ?2101?110? ??0?021312 00201?0200 0101021010 ??2?201211 ?????00022 01000????1  
1?0000??01 1012100000 12??10??0 0011020121 0111111110 202?0?0??0 0010?1??10 120??1??2?

????2130? 1?00000000 0????1?002 2110011110 1?10000{01}?? ?0??01???? ????0444040 311?101303  
0000??001 ??????02?? ?????????1? ?????1????? ??????1??? ?????????? ?????????1?? ??????????  
?????????? ?0000?0000 ?00??110?? ?????????? ??????????

Lycophidion\_capense 1100??001? ?400000111 1????0000? 0?23?0?231 1000301??0 1010012?00  
21?????00? 3??010????? 0??2?0?100 101??10000 2??1?1??2? 000?3??23 100000??20 10112?1?00  
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0??3?00??1 0?0??0000 420010110? ??0?021312 00201?0200 0101021000 ??2?200111 ?????00022  
01000????1 1?0010??01 1012100000 12??10??0 0011020121 0111111110 1?0?0?0??0 0310?1??0  
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311?1?1303 0000??001 ??????02?? ?????????1? ?????1????? ?????1????? ?????????1?? ??????????  
????????1?? ?????????? ?????????? ?0000?0000 ?00??11024 ???????01? 0?????????

Aparallactus\_weneri 10000?0010 ?000000101 1????0000? 0?0000?221 1000301??0 1010013?01  
1?????00? 31?010????? 0??0?0?100 100??10000 2??1?10?2? 000?3??023 100000??00 10112?1?00  
21????????? ??????????1? ??????02003 ?0?0??01 130?102100 1113100111 0022110011 101?003113  
0??3?00?01 0?03000100 42001?11?? ??0?021312 00001?0200 0101021000 ??2?200111 ?????20022  
01000????1 1?0??0??01 ?011?00010 12??11?00 001?020121 0111110110 1?2?0?0??0 0210?13?10  
1201?1??2? ??????2130? 1?00000000 0???242002 3110011110 1?10100020 00??01???? ????04420?0  
311?101303 0000??001 ??????02?? ?????????1? ?????1????? ?????1????? ?????????1?? ??????????  
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Atractaspis\_irregularis 110??02010 ?01000111 1????0000? 0?0000?231 1000321??0 0010012?01  
01?????1?? ?????????? ?????????100 100??20000 2??1?1??2? 0?0?????4? ???000??00 00112?1?00  
21????????? ??????????1? ??????00103 10010??01 130?40?040 1113100111 0022110011 10?003113  
0??3?00??1 0?0300010? ??01?11?? ??0?021312 ?0201?1??0 010?021000 ??2?200211 ?????00021  
01000????1 1?0010??01 3012000000 12??11??0 1001020121 0111111110 0??0?0??0 0210?11??0  
1201?1??2? ??????0130? 1?01????? 0??????001 0??01?110 ?????200?? ?0??01???? ????0444230  
311?1?1303 0000??001 ??????02?? ?????????1? ?????1????? ?????1????? ?????????1?? ??????????  
????????1?? ?????????? ?????????? ?0000?0000 ?00??11024 ???????01? 0???13????

Causus\_rhombeatus 110??001? 1400000211 1????0000? 0?2210?2?1 2001223??0 2010011?01  
21?????00? 31?010????? 0??4?0?100 100??10000 2??1?0?2? 0?0?????4? ???000??00 00212?1?00  
21????????? ??????????1? ??????00203 10010??01 1302402040 0113100111 0022110311 10?003113  
??12?00??1 0?0??02?0 4?0??????? ?1?021311 00201?0200 011?021010 ??2?200211 ?????00021  
01000????1 1?0000??01 1?12103000 12??10??0 0011020121 0111111110 0??0?0??0 0210?????0  
1200?1??2? ??????130? 1?00100000 0??????01 3110011110 1?0020001? 00??01???? ????0442030  
311?111303 0000??001 ??????02?? ?????????1? ?????1????? ?????1????? ?????????1?? ??????????  
????????1?? ?????????? ?????????? ?0000?0000 ?00??11024 ???????01? 0???13????

Azemiops\_fae 110??0101? 1400100211 1????0000? 0?1200?231 1000322??0 1010012?01 01?????00?  
31?110???? 0??4?1?100 100??20000 2??1?00?2? 0?0?????4? ???000??10 10212?1?00 21?????????  
?????????1? ??????00203 10010??01 1302402020 0113100111 0022110011 10?003113 0?12?00?01  
0?030?01?0 421??0110? ??1?021311 00201?0200 011?021000 ??2?200211 ?????00022 01000????1  
1?0010??01 (13)?12100000 12??10??0 0011020121 0111101110 1?2?0?0??0 0010??1?10 1200?1??2?  
?????2130? 1?00100000 0??????01 2110011110 1?10200010 00??01???? ????04430?0 311?111303  
0000??001 ??????02?? ?????????1? ?????1????? ?????1????? ?????????1?? ??????????  
????????? ?????????? ?????????? ?0000?0000 ?00??110?? ?????????? ???1?????

Daboia\_russelli 110??0101? 1400100211 1????0000? 0?23?0?2?1 2000323??0 2110011?01 11?????00?  
31?010???? 0??2?0?100 100??10000 2??1?0?2? 0?0?????4? ???000??00 13112?1?00 21?????????

?????????1? ?????00203 10010???01 1302402040 0113100111 0022110011 10??003113 ??22?00??1  
0?0??02?0 4?1??????? ?1?021311 00201?0200 011?021000 ??2?200211 ?????00022 01000????1  
1?0010??01 1?12123000 12???10??0 1021020121 0111110110 1??0?0?0?0 0210??1??0 1200?1??2?  
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0000??001 ??????02?? ????????1? ???1????1 ?????1???? ???????1?? ?????????? ???????1??  
????????? ?????????? ?0000?0000 ?00??11024 ???????01? 04?11????1

Agkistrodon\_contortrix 100??0101? 1400100211 1????0000? 0?2210?2?1 10003?3??0 2110011?01  
11?????00? 31?010???? 0??0?0?100 100??10000 2??1?0?2? 0?0?????4? ???00??00 10?12?1?00  
21????????? ????????1? ??????00203 10010???01 1302402030 0113100111 0022110011 10??003113  
??12?0{01}??1 0?0??00?0 421???12?? ?1?021311 00201?0200 011?021000 ??2?200111 ?????00022  
01000????1 1?0010??01 1?12123000 12???10?00 0021020121 0111110110 1?2?0?0?0 0310??1??0  
1200?1??2? ??????2130? 1?00100000 0???????01 2110011110 1?0020001? 00??01???? ???0442030  
312?111303 000021?001 ??????02?? ????????1? ???1????1 ?????1???? ???????1?? ??????????  
????????1?? ?????????? ?????????? ?0000?0000 ?00??11024 ???????01? 04?11????1

Bothrops\_asper 110??0101? 1400100211 1????0000? 0?2210?2?1 0000302??0 2110011?00 11?????00?  
31?010???? 0??0?0?100 100??10000 2??1?00?2? 0?0?????4? ???00??00 10?12?1?00 21?????????  
?????????1? ??????00203 10010???01 130240?040 0113100111 0022110011 10??003113 ??12?00?01  
0?0??00?0 421???12?? ?1?021311 00201?0200 011?021000 ??2?200211 ?????00022 01000????1  
1?0010??01 1?12123000 12???10??0 0021020121 0111100110 1??0?0?0?0 0310?????0 1200?1??2?  
?????2130? 1?00100000 0???????01 2110011110 1?002001?? 00??01???? ???04441?0 312?111303  
000021?001 ??????02?? ????????1? ???1????1 ?????1???? ???????1?? ?????????? ???????1??  
????????? ?????????? ?0000?0000 ?00??11024 ???????01? 0??1????1

Lachesis\_muta 110??0001? 1400000211 1????0000? 0?23?0?2?1 0000302??0 2110011?01 11?????00?  
31?010???? 0??0?0?100 100??10000 2??1?00?2? 0?0?????4? ???00??00 00?12?1?00 21?????????  
?????????1? ??????00203 10010???01 1302402030 0113100111 0022110011 10??003113 ??12?00??1  
0?0??00?0 421???12?? ?1?021311 00201?0200 011?021000 ??2?200211 ?????00022 01000????1  
1?0010??01 1?12123000 12???10??0 0021020121 0111100110 1??0?0?0?0 0010?????0 1200?1??2?  
?????2130? 1?00100000 0???????01 2110011110 1?00200020 00??01???? ???0444230 312?111303  
000021?001 ??????02?? ????????1? ???1????1 ?????1???? ???????1?? ?????????? ???????1??  
????????? ?????????? ?0000?0000 ?00??11024 ???????01? 0??1????0

Naja\_naja 1000??001? 1300100211 1????0010? 0?2200?221 2001323??0 1010012?01 21?????00?  
31?010???? 0??3?0?100 100??10000 2??1?00?2? 000?2????? 100?00??00 12212?1?00 21?????????  
?????????1? ??????00203 10010???01 1302402030 0113100111 0022110011 100?003113 0?12?00??1  
0?030?0000 ?20010120? ?1?021312 00201?0200 0101011?00 ??2?200211 ?????00022 01000????1  
1?0000??01 1012100000 12???12?00 0011020121 0111111110 1?2?0?0?0 0310?11??0 1201?1??2?  
?????2110? 1?00000000 0?????1?01 2110011110 1?00200{01}?? 00??01???? ???04441?0 312?111303  
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Notechis\_scutatus 110??0001? 1400000211 1????0000? 0?2200?221 1001323??0 1010012?01  
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??12?00?01 0?0??02?0 420010???? ?1?021312 00201?0200 0101011?10 ??2?200211 ?????00022  
01000????1 1?0000??01 1?12100000 12???12?00 1011020121 0111111110 1?2?0?0?0 0310?11??0  
1200?1??2? ??????2110? 1?00000?00 0?????1?02 3110011110 1?002001?? 00??01???? ???04430?0



311?111303 000021?001 ??????02?? ??????????1? ???1?1???1 ?????1???1 ???????1?? ???????????  
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*Laticauda\_colubrina* 1100??001? ?400000211 1???0000? 0?23?0?2?1 1000301??0 1110012?00  
 21?????00? 31?010???? 0?3?1?100 001??10000 2??1?10?2? 000?2???2? 10??00??00 03212?1?00  
 21????????? ??????????1? ??????00203 10010??01 1300402020 0???100111 0020110011 101?003113  
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 ???????1?? ??????????? ??????????? ?0000?0000 ?00??11024 ???????01? 04?113????0

*Micrurus\_fulvius* 1101??001? 1400000211 1???0000? 0?2200?221 1000321??0 1010013?00 21?????1??  
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*Natrix\_natrix* 1100??001? ?400000211 1???0100? 0?23?0?221 2001323??0 2010022?01 21?????00?  
 31?010???? 0??2?0?100 101??20000 2??1?00?2? 000?2???23 100000??00 10212?1?00 21?????????  
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 ??????????? ??????????? ?0000?0000 ?00??11024 ??????????1? 0??13????0

*Afronatrix\_anoscopus* 1100??001? ?400000211 1???0100? 0?23?0?221 1001322??0 2010012?01  
 21?????00? 31?010???? 0??3?0?100 101??20000 2??1?00?2? 000?2???23 100000??00 10212?1?00  
 21????????? ??????????1? ??????00203 11010??01 1302402030 0113100111 0032110011 10?003113  
 0?22?01?01 0?0??0100 42001011?? ??0?021312 00201?0210 0101022010 ??2?200211 ??????00022  
 01000?????1 1?0000??01 3012112010 12???10?00 0011020121 0111111110 1?2?0?0?0?0 0310?1??10  
 1201?1??2? ??????2130? 1?00000000 0???242003 3110011110 1?000001?? ?0??01???? ???04420?0  
 311?1?1303 0000??001 ??????02?? ??????????1? ???1?1???1 ?????1???1 ???????1?? ???????????  
 ???????1?? ??????????? ??????????? ?0000?0000 ?00??110?? ??????????? ???1????0

*Amphiesma\_stolata* 1100?0101? ?400000211 1???0100? 0?23?0?221 2001323??0 2010012?0?  
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 01000?????1 1?0010??01 3012112010 12???10?00 0011020121 0111111110 1?2?0?0?0?0 0310?1??10  
 1201?1??2? ??????2130? 1?00000000 0???242003 3110011110 1?001001?? ?0??01???? ???0442030  
 312?111303 000021?001 ??????02?? ??????????1? ???1?1???1 ?????1???1 ???????1?? ???????????  
 ???????1?? ??????????? ??????????? ?0000?0000 ?00??110?? ??????????? ???113????0

*Thamnophis\_marcianus* 1100??001? ?400000211 1???0100? 0?23?0?221 2001323??0 2010012?00  
 21?????00? 31?010???? 0??2?0?100 101??20000 2??1?00?2? 000?2???23 100000??00 10212?1?00  
 21????????? ??????????1? ??????00203 11010??01 1301402040 0113100111 0032110011 101?003113

??22?00??1 0?0??0100 42001?110? ??0?021312 00201?0210 0101022010 ??2?201211 ?????00022  
01000????1 1?0000?01 3012112010 12???11?00 1011020121 0111111110 1?2?0?0?0 0310?1??10  
1201?1??2? ?????2130? 1?00000000 0???242003 3110011110 1?000001?? 00??01???? ?0442030  
312?111303 000021?001 ??????02?? ?????????1? ???1????1 ?????1??1 ???????1?? ??????????  
??????1?? ?????????? ?????????? ?0000?0000 ?00??11024 ???????01? 04?113??1

Xenochrophis\_piscator 1100??001? ?400000211 1????0100? 0?23?0?221 2001323??0 2010012?01  
21?????00? 31?010???? 0??0?0?100 101??20000 2??1?0?2? 000?2??23 100000?00 10212?1?00  
21????????? ?????????1? ??????00203 11010??01 1302402030 0113100111 0032110011 100?003113  
??22?00?01 0?0??0100 420010110? ??0?021312 00201?0210 0101022010 ??2?201211 ?????00022  
01000????1 1?0000?01 3012112010 12???11?00 1011020121 0111111110 1?2?0?0?0 0310?11??0  
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Lampropeltis\_getula 1100??001? 1400000211 1????0000? 0?2200?221 2001323??0 2010014?01  
21?????00? 31?010???? 0?23?0?100 101??20000 2??1?00?2? 000?2??23 100000?00 10212?1?00  
21????????? ?????????1? ??????00203 11010??01 13024020?0 0113100111 0032110011 101?003113  
??22?00??1 0?0??0100 420010110? ??0?021312 00201?0210 0101021010 ??2?200211 ?????00022  
01000????1 1?0010?01 3012110010 1{12}??10?00 0011020121 0111111110 1?2?0?0?0 0310?1??10  
120??1??2? ?????2130? 1?00000000 0???240002 2110011110 1?100001?? 00??01???? ?04442?0  
312?101303 000021?001 ??????02?? ?????????1? ???1????1 ?????1??1 ???????1?? ??????????  
??????1?? ?????????? ?????????? ?0000?0000 ?00??11024 ?????????? 04?11????0

Coluber\_constrictor 1100??001? ?400000211 1????0000? 0?2200?221 2001323??0 2010024?01  
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01000????1 1?0010?01 3012100010 12???10?00 0011020131 0111111110 1?2?0?0?0 0310?1??10  
1201?1??2? ?????2130? 1?00000000 0???240002 2110011110 1?10000020 00??01???? ?044430?0  
312?101303 000021?001 ??????02?? ?????????1? ???1????1 ?????1??1 ???????1?? ??????????  
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Tropidophis\_cacuangoae 1100??001? 1300100201 1????0010? 0?2200?231 0000222??0 2010012?01  
01?????00? 31?110???? 0?24?1?100 111??20000 2??1?0?2? 000?2??22 1?0000?00 00102?1??  
11????????? ?????????1? ??????0?0? 00010??01 1300402??0 0113100111 0012111310 1000003002  
0?12?00?01 0?0?1?0110 421??0100? ??0?021311 00201?0200 0101011000 ??2?200111 ?????00022  
01000????1 1?00?0?01 3012?11010 12???11?00 100??20121 ?111111110 1?2?0?0?0 0010111?10  
1101?02?10 1200?2130? 1?101000?0 0???230003 3110011110 1?10000?? ?0??01???? ?0444140  
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Tropidophis\_taczanowskyi 1100??011? 1300100201 1????0010? 0?2200?231 0000221??0 2010012?01  
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11????????? ?????????1? ??????0?0? 00010??01 1300402??0 0113100111 0012111310 1000002002  
0?12?00?01 0?0?1?0110 421??0100? ??0?021311 00201?0200 0101011000 ??2?200111 ?????00022  
01000????1 1?00?0?01 3012?11010 12???11?00 100??20121 ?111111110 1?2?0?0?0 0010111?10  
1101?02?10 1200?2130? 1?101000?0 0???230003 3110011110 1?10000?? ?0??01???? ???????4?  
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??????0?? ?????????? ?????????? ?0000?0000 ?00??11024 ???????01? 0??110??1

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Tropidophis_melanurus 1100??011? 1300100201 1????0010? 0?2200?231 0000222??0 2011011?00
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11????????? ??????????1? ??????0?0?? 00010??01 1302402??0 0113100111 0012111310 1000002002
0?12?00?01 0?0?1?0110 420??0100? ??0?021311 00201?0200 0101012000 ??2?200101 ?????00022
01000?????1 1?00?0??01 3012?11000 12??????00 100??20121 ?111111110 1?2?0?0??0 0010111?10
1101?02?10 1200?2130? 1?101000?1 0???130103 2110011110 1?10000??? ?0??01???? ??????????
311?111303 000021?001 ??????02?? ??????????1? ???1?????0 ??????0??0 ??????????1?? ???????????
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Tropidophis_canus 1100??011? 1300100201 1????0010? 0?1200?231 0000222??0 2010011?00
01?????00? 31?110???? 0??4?1?100 111??20000 2??1?0??2? 000?2??21 1??000?000 00102?1???
11????????? ??????????1? ??????0?0?? 10010??01 1300402??0 0113100111 0012111310 1000002012
0?12?00?01 0?0?1?0110 420??0100? ??0?021311 00201?0200 0101011000 ??2?200101 ?????00022
01000?????1 1?00?0??01 3012?11000 12??????00 100??20121 ?111111110 1?2?0?0??0 0010111??0
1101?02?10 1200?2130? 1?101000?1 0???130103 2110011110 1?10000??? ?0??01???? ??????????
311?111303 000021?001 ??????02?? ??????????1? ???1?????0 ??????0??0 ??????????1?? ???????????
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END;

BEGIN ASSUMPTIONS;

OPTIONS DEFTYPE = unord PolyTcount = MINSTEPS;

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TYPESET * UNTITLED = unord: 1-2 4-6 8-9 11 13-17 19-24 26-32 34-37 40 42
44 46-47 50 52-55 57 59-62 64 68-69 71-79 81 85-89 91-92 94-96 98 100 103-104 107
109-110 112-113 115-119 121-125 127 131 134-139 142 144-148 150-151 153-154 156-
166 169-177 179-181 183 186 190-202 205-207 209-215 218-219 221-222 224-230 232-
237 239-241 243-247 249 252-255 257 259 261-262 264-267 269-270 272-275 278-282
284 286-287 289-299 304-305 307-308 310 313-315 317-325 327 329-336 338-339 341-
342 344-345 348 351-359 362-363 365-367 370-371 373-374 376-381 383-387 391 393
395 397-413 416-417 422-434 436-439 441-453 461-462 464-467 469-474 476 478-482
484-485 489-517 519-528 530-534 536-569 571 573-583 585-587 591-592 594-601 603-
610, ord: 3 7 10 12 18 25 33 38-39 41 43 45 48-49 51 56 58 63 65-67 70 80 82-84
90 93 97 99 101-102 105-106 108 111 114 120 126 128-130 132-133 140-141 143 149
152 155 167-168 178 182 184-185 187-189 203-204 208 216-217 220 223 231 238 242
248 250-251 256 258 260 263 268 271 276-277 283 285 288 300-303 306 309 311-312
316 326 328 337 340 343 346-347 349-350 360-361 364 368-369 372 375 382 388-390
392 394 396 414-415 418-421 435 440 454-460 463 468 475 477 483 486-488 518 529
535 570 572 584 588-590 593 602;
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END;

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END;