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PHYLOGENETIC RELATIONSHIPS OF A NEW SPECIES OF *APOSTOLEPIS* FROM BRAZILIAN CERRADO WITH NOTES ON THE *ASSIMILIS* GROUP (SERPENTES: COLUBRIDAE: XENODONTINAE: ELAPOMORPHINI)

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ABSTRACT

The *assimilis* species group is one of the several assemblages that can be distinguished within the genus *Apostolepis*. The group is characterized by a uniform red dorsal pattern, broad nuchal-cervical collars, enlarged light snout blotch, dark ventral head, and entirely black terminal shield. A new species is here recognized as a member of the *assimilis* group and its phylogenetic relationships to *A. assimilis* and *A. cearensis* is inferred by means of cladistic analysis. *Apostolepis ammodites* sp. nov. can be easily diagnosed from all congeners by many autapomorphies and an exclusive combination of features. Comparative data are presented on scalation, coloration, dentition, osteology, and geographic distribution, with some notes on feeding and reproductive biology. The new species occurs through central Brazilian Cerrado, filling a gap between the areas occupied by *A. assimilis* and *A. cearensis*. Although superficially resembling *A. assimilis*, parsimony analysis based on morphological data indicates its phylogenetic relationships closest to *A. cearensis*. Systematic analysis shows that two recently described species, *A. freitasi* and *A. tertulianoebui*, must be relegated as junior synonyms of *A. cearensis* and *A. assimilis*, respectively.

KEYWORDS: Serpentes, Colubridae, Elapomorphini, *Apostolepis*, *assimilis* group, *A. ammodites* sp. nov., phylogenetic systematics, biogeography.

INTRODUCTION

The South American fossorial snakes of the genus *Apostolepis* Cope 1862 consist of a highly speciose clade of about 30 species, and a number of yet undescribed ones. The taxonomy of such an already difficult group (Vanzolini, 1986; Ferrarezzi, 1993;

Harvey, 1999) has become increasingly complex, not only due to the lack of a comprehensive systematic review but, also because of a recent proliferation of poorly described new taxa (e.g., Lema, 2002, 2003, 2004a,b). This is the case of two new species, lately described by Lema (2004a,b) and based on a single specimen each: *Apostolepis freitasi* from central Bahia,

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and *Apostolepis tertulianobeni* from Minas Gerais, both being undistinguishable from *Apostolepis cearensis* and *Apostolepis assimilis*, respectively, but clearly referred to the *assimilis* group as defined by Ferrarezzi (1993).

Elapomorphus assimilis was described by Reinhardt (1861), from Minas Gerais, Brazil. Later, Gomes (1915) described *Apostolepis cearensis* based on four specimens from State of Ceará, Northeastern Brazil, comparing it to *A. assimilis* and *A. coronata* (= *Elapomorphus lepidus*). Apparently unaware of Gomes's species, Werner (1924, 1925) described in two subsequent papers *A. sanctaeritae*, based on a single specimen from "Santa Rita", Brazil (Brasilien Expedition V.F. Steindachner, 1903) and *A. amarali* based on a specimen from unknown South American locality. The last name has undisputedly been considered a junior synonymy of *A. cearensis* (Amaral, 1930, 1936; Peters & Orejas-Miranda, 1970). Recently, Ferrarezzi (1993), recognized the *assimilis* species group of *Apostolepis* to include *A. assimilis* and *A. cearensis*, and considered *A. sanctaeritae* as conspecific to *A. cearensis*, rather than a synonym of *flavotorquata* (Amaral, 1930, 1936; Peters & Orejas-Miranda, 1970) or a valid species (Lema & Fernandes, 1997; Lema, 2002).

The Instituto Butantan received, in the last few years, several specimens of a clearly distinctive but unnamed elapomorphine species of the genus *Apostolepis*, that seems to be quite common within the Cerrado domain of central Brazil. It appears to be intermediate between *Apostolepis assimilis* and *A. cearensis*, in superficial morphology and through its geographical distribution. The present paper refers to the formal definition and diagnoses of the *assimilis* species group along with an attempt to elucidate the taxonomic status and systematic relationships of its component species.

MATERIAL AND METHODS

Specimens: A total of 25 museum specimens known to represent the new species were examined. In addition to published figures and descriptions, representative individuals or samples of most species of *Apostolepis* were analyzed (Ferrarezzi, 1993), in order to fundament a brief character analyses of the group. Relevant material observed for external features (scallation, color pattern and proportions), cranial osteology, and hemipenial anatomy is listed in Appendix 1. Specimens from the following institutions with their respective acronyms were analyzed (used in the text, figures, and appendix): IB, Laboratório de Herpetologia, Instituto

Butantan, São Paulo; MNRJ, Museu Nacional, Universidade Federal do Rio de Janeiro; CHUNB, Coleção Herpetológica da Universidade de Brasília; MZUSP, Museu de Zoologia da Universidade de São Paulo; FUNED, Fundação Ezequiel Dias, Belo Horizonte, MG.

Along with the description of the new species we report the state observed for nearly all external characters currently thought to be diagnostic for the new species relative to its congeners (Ferrarezzi, 1993; Harvey, 1999; Harvey *et al.*, 2001). Morphological information about members of the *dorbignyi* species group were obtained from Harvey, 1999 and Embert (pers. comm.) on Ventral shields were counted using Dowling's (1951) method.

In addition to the observation of external morphology, we prepared osteological and hemipenial material of the new species and its closest relatives *Apostolepis assimilis* and *A. cearensis*, as well as of *A. pyymi* and *A. flavotorquata*, used as outgroups. Skulls of preserved specimens were prepared either dried (with the aid of dermestid beetles and by chemical maceration). Hemipenes were mounted with agar jelly, following the procedures described by Pesantes (1994) for inverted organs from preserved specimens, or by Manzani & Abe (1988) for freshly killed ones. The nomenclature used for hemipenial structures is based on Dowling & Savage (1960) and Zaher (1999).

Species habitat correlations were made by plotting distribution localities in the South American vegetation map of Hueck & Siebert (1972).

Comparative analyses: Monophyly of an ingroup comprising the *assimilis* species group (*Apostolepis assimilis*, *A. cearensis* and *A. ammodites* sp. nov. – *sensu* Ferrarezzi, 1993) has been assumed as a working hypothesis. Representatives of the *dorbignyi* group (*A. dorbignyi*, *A. multicolorata*) were included as the closest outgroup, whereas those belonging to the *flavotorquata* group (*A. flavotorquata*, *A. pyymi*) were taken as a more distant outgroup to root the tree resultant from cladistic analysis. The empirical justification for this assumption about ingroup-outgroup demarcation can be found in Ferrarezzi (1993), but it is also implicit in our character matrix. Character states observed were numerically coded in discrete binary and multistate transformation series, in order to construct the data matrix ready to be subjected to a parsimony analysis using Hennig86 applicative (Farris, 1982). Statements regarding evolutionary direction (polarity) of morphological transformation series (character states) were only assessed *a posteriori* to parsimony analyses, following the principles

recommended by Farris (1982) and Nixon & Carpenter (1993).

The criterion used to evaluate phylogenetic relationships between the new species and other ingroup taxa was apomorphy based (Hennig, 1966). Systematic relationships and biogeographic history of the new species are briefly discussed in a cladistic and vicariance context.

The *assimilis* species group

Definition and diagnosis: *Apostolepis* of medium size; nasal separated from preocular; fifth supralabial scale only in contact with the parietal; temporal 0+1; terminal shield pointed in a sharply edge; large internasal white blotch covering the snout and reaching the frontal shield; moderate to extremely broad and sharply evident white and black nucho-cervical collars; dorsal pattern uniformly red (without any trace of dark stripes); white ventral surface, except the gular region which is dark pigmented (black spotted) to mostly black; terminal shield black, undifferentiated from the tail tip coloration. Duvernoy's gland moderately developed; harderian gland well developed, reaching the temporal region, adductor jaw muscles moderately developed, reaching the dorsal surface of the brain case.

Distribution: Northeastern, central, and southeastern Brazil to neighboring northeastern Argentina; through the Caatinga and Cerrado domains to mesophytic forest of upper Paraná.

Content: At least *Apostolepis assimilis* (Reinhardt) (Fig. 1), *A. cearensis* Gomes (Fig. 2), and *A. ammodites* sp. nov. (Fig. 3). Perhaps also *A. quirogai*, *A. arenaria* and *A. gaboi* (see discussions and conclusions).

Remarks: The monophyly of the *assimilis* group, as here defined, is still uncertain due to the complete lack of osteological information for several species not analyzed in the present study.

Key to the *Apostolepis* of the *assimilis* species group

1. Dorsal pattern uniform red, without any vestige of dark stripes or lines; white and black nucho-cervical collars relatively wide, the posterior edge

- of black cervical collar reaching at least the 6th scale of the vertebral row; nasal well separated from preocular by prefrontal-supralabial contact; light snout blotch large, usually extensive to frontal 2
- 1'. Without the above combination of features other *Apostolepis*
- 2. Terminal shield mostly whitish, well differentiated from black tail tip coloration; three infralabials contacting anterior chinshields; temporals 0+0 (5th and 6th labial contacting parietal); symphial approaching to nearly in contact with anterior chinshields *dorbignyi* group
- 2'. Terminal shield uniformly black, undifferentiated from tail tip coloration; four infralabials contacting anterior chinshields; temporals usually 0+1 (last labial separated from parietal); symphial usually well separated from chinshields by first infralabials *assimilis* group
- 3. Light snout blotch cream; white supralabial blotch moderate sized; ventral surface of head lightly to moderately pigmented; rostral shortly rounded; nucho-cervical (white+black) collars about 2-3+3-4 scales long; ventral counts 236-267 in males and 246-270 in females (southeastern to central Brazil) *A. assimilis*
- 3'. Light snout blotch reddish; white supralabial blotch small to minute; ventral surface of head heavily pigmented to mostly black; rostral at least slightly prominent (if not pointed); nucho-cervical (white+black) collars about 4-6+4-7 scales long; ventral counts 215-235 in males, 225-252 in females 4
- 4. With an additional white post-cervical collar; rostral nearly roundish, its portion visible from above at most one half of interprefrontal suture length; (central to adjacent northeastern Brazil) *A. ammodites* sp. nov.
- 4'. Without an additional white post-cervical collar; rostral prominently pointed, its portion visible from above at least two thirds of interprefrontal suture length; (northeastern Brazil) *A. cearensis*

***Apostolepis assimilis* (Reinhardt, 1861)**

(Figura 1, 7a, 9a, 10a)

Elapomorphus assimilis Reinhardt, 1861:235. Type-locality: Minas Gerais, Brazil.

Apostolepis tertulianobeui Lema, 2004b:155-160 (New synonym).

TABLE 1. Selected external features diagnostic of *Apostolepis ammodites* sp. nov. relative to *A. cearensis* and *A. assimilis*.

Characters:	<i>A. assimilis</i> (N = 30)	<i>A. ammodites</i> sp. nov. (N = 25)	<i>A. cearensis</i> (N = 56)
Snout-rostral shape	Not prominent and rounded	Slightly prominent but rounded	Strongly prominent and pointed
Ventrals			
females	246-270	234-252	227-248
males	236-267	221-235	215-237
Subcaudals			
females	25-31	26-31	23-31
males	31-39	32-36	27-32
White nuchal collar	2-3 scales long	3-6 scales long	4-5 scales long
Black cervical collar	3-4 scales long	4-7 scales long	4-6 scales long
White postcervical collar	Absent	1-3 scales long	Absent
Light supralabial blotch	Moderate, exceeding forth labial	Small to indistinct, mostly confined to forth labial	Small to indistinct, mostly confined to forth labial
Ventral head coloration	Moderately pigmented	Heavily pigmented to mostly black	Heavily pigmented to mostly black
Geographic distribution	Mesophitic forest and cerrados of Upper Paraná, Upper São Francisco, and Eastern Paraguay basins	Cerrados of Middle São Francisco and Upper Tocantins basins	Caatinga domain

TABLE 2. Tooth counts for the species of the *assimilis* group of *Apostolepis*.

	<i>A. assimilis</i> (n = 11)	<i>A. ammodites</i> (n = 4)	<i>A. cearensis</i> (n = 2)
Maxillary teeth	3-4 (3.9) +, 2	4 +2	4 +2
Palatine teeth	5	5	5
Pterygoid teeth	3-4 (3.8)	3-4 (3.7)	2
Dentary teeth	7-9 (8.0)	9-10 (9.7)	7

Diagnosis: (Tables 1 and 2; Fig. 1) Rostral short and rounded, not prominent; little visible from above; ventrals 236-267 in males, 246-270 in females; subcaudals 31-39 in males, 25-31 in females (Fig. 8), light snout blotch cream (Fig. 7a); white supralabial blotch usually covering at least two supralabials; a single white nuchal color 2-3 scales long, followed by a black cervical color 3-4, restricted dorsally.

Distribution: Caatingas, central Brazilian cerrados and interspersing mesophytic forest of southeastern Brazil, but uncertain to northern Argentina (Giraud & Scrocchi, 1998); upper Paraná, upper São Francisco, and eastern Paraguay basins (Fig. 6).

Natural history: *Apostolepis assimilis* is an inhabitant of open vegetation areas from Atlantic forest and Cerrado, also considered an urban species (Pereira *et al.*, 2004). It preys on small amphisbaenians and scolecophidian snakes (Ferrarezzi, 1993; Marques *et al.*, pers. comm.). A female had six vitellogenic follicles and the largest measuring was 30,91 mm.

Remarks: *A. tertulianobeui* Lema, 2004 is clearly a member of the *assimilis* species group (*sensu* Ferrarezzi, 1993), judging from color pattern and scalation features. In most relevant diagnostic features presented by Lema (2004b), the holotype of *A. tertulianobeui* does not differ from the range of variation we have observed in a large sample of *A. assimilis* (Ferrarezzi, 1993). Eventually, a narrower cervical collar can be found in a few individuals as an intrapopulation polymorphism, but a reduced dark pigmentation, as referred by Lema (2004b), may be better explained by fading in the long time preserved holotype specimen. Although there is no specific type-locality, besides the state of Minas Gerais, the distribution of *A. tertulianobeui* is coincident with the distributional area of *Apostolepis assimilis* (Fig. 6). Therefore, even though we did not examine the holotype of *A. tertulianobeui*, we have no doubt that this name must be relegated as a junior synonym of *A. assimilis*.

Apostolepis cearensis Gomes, 1915

(Figuras 2, 7c, 9c, 10c)

Apostolepis cearensis Gomes, 1915:122. Type-locality: Estado do Ceará, Brazil.

Apostolepis sanctae-ritae Werner, 1924:43. Type-locality: Santa Rita, now Ibipetuba, Estado da Bahia, Brazil (New synonym).

Apostolepis amarali Werner, 1925:62. Type-locality: South America (here restricted to Northeastern Brazil).

Apostolepis sanctaeritae Lema & Fernandes, 1997:58.

Apostolepis freitasi Lema, 2004:3-7. Type-locality: Tanque do Aragoão, Bahia, Brazil (New synonym).

Diagnosis: (Fig. 2) Rostral somewhat pointed and prominent; nasal well separated from preocular; temporals usually 0+1, the 5th supralabial in contact with parietal (occasionally 0+0: 5th+6th in contact); ventrals 215-237 in males, 227-248 in females; subcaudals 27-32 in males and 23-31 in females (Table 1; Fig. 8); terminal caudal shield pointed and uniformly black; head black postero-laterally, with a large light area on snout (red in life, reaching frontal) (Fig. 7) and small to indistinct light supralabial spot; a broad white nuchal color (covering 4-5 scale rows) followed by a similar extensive black cervical color; dorsum uniform colored, without stripes; ventral surface uniform white, except by the heavily dark pigmented infralabial-gular region.

Distribution: Widespread within the Caatinga morphoclimatic domain of northeastern Brazil (Fig. 6).

Remarks: The recently described species *A. freitasi* Lema, 2004 is clearly a member of the *assimilis* species group (sensu Ferrarezzi, 1993), judging from the features of color pattern and scalation. In all diagnostic features presented by Lema (2004a), the holotype of *A. freitasi* is identical to *A. cearensis*. It is not surprising that Lema (2004a) traces no comparison of his new species with the last one, since if this have been done, the author would have failed to find any diagnostic feature at all. The same can be said about the type-locality which is within of the geographic distribution area of *A. cearensis* (Fig. 6). Therefore, even without having examined the holotype of *A. freitasi*, we have no doubt that this name must be included as a junior synonym of *A. cearensis*.

Apostolepis ammodites sp. nov.

(Figuras 3, 4, 7b, 9b, 10b, appendix 2)

Holotype: BRAZIL: TOCANTINS: Palmas (10°02'S, 47°20'W, 230 m altitude), adult ♀, IB 65267, deposited at "Coleção Herpetológica Alphonse Richard Hoge", Laboratório de Herpetologia, Instituto Butantan.

Paratypes: BRAZIL: ♂ BAHIA: Cocos (14°11'S, 44°32'W, 559 m altitude), IB 61525; Correntina (13°20'S, 44°38'W, 561 m) CHUNB s/n°; DISTRITO FEDERAL (15°46'S, 47°55'W), IB 49363; GOIÁS:

(IB 15723); Cana Brava, Rio Cana Brava (13°30'S, 48°21'W, 400 m), IB 40478; MZUSP 8007; São Domingos (13°23'S, 46°19'W, 667 m), IB 62593, 67392; MATO GROSSO: São Felix, Lago Itacy (11°37'S, 50°40'W, 195 m), IB 15723; MINAS GERAIS: Betim (19°58'S, 44°11'W, 860 m), FUNED 003; Curvelo (18°45'S, 44°25'W, 632 m), IB 22410; Serra do Cipó (19°24'S, 43°19'W, 689 m), MZUSP 7595; Três Marias (18°12'S, 45°14'W, 538 m), FUNED s/n°; Vazante (17°59'S, 49°54'W, 680 m), IB 48041; TOCANTINS: Gurupi (11°43'S, 49°04'W, 287 m); Lageado (09°45'S, 48°21'W, 202 m), IB 64533 (Adult ♀), IB 64534 (juvenile ♀), IB 64571 (Adult ♀), IB 64613 (Adult ♀), IB 65680 (juvenile ♂), IB 65681 (Adult ♀); Palmas (10°02'S, 48°20'W, 230 m), IB 65261 (Adult ♀), IB 65262 (Adult ♂), IB 65263 (Adult ♂), IB 65264 (Adult ♂), IB 65265 (Adult ♀), IB 65266 (Adult ♀), IB 65268 (juvenile ♂), IB 65269 (Adult ♀), IB 65664 (Adult ♂), IB 65688 (Adult ♀); Porto Nacional (10°42'S, 48°25'W, 212 m), IB 65682 (Adult ♂), IB 65683 (Adult ♀), IB 66166, (Adult ♀); Santa Isabel, Ilha do Bananal (15°17'S, 49°25'W, 611 m), IB 12324; unspecified locality: IB 71470 (juvenile ♀), IB 71471 (Adult ♀).

Etymology: Ambivalent connotation, from the Greek, ζῆσσω (ammos) meaning sand plus τ. δ. ι. κ. ω (dytes, the internal 'y' may be rendered by 'i' in Latin) meaning anyone that likes immersions or diving, but furthermore from the Latin *ammos* meaning around or having two plus *dites* meaning richly adorned or sumptuous. In allusion both to the habitat and habits of the new species and to its unique extravagant nuchal-cervical color pattern having two white collars around a black collar.

Diagnosis: Rostral nearly roundish but somewhat prominent, its portion visible from above about 1/3 to 1/2 of the interprefrontal suture length; ventrals 221-235 in males to 234-252 in females; subcaudals 32-36 in males and 26-31 in females (Table 1; Fig. 8); light snout blotch reddish in life (Fig. 7) (fading to yellowish in preservative) and a small to indistinct light supralabial spot; white nuchal collars about 3-6 scales long, black cervical collar 4-7 scales long, followed by an additional postcervical white collar 1-3 scales long; dorsum uniformly red (without stripes); ventral surface uniformly light (unpigmented), except under the head and neck; premaxillae bounded to maxillae; dorsal laminae of nasal contacting frontal and prefrontal; maxillary teeth 4+2, dentary teeth 9-10; pterygoid teeth 3-4 (Table 2).



FIGURE 1. *Apostolepis assimilis*. IB 72970 from Carapicuíba, São Paulo. Photo by A.C.O.R. Costa.



FIGURE 2. *Apostolepis cearensis*. Uncatalogued specimen from Feira de Santana Bahia. Photo by O.A.V. Marques.

Description and variation: Relatively large species of *Apostolepis* (maximum total length for a female 634 mm). Head subcylindrical, not distinct from neck, with somewhat prominent but rounded snout; body elongate cylindrical; tail short (males ($n = 10$): 9-11% of total length, mean 10%; females ($n = 14$): 7-9% of total length, mean 8%), thick and bluntly pointed (Appendix 2). Eye minute, with a subelliptic (nearly round when dilated) pupil.

Scalation: (Fig. 4) Rostral somewhat prominent but roundish, the portion visible from above about 1/2 to 1/3 of its distance to frontal. Nasal always separated from preocular by a broad prefrontal contact with second supralabial. Six supralabials (second and third entering eye). Temporals 0+1, usually only the fifth supralabial in contact with parietal (occasionally also the fourth making a slightly contact). Occipitals 3-5, the lateral very large. Synfissial separated from chinshields by contact between first infralabials; usually seven infralabials, the first four in contact with anterior

chinshields, and the fourth and fifth in contact with posterior chinshields; anterior chinshields wider and nearly equal to the posteriors in length. Ventrals 221-235 (mean = 229.2) in males ($n = 10$) to 234-250 (mean = 242.6) in females ($n = 14$); subcaudals 32-36 (mean = 33.4) ($n = 10$) in males and 26-31 (mean = 28.5) in females ($n = 13$) (Table 1; Fig. 8); terminal caudal shield short, high and blunt pointed, in contact with 5-6 scales around.

Dentition and cranial osteology: (Table 2; Figs. 9 and 10) Tooth series short and with stout teeth. Maxillary very short, with four solid teeth increasing in size posteriorly followed, after a distinct interspace, by a pair of large deeply grooved fangs, situated below the eye. Five palatine followed by three or four pterygoid teeth; the anterior end of pterygoid barely extending beyond its articulation with ectopterygoid, and just touching the palatine. Dentary short, bearing 9-10 subequal teeth, increasing in length to the fourth and then gradually decreasing to the last one. Reduced posterior process of dentary extending just behind splenial-angular hinge; meckelian channel closed along most of the



FIGURE 3. *Apostolepis ammodites* sp. nov. Paratype IB 61525, female, (total length 22 mm) from Cocos, Bahia, (Fazenda Francisco do Rio Formoso), in life. Photo by O.A.V. Marques.

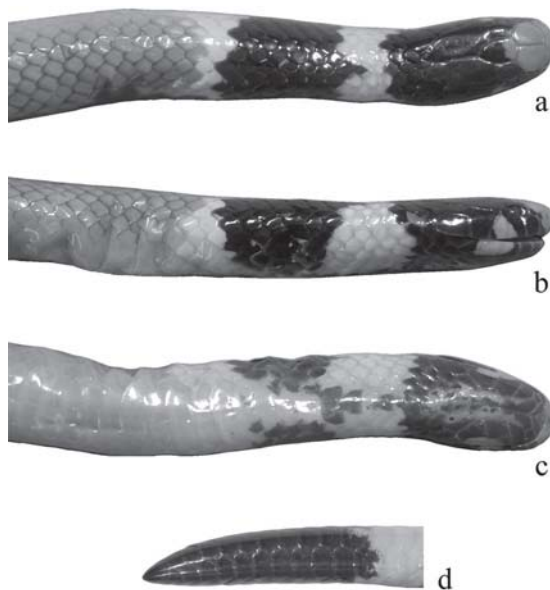


FIGURE 4. Head of the holotype of *Apostolepis ammodites* sp. nov. (IB 65267) in dorsal (A), lateral (B) and ventral (C) views, and tail tip in ventral view (D).

dentary length. Ectopterygoid flattened and deeply forked anteriorly, forming a fairly large maxiloepterygoid fenestra. Premaxillae very thick and robust, the lateral processes bounded to the maxillae, and with a stout dorsal process making very broad contact with the dorsal laminae of nasals, which is very wide and nearly rectangular, broader than and making an extensive transversal suture with the frontal and with the antero-dorsal edge of prefrontal. Supratemporals small, distantly separated from parietal and not reaching the posterior level of occipitals. Postorbital bone absent.

Hemipenis: The organ is subcylindrical and stout with a narrower base. Apex is just slightly bilobate, calyculate, and semicapitate. Spines are nearly uniformly distributed around the body. The *sulcus spermaticus* is forked slightly above the mid-length of the organ, with the branches running centrolineally to the extreme apex.

Coloration in life: (Fig. 3) Dorsum uniform vivid orange-red (without any vestige of dark stripes); head black postero-laterally (to firsts occipital rows), with a large reddish blotch on snout (covering entirely the prefrontals to reach the anterior end of frontal and supraoculars), a small to indistinct cream supralabial spot posterior to the eye is mostly restricted, if not confined, to the fourth supralabial; a broad white nuchal collar (3-6 scales long) followed by a similar extensive



FIGURE 5. Physiography of an area inhabited by *Apostolepis ammodites* sp. nov., in the locality of Correntina (Bahia state), where specimen CHUNB s/n° were collected. Photo by C. Nogueira.

black cervical collar (4-7 scales long); and an additional white postcervical collar (1-3 scales long); ventral surface uniformly light (unpigmented), except under the head and neck, where the infralabial, chin and gular regions are mostly black. The dorso-ventral tail coloration is similar to that of body, and with a distinct black band around the tail tip (7-11.5 scale long); terminal caudal shield uniformly black (not differentiated from tail tip coloration).

Distribution: All the known distribution records for the new species fall within the central and northeastern portion of the Cerrado morphoclimatic domain (Fig. 6).

Natural History: *Apostolepis ammodites* sp. nov. is an inhabitant of open vegetation areas of Cerrado (Fig. 5), where it appears to be restricted to sandy soils (F. Curcio, C. Nogueira and M.T. Rodrigues, pers. comm.).

A specimen (IB 64613) contained digested remains of skin of a small unidentified *Amphisbaena* and the head of an ant of the subfamily Attinae. The ant's head is most probably the secondary remain from the stomach content of the amphisbaenid prey.

The new species is oviparous (A. Silveira, pers. comm.). A female (IB 65261, 502 mm SVL) had three vitellogenic follicles and the largest measuring was 15,99 mm. Five males (IB 62593, IB 65262, IB 65263, IB 65268, and IB 65664) had large testes and convoluted deferent ducts. The largest male (IB 62593, 450 mm SVL) had the largest test, with 13,86 mm and was collected in August/2000. The smallest male (IB 65268) with large testes and opaque deferent ducts had 282 mm SVL. It was collected between December/2001 and January/2002.

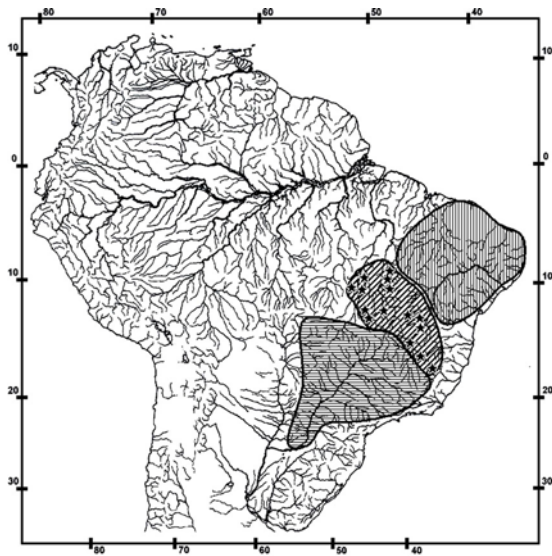


FIGURE 6. Geographic distribution of *Apostolepis ammodites* sp. nov. (plotted stars represent localities for the type-series – an encircled star indicates the type-locality), with regards to the distribution area of its closest relatives *A. cearensis* (vertical lines) and *A. assimilis* (horizontal lines). Note the tight distributional limits of this allopatric pattern exhibited by the components of the *assimilis* species group.

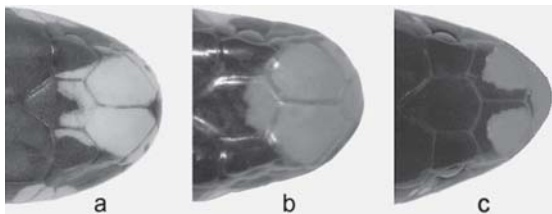


FIGURE 7. Dorsal view of the snouts of representatives of the *Apostolepis assimilis* species group. (A) *A. assimilis* (IB 68794), (B) *A. ammodites* sp. nov. (holotype IB 65267), and (C) *A. cearensis* (uncatalogued specimen, field number ESTR043).

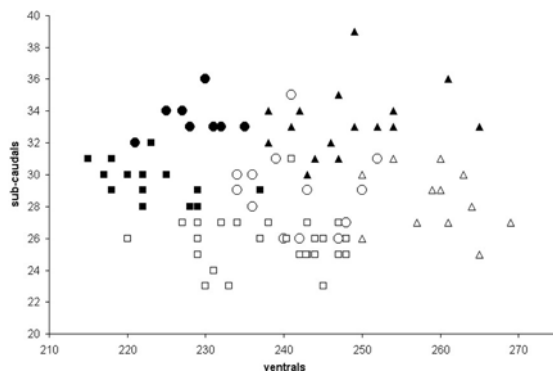


FIGURE 8. Numbers of ventrals and subcaudals plotted for the type series of *Apostolepis ammodites* sp. nov. (circles), in comparison with a sample of *A. assimilis* (triangles) and *A. cearensis* (squares). Empty symbols represent females and full symbols represent males.

Characters and character states coded for the cladistic analysis

Characters and respective character states numerically coded and listed below correspond to those in the data matrix of Table 3, which are optimized in the cladogram presented in Figure 11. Linearly ordered multistate transformation series (denoted by NA) were managed under the assumption of additivity during parsimony analysis.

Characters

Coloration (Figs. 1-4, 7):

- Light snout blotch color (Fig. 7):
 - cream or whitish
 - reddish
- Light snout blotch shape:
 - moderate sized irregularly edged blotch(es), confined to prefrontals dorsally
 - a broad regular blotch covering all snout, reaching frontal and supraoculars
- White supralabial blotch:
 - moderate sized, fairly exceeding fourth labial
 - small (mostly confined on fourth labial) to minute or eventually absent
- Pigmentation of the ventral head surface:
 - virtually immaculate
 - irregularly dark blotched.
 - mostly black
- White nuchal collar:
 - narrow (1-2 scales long) if present
 - moderately broad (2-4 scales long)
 - large (4-6 scales long)
- Black cervical collar:
 - narrow (1 scale long)
 - moderate (2-3 scales long)
 - wide (4-6 scales long)
 - extremely long (5-7 scales long)
- Anterior indentation of black cervical collar along vertebral row:
 - absent
 - present
- Ventral extension of black cervical collar:
 - absent without vestiges
 - variable, but usually at least a vestige
- White post-cervical collar:
 - absent
 - present
- Terminal shield color:
 - mostly whitish, differentiated from tip of tail
 - uniformly black, undifferentiated from tip tail

Scalation (Figs. 4, 7):

11. Rostral shield:
 - (0) short and rounded
 - (1) slightly prominent but roundish
 - (2) prominently pointed
 12. Temporals: Comment: The usual condition in *A. cearensis* is state (0), although polymorphism has been observed in some populations. A single species of the *flavitorquata* group exhibits intraspecific polymorphism.
 - (0) 0+1 (posterior temporal present between last supralabial and parietal)
 - (1) 0+0 (no temporals, last two supralabial contacting parietal)
 13. Infralabials contacting anterior chinshields:
 - (0) four
 - (1) three
 14. Ventral counts (modal): Comment: The *dorbigny* group exhibits interspecific variation and were coded as missing data.
 - (0) 217-232 in males, 227-248 in females
 - (1) 241-261 in males, 254-265 in females
 15. Subcaudal counts (modal):
 - (0) 32-36 in females, 37-41 in males
 - (1) 27-31 in females, 32-37 in males
 - (2) 23-27 in females, 28-31 in males
- Cranial osteology (Figs. 9, 10, Tab. 2):
16. Number of pterygoid teeth:
 - (0) 3-4 (mode 4)
 - (1) 2
 17. Number of dentary teeth (mode):
 - (0) 7-8
 - (1) 9-10
 18. Dentary shape:
 - (0) nearly straight
 - (1) curve
 19. Prearticular crest of compound bone:
 - (0) higher than surangular crest posteriorly
 - (1) as low as surangular crest
 20. Shape of mentonian foramen:
 - (0) elongate groove
 - (1) rounded
 21. Shape of premaxillae:
 - (0) roughly T-shaped, with a distinct ascending process
 - (1) stoutly enlarged without a distinct ascending process, but not pointed
 - (2) strongly enlarged and prominently pointed
 22. Septomaxillary process of premaxillae:
 - (0) short and widely separated from each other.
 - (1) moderately long and close to each other
 - (2) long and closer to each other

23. Contact between premaxillae and maxillae:
 - (0) distantly separated
 - (1) separated
 - (2) bound to each other
24. Width of facial segment of skull:
 - (0) relatively wide, conferring a larger palatine-ectopterygoid distance
 - (1) relatively narrower
25. Ectopterygoid shape:
 - (0) wider and flat
 - (1) narrow and sub cylindrical
26. Contact between dorsal laminae of nasals and frontals:
 - (0) absent
 - (1) present, forming a transverse suture
27. Shape fronto-parietal suture in dorsal view:
 - (0) U-shaped, no parietal indentation between frontals
 - (1) W-shaped, with an antero-median parietal indentation between frontals
28. Width of fronto-parietal suture:
 - (0) short and wide
 - (1) narrower and longer
29. Contact between nasal and prefrontal:
 - (0) absent
 - (1) present dorsally
 - (2) present laterally

Ecology (Fig. 5):

30. Habitat (soil):
 - (0) non sandy soils
 - (1) sandy soils
31. Habitat (physiognomy):
 - (0) mesophytic forests
 - (1) mesic savannas
 - (2) semiarid caatingas

Results of Cladistic analysis

Parsimony analysis of the data matrix in Table 3 resulted in a single most parsimonious tree, which was rooted in the *flavitorquata* species group (Fig. 11). This cladogram presents a highly consistent pattern of character congruence, as denoted by its consistency and retention indexes: length = 43; CI = 0.97, RI = 0.97 (the values are the same under both Wagner and Fitch parsimony options applied to ordered multistate characters). Even if the total amount of data is partitioned into different character classes (*viz.*: coloration, scalation, osteology, or ecology), the same single tree topology is obtained from each independent analyses of the four subsets.

The results of the cladistic analysis demonstrate that *A. ammodites* sp. nov. is closer to *A. cearensis* than *A. assimilis* (Fig. 11). This last species appears as the most conservative lineage within the clade. At least with regard to the character sample analyzed here, it remains nearly identical to the common ancestor of the tree species. On the other hand, the lineage leading to *A. ammodites* sp. nov. and *A. cearensis* is the most divergent lineage morphologically, judging from an amount of synapomorphic and autapomorphic traits of coloration and, especially, cranial osteology (Figs. 9, 10 and 11).

Regarding the evolutionary rate of the different classes of morphological data, the scalation features represent the most conservative ones, while the cranial osteology is the most divergent.

DISCUSSION AND CONCLUSIONS

At least three other species exhibiting entirely black terminal shield may be further proven to belong to the *assimilis* group Ferrarezzi, unpublished data). These are *Apostolepis arenaria* Rodrigues, 1993,

and *A. gaboi* Rodrigues, 1993, a pair of closely related species that shares apomorphies with both *A. ammodites* sp. nov. and *A. cearensis*, plus a few additional features only with the latter, (and thus, may be sister to *A. cearensis*). On the other hand *A. quirogai* Giraud & Scrocchi, 1998 lacks most derived features of the other species, and may represent the sister taxa of the whole group. The phylogenetic relationships of all of them are left to be discussed in a further study. By now, it is sufficient to explain that keeping them out of here will not disqualify our analysis about the pattern of cladistic relationships of the other species, since they have also been excluded from outgroup comparison.

At least one of the apomorphies determined within the *assimilis* group, a higher degree of rostral prominence, is also shared by several species referred to the *dimidiata* and *arenaria* groups of *Apostolepis* (Ferrarezzi, 1993). Absence of rostral prominence is inferred as a plesiomorphic within *Apostolepis* since it is the common condition in the closely related genera *Elapomorphus* and most species of *Phalotris* (excluding the *nasutus* group, Ferrarezzi, 1993, 1994). An *ad hoc* assumption of our present phylogenetic hypothesis is

TABLE 3. Data matrix depicting the taxonomic distribution of morphological character states scored for the cladistic analysis of the *assimilis* species group of *Apostolepis*. Numbered characters and respective states coded as listed and described in the text (1-10 = coloration; 11-15 scalation; 16-29 = osteology; 30-31 = ecology). (-) = missing information, (?) = variable.

Taxa	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	
<i>A.gr.flavatorquata</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	-	1	0	0	0	0	?	0	0	?
<i>A.gr.dorbignyi</i>	0	1	0	1	1	1	0	0	0	0	0	1	1	?	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0
<i>A.assimilis</i>	0	1	0	1	1	1	0	0	0	1	0	0	0	1	1	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0
<i>A. ammodites</i> sp.n.	1	1	1	2	2	3	1	1	1	1	1	0	0	0	1	0	1	1	0	1	1	1	2	1	1	1	1	1	2	1	1	
<i>A.cearensis</i>	1	1	1	2	2	2	1	0	0	1	2	0	0	0	2	1	0	0	1	0	2	2	0	1	1	0	1	0	1	1	2	

Made with NEXUS Data Editor

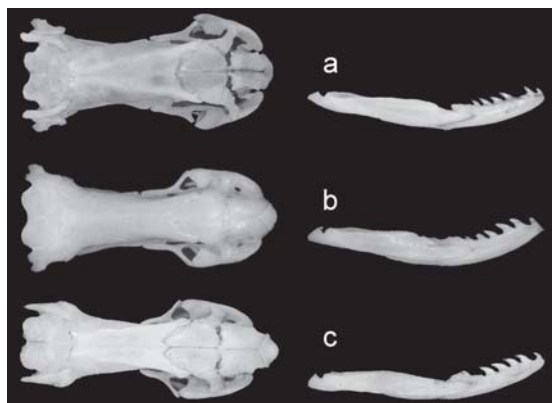


FIGURE 9. Dorsal view of the skulls and lateral view of mandibles of representatives of the *Apostolepis assimilis* species group. (A) *A. assimilis* (IB 70356), (B) *A. ammodites* sp. nov. (paratype IB 65681), and (C) *A. cearensis* (IB 20220).

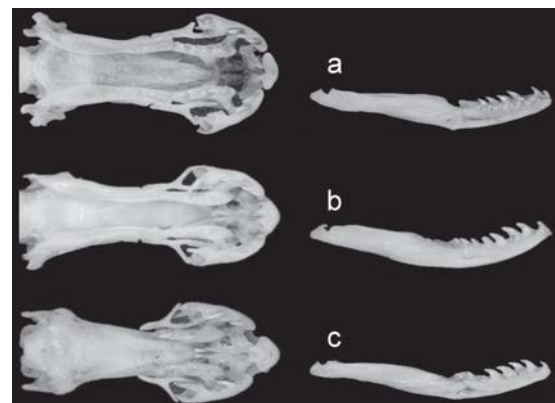


FIGURE 10. Ventral view of the skulls and lingual view of mandibles of representatives of the *Apostolepis assimilis* species group. (A) *A. assimilis* (IB 70356), (B) *A. ammodites* sp. nov. (paratype IB 65681), and (C) *A. cearensis* (IB 20220).

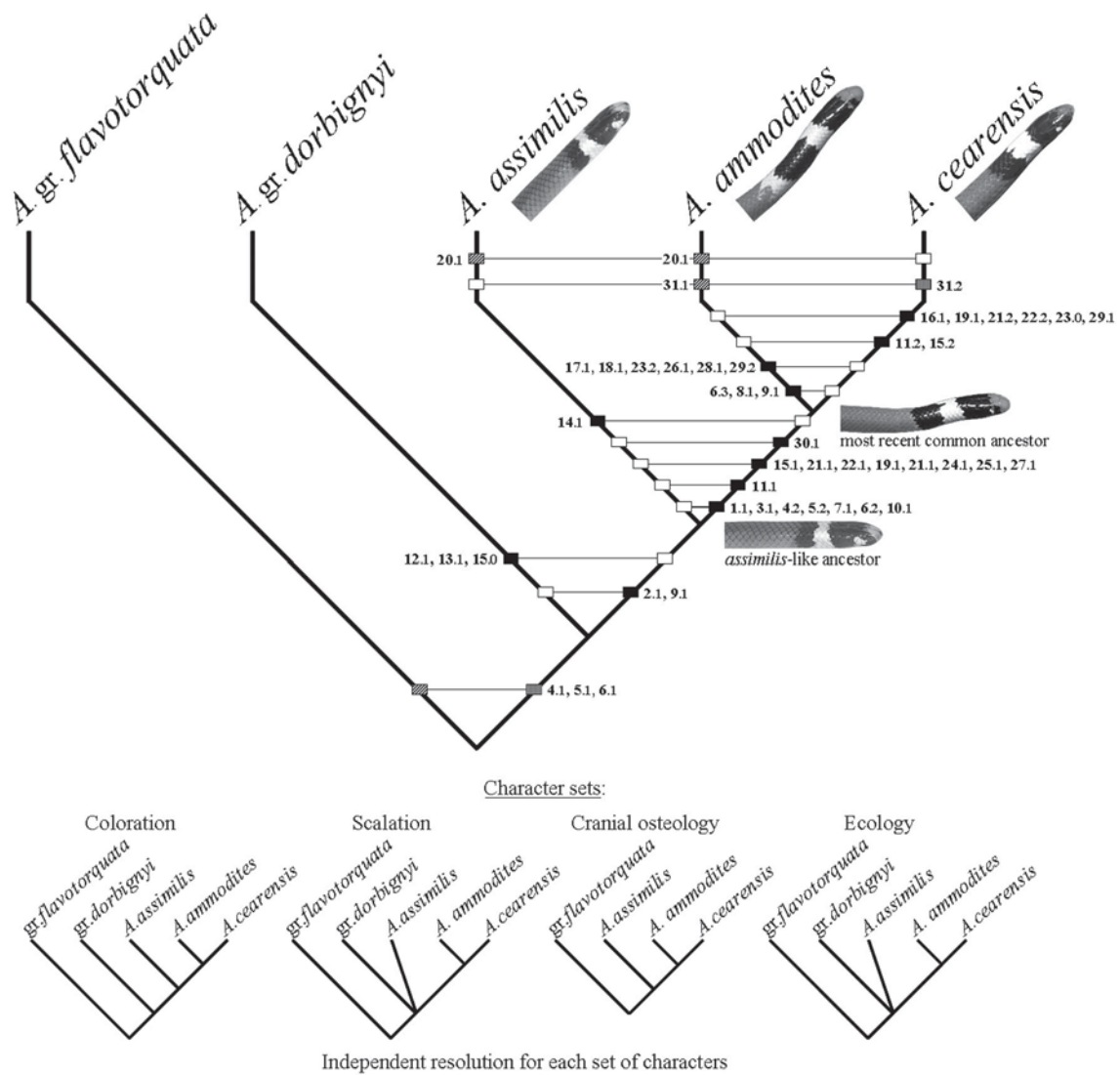


FIGURE 11. Cladogram depicting the phylogenetic relationships among the components of the *assimilis* species group of *Apostolepis*. This is the single most parsimonious tree derived from the cladistic analysis of the data matrix of Table 3 (length = 43; CI = 0.97, RI = 0.97 under both Wagner and Fitch parsimony options applied to ordered multistate characters). The head and neck external morphology was reconstructed for the hypothetical common ancestors, as a corollary of our theory about cladistic relationships and character state polarities. Differently colored numbers represents four sets of characters. The four small cladograms below represents the tree topology derived from independent analyses of each character set.

that rostral prominence has evolved independently in several elapomorphine lineages. However, a better understanding of phylogenetic relationships, in addition to detailed information on morphometrics and, hopefully, also on ecology (including detailed descriptions of microhabitat use) are still necessary for reliable interpretations of the possible phylogenetic meaning and adaptive value of an enlarged rostral scale in these groups of *Phalotris* and *Apostolepis*.

The present discovery of new diagnostic characters arranged in a simple congruent pattern of relationships, although just for a few species, stands as a first step towards a comprehensive resolution of the whole group. The original synapomorphy scheme proposed here represents a testable phylogenetic hypothesis to be corroborated, modified or (mostly important) even refuted, after an advanced survey on these character states for other putative members of a broad-

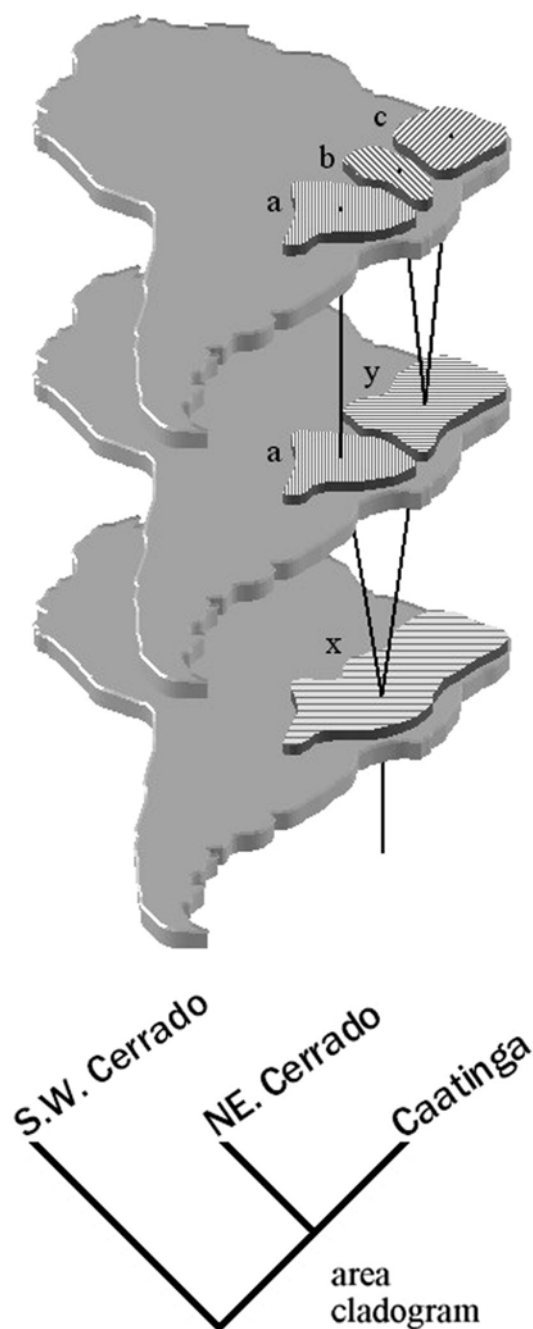


FIGURE 12. History and pattern of biogeographic relationships among the distribution areas of the species belonging to the *assimilis*-group, as hypothesized following a vicariance model of speciation.

based *assimilis* group, as well as other *Apostolepis* in general.

Finally, given the allopatric pattern of distribution (Fig. 6), a hypothesis of the biogeographic history under the assumption of a vicariance model is

developed (Fig. 12). The biological area cladogram resulting from the recovered cladistic relationships for the *assimilis* group of *Apostolepis* indicates that the northeastern portion of the Cerrado is more closely connected to the Caatinga than to the southwestern Cerrado region. Further area cladograms derived from other groups of organisms exhibiting the same areas of endemism are needed in order to test the generality of this conjecture.

RESUMO

As espécies do grupo assimilis se caracterizam por um padrão dorsal vermelho uniforme, colares nuco-cervicais largos, mancha clara do focinho larga, região ventral da cabeça densamente pigmentada e escudo terminal completamente preto, é um dos vários grupos que podem ser distintos dentro do gênero Apostolepis. Uma nova espécie é aqui reconhecida como membro do grupo assimilis e suas relações filogenéticas para A. assimilis e A. cearensis são inferidas por meio de uma análise cladística. A. ammodites sp. nov. pode ser diagnosticada facilmente de todos os congêneres por muitas autapomorfias e uma combinação exclusiva de caracteres. Dados comparativos são apresentados sobre escutelação, coloração, dentição, osteologia e distribuição geográfica, junto com notas sobre alimentação e biologia reprodutiva. A espécie nova ocorre através do Cerrado brasileiro central, preenchendo o intervalo entre as áreas ocupadas por A. assimilis e A. cearensis. Embora se assemelhe superficialmente a A. assimilis, análises de parcimônia baseadas em dados morfológicos indicam maior parentesco filogenético com A. cearensis. Análises sistemáticas mostram que duas espécies recentemente descritas, A. freitasi e A. tertulianoebui, devem ser consideradas como sinônimos juniores de A. cearensis e A. assimilis, respectivamente.

PALAVRAS-CHAVE: Serpentes, Colubridae, Elapomorphini, *Apostolepis*, grupo *assimilis*, *A. ammodites* sp. nov., sistemática filogenética, biogeografia.

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APPENDIX 1

Material Examined

Museum Collections:

IB (Laboratório de Herpetologia, Instituto Butantan, São Paulo);
MZUSP (Museu de Zoologia, Universidade de São Paulo);
MNRJ (Museu Nacional do Rio de Janeiro);
UNB (Dept. Zoologia, Universidade de Brasília);
LAPH (Lab. An. Peç. e Herpet., Universidade Estadual de Feira de Santana, Bahia).

Apostolepis assimilis: BRAZIL: SÃO PAULO: Carapicuíba (IB 72970); Icem/Fronteira (IB 40008); Itu (MZUSP 4180, 6606); São Paulo (IB 24180, 24548, 24873, 27598, 31716, 33316; IB-MSP348), Pirituba (IB 70351 SKULL), Jaraguá (IB 70356 SKULL); Santana do Parnaíba (IB 61761); DISTRITO FEDERAL: Brasília (IB 20566, 28734, CHUNB24456, 24474); MINAS GERAIS: Conceição dos Ouros (IB 33206); Uberlândia (MZUSP 3841, 3845). GOIÁS: Jataí (MZUSP 3783); Mineiros (IB 55495); MATO GROSSO: Buriti, Chapada dos Guimarães (MZUSP 5346); MATO GROSSO DO SUL: Amambaí (IB 41163); Campo Grande (IB 42978, 57222; MZUSP 10155); Nova Andradina (IB 27489); Paranaíba (IB 45615); Ponta-Porã (IB 44065); PARANÁ: Londrina (IB 37462, 40008).

Apostolepis cearensis: BAHIA: Brumado (IB 33685); Camaçari (LAPH371); Capim Grosso (LAPH294); Feira de Santana (LAPH012, 019, 070, 071, 074 086, 130, 162, 166,203, 277, 310, 315, 429, 434, 463, 464, 505, 515, 615, 624, IB 53700); Mina Caraíba, Jaguarari river (IB 26203); Santo Inácio (MZUSP -MTR.field# 916639, 916640, 916641 (incl.HEMIPENIS); São Gonçalo (LAPH073); CEARÁ: (IB 14948), (IB 0882, holotype, 0910, 0911, 20220 including skull); Crato, Serra do Araripe (IB 20385); Fortaleza (IB 2106, 20020, 55318, 40262); Juazeiro do Norte (IB 20164); Lima Campos, Icó (IB 20190); Limoeiro do Norte (IB 12775); Northeastern Ceará (IB 20097); RIO GRANDE DO NORTE: Natal (IB 43960, 55064-67); PERNAMBUCO: Recife (IB 56983); PIAUÍ: Terezina (IB 49743); PARAÍBA: Cabaceiras (MZUSP 9013); Campina Grande (IB 9050); João Pessoa (MZUSP 7975); (MNRJ r3371a, r3371b).

Apostolepis ammodites sp. nov.: BAHIA: Cocos (IB 61525), Correntina (CHUNB s/n°); DISTRITO FEDERAL (IB 49363); GOIÁS: (IB 15723); Cana Brava, Rio Cana Brava (IB 40478); São Domingos (IB 62593, 67392); MATO GROSSO: São Felix, Lago Itacy (IB 15723); MINAS GERAIS: Betim (FUNED003); Curvelo (IB 22410); Serra do Cipó (MZUSP 7595); Três Marias (FUNED s/n°); Vazante (IB 48041); TOCANTINS: Gurupi (MZUSP 8007); Lajeado (IB 64533, 64534, 64571, 64613, 65680, 65681); Palmas (IB 65261-69, 65664, 65688); Porto Nacional (IB 65682, 65683, 66166); Santa Isabel, Ilha do Bananal (IB 12324); unspecified locality (IB 71470, 71471).

Apostolepis flavotorquata: BAHIA: Coribe (UNB1213); GOIÁS: Anápolis (IB 18851); Nerópolis (UNB0948); MATO GROSSO: Chapada Matogrossense (IB 32530); MATO GROSSO DO SUL: Ilha Solteira (IB 36449, 36450 SKULL).

Apostolepis pygmy: AMAZONAS: Balbina (IB 51396); Manaus (MZUSP 8423, 8657); PARÁ: Belém (IB 3033, 3034); Canindé, Rio Gurui (MZUSP 2001); (uncataloged specimen- SKULL),

APPENDIX 2

Apostolepis	Rostral length *	Nasal/preocular	Temporals	Contact between parietal and 4th upperlabial	Total number of infraorbitals **	Nuchal-cervical collars			Light snout blotch extended from rostral to:	Ventral extension of black cervical color	Chinshield/infraorbital pigmentation	Black occiput ventral extension	White supralabial blotch (oval)	Supralabials	Mental/chinshield
						white	black	white							
IB 65267	~1/2	separate	0+1	absent	7 (4)	4	5-6	3	frontal	complete	mostly black	gular	3+4+5 th sup	6 (2-3)	absent
IB 62593	~1/2	separate	0+1	absent	7 (4)	4	4-5	0	s.ocul. - frontal	incomplete	havely blotched	gular	3+4+5 th sup	6 (2-3)	absent
IB 64533	~1/2	separate	0+1	present	7 (4)	3	6-7	1	parietals	absent	mostly black	gular	oval 4 th	6 (2-3)	absent
IB 64534	~1/2	separate	0+1	absent	7 (4)	4	5-6	0	s.ocul. - frontal	incomplete	mostly black	gular	1/3 sup of 4 th	6 (2-3)	absent
IB 64571	~1/3	separate	0+1	absent	7 (4)	5	6-7	2	s.ocul. and pre frontal	incomplete	mostly black	gular	oval 4 th	6 (2-3)	absent
IB 64613	~1/2	separate	0+1	absent	7 (4)	5	5-6	0	s.ocul. and pre frontal	absent	mostly black	gular	4 and 5 th sup	6 (2-3)	absent
IB 65261	~1/2	separate	0+1	absent	7 (4)	4	4-5	2	s.ocul. - frontal	incomplete	mostly black	gular	3+4+5 th sup	6 (2-3)	absent
IB 65262	~1/2	separate	0+1	absent	7 (4)	5	4-5	3	s.ocul. - frontal	incomplete	mostly black	gular	oval 4 th	6 (2-3)	absent
IB 65263	~1/2	separate	0+1	absent	7 (4)	5	5-6	1	s.ocul. - frontal	complete	mostly black	gular	absent	6 (2-3)	absent
IB 65264	~1/2	separate	0+1	absent	7 (4)	3	6-7	2	s.ocul. - frontal	complete	mostly black	gular	4+5 th sup	6 (2-3)	absent
IB 65265	~1/3	separate	0+1	absent	7 (4)	4	5-6	1	s.ocul. - frontal	incomplete	mostly black	gular	4+5 th sup	6 (2-3)	contact
IB 65266	~1/3	separate	0+1	absent	7 (4)	5	4-5	1	s.ocul. - frontal	incomplete	mostly black	gular	4+5 th sup	6 (2-3)	absent
IB 65268	~1/2	separate	0+1	just a point	7 (4)	4	5-6	1	frontal-parietals	incomplete	black	gular	point on 4 th sup	6 (2-3)	absent
IB 65269	~1/2	separate	0+1	present/absent	7 (4)	3	6-7	1	s.ocul. - frontal	incomplete	black	gular	absent	6 (2-3)	absent
IB 65664	+ 1/2	separate	0+1	absent	7 (4)	6	5-6	2	frontal	incomplete	mostly black	gular	4+5 th sup	6 (2-3)	absent
IB 65680	~1/2	separate	0+1	absent	7 (4)	4	6-7	2	supra oculars	incomplete	mostly black	gular	4+5 th sup	6 (2-3)	absent
IB 65681	~1/2	separate	0+1	absent	7 (4)	6	3-4	2	supra oculars	incomplete	mostly black	gular	4+5 th sup	6 (2-3)	absent
IB 65682	~1/3	separate	0+1	absent	7 (4)	5	5-6	1	s.ocul. - frontal	incomplete	mostly black	gular	4 sup+5 th sup	6 (2-3)	absent
IB 65683	~1/2	separate	0+1	absent	7 (4)	5	6-7	1	frontal	incomplete	blotched	gular	4 th	6 (2-3)	absent
IB 65688	~1/3	separate	0+1	absent/present	7 (4)	4	5-6	2	frontal	incomplete	mostly black	gular	point on 4 th sup left	6 (2-3)	absent
IB 66166	~1/3	separate	0+1	absent	7 (4)	4	5-6	1	frontal	incomplete	mostly black	gular	4+5 th sup	6 (2-3)	absent
IB 67392	~1/3	separate	0+1	absent	7 (4)	5	4-5	0	frontal	incomplete	mostly black	gular	inf 3+4+5 th sup	6 (2-3)	absent