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Revisiting the taxonomic status of *Apostolepis sanctaeritae*, a forgotten Neotropical dipsadid snake

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Abstract. *Apostolepis* Cope, 1862 is a highly diversified and speciose Neotropical dipsadid genus, encompassing almost 40 species of fossorial or cryptozoic snakes, widely distributed east of the Andes. In this work, we revisit the taxonomic status of *A. sanctaeritae* Werner, 1924, a rather controversial taxon described from a single specimen. *Apostolepis sanctaeritae* has been subject to several synonymizations and revalidations, being currently relegated as a junior synonym of *Apostolepis cearensis* Gomes, 1915. A careful reanalysis of its coloration pattern, pholidosis, and a detailed description of the skull morphology of *A. sanctaeritae*, based on CT-scan data of the holotype, provide compelling evidence for its revalidation. Furthermore, we consider *A. ammodites* Ferrarezzi, Barbo & Albuquerque, 2005 as a junior synonym of *A. sanctaeritae*, considering a total overlap of important diagnostic characters of coloration (large snout blotch reaching up to the frontals, wide black nuchal collar), pholidosis (rostral scale does not reach one/half of its interprefrontal suture), osteology (curved dentary, with 8–9 teeth loci; prearticular crest slightly higher than surangular crest), and geographic distribution (recorded from the Cerrado of Brazil). We also present a detailed osteological description and taxonomic account for *A. sanctaeritae* plus brief comments on the taxonomy of *Apostolepis*, suggesting major changes for the current framework seen in recent publications.

Key words. Coloration pattern, cranial morphology, CT-Scan, Elapomorphini, morphology, pholidosis.

Introduction

The Elapomorphini Jan, 1862 tribe is a monophyletic assemblage of Neotropical dipsadid snakes, encompassing the genera *Apostolepis* Cope, 1862, *Coronelaps* Lema & Hofstadler-Deiques, 2010, *Elapomorphus* Wiegmann, 1843, and *Phalotris* Cope, 1862 (Ferrarezzi 1993, Zaher et al. 2009). The monophyly of the tribe is supported by both molecular and morphological synapomorphies, such as a relatively reduced number of supralabial scales (5–6) when compared to other dipsadids, entire nasal plate, short dentary dentigerous process, "U"-shaped fronto-parietal suture, reduction or loss of the quadrato-maxillary ligament, two or less teeth in the pterygoid palatine process anteriorly to the ectopterygoid articulation, and the second supralabial in contact with the eye (Ferrarezzi 1993, 1994, Savitzky 1979, Zaher 1995, Zaher et al. 2009). The approximately 50 species occur throughout most of cis-Andean South America, northernmost in the Guyana shield Amazon forest to the southernmost in the open areas of Patagonia (Ferrarezzi 1993, Guedes et al. 2018a, Uetz et al. 2019).

The most speciose Elapomorphini genus is *Apostolepis*, with nearly 40 species, readily diagnosed based on the presence of fused prefrontal and internasal scales (Ferrarezzi 1993). *Apostolepis* presents a particularly unstable taxonomy, as addressed by several authors (e.g. Vanzolini 1986, Ferrarezzi 1993, Harvey 1999, Nogueira et al. 2012, Ferrarezzi et al. 2005, Guedes et al. 2018b, Entiauspe-Neto et al. 2019, Entiauspe-Neto et al. 2020). Additionally, several species are known from small series, poorly supported by brief descriptions, and present an incomplete knowledge of their morphological variation and geographic distribution (see Entiauspe-Neto et al. 2019 for a discussion). It is noteworthy that the phylogenetic relationships of *Apostolepis* species also remain unresolved.

FERRAREZZI (1993) proposed the first outline of a phylogenetic arrangement for the genus, strictly supported by morphology, and tentatively partitioned the genus into six species groups (in use until nowadays), based on coloration patterns and morphological character states. Later, ZAHER et al. (2009) recovered a monophyletic *Apostolepis* based on molecular data, although including only two terminals. The poor representation of *Apostolepis* taxa in modern molecular phylogenies has not improved much since then. A most recent work from ZAHER et al. (2019) still bears only seven species, and most questions regarding the internal relationships of the genus remain unanswered.

The *Apostolepis assimilis* species Group (sensu FERRAREZZI 1993) currently comprises at least three species with a long and convoluted taxonomic history: *Apostolepis ammodites* FERRAREZZI, BARBO & ALBUQUERQUE, 2005, *Apostolepis assimilis* (REINHARDT, 1861), and *Apostolepis cearensis* GOMES, 1915. *Elapomorphus assimilis* was described based on one specimen (ZMUC 63806), assigned by the author to "Brumado I Campos-Egnene af Provindsen Minas geraes vest for Serra do Espinhaço" (REINHARDT 1861: 235), which has been tentatively assigned to the municipality of Brumadinho, at the time referred to as "Brumado" and "Brumado Velho", in the hills of Minas Gerais state, southeastern Brazil. The description by REINHARDT (1861) is particularly informative, providing detailed information on its morphology and coloration, allowing for an unambiguous identification of the species, while also comparing it with two "close" congeners, *Elapomorphus d'Orbignyi* (*A. dorbignyi*) (SCHLEGEL, 1837) and *Elapomorphus flavotorquatus* (*Apostolepis flavotorquata*) (DUMÉRIL, BIBRON & DUMÉRIL, 1854). JAN (1865) and STRAUCH (1884) provided brief comments on the morphology and relationships of the species. Later, BOULENGER (1896) allocated *E. assimilis* in the genus *Apostolepis*, a decision which has gone unchanged since then.

GOMES (1915) presented a description of four snake species from the "Museu Rocha", including *A. cearensis*, described upon four specimens from the state of Ceará, northeastern Brazil. The work of GOMES (1915) is particularly well illustrated, while also presenting comparisons between the novel taxa and *A. assimilis*. This was followed by the works of WERNER (1924, 1925), who described two *Apostolepis* species from Brazil; the first, named as *Apostolepis sanctae-ritae* (hereafter *A. sanctaeritae* sensu LEMA & FERNANDES 1997), was described based on a specimen from "Santa Rita, Brasilien (Brasil. Expedition)." (WERNER 1924: 43), and the second, *Apostolepis amarali*, bearing no specific type locality (WERNER 1925: 62). The description of *A. sanctaeritae* was composed by pholidosis counts, morphological description of the type (NMW 23452), measurements, and comparisons with *A. flavitorquata* (misspelling of *A. flavotorquata*) and *A. pymi* BOULENGER, 1903. The description of *A. amarali* was even briefer, having only the pholidosis counts, a short description of morphology, and comments of resemblance to *A. assimilis*.

Shortly after, AMARAL (1929) proposed the synonymization of *A. amarali* with *A. cearensis*, and of *A. sanctaeritae* with *A. flavotorquata*. In both cases, only a brief commentary was given for these taxonomic actions; for *A. amarali*, the author argues that after examining the type, he could not distinguish it from *A. cearensis*, while for *A. sanctaeritae*, there is only a mention that the "nasal-preocular separation" should not be of taxonomic significance, and that the former species should be relegated as a synonym of *A. flavotorquata*, together with *Apostolepis nigrolineata* (PETERS, 1869). Subsequent studies have followed this arrangement, while PETERS & OREJAS-MIRANDA (1970) remarked that the type locality of *A. sanctaeritae*, given as "Santa Rita", referred to the municipality of Santa Rita do Araguaia, in Goiás, southeastern Brazil.

Although never formally published, the work of FERRAREZZI (1993) proposed several changes on the taxonomy of the genus (notably, the recognition of the *A. assimilis* Group, composed of *A. assimilis*, *A. cearensis*, and two other candidate new species that remained undescribed). *Apostolepis sanctaeritae* is cited as a synonym of *A. cearensis*. It is unclear to us whether the author examined the holotype of *A. sanctaeritae* although there seems to be an unpublished congress abstract authored by FERRAREZZI and collaborators, on the matter, that could not be examined by us. The two proposed new species could also not be examined by us since they appear to have been lost in the Instituto Butantan fire event of 2010 (G. PUORTO pers. comm.).

LEMA & FERNANDES (1997) proposed a revalidation of *A. sanctaeritae* and redescribed the holotype, housed in the Naturhistorisches Museum Wien, Austria, with comments on its morphology and relationships. These authors also proposed the recognition of "Santa Rita, Ibipetuba, Bahia, Brazil" as the type locality of *A. sanctaeritae*. HARVEY (1999), seemingly unaware of this work, cited *A. sanctaeritae* as a synonym of *A. cearensis*, attributing this to AMARAL (1929) and FERRAREZZI (1993). This statement is largely incorrect because, as already mentioned, AMARAL (1929) synonymized *A. sanctaeritae* with *A. flavotorquata*, rather than *A. cearensis*. LEMA (2002) provided another redescription for the type of *A. sanctaeritae* while also correcting some of the mistakes made by AMARAL (1929) and LEMA & FERNANDES (1997), which were largely related to pholidosis and coloration.

The works of LEMA (2004a, 2004b) described two new species belonging to the *A. assimilis* Group; *Apostolepis freitasi* LEMA, 2004 and *Apostolepis tertulianobeui* LEMA, 2004, respectively. FERRAREZZI et al. (2005) presented a taxonomic revision of the *A. assimilis* Group, proposing a parsimony-based phylogenetic arrangement, describing *A. ammodites* based on a specimen from the locality of Palmas, Tocantins state, northeastern Brazil while also allocating *A. sanctaeritae* and *A. freitasi* as synonyms of *A. cearensis*, and *A. tertulianobeui* as a synonym of *A. assimilis*. Later, LEMA & RENNER (2007) proposed a revalidation of *A. tertulianobeui*, comparing its holotype with a large series of *A. assimilis* specimens. Another species, *Apostolepis parassimilis* LEMA & RENNER, 2012 was described based solely upon a single specimen (MNRJ 6524, ex MCN 8535) from

"Bahia", without further comments on its locality. Costa & Bérnils (2015) recognized *A. parassimilis* as an objective synonym of *A. tertulianobeui*, as both species shared the exact same type specimen.

Considering the taxonomic instability of the group, we examined the holotypes of both *A. sanctaeritae* and *A. ammodites*. Our detailed analysis including the type-series and a large number of additional specimens provided us with compelling evidence to consider *A. sanctaeritae* as a valid species, which has been referred to *A. ammodites* in recent works. In this work, we present a translation of its original description, revalidation, and an emended diagnosis for *A. sanctaeritae* while also considering *A. ammodites* as a junior synonym of this species. We also provide a detailed description of the skull morphology of *A. sanctaeritae* based on CT-scan data of the holotype and comments on the taxonomy of *Apostolepis*.

Materials and methods

We examined a total of 642 specimens of *Apostolepis* from the following collections: Academy of Natural Sciences, ANSP, USA; The Natural History Museum, BMNH, United Kingdom; Coleção Herpetológica da Universidade Federal do Ceará, CHUFC, Brazil; Coleção Herpetológica da Universidade Federal de Sergipe, CHUFS, Brazil; Instituto Butantan, IBSP, Brazil; Instituto de Ciencias Naturales, Universidad Nacional de Colombia, ICN, Colombia; Coleção Herpetológica, Instituto de Pesquisas Amazônicas, INPA, Brazil; Museu de Ciências e Tecnologia da Pontifícia Universidade Católica do Rio Grande do Sul, MCP, Brazil; Muséum National d'Histoire Naturelle, MNHN, France; Museo de Historia Natural Para la Tierra, MHNP, Paraguay; Museu Nacional, MNRJ, Brazil; Museu de História Natural da Universidade Federal de Alagoas, MUFAL, Brazil; Museu de Zoologia, Universidade Estadual de Feira de Santana, MZUEFS, Brazil; Museu de Zoologia da Universidade Federal da Bahia, MZUFBA, Brazil; Museu de Zoologia da Universidade de São Paulo, MZUSP, Brazil; Naturhistorisches Museum Wien, NMW, Austria; Coleção Herpetológica da Universidade Federal do Mato Grosso, UFMT-R, Brazil; Coleção Herpetológica da Universidade Federal de Rondônia, UFRO-H, Brazil; University of Michigan Museum of Zoology, Herpetology collection, UMMZ, USA; Zoologisches Forschungsmuseum Alexander Koenig, ZFMK, Germany; Zoologisches Museum für Naturkunde Berlin, ZMB, Germany. A list of examined material is provided in Appendix 1.

Measurements were taken to the nearest 0.01 mm with a caliper, except for snout-vent (SVL) and tail length (TL), which were taken with a flexible ruler. Scale counts follow Dowling (1951). Sex determination was done with a ventral incision in the base of the tail. Our final dataset was improved with literature data for *A. ammodites* (Ferrarezzi et al. 2005, Lema & Renner 2007) and *A. assimilis* (Ferrarezzi et al. 2005). Coordinates are given in SIRGAS2000 Datum. An emended diagnosis, as well as meristic and morphometric characters were selected based on the nomenclature used by Entiauspe-Neto et al. (2020), and are as follows: head length, measured from centre of rostral to the corner of mouth; head width, measured at the corner of mouth; snout-vent length, ventrally measured from centre of rostral to the posterior margin of cloacal scale; tail length, measured from posterior margin of cloacal scale to terminal scale. Adopted phylogenetic relationships of the *A. assimilis* clade follow Zaher et al. (2019). Speciation concepts follow de Queiroz (2005, 2007).

Osteological description of the skull of the holotype of *A. sanctaeritae* (NMW 23452) is based on a high-resolution micro-CT scan, performed with a Bruker SkyScan 1173 at ZFMK. The scan was conducted at an X-ray beam with 43 kV source voltage and 114 µA current without the use of a filter. Rotation steps of 0.25° degrees were used with a frame averaging of 5, recorded over a 180° rotation, resulting in 960 projections of 550 ms exposure time each and a total scan duration of 1 h 03 min. The magnification setup generated data with an isotropic voxel size of 9.94 µm. The CT-dataset was reconstructed using N-Recon software version 1.7.1.6 (Bruker MicroCT) and rendered in three dimensions through the aid of CTVox 2.6 (Bruker MicroCT) and Amira visualization software (FEI, Thermo Fisher Scientific). Segmentation to separate bones was done with Amira. Osteological terminology follows Bullock & Tanner (1966) and Cundall & Irish (2008). We compared our osteological description with data available for *Apostolepis* from Ferrarezzi et al. (2005).

Results

Reanalysis of type specimen and comparisons

We have carefully re-analysed the work of Ferrarezzi et al. (2005), running the holotype of *Apostolepis sanctaeritae* through the proposed dichotomous key (see Ferrarezzi et al. 2005: 217) and it is not possible to determine if the type specimen of *A. sanctaeritae* presents or not an additional post-cervical white collar, as we have observed that it becomes indistinct in long-term preserved and discolored specimens. To the second character, we observed the rostral scale of *A. sanctaeritae* matches the condition presented by *A. ammodites* since it does not reach one/half of its interprefrontal suture. Additionally, the white snout blotch in *A. sanctaeritae* and *A. ammodites* are similar, reaching up to the frontal scale, while in *A. cearensis* it is restricted to the prefrontals. The holotype of *A. sanctaeritae* bears 4–5 pterygoid teeth loci (vs. 2 in *A. cearensis*; 3–4 in *A. ammodites*), curved dentary, with 8–9 teeth loci (vs. nearly straight, 7–8 teeth in *A. cearensis*; curved, 9–10 teeth in *A. ammodites*), prearticular crest slightly higher than surangular crest (vs. straight in *A. cearensis*, higher than surangular crest posteriorly in *A. ammodites*) (Ferrarezzi et al. 2005). Our analysis of the *A. sanctaeritae* type specimen (NMW 23452) revealed minor incongruences with the description provided by Werner (1924): the number of ventrals should be corrected to 241, and the number of subcaudals to 31/31. This is very close to the range reported for males of *A. ammodites* (ventrals 219–240, subcaudals 32–36) by Ferrarezzi et al. (2005), Lema & Renner (2007), and in this study. In light of this, we conclude *A. sanctaeritae* is actually synonymous with *A. ammodites*, and therefore, *A. ammodites* should be relegated as a junior synonym of *A. sanctaeritae*.

Original description translation

The description of *A. sanctaeritae*, originally presented by Werner (1924: 43–44) in German, is translated (by coauthor Arthur Tiutenko) and presented below.

"*Apostolepis sanctae-ritae* n. sp. Santa Rita, Brazil (Brazil Expedition).

Closely related to *A. flavitorquata* (sic) Cope and *A. pymi* Blngr.

The part of the rostral that is visible from above is almost as long as the distance from the frontal. The frontal is 1 1/2 times as long as wide, longer than the distance from the rostral, much shorter than the parietals which are twice as long as wide. The nasal separated from the preocular, prefrontal in contact with the 2nd supralabial; 1 pre-, 1 postocular; 6 supralabials, 3rd, 4th at eye, 5th, 6th at parietal; 4 infralabials in contact with the anterior chin shields which are as long as the posterior.

V. 245, A 1/1, Sc. 32/23+1.

Forehead yellow; parietals, the rear corner of the frontal, sides of the head, starting from the 3rd supralabial, and the foremost three scale rows are black; a yellow longitudinal stripe at the inner margin of every parietal; gulars black, infralabials dark outlined; symphisal and chin shields dark (grey) along the midline.

Otherwise yellow-brown from above, venter whitish; rear tail half (from 23rd subcaudal pair on) black from above and from below.

Length 555 (50) mm.

It differs from *A. flavitorquata* (sic) by from the nasal separated preoculars, only four infralabials contacting the chin shields, as well as by yellow snout; from *A. pymi* by a higher rostral, also by from nasal separated preocular, smaller number of ventrals and a different pattern (no black bands)."

A detailed redescription of the type specimen is provided by Lema (2006).

Redescription

Apostolepis sanctaeritae **Werner, 1924 revalidated.**
Apostolepis ammodites Ferrarezzi, Barbo & Albuquerque, 2005 **new synonymy.**
Heterochresonymy
Apostolepis flavotorquata (part.) Amaral, 1930;
Apostolepis cearensis (part.) Ferrarezzi et al. 2005.

Holotype (Fig 1): NMW 23452, adult male collected by Franz Steindachner, from "Santa Rita Brasilien", Santa Rita de Cássia, Ibipetuba municipality, Bahia state, northeastern Brazil.

Type locality: The type locality "Santa Rita Brasilien" mentioned by Werner (1924) was later referred to "municipality of Santa Rita do Araguaia, Goiás state" by Peters & Orejas-Miranda (1970), and then to "Santa Rita de Cássia, Ibipetuba municipality, Bahia state" by Lema & Fernandes (1997). The type locality suggested by Lema & Fernandes (1997) is considered the most probable since it is inside the area of occurrence of the species in the Cerrado (Fig. 2). However, the current name assigned to the municipality is Santa Rita de Cássia, Bahia state (11°00'31.3" S, 44°33'29.5" W).

Emended diagnosis (n = 11): *Apostolepis sanctaeritae* can be distinguished from all its congeners by the following combination of characters: (1) 15/15/15 smooth dorsals without apical pits; (2) 1+1 postoculars; (3) loreal absent; (4) temporals 0+1, 1+1; (5) supralabials 6, with 2nd and 3rd in contact with orbit; (6) infralabials 7, with first four in contact with chin shield; (7) ventrals 219–253 (219–240 in males, 221–253 in females); (8) subcaudals 25–36 pairs (32–36 in males, 26–32 in females); (9) in life, dorsal pattern uniform orange or red, head dorsally black, with a white blotch ranging from rostral to frontal scales, supralabial blotch small on 4th supralabial scale, white nuchal collar wide (2–6 scales long), black nuchal collar wide (4–7 scales long), followed by a small or absent white nuchal collar (1–3 scales long, if present), black dorsal tail blotch present (in preservative, white, orange, and red colorations can become indistinct); (10) in life, ventral pattern similar to dorsal, uniform orange, with infralabial and gular black markings, sometimes with indistinct black markings below the white and black nuchal collar, terminal caudal spine black (Fig 2).

Osteology (NMW 23452; Figs 3–7).

Snout: Premaxilla thick and robust, 1.4 times broader than high, with a stout, posterodorsally oriented ascending process approaching, but not contacting, anterior end of nasals; lateral processes short and distinctly separated from maxillae; vomerine processes short and broad, posteriorly oriented, dorsal part almost contacting anteroventral part of septomaxilla, largely separated from anterior end of vomers.

Septomaxillae separated from each other; each with a broad ascending conchal process, freely extending laterally beyond lateral margin of nasal in dorsal view; posterior process contacting posterior process of nasal and almost contacting frontal; contacting vomer posteriorly.

Nasals almost as broad as frontals, about rectangular in dorsal view; in contact medially, the front edges reach close to the premaxillary and frame its ascending process, lateral edges curved downwards; posterior processes of nasals contacting ventral part of frontals anteriorly; vertical lamina of nasals approaching, but not contacting medial part of septomaxillae.

Vomers in contact medially; almost contacting anterior region of palatine laterally; bifurcate vertical posteromedial laminae, diverging dorsally and ventrally, framing but not contacting choanal process of palatine anteriorly.

Braincase: Prefrontals forming anterior margin of orbits; oriented oblique, anterior margin irregular, posterior margin slightly concave; in contact with frontal dorsally; ventral portion contacts dorsal surface of maxilla laterally and maxillary process of palatine medially; in rear view, lacrimal foramen visible in most basal portion.

Frontals paired, almost in contact medially with a straight medial suture; lateral and posterior margins irregularly notched, only a small part of the lateral margin participates in the formation of the dorsal margin of orbit; anterolateral edges of frontals forming an oblique suture with prefrontals; loose, curved suture between frontals and parietal, with long anterolateral processes of the parietal extending almost completely along the lateral edges of the frontals and excluding major parts of the frontals from the orbit; ventral edges of vertical laminae of frontals in medial contact anteriorly, separated in the posterior two-thirds by the intervening parabasisphenoid.

Parietal single, elongate, distinctly longer than broad, with long and robust anterolateral processes framing lateral borders of frontals and forming posterior and most of dorsal margin of orbit; anterior border irregular and notched, especially in central region; a ridge extends dorsally on both sides from the anterolateral process in posteromedial direction, both ridges merge in the posterior fifth of the parietal, and reach to the suture with the supraoccipital; lateroventrally contacting posterior portion of parasphenoid rostrum and basisphenoid portion of parabasisphenoid, posterolaterally contacting dorsal and anterior margin of prootics in dorsal and lateral view, and posteriorly contacting supraoccipital.

Postorbitals absent.

Supraoccipital single, diamond-shaped, 1.4 times broader than long, contacting prootics anterolaterally and exoccipitals posteriorly; not in contact with supratemporals; anterior region elevated, a slight medial ridge emerges posterior to the elevated part and reaches to the suture with exoccipitals.

Exoccipitals subhexagonal, each with a lateral ridge parallel to inner margin of supratemporals; contact supraoccipital anterodorsally, prootics anterolaterally, basioccipital ventrally and supratemporals laterally; fenestra ovalis is situated at suture between prootic and exoccipital, and exoccipitals forming posterior margin of fenestra; posteriorly, exoccipitals forming dorsal, lateral, and lateroventral border of foramen magnum.

Basioccipital hexagonal, contacting parabasisphenoid complex anteriorly, prootics anterolaterally, exoccipitals posterolaterally, and forming ventral border of foramen magnum posteriorly; in the first anterior third is a slight

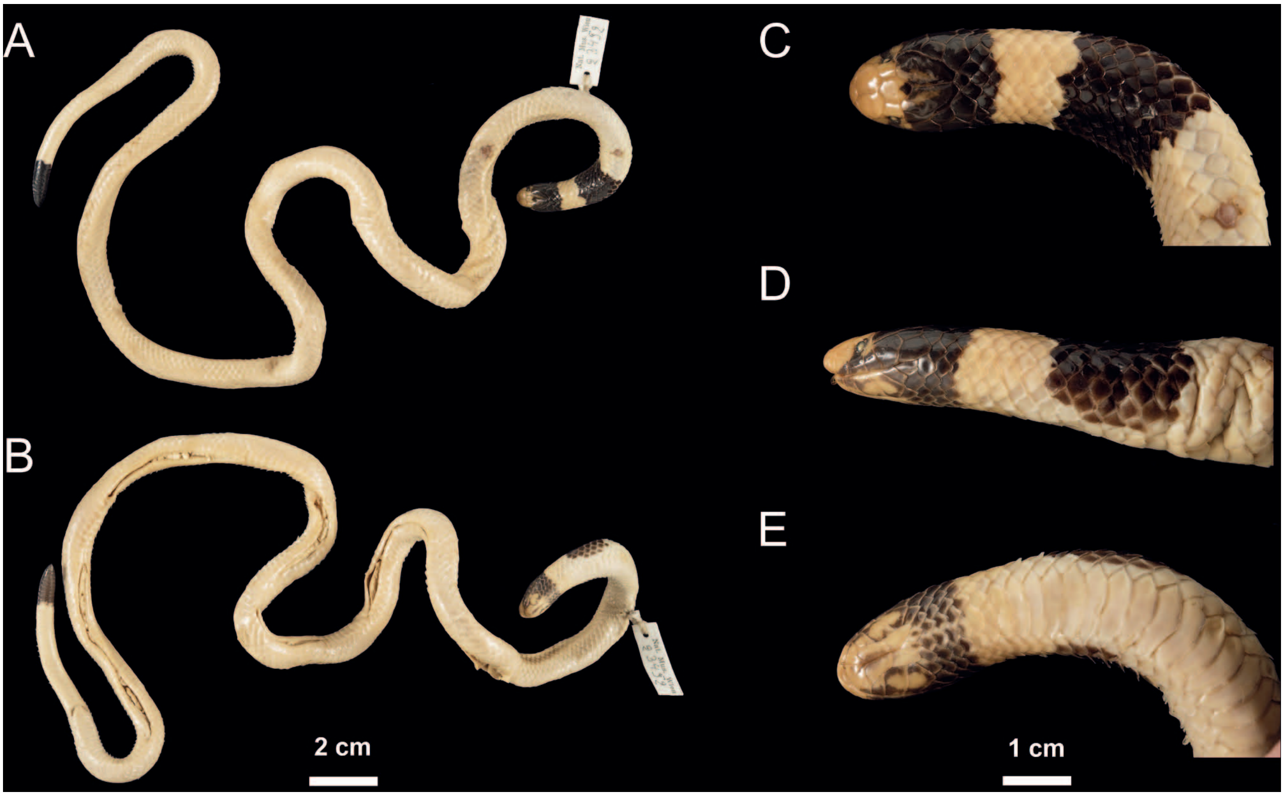

Figure 1. The holotype of *Apostolepis sanctaeritae* (NMW 23452): entire specimen in A) dorsal, and B) ventral views; close-up of head in C) dorsal, D) lateral, and E) ventral views. Images by M. Flecks.

elevation medially which ends posteriorly in two symmetrical bulges, each lateral to the midline; at the widest point, approximately at the beginning of the posterior half of the basioccipital, is a short, blunt, backwards pointing projection on each side of the outer lateral edges.

Prootics ovaloid in lateral view, each with a large foramen at the lateral suture with the parietal and a second large foramen slightly posterior and slightly below the central part of the prootic in lateral view, in between are two small foramina in the lower third of the bone; trapezoidal in dorsal view, with a depression in the posterior half in which the anterior quarter of the supratemporal rests; contacting parietal anteriorly and anterodorsally, supraoccipital posterodorsally, exoccipitals posteriorly, parabasisphenoid complex anteroventrally, and basioccipital posteroventrally; posteriorly forming anterior margin of fenestra ovalis at suture with exoccipitals.

Parasphenoid and basisphenoid fused; basisphenoid portion ovaloid; parasphenoid rostrum lanceolate with a blunt anterior tip, which contacts dorsally the lower part of the frontals in anteromedial region; anterior tip of parasphenoid rostrum neither contacting and nor surpassing choanal process of palatine, largely separated from posterior ending of vomers, nasals, and septomaxillae; parasphenoid rostrum with lateral groove on each side along anterior two-thirds of its length; a small foramen in the central part of the anterior third of basisphenoid; two further foramen are located in the posterior part of the basisphenoid, each at the lateral edge of the bone shortly before the suture with the prootic.

Palatomaxillary arch: Maxillae short and robust, extending from level of vomerine processes of premaxilla to about central region of orbit, forming the anterior, inferior margin of orbit laterally; slightly arched towards premaxilla; ventral surface of maxillae with four solid, curved, and rear facing anterior teeth, slightly increasing in size posteriorly, followed posteriorly, after a distinct interspace, by a pair of large deeply grooved fangs, situated bellow the eye; posterior end of maxillae with a short, rear facing tooth-like sporn at the lateral margin of the ventral surface; palatine process very short, not in contact with maxillary process of palatine; dorsally contacting ventral part of prefrontal at level of maxillary interspace; ectopterygoid process not evident; maxilla corresponds to less than one-third of length of skull.

Ectopterygoids divining rod-shaped, deeply forked anteriorly; in dorsal view of skull, not covered by any roofing skull bones and thus almost entirely visible; anterior processes framing but not contacting the posterior end of the maxillae laterally and medially, forming a fairly large maxilo-ectopterygoid fenestra; rod-like posterior process, overlaying but not contacting anterolateral portion of pterygoid.

Pterygoids elongate, corresponding approximately to half-length of skull; in dorsal view of skull, lateral edges are visible and not covered by parietal; ventral surface with 4–5

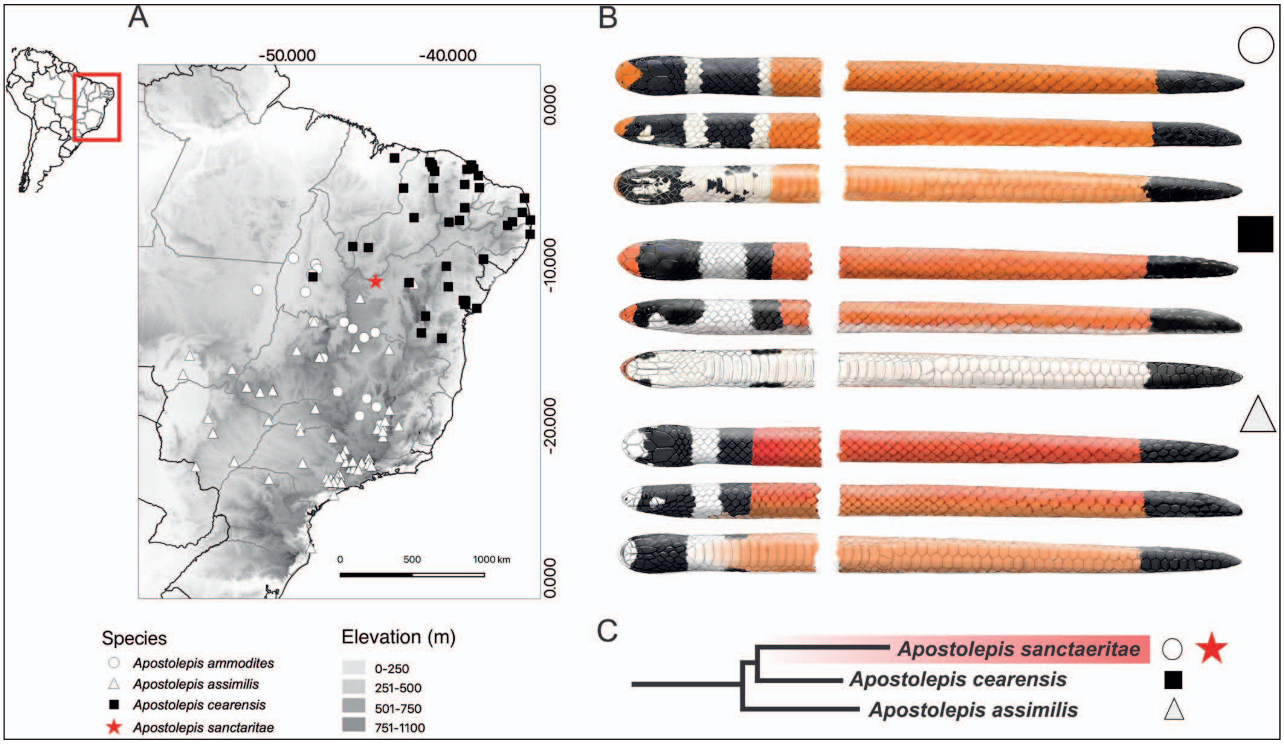

Figure 2. Overview of the *Apostolepis assimilis* Group. A) Geographic distribution of *A. assimilis*, *A. cearensis*, *A. sanctaeritae* (type locality), and populations formerly assigned to *A. ammodites* (synonym of *A. sanctaeritae*); B) Illustrations of *A. sanctaeritae* (circle; based on holotype of *A. ammodites*, IBSP 65267), *A. cearensis* (square), and *A. assimilis* (triangle); C) Phylogenetic relationships of the *A. assimilis* Group, modified from Zaher et al. (2019).

tooth loci; teeth subequal, small, slightly curved, and rear facing; anterior tip of pterygoid not extending beyond its articulation with ectopterygoid, and dorsally just marginally overlain by posterior toothless tip of palatine, but not contacting it; lateral borders of pterygoids slightly sigmoidal; medial borders nearly parallel in anterior two-thirds, with smallest distance between each other shortly after tooth line; medial border of last third of bone gradually

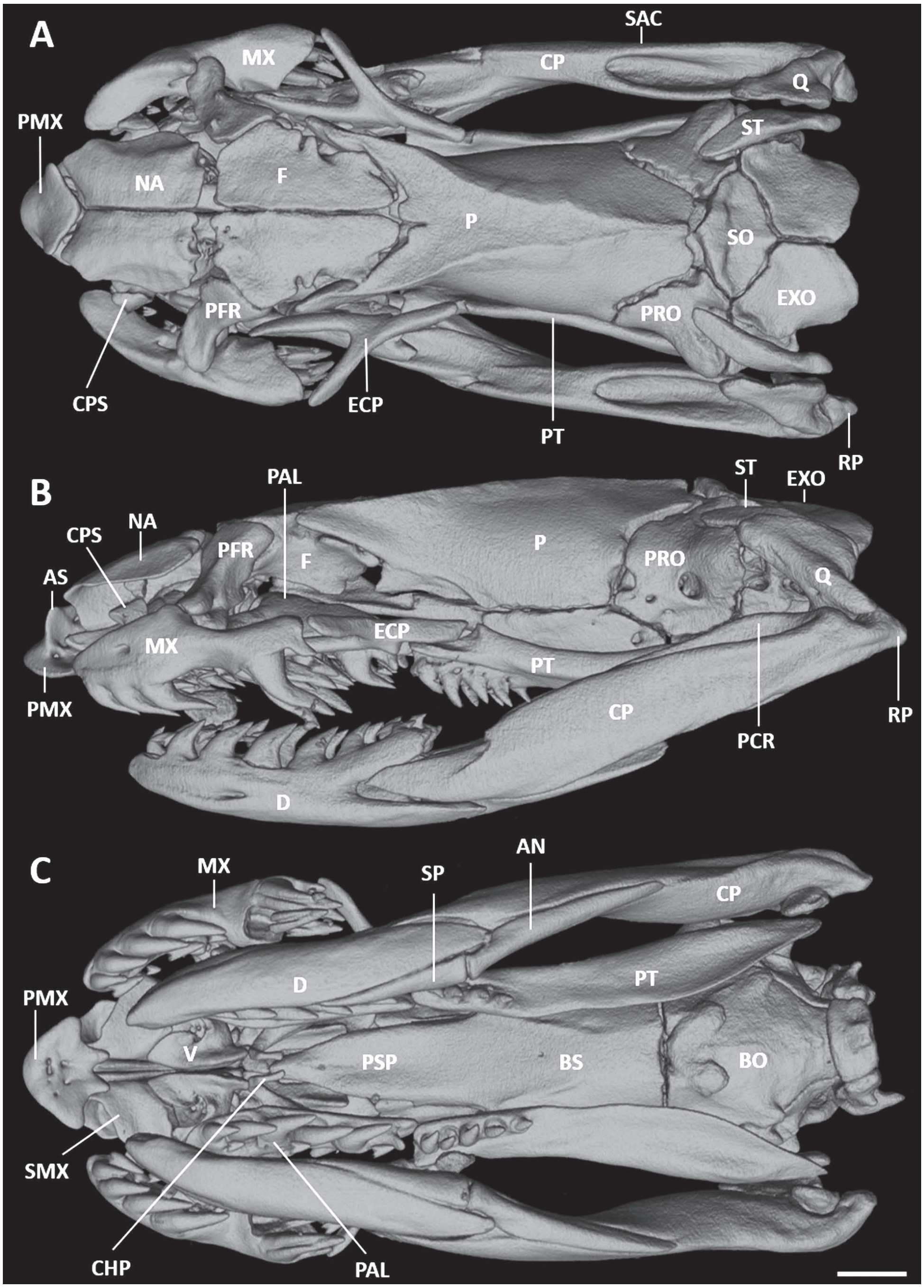

Figure 3. Micro-CT images of the skull of the holotype of *Apostolepis sanctaeritae* (NMW 23452) in A) dorsal, B) lateral, and C) ventral views; AN (angular); AS (ascending process of premaxilla); BO (basioccipital); BS (basisphenoid); CHP (choanal process of palatine); CP (compound bone); CPS (conchal process of septomaxilla); D (dentary); ECP (ectopterygoid); EXO (exoccipital); F (frontal); MX (maxilla); NA (nasal); P (parietal); PAL (palatine); PCR (prearticular crest of compound bone); PFR (prefrontal); PMX (premaxilla); PRO (prootic); PSP (parasphenoid rostrum); PT (pterygoid); Q (quadrate); RP (retroarticular process of compound bone); SAC (surangular crest of compound bone); SMX (septomaxilla); SO (supraoccipital); SP (splenial); ST (supratemporal); V (vomer). Scale bar = 1 mm. Images by C. Koch.

tapering posterolaterally, resulting in the greatest distance between both pterygoids at their posteriormost tips; posterior end of pterygoid approaching ventromedial portion of quadrate; dorsal surface with a lateral longitudinal ridge along most of its length, beginning at about level of third tooth, and reaching to posterior tip of pterygoid.

Palatines short and robust, almost straight and parallel, shortest of all toothed bones; ventral surface with 5 tooth loci; teeth solid, subequal, curved, and rear facing; anterior portion of palatines almost contacting ventrolateral part of vomers dorsally; dorsomedially, a long, thin choanal process curves downwards in a semicircle, approaching but not contacting its counterpart medially; short, stout, maxillary process situated on lateral surface of palatine at level of second tooth, directed laterally, anterior region almost contacting palatine process of maxilla, dorsal surface contacting medioventral region of prefrontal; posterior part of palatine bifurcating, with a slightly shorter lateral branch and a slightly broader, medial branch, both flattened and tapering towards the posterior end, the medial branch approaching but not contacting anterior part of pterygoid.

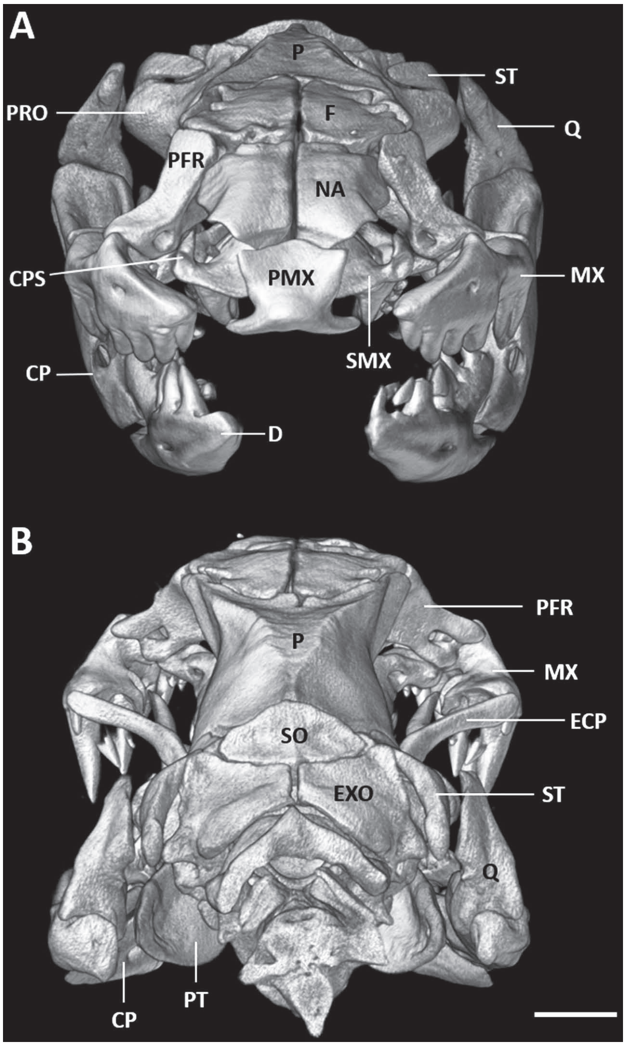

Figure 4. Micro-CT images of the skull of the holotype of *Apostolepis sanctaeritae* (NMW 23452) in A) anterior, and B) posterior views; CP (compound bone); CPS (conchal process of septomaxilla); D (dentary); ECP (ectopterygoid); EXO (exoccipital); F (frontal); MX (maxilla); NA (nasal); P (parietal); PFR (prefrontal); PMX (premaxilla); PRO (prootic); PT (pterygoid); Q (quadrate); SMX (septomaxilla); SO (supraoccipital); ST (supratemporal). Scale bar = 1 mm. Images by C. Koch.

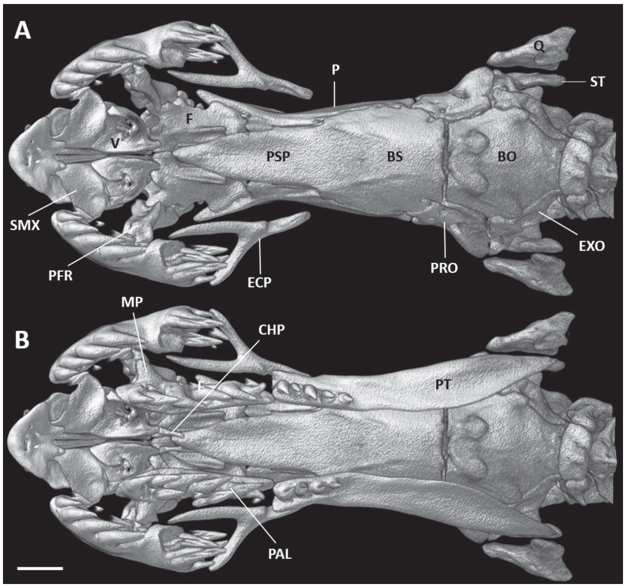

Figure 5. Micro-CT images of the skull of the holotype of *Apostolepis sanctaeritae* (NMW 23452) in ventral view: (A) mandibulae, palatines, and pterygoids removed, (B) mandibulae removed; BO (basioccipital); BS (basisphenoid); CHP (choanal process of palatine); ECP (ectopterygoid); EXO (exoccipital); F (frontal); MP (maxillary process of palatine); P (parietal); PAL (palatine); PFR (prefrontal); PRO (prootic); PSP (parasphenoid rostrum); PT (pterygoid); Q (quadrate); SMX (septomaxilla); ST (supratemporal); V (vomer). Scale bar = 1 mm. Images by C. Koch.

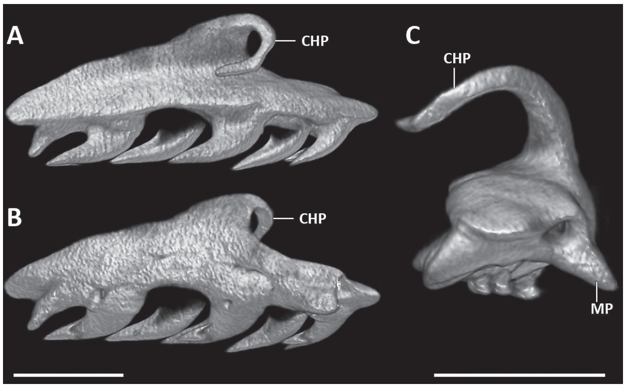

Figure 6. Micro-CT images of the left palatine of the holotype of *Apostolepis sanctaeritae* (NMW 23452) in A) medial, B) lateral, and C) anteroposterior views; CHP (choanal process of palatine); MP (maxillary process of palatine). Scale bars = 1 mm. Images by C. Koch.

Suspensorium and mandible: Supratemportals laminar, elongate; anterior end overlaying and firmly contacting posterior half of prootic in dorsal view, distantly separated from parietal; central part overlaying anterolateral part of exoccipital; central and posterior part, except ultimate end, laterally articulating with quadrate; posterior end free, surpassing quadrate but not reaching posterior end of exoccipital.

Quadrates flattened and broad dorsally, tapering dorsoventrally in lateral view, but gradually increasing in width in rear view; oblique oriented, from anterodorsally to posteroventrally; medial portion with short process corresponding to region of contact with columella auris, however, no columella visible; ventral portion slightly bifurcate, straddling glenoid cavity of retroarticular process of mandible.

Dentaries short; dorsal surface with 8–9 tooth loci; teeth subequal, curved and rear facing, increasing in length to the fourth or fifth and then gradually decreasing to the last one; lateral face slightly convex with a mental foramen located at about level of 3rd–4th tooth, slightly anterior to midregion of dental tooth line; at about level of 6th–7th tooth, dentary branches into a shorter dorsal process, which overlays anterior part of compound bone, and a longer lanceolate ventral process, which contacts splenial and anterior part of angular, and runs with its dorsal surface parallel and close along anterior part of medioventral region of compound bone without touching it; at level of 7th–8th tooth, dorsal process branches again into a short medial process and a longer tooth-bearing dorsal process.

Splenials elongate, triangular, tapered anteriorly, with anterior mylohyoid foramen in dorsal region at about the beginning of the fourth quarter; posterior edge contacting anterior region of angular.

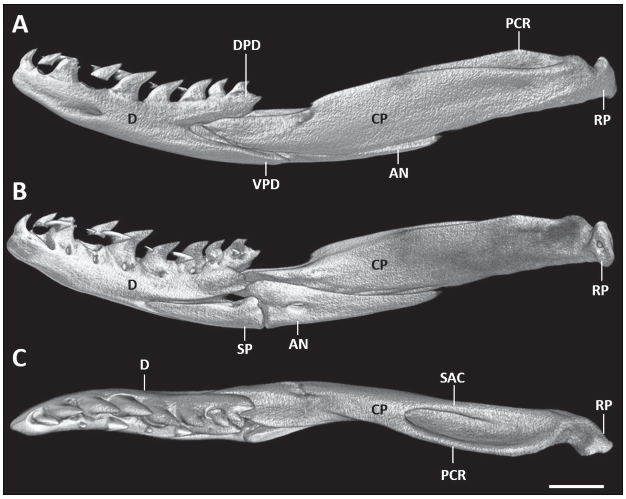

Figure 7. Micro-CT images of the right mandibula of the holotype of *Apostolepis sanctaeritae* (NMW 23452) in A) lateral, B) medial, and C) dorsal views; AN (angular); CP (compound bone); D (dentary); DPD (dorsal process of dentary); PCR (prearticular crest of compound bone); RP (retroarticular process of compound bone); SAC (surangular crest of compound bone); SP (splenial); VPD (ventral process of dentary). Scale bar = 1 mm. Images by C. Koch.

Angulars elongate, triangular, tapered posteriorly; contacting compound bone laterally; anterodorsal process approaching but not contacting medial process of dentary; posterior mylohyoid foramen on lateral surface in first quarter of angular.

Compound bones elongate, approximately two-thirds length of mandible; prearticular crest slightly higher than surangular crest and thus visible in lateral view, the latter not visible in medial view; in lateral view, compound bone tapering anteriorly, fitting between dorsal and ventral processes of dentary; anterodorsally oriented foramen shortly behind level where posterior tip of ventral process of dentary ends; retroarticular process short, reaching just beyond the posterior end of the exoccipitals, slightly medially directed.

Discussion

Previous authors (e.g. Lema & Fernandes 1997; Lema 2002) had already highlighted significant differences among the holotype of *Apostolepis sanctaeritae* and other species of the *A. assimilis* Group. Lema (2002) provided a dichotomous key and comments on other *Apostolepis* from northeastern Brazil, diagnosing *A. sanctaeritae* from *A. cearensis* (in parenthesis) based on a broader head (slender), snout not projected beyond jaws (projected), black cervical (in our interpretation, nuchal) collar without anterior projection (with anterior vertebral projection), light supralabial blotch usually large (small), snout tip yellow (red) (Fig. 8). However, some of these characters are known to exhibit large variation, such as the nuchal collars, supralabial blotches and snout coloration (see Entiauspe-Neto et al. 2020). It is also noteworthy that we have observed photographs from an unvouchered specimen of *A. sanctaeritae* from Tocantins, central Brazil, with a vestigial second nuchal collar (half scale long). These pattern variations likely led Amaral (1930), Ferrarezzi (1993), and Ferrarezzi et al. (2005) to assigning *A. sanctaeritae* to distinct synonymies over the last centuries.

Apostolepis is quite likely one of the most unstable Neotropical snake genera, considering the number of valid species over time, their nomenclature, and historical status modifications (Entiauspe-Neto et al. 2019). The proliferation of descriptions, based upon small series, not taking into account intraspecific variation, or integration of multiple lines of evidence, may be accountable for severe instability over its taxonomic history, riddled with revalidations and synonymizations (Entiauspe-Neto et al. 2019; Entiauspe-Neto et al. 2020; Entiauspe-Neto & Tiutenko 2020). For instance, the taxa *A. adhara* França, Barbo, Silva-Júnior, Silva & Zaher, 2019, *A. breviceps* Harvey, Gonzales & Scrocchi, 2001, *A. cerradoensis* Lema, 2003, *A. christineae* Lema, 2002, *A. dorbignyi* (Schlegel, 1837), *A. kikoi* Santos, Entiauspe-Neto, Araújo, Souza, Lema, Strüssmann & Albuquerque, 2018, *A. lineata* Cope, 1887, *A. niceforoi* Amaral, 1935, *A. phillipsae* Harvey, 1999, *A. roncadori* Lema, 2016, *A. serrana* Lema & Renner, 2006, *A. striata* Lema, 2003, *A. tenuis* Ruthven, 1927, *A. underwoodi* Lema & Campbell, 2017, and *A. vittata* Cope, 1887, remain known from less than five specimens, some of these even after a large timespan since their description; although some of these works have been consolidated over multiple lines of evidence (e.g. Santos et al. 2018), most lack comprehensive integration and analysis of data. We urge authors to conduct a careful re-examination of historical synonyms, in order to avoid describing new taxa that might have already available names in the literature.

Current diagnosis for *Apostolepis* species are largely based upon variable characters of pholidosis and coloration (see Entiauspe-Neto et al. 2020); these differences are, in some cases, shown to be subjective (see Nogueira et al. 2012), which might force taxonomists to undergo to geographic comparisons each time a new specimen needs identification. It is imperative to review and re-analyse the selected characters and how they are being employed for species delimitation in *Apostolepis*; its scarcity in collections and the intermittent attaining of specimens are factors that also should be taken into account. We argue for three major changes in the current taxonomic outlook for the genus: (1) researchers should integrate multiple lines of evidence when dealing with taxonomic decisions or determinations, therefore reducing subjectivity; (2) during fieldwork, researchers herpetologists should take additional steps in preserving specimens, such as the in-field preparation of hemipenis and tissue sample collection; (3) coordinate efforts in data sharing and availability, in order to conduct an integrative systematic and taxonomic review for the genus. Several questions remain unanswered for *Apostolepis*, for instance, the phylogenetic relationships for the genus have not been consistently tested. The most comprehensive phylogeny of *Apostolepis* (see Zaher et al. 2019) encompasses only seven terminals, with variable node support (>70–90%). It is not clear if the proposed species groups actually reflect monophyletic entities. Most species also lack basic information on hemipenial morphology and osteology. A throughout revision and large-scale collaboration is warranted in order to increase taxonomic stability for the group. We also suggest that micro-CT scanning is a non-invasive method, that can be used to gather important information on delicate, old, and preserved specimens, raising the possibility of a genus-wide employment for solving particularly difficult issues.

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Figure 8. Specimen of *Apostolepis sanctaeritae* in life. Image by Otávio A. V. Marques.

type of *A. sanctaeritae* and to M. Flecks (ZFMK) for taking pictures of the type. For allowing the revision of specimens in their museum collections and/or the loan of material we are indebted to N. Gilmore (ANSP), P. Campbell (BMNH), D. Loebmann (CHFURG), D. Borges (CHUFC), G. Colli and F. Domingos (CHUNB), G. Puorto (IBSP), F. Werneck (INPA), G. M. Funk Pontes (MCP), N. Vidal (MNHN), P. Cacciali (MHNP), I. Biondi and F. Juncá (MZUEFS), R. Lira-da-Silva (MZUFBA), H. Zaher (MZUSP), A. L. C. Prudente and J. C. Costa (MPEG), D. Meneghelli (UFRO-H), F. Curcio (UFMT-R), A. G. Kluge (UMMZ), F. Tillack (ZMB), D. K. Johansson (ZMUC), and P. R. Manzani (ZUEC). O. M. Entiauspe-Neto thanks CNPq for a PIBIC grant (136628/2016-8); T. B. Guedes thanks Fundação de Amparo à Pesquisa do Estado de São Paulo (postdoc fellowship FAPESP 2013/04170-8 and 2014/18837-7) and Universidade Estadual do Maranhão (Senior Researcher fellowship). We would also like to thank Otávio A. V. Marques for sending us a photograph of a specimen in life.

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Appendix I
Material examined

Countries are given in capitals, states in small capitals, followed by municipalities and localities.

Apostolepis arenaria (n = 5). BRAZIL: Bahia: Alagoado (MZUSP 10027, 10028, 10029, 10030, 10289).

Apostolepis assimilis (n = 143). BRAZIL: Bahia: Barreiras (UMMZ 20411), Distrito Federal: Brasília (CHUNB 24456, 24474, IBSP 20566, 28734, USNM 148790); Goiás: Ilha do Bananal, Santa Isabel (IBSP 12324); Jataí (MZUSP 3783); Mineiros (IBSP 55495); Rio Verde (IBSP 10326, 12945, MZUSP 3194), Uruaçu, Cana Brava (IBSP 9154); Minas Gerais: Cabo Verde (IBSP 29448); Cambuí (IBSP 44222), Capão dos Porcos, Mariana (ZMUC 63806, holotype of *Apostolepis assimilis*), Caxambu (IBSP 816), Conceição dos Ouros (IBSP 33206), Entre Rios de Minas (FUNED 691), Gonçalves (IBSP 49666), Ibirité (FUNED 603), Itajubá (IBSP 9115, 9407, 9592), Itamonte (IBSP 22405), Itatiaiaçu (FUNED 510), Jaíba (FUNED 1465), Maria da Fé (IBSP 5597), Moéda (FUNED 02), Nova Lima (FUNED 550), Ouro Fino (IBSP 34306), Munhoz (IBSP 66376), Passa Quatro (IBSP 3264, 3274, 34306), Poços de Caldas (IBSP 45737, 23985, 14256), Pouso Alegre (IBSP 42162, 44597, 49942), Santa Rosa da Serra (IBSP 46088), Serra do Cipó (MZUSP 7595), Uberabinha (IBSP 888) Uberlândia (IBSP 3841, 3845, 6388, 3841), Vespasiano (FUNED 04); Mato Grosso do Sul: Amambaí (IBSP 41163), Campo Grande (IBSP 41163, 42978, 57222, MHNCI 6719, MZUSP 10155) Nova Andradina (IBSP 27489, 27489), Paranaíba (IBSP 45615), Ponta Porã (IBSP 44065); Mato Grosso: Buriti (IBSP 5346), Cuiabá (MNRJ 2031); Paraná: Londrina (IBSP 37462, 40008); Santa Catarina: Florianópolis (BGSS5344); São Paulo: Araçariguama (IBSP 83132), Barueri (IBSP 23206), Bauru (MHNCI 4790), Cabreuva (IBSP 26565), Caieiras (IBSP 40320), Caixa d'Água (IBSP 6659), Carapicuiba (IBSP 87769, 82260), Cajamar (IBSP 30408, 87083, 3186), Campo Largo (IBSP 4498), Campo Limpo (IBSP 6532), Campos do Jordão (IBSP 26796, UMMZ 204112), Carapicuíba (IBSP 72970), Cotia (IBSP 24588), Ibiúna (IBSP 32672, 79312, 78900), Itapevi (IBSP 30436, 86908, 79489), Itatiba (IBSP 5703), Itu (IBSP 4180, 6606, 82230, , MHNCI 6969, MZUSP 4180, 6606), Jaguara (IBSP 70356), Jandira (IBSP 31694, 40493), Jarinu (IBSP 30019), Jundiaí (IBSP 16688), Mairinque (IBSP 41065, 89049), Osasco (IBSP 23889, 40480, 6141, 62362, 78442, MCP 64), Pirituba (IBSP 70351, 78948,), Rio Grande (IBSP 40008), Santana de Parnaíba (IBSP 61761, 81066,), São Caetano do Sul (IBSP 81238), São Paulo (IBSP 318, 348, 6401, 6558, 8040, 8945, 21993, 22221, 24180, 24548, 24873, 27598, 30153, 30586, 31716, 32441, 33316, 84949, 78948), São Roque (IBSP 23548, 78641, , 79658, MHNCI 4495, 6970), Sorocaba (IBSP 15760, 40008); PARAGUAY: Trinidad (MZUM 108810).

Apostolepis cearensis (n = 140). BRAZIL: Alagoas: Piranhas (CHUFS 3217, 3365, MUFAL 1315); Bahia: Brumado (IBSP 33651, 33685), Camaçari (MZUEFS 371), Capim Grosso (MZUEFS 294), Feira de Santana (MZUEFS 12, 19, 70, 71, 74, 86, 130, 162, 166, 203, 277, 310, 315, 429, 434, 463, 464, 505, 515, 615, 624, 637, 669, 672, 689, 771, 804, 836, 841, 895, 927, 1007, 1040, 1053, 1067, 1069, 1070, 1071, 1077, 1080, 1110, 1146, 1157, 1158, 1195, 1196, 1208, 1209, 1210, 1236, 1240, 1241, 1244, 1260, 1302, 1310, 1313, 1369, 1377, 1405, 1445, 1446, 1477, 1478, 1479, 1499, 1539, 1559, 1570, 1587, 1604, 1611, 1622, 1629, 1645, 1673, 1674), Poções (MZUFBA 1595, 1796, 1805, 1813, 1826, 1827), São Gonçalo dos Campos (MZUEFS 73, 825), Jaguarari (IBSP 26203); Ceará: Aquifaz (CHUFC 1185), Beberibe (CHUFC 1628), Cratéus (CHUFC 2238), Crato (IBSP 20385), Fortaleza (CHUFC 208, 826, 1240, 1242, 1243, 1524, 1525, 1526, 1527, 1528, 1529, 1531, 1539, 1620, 1621, 1622, 1623, 1623, 1624, 1625, 1626, 1627, 1629, 2001, 2236, 2287, 2243, 2633, IBSP 20020, 40262, 55318, 18219, 18220), Icó (IBSP 12106), Juazeiro do Norte (IBSP 20164), Limoeiro do Norte (IBSP 12775), Maranguape (CHUFC 2235), Quixadá (CHUFC 1221), São Benedito (CHUFC 2114, 2147), Tianguá (IBSP 77109), Ubajara (IBSP 75855, 77101), Viçosa do Ceará (IBSP 77509); Paraíba: Cabaceiras (MZUSP 9013), Campina Grande (IBSP 9050), Lagoa de Dentro (MNRJ 17055); Piauí: Teresina (IBSP 49743), Redenção do Gurgeia (IBSP 80942).

Apostolepis cerradoensis (n = 1). BRAZIL: Goiás: Minaçu (MCP 15219, holotype of *Apostolepis cerradoensis*).

Apostolepis christineae (n = 2). BOLIVIA: Santa Cruz: Puerto Suarez, German Busch (BMNH 1907.10.31.62). BRAZIL: Mato Grosso: Cáceres (MCP 12515, holotype of *Apostolepis christineae*).

Apostolepis dorbignyi (n = 1). "AMÉRIQUE MÉRIDIONALE": Unknown locality (MNHN 3664, holotype of *Apostolepis dorbignyi*).

Apostolepis gaboi (n = 34). BRAZIL: Bahia: Ibiraba-Barra (MZUFBA 1673, 1674, 1675, 1676, 1677, 1678, 1679, 1680, 1681, 1682, 1683, 1684, 1685, 1686, 1687, 1688, 1689, 1690, 1691, 1692, 1693, 1694, 1695, 1696, 1697, 1698, 1699, 1700, 1701, 1702, 1702, 1704), Icatú-Barra (MZUEFS 981), Queimadas (MZUSP 10290).

Apostolepis goiasensis (n = 1). BRAZIL: Minas Gerais: Três Lagoas (CHFURG 1344).

Apostolepis intermedia (n = 2). PARAGUAY: San Pedro: Laguna Blanca (MHNP 11533, 11636).

Apostolepis kikoi (n = 5). BRAZIL: Mato Grosso: APM Manso, Chapada dos Guimarães (MCP 12096, 14524, 14525, 11372, UFMT-R 1933).

Apostolepis longicaudata (n = 1). BRAZIL: Tocantins: Estação Ecológica Serra Geral (MZUSP 14122).

Apostolepis multicincta (n = 3). BOLIVIA: Santa Cruz: San Juan (ZFMK 66375, paratype of *Apostolepis multicincta*), Florida (ZFMK 75025, 75026).

Apostolepis nelsonjorgei (n = 2). BRAZIL: Goiás: Campinaçú (MZUSP 20636). Tocantins: Estação Ecológica Serra Geral (MZUSP 17615).

Apostolepis nigrolineata (n = 217). SOUTH AMERICA (ZMB 6447, *A. nigrolineata* holotype). BRAZIL (BMNH 1946.1.9.82, *A. pymi* holotype). Maranhão: Paruá, BR 316 (MPEG 10835, 13641, 14352). Maranhão and Pará border: BR 316, km 74 (MPEG.1064, 1084, 3581, 8192, 10851). Mato Grosso: Paranaita (MZUSP 22344). Pará: Acará (MPEG 10939). Ananindeua (MPEG 6943, 9459). Apeú (MPEG 586, 587, 696, 1174, 1476, 1479, 2657, 2666, 3331, 3332, 3334, 3335, 5718, 6916, 6919, MCP 11317). Augusto Correa (MPEG 3905, 3954, 5399, 6712, 6713, 6721, 6724, 6737, 8999, 9937, 10764, 12450, 13074). Baião (MPEG 1596, 1600–1605, 1891–1897, 2101, 2422, 2423, 2560, 2822, 2826, 2864–2866, 3386, 3387, 3389, 3390, 3448, 3949, 3950, 3951, 4086, 4094, 4801, 4802, 4807, 4808, 4811, 4813–4817, 4828, 4858, 8187). Belém (IBSP 3033, 3034, 54152; KU 127256, 127257, 140153, 140154, MPEG 12769, 12770, 12771). Benevides: Genipaula Road, Pratinha (MPEG 7570, 8399, 8615, 8631, 12575, 14285, 15476); Cachoeira do Piriá (MPEG 2174, 2970, 5160, 7821, 7827, 9546, 9558, 9818, 9829, 11486, 11488, 11933, 11937, 12882, 12883, 15060, 15063, 15863). Castanhal (MPEG 5878, 7163, 7173, 10912, 10913, 11794, 12693). Gurupá (MPEG 16324). Igarapé-Açu (MPEG 868, 869, 870, 871, 910, 912, 913, 924, 925). Inhangabi (MPEG 1464, 1568, 1571). Marabá (MPEG 17304). Ilha de Outeiro (MCP 10718). Ourém (MPEG 4224, 5004, 5005, 5012, 7016, 7019). Santa Bárbara do Pará (MPEG 1855, 2608, 3952). Santarém (MPEG 8011). Santarém Novo (MPEG 1841, 1977, 3251, 4154, 4796, 7081). Santo Antônio do Tauá (MPEG 1000, 1453, 1872, 1873, 1879, 2375, 2376, 2643, 3306, 3940, 3940, 4718, 4720, 4721, 4723, 4730, 6958, 7557). Serra dos Carajás (MZUFV 1071). Serra de Kukoinhokren (MZUSP 10684–85). Uruá (IBSP 7285, MZUSP 7287). Utinga (KU 128094). Viseu (MPEG 1735, 1787, 2292, 2293, 2323, 2349, 3142–43 3714, 3953, 4458, 5239, 5249, 5320, 5321, 5324, 5325, 5327, 5329, 6633, 7291, 7325, 7338, 7701, 8959, 10010, 10884, 10886, 10887, 11267, 11268, 13260, 15126, 15127, 17279). Rondônia: Machadinho do Oeste (MZUSP 21888). Pontes e Lacerda (MPEG 2500).

Apostolepis quinquelineata (n = 4). GUYANA: Georgetown (BMNH 89.9.30.12 holotype of *Apostolepis quinquelineata*). BRAZIL: Amazonas: Presidente Figueiredo (INPA-H 31440); Rondônia: Porto Velho (UFRO-H 228, 229).

Apostolepis nigroterminata (n = 3). BRAZIL: Mato Grosso: Comodoro (MPEG 26500). Vila Bela da Santíssima Trindade (MZUSP 6408). PERU: Cayaria (BMNH 1946.1.9.77, holotype).

Apostolepis quirogai (n = 1). BRAZIL: Rio Grande do Sul: Santo Ângelo, Campus URI (MCP 12185).

Apostolepis sanctaeritae (n = 31). BRAZIL: Bahia: Unknown locality (MCP 8442), Cocos (IBSP 61525, CHUNB 51360, CHUNB 23715), Correntina (CHUNB 39079), Santa Rita, Ibipetuba (NMW 23452, holotype of *Apostolepis sanctaeritae*, MZUFBA 728, topotype); Distrito Federal: Brasília (IBSP 49363); Goiás: Unknown locality (IBSP 15723); Minaçu (IBSP 40478), São Domingos (IBSP 62593, IBSP 67392); Mato Grosso: Nova Xavantina (MCP 8002), Ribeirão Cascalheira (MCP 19481), São Félix do Araguaia (IBSP 15723); Minas Gerais: Betim (FUNED 03), Curvelo (IBSP 22410), Pirapora (MPEG 18347), Serra do Cipó (MZUSP 7595); Três Marias (FUNED, Without voucher); Vazante (IBSP 48041); Tocantins: Gurupi (MZUSP 8007); Lajeado (IBSP 64533, IBSP 64534, IBSP 65571, IBSP 65680, IBSP 65681), Palmas (IBSP 65267, holotype of *Apostolepis ammodites*), Porto Nacional (IBSP 65682, IBSP 65683, IBSP 66166), Santa Isabel (IBSP 12324).

Apostolepis tenuis (n = 1). BOLIVIA: Santa Cruz: Buena Vista (UMMZ 64436, holotype of *Apostolepis tenuis*).

Apostolepis thalesdelemai (n = 39). BRAZIL: Ceará: Guaramiranga (CHUFC 1950, 2067, 2353, 2371); Ibiapina (CHUFC 2337, 2340, 2342, 2343, 2351, 2437); Maranguape (CHUFC 2102, 2208, 2212, 2213, 2218, 2339, 2347, IBSP 80734); Pacoti (CHUFC 2344, 2346, 2463, 2731, 2841); São Benedito (CHUFC 2338); Ubajara (CHUFC 1349, 2085, 2110, 2137, 2154, 2341, 2350, 2769, 2954, IBSP 80735, ZUEC 3384).

Apostolepis vittata (n = 5). BRAZIL: Mato Grosso: Chapada dos Guimarães (ANSP 11293, holotype of *Rhynchonyx ambiniger vittatus*, CHUNB 30656), Parque Nacional Chapada dos Guimarães (UFMT-R 12259), Rio da Casca (MCP 13283), Serra do Roncador, Rio Araguaia (BMNH 1972.429, Holotype of *Apostolepis roncadori*).