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A New Genus of Microteiid Lizard from the Atlantic Forests of State of Bahia, Brazil, with a New Generic Name for *Colobosaura mentalis*, and a Discussion of Relationships Among the Heterodactylini (Squamata, Gymnophthalmidae)

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ABSTRACT

A new genus and species of microteiid lizard is described from a series of specimens obtained in the leaf litter at Una (15°10′S, 39°03′W) in the Atlantic forest of southern Bahia, Brazil. It is characterized by the presence of prefrontals, frontoparietals, parietals, and interparietal; parietals longer than wide; distinct ear openings and eyelids; two pairs of genials, absence of collar and occipital scales; dorsal scales anteriorly smooth and becoming gradually lanceolate and mucronate posterior to the forelimb; and four regular transverse series of smooth ventrals that are longer than wide, identical in size. A phylogenetic analysis based on external morphology, osteology, and molecular data confirms this new lizard as a member of the Heterodactylini radiation of Gymnophthalminae. The topology recovered by maximum parsimony (MP) analyses reveals that its closest relatives are the sister taxa *Colobosaura modesta* and *Iphisa elegans* (BS = < 50%;

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Bremer value = 2) and the partitioned Bremer indexes indicated that the largest contribution to this relationship comes from morphology; *Colobosaura mentalis*, for which a new generic name is here proposed, is basal to this radiation. Our analyses confirm a previous hypothesis suggesting *Stenolepis* as a member of the Heterodactylini radiation and that the clade composed of *Colobodactylus* and *Heterodactylus* is the sister group of the clade formed by *Colobosaura mentalis*-*Stenolepis* (BS = 100; Bremer value = 18), *Colobosaura modesta*-*Iphisa* (BS = < 50%; Bremer value = 1), and the new genus here described. The support for Heterodactylini monophyly, on the basis of combined MP analyses is higher (BS = 96, Bremer value = 11) than that previously found in molecular-based studies only. Partitioned Bayesian methodology combining molecular and morphological data sets recovered the new genus as the sister taxon (PP = 0.94) of the clade (PP = 0.94) formed by *I. elegans*-*C. modesta* (PP = 0.51) and *C. mentalis*-*S. ridleyi* (PP = 1.0). An alternative topology demonstrating a paraphyletic Heterodactylini is only weakly supported (PP = 0.63). Based on the MP topology we discuss tentative scenarios for the evolution of Heterodactylini.

INTRODUCTION

The Gymnophthalmidae represent a large South and Middle American radiation (41 genera and about 180 species) of small to medium-sized lizards occurring in terrestrial, arboreal, fossorial, and semiaquatic habitats extending from sea level to the high Andes (Pellegrino et al., 2001; Doan, 2003; Doan and Castoe, 2005; Rodrigues et al., 2005). Taxonomic study of these so-called "microteiid" lizards (Ruibal, 1952) has been complicated by the rarity of specimens in collections, which limits studies of geographical and individual variation, and convergence in character complexes (e.g., body elongation, limb reduction, earlessness, lack of eyelids, and the fusion/fission of some major head scales), which has rendered higher-level taxonomy of the Gymnophthalmidae problematic. Boulenger (1885) first organized their chaotic taxonomy by recognizing three groups of microteiids and another group (macroteiids) in the Teiidae. After this, several attempts were made to validate or understand intergeneric relationships between and within the boulengerian groups (Ruibal, 1952; MacLean, 1974; Presch, 1980; Harris, 1985; Sullivan and Estes, 1997; Hoyos, 1998). The relationships between gymnophthalmids and teiids (macroteiids) were generally recognized, with microteiids considered either as a distinct family (Presch, 1983, 1988; Estes, 1983; Estes et al., 1988) or as a subfamily (MacLean, 1974; Presch, 1978, 1980) of Teiidae. In the last two decades, several new taxa of the Gymnophthalmidae have been described (Rodrigues, 1991a, 1991b, 1991c, 1997; Myers and Donnelly, 2001; Kok, 2005); some attempts have been made to infer relationships among the genera (Myers and Donnelly, 2001; Hoyos, 1998), and one entirely new clade of microteiids (characterized by scincoid scales) was recognized (Rodrigues, 1991a, b, c). All of these initiatives were based on morphology.

Only in this century, the first extensive molecular-based phylogenetic hypothesis was proposed for Gymnophthalmidae, which were recovered as monophyletic (Pellegrino et al., 2001). Based on the study of 26 representatives of the 36 genera recognized at the time, four subfamilies were recognized: Alopoglossinae, Rhachisaurinae, Cercosaurinae (with two tribes, Cercosaurini and Ecpleopini), and Gymnophthalminae (also with two tribes: Gymnophthalmini and Heterodactylini). Genera not represented in the molecular analysis of Pellegrino et al. (2001) were tentatively allocated to the recognized clades on the basis of morphology. Pellegrino et al. also demonstrated the paraphyly of several microteiid genera, giving support to previous hypotheses suggesting extensive character convergence, and making understandable the unsuccessful attempts of previous classifications.

Castoe et al. (2004) using only four of the five genes explored by Pellegrino et al. (2001) and a slightly improved sampling design (twelve additional species and one additional genus), reanalyzed the Pellegrino et al. (2001) data. Their results, based on partitioned Bayesian analyses, were highly consistent with those obtained by Pellegrino et al. (2001) with the following higher-level taxonomic changes: (1) *Ptychoglossus* was included in Alopoglossinae; (2) Heterodactylini and Gymnophthalmini were combined in a Gymnophthalminae without tribal divisions; (3) Ecpleopini was raised to subfamily status, and (4) *Bachia* was allocated to the new tribe Bachiini within the Cercosaurinae.

Since then, both schemes have been referred in the literature (Doan and Castoe, 2005; Rodrigues et al., 2005). In a paper focused on clarification of the phylogenetic taxonomy of the cercosaurines, Doan and Castoe (2005) followed the arrangement of Castoe et al. (2004). They described two new genera (*Potamites* and *Petracola*) to accommodate a group of species formerly included in *Neusticurus* and *Proctoporus,* respectively, and resurrected *Riama* to allocate another group of *Proctoporus*. Rodrigues et al. (2005) fully agreed with the reallocation of *Ptychoglossus*, but continued to follow the proposal by Pellegrino et al. (2001) in other respects because they considered the other changes proposed by Castoe et al. (2004) premature; this decision was based on the evidence provided by morphological characters included in the study of Rodrigues et al. Although the study by Rodrigues et al. (2005) was based on a smaller data set, they included representatives of the major clades to test the relationships of the new genus described (*Dryadosaura*) in that paper, and their combined morphological and molecular data recovered monophyly for the Heterodactylini and Gymnophthalmini, as well as a sister-group relationship between them, and all with strong support (their fig. 5B). They also recovered the ecpleopines as a monophyletic group unrelated to Cercosaurini, in agreement with Castoe et al. (2004). Nevertheless, based on the shape of the postorbital, its contact with the postfrontal, and the shape of the interclavicle all suggesting a close relationship between Ecpleopini and Cercosaurini, Rodrigues et al. (2005) retained the tribal assignment of Pellegrino et al. (2001) while awaiting additional evidence. Additionally, based on the limited taxonomic and character sampling of cercosaurines, Rodrigues et al. (2005) did not adopt the Bachiini proposal of Castoe et al. (2004).

Although molecular studies have highlighted and greatly improved our understanding of microteiid relationships, geographic distributions, character evolution, and Neotropical biodiversity, phylogenetic relationships within the family Gymnophthalmidae remain poorly known. We therefore follow Rodrigues et al. (2005) and use the classification proposed by Pellegrino et al. (2001) for the Gymnophthalminae until extensive character and taxon sampling has been completed.

Pellegrino et al. (2001) defined the tribe Heterodactylini, on the basis of molecular evidence, to include the genera *Colobodactylus, Colobosaura, Heterodactylus, Iphisa*, and probably the genus *Stenolepis* (which was not sampled by Pellegrino et al.; or Castoe et al. 2004) on the basis of morphology. In this paper we include the latter genus and add morphological data (completely absent from the studies of both Pellegrino et al., and Castoe et al.) to extend our studies of relationships within the Heterodactylini. We describe an unknown genus and species within this clade, and discuss its relationships to the other heterodactyline genera. The first specimen of the new taxon came to our attention in the mid-1990s, when the first author received for examination a lizard obtained at Ilhéus, state of Bahia, Brazil. It was sent by P.E. Vanzolini with a note saying that it was possibly a new species of *Colobosaura*. That specimen was discovered during the process of reorganization of the herpetological collection of the late Werner Bokermann, now at the Museum of Zoology, University of São Paulo. Some years later, two additional specimens were obtained near Itabuna, state of Bahia by one of us (A. Argolo). It was not until 2000 that a large series of specimens was collected in pitfall traps at Una by M. Dixo during a survey of the herpetofauna of the Atlantic forests of southern Bahia. Additional specimens were subsequently obtained at Serra do Teimoso in the same general region.

Vanzolini's tentative generic allocation was accurate in the context of the taxonomy of that time, and this was also its provisional allocation in the molecular study of Pellegrino et al. (2001), where it was referred as *Colobosaura* sp. and recovered deeply nested within the Heterodactylini. Nevertheless, as recommended by that study and demonstrated hereinafter, we allocate this taxon to its own genus to render classification compatible with the recovered phylogenetic structure. Our study also shows that as currently recognized the genus *Colobosaura* is paraphyletic, and, for this reason, a new generic name is proposed to allocate the former *Colobosaura mentalis*.

The discovery of this new taxon in Atlantic forests of southern Bahia, one of the most threatened habitats in the world (Myers et al., 2000; Rodrigues et al., 2002a, b), reveals further undisclosed biological diversity and refines our understanding of heterodactyline relationships. This combined estimate of the evidence of phylogenetic relationships of the Heterodactilini also raises additional questions about historical biogeography and speciation mechanisms of this interesting group of lizards.

MATERIAL AND METHODS

Snout-vent length was measured to the nearest mm with a rule; scale counts and osteological data on cleared specimens (appendix 1) were taken with the aid of a stereomicroscope. Scale counts and scale nomenclature are according to Rodrigues and Borges (1997), and osteological nomenclature follows Presch (1980) and Estes et al. (1988). Sex was determined by the presence/absence of femoral pores and confirmed by dissection in previously opened specimens. All data were taken from preserved specimens housed at MZUSP (Museu de Zoologia, Universidade de São Paulo), MNRJ (Museu Nacional, Rio de Janeiro), MZUESC (Museu de Zoologia, Universidade Estadual de Santa Cruz), and RNHM (Nationaal Natuurhistorisch Museum, Leiden). To compare abundance of males and females and total abundance among habitats of the new taxon sampled we used one-way analysis of variance (ANOVA; Zar, 1996). When significant differences were obtained, differences between pairs of habitats were tested with a Tukey's test (Zar, 1996). Association among habitat categories and species or sex was detected by chi-square test. All analyses were done using Statistica (StatSoft, 1998). Appendix 2 presents the 19 species, assigned to 17 genera of Gymnophthalmidae (including the new one herein described), used in the present study. External morphological characters included in appendix 2 were selected among those not presenting intraspecific polymorphism after the examination of the MZUSP collections. Hemipenes were examined when partly or totally everted in preserved specimens in order to improve descriptions and comparisons, but due to their limited availability among the genera included here, they were not used in the subsequent analyses.

The majority of DNA sequences used here were those from Pellegrino et al. (2001), but new sequences for the same mitochondrial (12S, 16S and ND4) and nuclear (c-mos and 18S) gene regions were included for the previously unsampled ingroup taxon *Stenolepis ridleyi* (GenBank accession numbers EF 405618-405622). The present molecular partition is composed of 2,333 bp of aligned sequences; some adjustments on the original Pellegrino et al. (2001) alignments for the ribosomal 12S, 16S, and 18S regions were performed manually on the reduced matrix used in this study. This was necessary to accommodate the sequences of *Stenolepis* and exclude unnecessary gaps. Regions of ambiguous alignment for the 12S and 16S were excluded from the final analyses on the reduced matrix.

Phylogenetic inference was first conducted on the separate morphological partition followed by a combined analyses with the molecular partitions under equally weighted parsimony (MP) in PAUP* v4.0b10 (Swofford, 2002). For a matrix of 42 morphological characters (appendix 2), with all character states coded as unordered and all transformations uniformly weighted, a search with the branch-and-bound algorithm was performed. The analysis of the combined data set included an MP heuristic search with 1,000 replicates of random stepwise addition and TBR branch-swapping.

Nodal support was assessed by bootstrap analysis (BS; Felsenstein, 1985) with a 1,000 random stepwise additions per bootstrap pseudoreplicate, and TBR branch-swapping, in both branch-and-bound (morphology) and heuristic (combined data) searches; bootstrap values greater than 70% (Hillis and Bull, 1993) were interpreted as strong support for a node. Total and partitioned Bremer support (PBS) values (Baker and DeSalle, 1997), the latter representing the contribution of each specified data partition to each node, were calculated for all nodes of the combined data-partition topology using the program TreeRot v. 2.0 (Sorenson, 1999).

Modeltest v.3.06 (Posada and Crandall, 1998) was used to select the appropriate model of evolution for each molecular data partition: 12S (TrN+Γ), 16S (TrN+I+Γ), ND4 (TVM+I+Γ), c-mos (K80+Γ) and 18S (JC). Using the combined data set (molecular and morphology) a partitioned Bayesian analysis was implemented in Mr.Bayes 3.0 (Huelsenbeck and Ronquist, 2001), under the best fit models of substitution for individual gene regions and morphological data set as "standard", with 3,000,000 generations, four chains, and trees sampled at intervals of 1,000 generations. Two independent runs were conducted. Trees prior to stationarity were discarded as "burn-in", and a 50% majority-rule consensus tree was obtained from 2,900 data points. Nodes on consensus trees from both runs with posterior probability (PP values) ≥ 0.95 were considered as evidence of significant support for a given clade (Huelsenbeck and Ronquist, 2001).

Two species of *Alopoglossus*, members of the subfamily Alopoglossinae formally recognized by Pellegrino et al. (2001) and Castoe et al. (2004) and strongly supported as basal to all other clades of Gymnophthalmidae in both studies, were constrained to monophyly and used as the outgroup. Selected taxa from Gymnophthalmini, Cercosaurini and Ecpleopini were also included to give *Stenolepis* a chance to fail to be recovered within the Heterodactylini (see appendix 2).

RESULTS

TAXON DESCRIPTION

Alexandresaurus, new genus

DEFINITION: A large and slightly elongate gymnophthalmid (maximum SVL 70 mm) with distinctive ear opening and eyelid, large tail (1.63%–2.36% SVL), and slender pentadactyl limbs; first toe lacking a claw. Frontonasal single; prefrontals, frontoparietals, parietals, and interparietals present. Parietals and interparietal longer than wide. Collar fold absent. Two pairs of genials and three supraoculars. Dorsal scales anteriorly smooth, isodiametric or subrectangular in occipital region, becoming progressively narrower, more elongate and rounded toward arm level and then lanceolate, strongly keeled, with lateral sides almost juxtaposed. Occipitals absent. Ventrals longer than wide, smooth, in four regular transverse series identical in size. Males with a continuous series of very conspicuous pores with no gap between preanal and femoral; pores absent in females. Hemipenis without evident bilobation, sulcus spermaticus single, marginated by a naked area which is also present on the opposite side of sulcus. Between naked areas two symmetrical series of continuous transverse rows of comb-like flounces with minute spines or irregular tooth-like structures. A series of enlarged spines near the base of hemipenis.

CONTENT: *Alexandresaurus camacan* new species; monotypic.

ETYMOLOGY: A homage to the Brazilian naturalist Alexandre Rodrigues Ferreira, born in Salvador, state of Bahia, as a recognition for his effort to document the natural history of Brazil at the end of the 18th century. After pursuing natural history studies under Vandelli at the University of Coimbra, Alexandre headed the famous *viagem filosófica* ("philosophical voyage") to Brazil at the end of 18th century. He remained in Brazil until 1789 where, among other places, he traveled extensively along the Rio Negro, Madeira and Guaporé in the Brazilian Amazon. The travels of Alexandre were part of a larger project to publish what was meant to be a monumental natural history of the Portuguese colonies (Farias, 2001). The plan was abandoned by the end of 1807 when the royal family escaped to Brazil against the backdrop of Lisbon's imminent conquest by Napoleonic forces. Most of the collections assembled by Alexandre during the more than 35,000 km traveled in Brazil were published by other naturalists following the request of part of the material by Étienne Geoffroy Saint Hilaire, who was present in Lisbon during the subsequent conquest.

COMPARISONS: Considering the now recognized multiple origins of character complexes associated with fossoriality in gymnophthalmid lizards, and the chaotic state of their taxonomy based on external attributes (until recently), we compare *Alexandresaurus* with all other gymnophthalmids while emphasizing the external morphological differences with the genera *Iphisa, Colobosaura, Colobodactylus, Heterodactylus*, and *Stenolepis*. Except for the latter, this group of genera was recovered by Pellegrino et al. (2001) as a well-supported clade that included the closest relatives of *Alexandresaurus*. *Stenolepis*, although not included in that study, was tentatively allocated to the same radiation.

Most character states for the taxa compared here are summarized in appendix 1. *Alexandresaurus* differs from *Iphisa* (data for the latter in parenthesis) by having: two pairs of genials (one); several rows of lanceolate and keeled dorsal scales (smooth, in two longitudinal rows); ventral scales regularly transverse in four longitudinal rows (not in transverse rows and in two longitudinal rows); and regularly transverse rows of gulars (not regular). *Alexandresaurus* also differs from *Iphisa* in having a naked area opposite to the sulcus spermaticus and large spines at the base of the hemipenis (naked area absent and only small spines at base of the organ). From *Colobosaura Alexandresaurus* can be distinguished from *Colobosaura* by its smooth neck scales and small, smooth, and posteriorly rounded scales in the first 7–8 dorsal rows, rarely two enlarged nuchals are present at the central part of the second dorsal row; occipitals are never present. In *Colobosaura* neck scales have keels; there are several enlarged scales, much wider than long, in the first eight dorsal rows, the first two characteristically smooth and enlarged, forming an occipital pair separated or not by a smaller scale; the posterior 5–6 dorsal rows are striate or multicarinate. Ventral scales in *Alexandresaurus* are longer than wide, laterally juxtaposed, rounded posteriorly, identical in size and shape, regularly arranged transversally and in four longitudinal series. In *Colobosaura* there are also four longitudinal rows of quadrangular ventral scales, but they are not regularly transversal and are irregular in size and shape, laterally imbricate, and in the first ventral rows midline scales always distinctively wider than long; the external ventral rows are slightly wider than long in *Colobosaura mentalis*, whereas the reverse occurs in *Colobosaura modesta*. The latter species also differs from *Alexandresaurus* by having only three pairs of genials. As in *Alexandresaurus,* the hemipenis of *Colobosaura mentalis* also has a naked area on the side of organ opposite to the sulcus, as well as flounces of right and left lobes medially interrupted by a naked area, a character absent in the former species. The only other species referred to *Colobosaura* was *Perodactylus kraepelini*. It is a young female (SVL = 40 mm) described by Werner in 1910 having Puerto Max: Paraguay as type locality. We have not examined the holotype, which is lost from the Hamburg Zoological Museum according to Dr. J. Hallermann (in litt.); based on the original description, this species is identical to *Colobosaura modesta*, an opinion advanced long ago by Amaral (1933). The distributional data agree with this interpretation because the type locality is in the area of occurrence of *C. modesta.* The only character that until now has precluded synonymy between *C. modesta* and *C. kraepelini* was Werner's reference to the tongue of his specimen as having "oblique plicae like *Alopoglossus*". Based on the agreement of all other characters mentioned in the description we think that Werner was in error in describing the tongue, evidently a strange character and restricted to Alopoglossinae. *Alexandresaurus* differs from *Stenolepis, Colobodactylus*, and *Heterodactylus* in having a pair of prefrontals (absent). It further differs from *Stenolepis* by having small dorsal neck scales (large, in 3–4 longitudinal rows), larger scales on the sides of neck (small, some almost granular), ventral and gulars in regularly transverse rows (not so), and smooth scales near venter (keeled). In *Colobodactylus* and *Heterodactylus* the parietals are wider than long in contrast to the longer than wide parietal scale observed in *Alexandresaurus* and other Heterodactylini. This difference is probably due to a possible scale rearrangement in *Heterodactylus* and *Colobodactylus* in which parietals (and interparietal in *Colobodactylus*) were divided and their posterior regions incorporated into the highly conspicuous occipitals that characterize both genera. This hypothesis, further discussed under a phylogenetic framework below, reveals that even head scales traditionally used in taxonomic descriptions may not be strictly homologous. This is another example of the taxonomic confusion that may result from uncritical use of morphological characters in microteiid systematics. *Alexandresaurus* also differs from *Colobodactylus* and *Heterodactylus* in having five toes and smooth flank scales (only four toes and flank scales keeled in the latter genera). *Heterodactylus* further differs from *Alexandresaurus* by the absence of external ear, absence of frontoparietals, and absence or extreme reduction of interparietal. Finally, the hemipenis of *Heterodactylus* is very different from that of *Alexandresaurus*. The organ is distinctively bilobate with a centripetal sulcus spermaticus surrounded by a naked area. The asulcate side of the organ has a series of continuous and unornamented naked flounces containing only one spine at each edge, very different from the interrupted flounces containing spines in a comb-like arrangement observed in *Alexandresaurus*.

Alexandresaurus differs from members of Alopoglossinae by having imbricate, scalelike papillae covering the tongue (oblique plicae), and from Rhachisauridae by having a distinctive ear opening and eyelid (absent), five toes (four), a normal body (clearly elongate), presence of frontoparietals (absent), and a nostril at the nasal border (in the center of the nasal scale). From all other Gymnophthalminae *Alexandresaurus* differs by having five toes (fifth toe reduced or absent), a distinctive eyelid (absent in all Gymnophthalmini except for *Tretioscincus*), nostril at the nasal border (in the center of the nasal scale), a wide and flattened clavicle enclosing a fenestra (simple, boomerang shaped and without fenestrae), nasal bones in contact at midline but broadly separated anteriorly (totally separated by contact between frontal and premaxilary), and, among other characters, by having straight lateral processes of the interclavicle (posteriorly oriented). *Alexandresaurus* also differs from all Cercosaurinae by having a distinctive sternal fontanelle process (absent), a glossohyal separated from basiyal (fused), nasal bones broadly separated anteriorly (in broad contact), and postorbital covering postfrontal (covered by postfrontal).

Alexandresaurus camacan, new species

figures 1–4

HOLOTYPE: MZUSP 93201, an adult male from Una (15°10′S, 39°03′W): state of Bahia: Brazil, collected by Marianna Dixo on 01 November 1999, field number md-1106.

PARATYPES: All from the state of Bahia, Brazil. MZUSP 93179–93200, Una, collected by M. Dixo between 24 January 1999 and 27 February 2000; MZUSP 93331, Ilhéus, collected by W. Bokerman on December 1971; MZUSP 93462–93464 Ilhéus (CEPLAC, sede regional), A. Argolo leg., collected respectively on July 1990, 24 April 1991, and 12 May 1999; MZUSP 93227–93228, Jussari (Serra do Teimoso) collected by M. T. Rodrigues, D. Pavan, M. Dixo, and V. K. Verdade on March 2001; MZUESC 2431, Ilhéus (Campus UESC), collected by C. N. Souza on 8 March 2002; RMNH 29741, from Una, Ilhéus.

ETYMOLOGY: The specific epithet is a homage to the extinct Camacan Indians, a Botocudo group who lived in the exuberant forests of Bahia from north of Rio Pardo to Ilhéus.

DIAGNOSIS: A gymnophthalmid with ear openings and eyelids, and slender pentadactyl limbs lacking the claw on first toe. Frontonasal single; prefrontals, frontoparietals, parietals, and interparietals present. Parietals longer than wide. Collar fold absent. Two pairs of genials; three supraoculars. Dorsal scales in 30–38 rows, anteriorly smooth, isodiametric or subrectangular in occipital region, becoming progressively narrower, more elongate and rounded toward the arm, and posterior to the arm becoming more lanceolate, strongly keeled, with lateral sides almost juxtaposed. Occipitals absent. Ventrals longer than wide, smooth, in four regular longitudinal and 15–19 transverse rows, identical in size. Scales around body 29–35; 11–15 and 16–20 infradigital lamellae under finger IV and toe IV respectively. Males with a series of 20–25 very conspicuous pores without gap between preanal and femoral; pores absent in females.

DESCRIPTION OF HOLOTYPE (fig. 2A–C): Rostral broad, wider than high, contacting first supralabial, nasal, and frontonasal. Frontonasal pentagonal, twice as wide as long, contacting rostral, nasal, loreal, and

Fig. 1. *Alexandresaurus camacan* (MZUSP 93228), an adult male (57 mm) from Serra do Teimoso, state of Bahia, Brazil.

prefrontals. Prefrontals slightly wider than long, in broad contact at midline. Frontal hexagonal, with almost parallel lateral margins, slightly longer than wide, anteriorly indenting the prefrontal and posteriorly the frontoparietal sutures. Frontoparietals pentagonal, larger than prefrontals, in slight contact, strongly indented by the interparietal. Interparietal longer than wide, longer and narrower than frontal, as long as and narrower than parietals. Parietals heptagonal, marginated laterally by two temporal scales with approximately the same size, anteriorly by the third supraocular and frontoparietal, medially by the interparietal, and posteriorly by the first dorsals. Three supraoculars, first the smallest, second and third about the same size, second slightly wider, its longest suture with frontal, third slightly longer, in broad contact with frontoparietal. Nasal above first supralabial, large, longer than high, with the nostril in the center and lower part of scale, indenting suture with labial. Loreal posterior to nasal, narrower and diagonally oriented; contacting posteriorly first superciliary, preocular, and frenocular. Frenocular below preocular, followed posteriorly by a long subocular wider anteriorly and indenting suture between preocular and frenocular. Seven supralabials, third and fourth under the eye, fifth the highest and contacting two smaller scales following posteriorly the subocular, the smallest one clearly a postocular; seventh supralabial the smallest, in contact with the granules surrounding anterior margin of ear. Three superciliaries, first largest, wider anteriorly, longer than first supraocular, contacting preocular, loreal, first and second supraoculars, second superciliary and upper eyelid. Central part of eyelid with a semitransparent undivided disc surrounded by small and slightly pigmented granular smooth scales. Lower eyelid with eight strongly pigmented palpebrals. Temporal region with few smooth and juxtaposed scales, irregular in size and shape, between parietals and supralabials; the larger as large as the sixth supralabial. Ear opening surrounded by a series of very small and juxtaposed rounded granules; external auditory meatus large, tympanum distinct, subovoid, recessed. Lateral surface of neck with smooth, imbricate and mostly longer than wide scales, larger dorsally. All head scales smooth and juxtaposed with scattered sensorial organs.

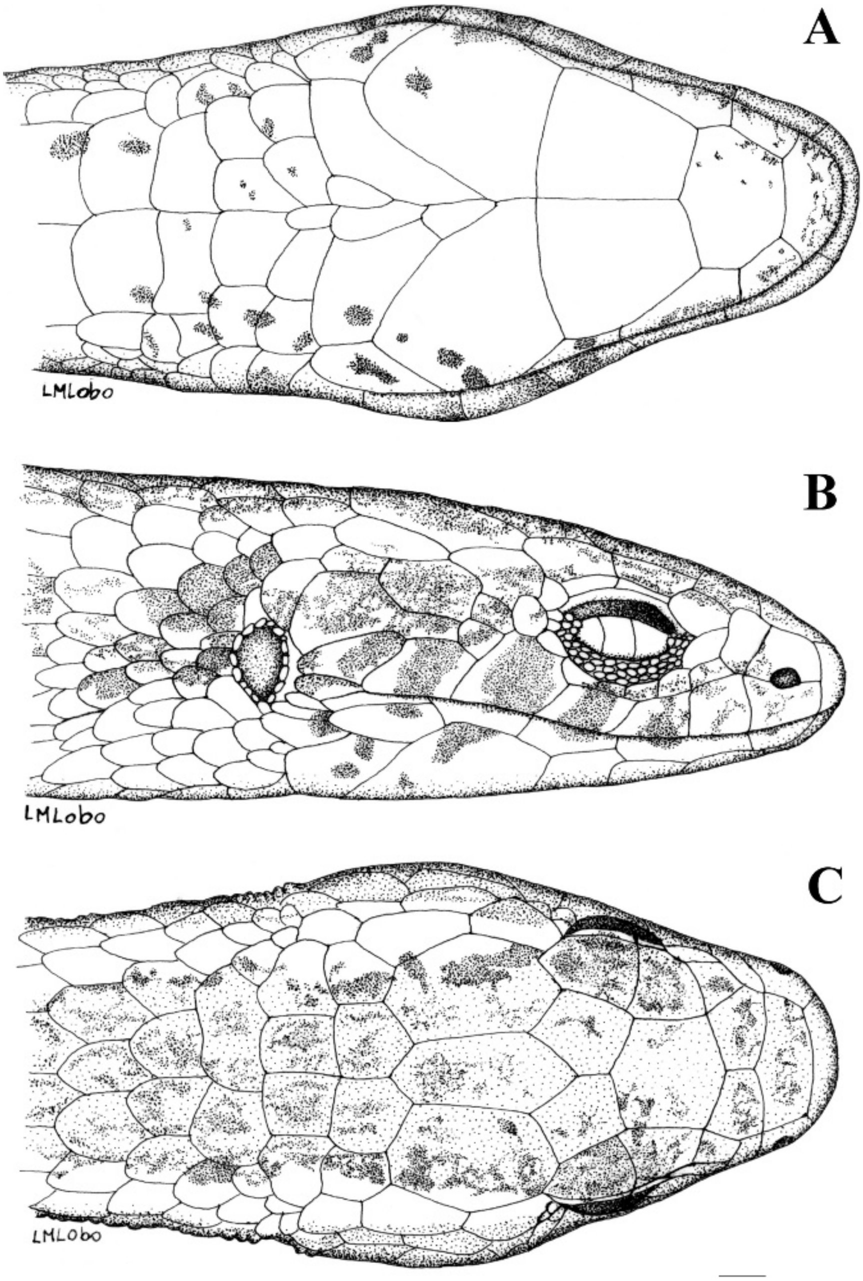

Fig. 2. Ventral (A), lateral (B), and dorsal (C) views of the head of the holotype of *Alexandresaurus camacan* (MZUSP 93201). Scale = 1 mm.

Mental broad, wider than high. Postmental heptagonal, wider than long. Two pairs of genials, both contacting infralabials; the first smaller, in broad contact at midline; second pair contacting only anteriorly and reaching the level of labial comissure. An enlarged pair of symmetric flat and chevron-like scutes follows second pair of genials, preventing their contact posteriorly. Six infralabials, second the largest. Gulars smooth, imbricate,

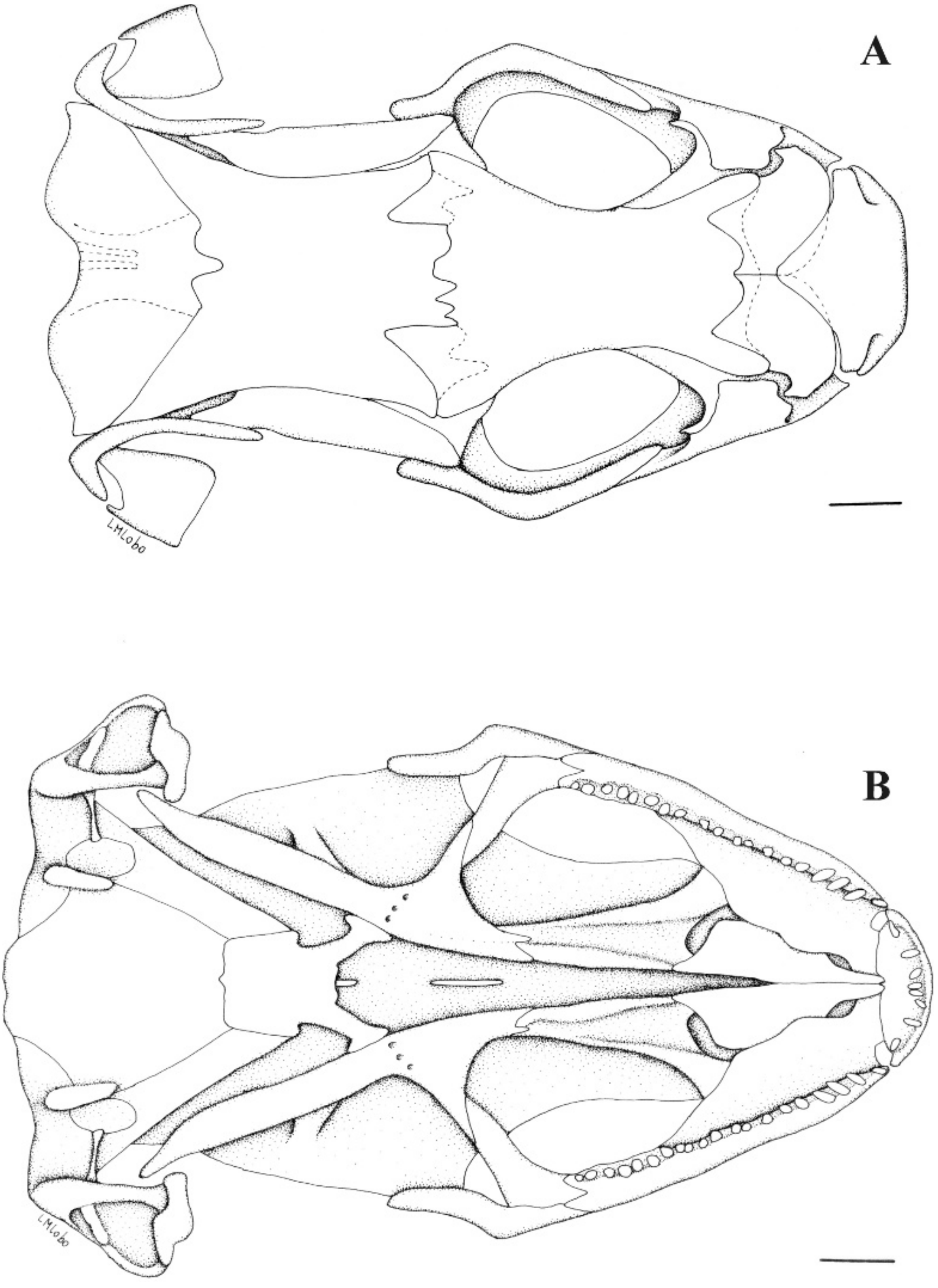

Fig. 3. Dorsal (A) and ventral (B) views of the skull of *Alexandresaurus camacan* (MZUSP 94252-53). Scale = 1 mm.

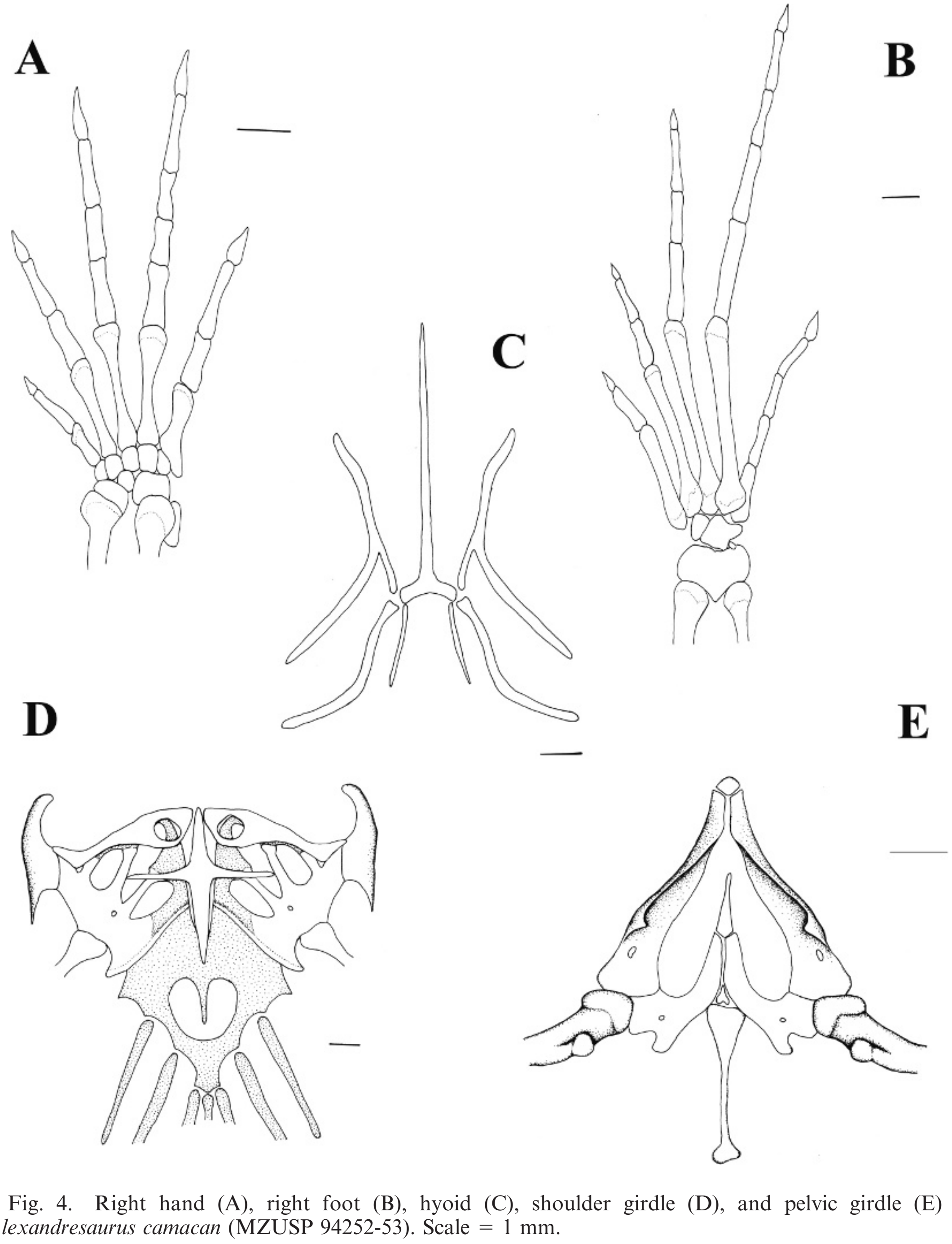

Fig. 4. Right hand (A), right foot (B), hyoid (C), shoulder girdle (D), and pelvic girdle (E) of *Alexandresaurus camacan* (MZUSP 94252-53). Scale = 1 mm.

rounded posteriorly, in seven transversal rows; at midline similar to ventrals, much smaller toward side of neck. Gulars followed by a distinct interbrachial region with seven much larger and elongate scales, about twice as long as gulars. Collar fold absent.

Dorsal scales imbricate and arranged in regular transversal rows; smooth, isodiametric or subrectangular in occipital region, becoming progressively narrower, more elongated and rounded at arm level and then posteriorly lanceolate, strongly keeled, with lateral sides almost juxtaposed. Thirty transverse rows between interparietal and the posterior level of hind limbs. Lateral scales about the same size as dorsals but smooth, strongly imbricate laterally, less acuminate and more diagonally arranged than dorsals; those closer to ventrals larger. A distinctive area with granular scales surrounds the area of arm insertion. Thirty-one scales around midbody. Ventral scales smooth, longitudinally imbricate, laterally juxtaposed, longer than wide, rounded posteriorly; 17 transverse rows from interbrachials (excluded) to preanals. Six scales in precloacal region, central and paramedials the largest. Total pores 23, continuous, with no gap between femoral and preanal ones.

Scales of tail smaller than midbody dorsals, but otherwise identical; keeled, lanceolate, strongly imbricate longitudinally; those from base of tail slightly larger ventrally, becoming gradually identical around tail toward the extremity.

Forelimbs with large, smooth, and imbricate scales; those on ventral part of brachium much smaller. Anterior and ventral parts of hind limbs with irregularly large, smooth, and imbricate scales, identical to the correspondent parts of fore-limbs. Posterior part of hind limbs with granular, juxtaposed scales, grading progressively to larger, imbricate, and keeled scales in dorsal part of tibia. Carpal and tarsal scales large, imbricate; supradigital lamellae, smooth imbricate. Palmar and plantar surfaces with smooth, small granules; infradigital lamellae single, 12 on Finger IV and 19 on Toe IV. Toes and fingers, except for Finger I, clawed, and respectively in the following relative sizes: $1 < 2 = 5 < 3 = 4$ and, $1 < 2 < 5 < 3 < 4$.

Dorsal surfaces of body and tail and lateral part of tail dark brown with an irregularly distributed darker punctuation smaller than one fourth of the scale size. Flanks predominantly yellowish to cream, as the ventral parts of body and tail, but strongly mottled by an irregularly black pattern. Lateral parts of head with an identical pattern, black blotches concentrated in central parts of supra- and infralabials, yellow at their sutures. Ventral parts of body and tail creamy yellow, immaculate, except in the external rows of gulars and ventrals, which present irregular black spots. Ventral part of tail becomes gradually darker toward the extremity. Limbs dark brown dorsally, irregularly mottled with yellow; creamy yellow and immaculate ventrally.

Hemipenis partly everted at preservation except for the apex; bilobation not evident; sulcus spermaticus single, marginated by an enlarged naked area that is also present, but narrower, on the opposite side of sulcus. Between naked areas of the organ, two symmetrical series of 29 (or more) continuous transverse rows of comb-like flounces with minute spines or irregular tooth-like structures. Flounces continuous even near basal part of the organ where their ornamentation is medially interrupted by a small area without spines. A basal series of very enlarged spines is present near the base of hemipenis in its asulcate face.

Measurements of the holotype: snout-vent length: 66 mm; tail length: 145 mm.

VARIATION: Males are slightly larger than females but have much longer tails: maximum SVL for males and females was 70 mm and 66 mm. Tail length varied respectively in males and females from 1.76 to 2.36 and 1.8 to 2.03 times SVL (fig. 5: r^2 males 0.93; r^2 females 0.29). No sexual differences were found in squamation. Variation in meristic characters ($N = 28$) was the following (mean and standard error, respectively, in the parenthesis): dorsal rows, 28–30 (29 and 0.72); ventrals 15–19 (16.8 and 1.06); scales around midbody 29–35 (31.5 and 1.42); infradigital lamellae under finger IV 11–15 (12.9 and 0.19); and infradigital lamellae under Toe IV 16– 20 (18.1 and 1.0). All specimens show three supraoculars and three superciliaries. All the specimens have seven supralabials, and all have six infralabials except RM 29791, which has seven. One specimen (MZUSP 93187) has four ventral rows fused midventraly resulting in two longitudinal rows of ventrals. We note that this arrangement is similar to the pattern found in *Iphisa*, but differs from it because the rows of scales are regularly arranged transversally in *Alexandresaurus* and not so in *Iphisa*. Only males have pores, they are absent in

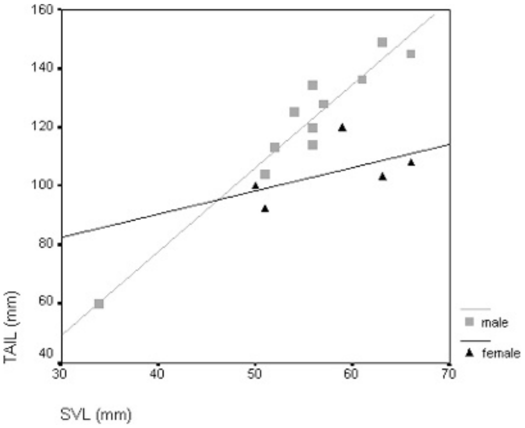

Fig. 5. Regression lines between body length and tail length for males and females of *Alexandresaurus camacan* from Una, State of Bahia, Brazil.

females. Pores are highly conspicuous, placed in distinctively elevate scales, aligned on each side without gaps between preanal and femoral. Total number of pores varied from 20–25 (*N* = 16). Sexual color dichromatism is evident; males are characterized by dark coloration in the flanks mottled with yellowish or whitish blotches and a reddish venter; females and juveniles are more dull colored having unpatterned light brown flanks and a creamy white venter.

OSTEOLOGY (figs. 3–4): The following description is based on two alizarin-prepared skeletons (MZUSP 94252–53). Premaxillary as long as wide, contacting but not articulating laterally with the maxillary. Its dorsal lamina triangular posteriorly, long, just covering anteriorly the nasals and deeply indenting their suture, preventing their anterior contact. Twelve premaxillary conical teeth. Nasals large, longer than wide, wider anteriorly, diagonally arranged, widely separated anteriorly, posterior third in midline contact, covering frontal anteriorly. Frontal longer than wide, wider posteriorly, covering parietal and articulating with it by a pair of frontoparietal tabs. Parietal longer than wide, wider and concave posteriorly and covering laterally the occipital region. Epipterygoid contacting externally a descending epipterygoid process of parietal. Maxillary dorsally contacting nasal, and lateral parts of frontal and lacrimal, without overlapping, and extensively covering prefrontal and jugal; 21 maxillary teeth. Prefrontal large, its posterior process long but not reaching the level of middle of orbit; in broad contact with frontal. Lacrimal large, very conspicuous, contacting prefrontal and maxillary and indenting the orbit. Postfrontal and postorbital single. Postfrontal triangular, contacting jugal, frontal, postorbital and jugal, closing posteriorly the orbita. Postorbital long and wide, contacting squamosal posteriorly, almost closing the supraorbital fenestra. Squamosal long, posteriorly curved and abutting the top of quadrate. Supratemporal fenestra almost closed and strongly constrained laterally by parietal and postorbital. Supratemporal present, in straight contact with posterior part of parietal and squamosal. Fifteen scleral ossicles in the eye. Vomer, palatine, pterygoid, ectopterygoid, and pterygoid present. Vomer, palatine, premaxillary, and maxillary in contact restricting the fenestra exochoanalis. Infraorbital fenestra large, bordered posteriorly by ectopterygoid. Stapes rodlike, wider at the base. Sutures between supraoccipital, exoocipital, basioccipital and the otic area of skull are not as visible as those between basioccipital and basisphenoid. In the lower jaw dentary, articular, splenial, angular, and supraangular are distinct; there are 14–15 dentary teeth, conic anteriorly, bicuspid or tricuspid posteriorly.

Glossohyal long, fused to basihyal. First ceratobranchial curved posteriorly; hypohyal and ceratohyal present. A second short pair of ceratobranchials is present and positioned parallel to the anterior part of trachea.

Anterior part of clavicle very enlarged, flattened, enclosing a fenestra. Interclavicule long, cruciform, with very long lateral processes reaching the sternum but not sternal fenestra. Scapulocoracoid with coracoid, scapular, and scapulocoracoid fenestrae; suprascapula present. Sternum with a large fenestra, receiving three sternal ribs and a xiphisternum with two inscriptional ribs. Ilium, ischium, and pubis present, the latter with a conspicuous pectinate apophysis. Hypoischium long, larger at the base, almost reaching the preanal border; a small elongate preischium and a small quadrangular ossificate prepubis are present.

Twenty-seven procoelous presacral vertebrae, neural spines low, higher anteriorly hypopophyses present in the first six vertebrae; zigantrum-zygosphene present. Last presacral vertebra lacking ribs. Two sacral vertebrae. First caudal vertebrae with long transverse processes, lacking autotomic septa.

Humerus and femur are slightly larger than radius and ulna and tibia and fibula. Remaining elements of the forelimbs and hind limbs as in figure 4.

Distribution and Natural History

Alexandresaurus camacan is currently known only from four localities in the southern Atlantic rainforest region of the state of Bahia: Ilhéus, Una, Jussari (Serra do Teimoso), and Uruçuca. The maximum straight-line distance between the most distant of these localities is less than 60 km. Pristine tropical forest with high levels of humidity and rainfall (about 2,000 mm) regularly distributed throughout the year, with a dense leaf litter, large trees reaching up to 30 m high and more than 50 cm diameter at breast height, and an abundance of bromeliads and other epiphytes, was the typical habitat in the Atlantic rainforest at this latitude. Most of this area is dominated by lowlands or low hills dissected by small- to medium-sized streams, interrupted by isolated higher mountains. The Serra do Teimoso is one these higher mountains reaching about 1,000 m altitude and receiving the highest levels of humidity at the top as a result of the orographic effect and condensation of air masses coming from the sea. Currently most of the forest cover is restricted to scattered patches of remnant forest, the Una reserve (Reserva Biológica de Una—ca. 11,500 ha) being the largest one. The largest area of original forest was destroyed by agriculture (for cacao plantations), cattle ranching, and timber harvest activities. In cacao groves (“cabrucas” locally) where large and emergent trees have been preserved to shade the understory cacao plants, leaf litter is abundant and humidity is higher than in other disturbed areas.

The localities where *Alexandresaurus camacan* was collected show slight differences related to soil type, levels of humidity, and distance from the coast. Uruçuca (14°33′S, 39°18′W) is located on fertile soils originating from volcanic deposition and is intensely cultivated for cacao production. Ilhéus and the Reserva Biológica do Una (15°10′S, 39°03′W) are located near the coast on the sandy soils of Barreiras Formation and receive more rainfall. The RPPN (Reserva Particular do Patrimônio Natural; Serra do Teimoso; 15°19′S, 39°31′W) is an isolated peak toward the interior of the state and is covered by a semideciduous forest, along with cacao groves at the lower areas and tropical rainforest with high humidity levels near the top.

Pitfall traps were installed at Una, Serra do Teimoso, and Uruçuca to sample areas of primary and secondary forest and cacao groves. At Serra do Teimoso a series of pitfall traps also sampled semideciduous forest. *Alexandresaurus camacan* was always obtained in sheltered areas in primary forest or cacao groves, never in secondary forests. At Serra do Teimoso the only individual collected was found in semideciduous forest at high elevation (about 900 m) in the humid forest. No association between habitat categories and sex was detected ($p > 0.05$, chi-square test). *Alexandresaurus camacan* was always found in shady areas in primary forest or cacao groves, and never in secondary forests. Total abundance ($F_{(2,\ 27)} = 1{,}06$, $p = 0.36$) and female abundance ($F_{(2,\ 27)} = 0.32$, $p = 0.73$) did not vary significantly among habitats (forest interior, forest edge, and cacao groves), while male abundance did ($F_{(2,\ 27)} = 4.70$, $p = 0.018$). Male abundance was significantly higher in forest edges than in cacao groves ($p = 0.03$) and marginally higher than in forest interior ($p = 0.06$).

Phylogenetic Analyses

Parsimony analyses to determine the phylogenetic placement of *Alexandresaurus camacan* and its relationships within the Heterodactylini, were first conducted on the partition composed of 42 morphological characters (38 of which are parsimony informative; appendix 2) with all states coded as unordered. This analysis recovered 211 most parsimonious trees; the poorly resolved strict consensus tree (L = 106; CI = 0.55 and RI = 0.72; fig. 6A) left the position of *Alexandresaurus* unresolved within the Heterodactylini, but, although weakly supported, recovered the tribe as monophyletic (BS = 58, Bremer value = 4). Except for a well-supported sister relationship between *Colobodactylus taunayi*-*Heterodactylus imbricatus* (BS = 95, Bremer value = 4) this tree left all other ingroup taxa as an unresolved polytomy. Two other well-supported sister-group relationships recovered by the morphological partition were those of *Procellosaurinus tetradactylus*-*Micrablepharus maximiliani* (BS = 99, Bremer value = 4) and *Colobosauroides cearensis*-*Anotosaura vanzolinia* (BS = 88, Bremer value = 2).

Combined analyses of the morphological and molecular partitions resulted in a single most parsimonious tree of 2,740 steps, 660 parsimony-informative characters, and CI = 0.47 and RI = 0.43 (fig. 6B). The recovered relationships are very similar to those suggested by the previous study of Pellegrino et al. (2001) based on molecular data only. The Heterodactylini was recovered with strong support (node 8: BS = 92, Bremer value = 11; see appendix 4). Within the Heterodactylini, *A. camacan* is weakly resolved as the sister group of *I. elegans*-*C. modesta* (node 5: BS < 50; Bremer value = 2; see appendix 4); (*C. mentalis* + *S. ridleyi*) is recovered as a strongly supported clade (node 6: BS = 100, Bremer value = 18, see appendix 4); and both the monophyly of the clade (*Colobodactylus taunayi* + *H. imbricatus*) and that of its sister group (*A. camacan, C. modesta, I. elegans* + *C. mentali* -*S. ridleyi*) are strongly and moderately well supported (respectively, node 3: BS = 99, Bremer value = 13, and node 7: BS = 75, Bremer value = 5; appendix 4). The Gymnophthalmini represented by the *Procelosaurinus*-*Micrablepharus* clade (node 9: BS = 100, Bremer value = 28) is resolved as the sister clade of the Heterodactylini with high support (node 10: BS = 96, Bremer value = 11). Slightly different from the Pellegrino et al. (2001) hypothesis are the weakly supported sister relationship *Rhachisaurus*-*Bachia* (node 1: BS < 50, Bremer value = 1) and the placement of *Arthrosaura reticulata* as the sister taxon of the *C. cearensis*-*A. vanzolinia* clade (node 13: BS = 63, Bremer value = 8). The monophyly of the ecpleopines was also strongly supported (node 15: BS = 92, Bremer value = 11).

Externally, the (*C. ocellata* (*Rhachisaurus brachylepis*-*B. bresslaui*)) clade was weakly supported (node 2: BS < 50, Bremer value = 6), and the Heterodactylini-Gymnophthalmini clade (node 10) and the Ecpleopini clade (node 15) were recovered with high support indexes (BS = 96, Bremer value = 11; BS = 92, Bremer value = 11; fig. 6B, respectively).

Figure 7 shows the majority-rule consensus tree estimated using partitioned Bayesian method, which differs from that recovered from parsimony analysis (fig. 6B). The major difference refers to the paraphyly of the Heterodactylini with respect to the Gymnophthalmini, but this alternative topology is only weakly supported by posterior probabilities (PP = 0.63). Bayesian tree is unique in recovering a quite well-supported sister relationship (PP = 0.94) between *I. elegans*–*C. modesta* (PP = 0.51) and *C. mentalis*–*S. ridleyi* (PP = 1.0), with *Alexandresaurus* basal to this grouping (PP = 0.94). Also, the sister-group relationship between *Bachia* and *Cercosaura* is highly supported (PP = 0.99). Similar to the MP tree (fig. 6B), the support for Ecpleopini monophyly is high (PP = 1.0), although its position is unresolved (fig. 7).

TAXONOMIC IMPLICATIONS: Our results show that the position of *Colobosaura mentalis* in the tree is incompatible with a monophyletic *Colobosaura*. This was also indicated in the analysis of Pellegrino et al. (2001), which although based exclusively on molecular data incorporated a much larger dataset. The sister-group relationship between morphologically highly divergent species like *Iphisa elegans* and *Colobosaura modesta*, suggests the recognition of another new genus to allocate *Colobosaura mentalis*. We propose the following name to accommodate it:

Acratosaura, new genus

DEFINITION: A microteiid characterized by a distinctive ear opening and eyelid, large tail, and slender pentadactyl limbs. Frontonasal

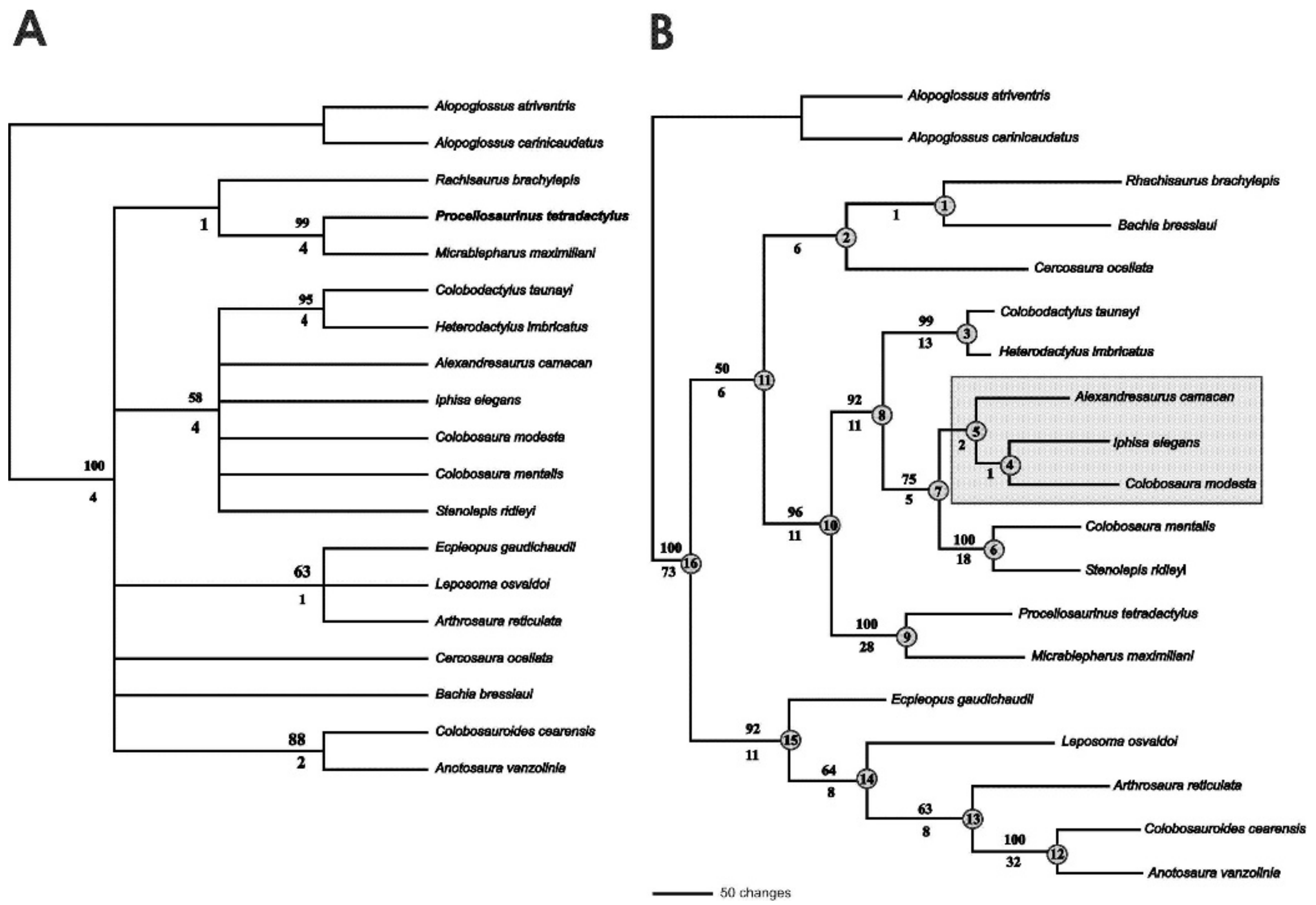

Fig. 6. Phylogenetic trees inferred from maximum parsimony analyses. (**A**) Strict consensus of 211 equally parsimonious trees estimated from morphology partition (L = 106; CI = 0.55; RI = 0.72). (**B**) Single most parsimonious tree recovered from analyses of combined morphology and molecular partitions (L = 2.740, CI = 0.47, RI = 0.43). The internal nodes are numbered (circles) and the partitioned Bremer support indexes are listed in appendix 4 for each node. Bootstrap support values (> 50%) and decay indexes are presented above and below branches, respectively. The inset includes *Alexandresaurus camacan* and its closest relatives.

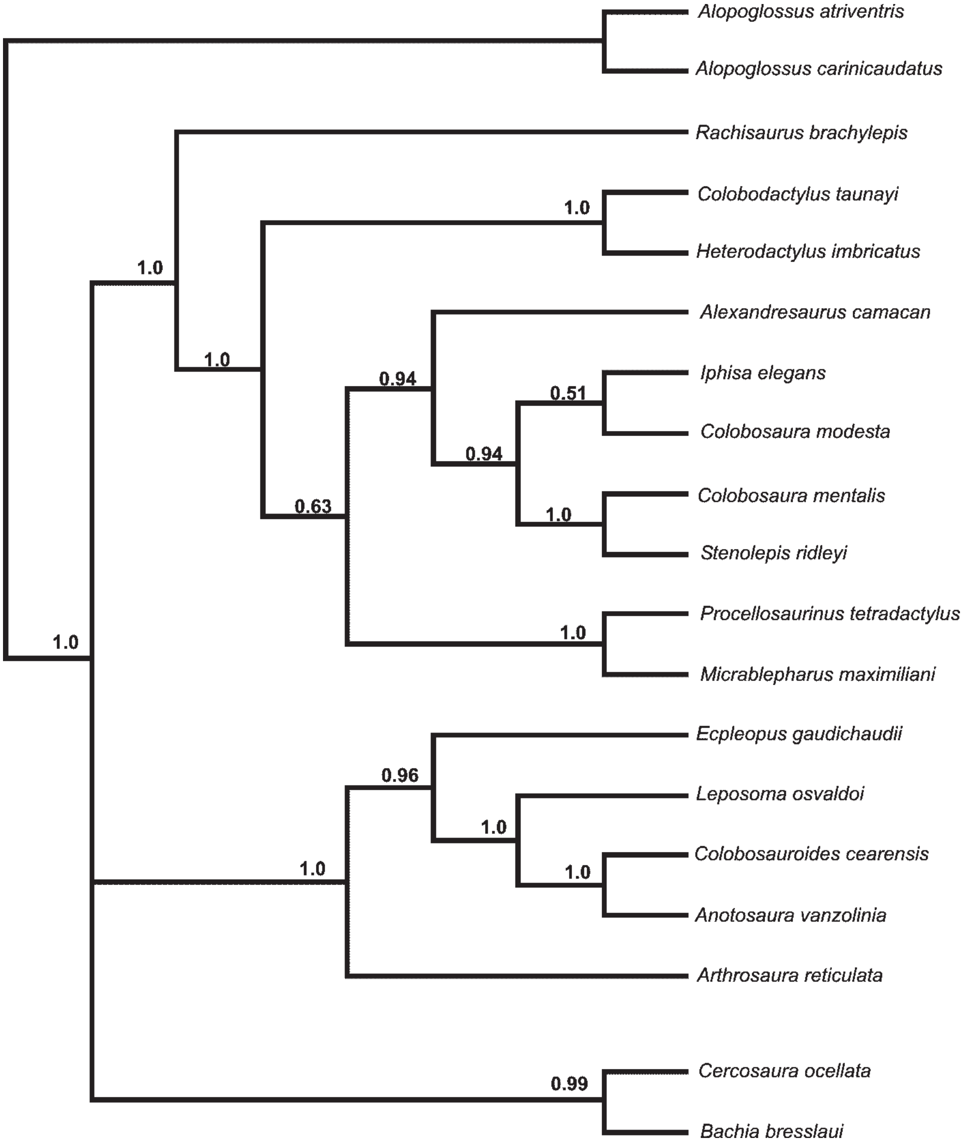

Fig. 7. Phylogenetic tree estimated under Bayesian method of the combined morphology and molecular data set and posterior probabilities (above nodes) for clades recovered at the 50% majority rule consensus topology.

single; prefrontals, frontoparietals, parietals, and interparietals present. Parietals longer than wide. Collar fold absent. Three pairs of genials and three supraoculars. Dorsal scales anteriorly smooth, large in the occipital region, becoming gradually elongated, lanceolate, and strongly keeled posteriorly. Occipitals present. Ventral scales quadrangular, in longitudinal but not in regularly transverse rows; laterally imbricate, irregular in size and shape, scales of external rows slightly wider. Males with continuous series of very conspicuous pores without gap between preanal and femoral; pores absent in females. Frontal bone anteriorly divided.

CONTENT: *Acratosaura mentalis*, new generic name for *Colobosaura mentalis* Amaral, 1933.

ETYMOLOGY: From the Greek *akratos*, meaning "unmixed, pure"; here intended to reflect its unmixed condition after being dismembered from the polyphyletic *Colobosaura*.

DISCUSSION

Our study provides evidence for the monophyly of the Heterodactylini and its sister relationship with Gymnophthalmini (nodes 8 and 10 respectively; fig. 6B). Castoe et al. (2004) admitted monophyly of Gymnophthalminae as proposed by Pellegrino et al. (2001), but removed their tribal arrangement. In contrast to Castoe et al. (2004), our parsimony analyses (MP) recover both the monophyly of the Heterodactylini and Gymnophthalmini (nodes 8 and 9; fig. 6) and their sister-group relationship (node 10; fig. 6B). The support for Heterodactylini monophyly, on the basis of combined analyses of molecular and morphological characters, is higher (BS = 96, Bremer value = 11) than that previously obtained using molecular data only (BS = 71, Bremer value = 2 in Pellegrino et al., 2001). The partitioned Bayesian analyses we performed here differently from Castoe et al. (2004), included 42 morphological characters. Agreeing with them, our analyses also recovered a paraphyletic Heterodactylini with respect to the Gymnophthalmini, but there is low support for such alternative topology (PP = 0.65). More extensive sampling of morphological and molecular characters is essential to confirm the result of our Bayesian analyses; these studies are in progress, but until they are complete we accept the tree topology recovered by MP analyses as the best hypothesis.

Monophyly of the Heterodactylini is reinforced by the unique condition of the shape of their interclavicle and the condition of their nasals (characters 25 and 34, appendix 1). The better support now obtained is due not only to the inclusion of morphological characters in this analysis but also to the addition of the genus *Stenolepis*, absent in the Pellegrino et al. (2001) study. Our results also indicate that the Heterodactylini consists of two strongly supported clades, and that morphological characters are the major contribution to each (appendix 4). One is the *Heterodactylus*-*Colobodactylus* assemblage; the other assembles all other Heterodactylini (respectively nodes 3 and 7, fig. 6B). This conclusion is supported by the condition of the supratemporal fenestra, the lateral expansion of the parietals, the postorbital width, shape of postfrontal, and the shape and size of parietal scale (characters 23, 31, 33, 35, 37 and 39; appendix 1). The assemblage *Colobodactylus*-*Heterodactylus* also differs from the remaining Heterodactylini by their more elongated body and degree of limb reduction (characters 17 and 21). The genera *Alexandresaurus, Colobosaura, Iphisa, Acratosaura*, and *Stenolepis* are also characterized by a strong sexual dichromatism absent in *Colobodactylus* and *Heterodactylus*. Reproductive males of all genera in the first clade exhibit a reddish venter and have a lateral color pattern consisting of cream, white, or yellowish blotches against a dark brown or black ground color, which is absent in females.

Alexandresaurus camacan was recovered as the sister group of the (*Iphisa elegans*-*Colobosaura modesta*) clade with weak support, and the partitioned Bremer index shows that the largest contribution to this relationship comes from morphology (node 5, fig. 6B, appendix 4). The present study also confirms the previously hypothesized inclusion of the genus *Stenolepis* within the Heterodactylini, in contrast to its affinities with *Tretioscincus* as suggested by Presch (1980). *Acratosaura* (*Colobosaura mentalis* in fig. 6B) is recovered as the sister group of *Stenolepis*, and this relationship received high support (BS = 100, Bremer value = 18).

Although our taxonomic sampling is limited with respect to total microteiid diversity and is focused primarily on the Heterodactylini, the monophyly of the Ecpleopini was also confirmed. Relationships among the genera are similar to those obtained by Pellegrino et al. (2001), except for the position of *Arthrosaura*, which was basal and here is recovered as the sister group to the (*Colobosauroides*-*Anotosaura*) clade (node 13; fig. 6B), with morphology making the second largest contribution to the partitioned Bremer index (node 13, appendix 4). In contrast to Pellegrino et al. (2001), Castoe et al. (2004)

recovered the Ecpleopini assemblage distantly related to Cercosaurini, which led them to raise the status of the former to subfamilial level. Our results confirm monophyly of the Ecpleopini with higher support than previously obtained (BS = 92, BS = 11 vs. BS = 75, BS = 6 in Pellegrino et al., 2001) and not related to Cercosaurini, a result consistent with the position suggested by Castoe et al. (2004).

In a different part of the tree, we recovered the Rhachisaurinae *Rhachisaurus brachylepis*, as nested with *Bachia* and *Cercosaura*, a result we regard as highly suspect. Pellegrino et al. (2001) recovered the Rhachisaurinae as the sister group of Gymnophthalminae, and appendix 4 shows that the strongest contribution for this relationship (node 1) comes from morphology, specifically from characters classically subject to convergence (see appendix 2). Further, because our taxonomic sampling of Cercosaurini is limited (of the 13 genera now accepted [Doan, 2003] only *Bachia* and *Cercosaura* are represented here), we prefer to keep the scheme adopted by Pellegrino et al. (2001) until more complete taxonomic sampling and additional data sets provide better resolved phylogenetic hypothesis upon which sound taxonomic decisions can be made.

Most of the Heterodactylini are restricted to eastern Brazil. The two species of *Colobodactylus* (*C. dalcyanus* and *C. taunayi*) are restricted to the Atlantic forest of southeastern Brazil (Vanzolini and Ramos, 1977). The genus *Heterodactylus* includes one species (*H. imbricatus*) occurring in the Atlantic forests of southern Brazil but extending into elevated areas in the mountains of the state of Minas Gerais, where the only other species (*H. lundi*) seems to be restricted. Apart from some records near the coast, the distribution of *Colobodactylus*-*Heterodactylus* appears to be restricted to mountainous terrain once covered by or influenced by the Atlantic Forest Domain (see Vanzolini and Ramos, 1977). Except for *Iphisa elegans* and *Colobosaura modesta*, the other genera of the Heterodactylini are also associated with Atlantic forest or contiguous elevated areas. *Alexandresaurus camacan* is restricted to the Atlantic forests of southern Bahia. *Stenolepis ridleyi* occurs in the Atlantic forest north of the Rio São Francisco, but its association with mountainous areas is evident because it also occurs in isolated remnant forests of the semiarid northeastern Brazil (for example, Serra de Baturité [1115 m altitude], state of Ceará, and Pico do Jabre [1044 m], state of Paraiba). *Acratosaura mentalis* has a larger but seemingly insularized distribution; it is known from some isolated areas in the Caatingas of northeastern Brazil, and elsewhere in the Serra do Espinhaço, a large mountain range reaching to 2,400 m in altitude that extends from the state of Minas Gerais to Bahia. *Colobosaura modesta* and *Iphisa elegans* are the only Heterodactylini not directly associated with mountains or Atlantic forests; the first is a typical Cerrado lizard occurring both in open areas and in gallery forests, and the second is restricted to Amazonian forests.

We are aware that the ideal approach to understand the historic biogeography of the heterodactyline should be based on a well-supported phylogenetic hypothesis derived from more extensive molecular and morphological character sampling than that now available. In our hypothesis, for example, it is evident that nodes 4, 5, and 7 need additional support. However, some considerations based on the present topology might be appropriate at this time and advanced as a preliminary working hypothesis to be tested by additional data.

Assuming the topology of figure 6B, an important point to note is the ancestral position of Atlantic forest forms compared to those from central Brazilian Cerrados (*Colobosaura modesta*) or Amazonia (*Iphisa elegans*). Another interesting issue suggested by the resulting topology is the insularized distribution of the older genera as originally hypothesized by Vanzolini and Ramos (1977). They hypothesized specifically that *Colobodactylus* and *Heterodactylus* were more widely distributed during colder episodes of the Quaternary, and are presently isolated in mountains or especially favorable areas. The occurrence of *Stenolepis ridleyi* in a forest refuge in northeastern Brazil also suggests a range contraction from times when the Atlantic forest extended more to the west than the present day distribution indicates. The sister relationship recovered between *Stenolepis ridleyi* and *Acratosaura mentalis* confirms this pattern. Although we did not have any previous idea of the relationships between entities grouped at node 7 (fig. 6B), in hindsight the recovery of *Stenolepis* and *Acratosaura* as sister species is not unexpected. This hypothesis is consistent with an emerging biogeographic pattern based on sister group relationships between Atlantic forest species and those occurring along the Serra do Espinhaço in other taxa (see for example Parrini et al. 1999). Third, why are *Iphisa elegans* and *Colobosaura modesta* so widespread compared to their relatives? Is their broad distribution across Amazonia and the Cerrados due, respectively, to recent origin and dispersal under favorable conditions?

To answer this last question we should have more data on divergence times for the species involved, particularly for those with currently isolated populations. Calibration of divergence times could also help us to understand another intriguing feature of the Heterodactylini radiation. The monophyletic assemblage formed by *Alexandresaurus, Iphisa, Colobosaura, Acratosaura,* and *Stenolepis* consists of monotypic genera, which is surprising when compared with other genera of Gymnophthalmidae occurring in the same areas. *Leposoma*, for example, is a much more speciose genus, and morphological differences between its species are slight, sometimes inconspicuous, contrasting with the strong morphological gaps we observe among the genera under study. In the latter, anteroposterior axes of differentiation affecting size, shape, and ornamentation of body scales are clearly observable. This suggests that developmental processes might be differentially associated with or contributing to speciation among these lineages.

Since the submission of this paper two highly distinctive new Heterodactylini were discovered from widely isolated mountains of eastern Brazil. Our initial observations of their tentative phylogenetic positions suggest that they support the primary split of this interesting radiation, and the biogeographic scenario outlined above. Considering the rate of habitat loss in Brazil and the high sensitivity of these lizards to deforestation, accelerated study is needed in order to understand better the interesting biological problems they present.

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APPENDIX 1

MORPHOLOGICAL CHARACTERS AND CHARACTER STATES USED FOR PHYLOGENETIC ANALYSES

External morphology and scalation:

1. External ear opening: (0) present; (1) absent
2. Ornamentation of head scales: (0) smooth; (1) rugose
3. Posterior margin of head scutes: (0) curved; (1) straight
4. Prefrontal scales: (0) present; (1) absent
5. Frontoparietal scales: (0) present; (1) absent
6. Superciliary scales: (0) four or more; (1) three or less
7. Number of temporal scales: (0) six or more; (1) four
8. Pairs of enlarged genials: (0) three; (1) two; (2) one
9. Size of interparietal scale: (0) reaching anteriorly the level of the parietal; (1) shorter
10. Anterior dorsal scales: (0) keeled; (1) smooth
11. Posterior dorsal scales: (0) keeled; (1) smooth
12. Shape of dorsal scales at midbody: (0) lanceolate; (1) quadrangular or slightly mucronate; (2) cycloid
13. Ventral scales: (0) strongly imbricate; (1) juxtaposed
14. Flank scales: (0) lanceolate, imbricate; (1) rectangular, smooth, imbricate; (2) quadrangular, juxtaposed; (3) cycloid
15. Collar: (0) absent; (1) present
16. Limbs: (0) normal, slender; (1) stout, compact; (2) reduced
17. Body form: (0) normal, 29 presacral vertebrae (pv.) or less; (1) elongate, more than 29 pv.
18. Eyelid: (0) present; (1) absent
19. Disc of lower eyelid: (0) divided; (1) single
20. Position of nostril: (0) in nasal border; (1) in center of nasal
21. Number of toes: (0) five, without reduction; (1) less than five
22. Interparietal scale: (0) present, large; (1) vestigial or absent
23. Parietal scale: (0) longer than wide; (1) short, as wide as long
24. Enlarged occipitals: (0) absent, (1) present

Osteology:

25. Interclavicle: (0) cross-shaped, with central area extremely enlarged, lateral processes large but pointed; (1) same, but lateral processes short, ending abruptly, not pointed; (2) cruciform, central area reduced and lateral processes extremely long and straight; (3) cruciform, central area reduced, lateral processes posteriorly oriented; (4) a longitudinal rod-shaped element, lateral processes absent; (5) transversal, clavicular, and sternal processes absent.
26. Sternal process of interclavicle: (0) long, reaching sternal fontanelle; (1) small, not reaching fontanelle.
27. Sternal fontanelle process: (0) absent; (1) present
28. Number of sternal ribs: (0) three; (1) two; (2) one
29. Glossohyal: (0) separated from basihyal; (1) fused
30. Second pair of ceratobranchials: (0) present; (1) absent
31. Supratemporal fenestra: (0) almost closed; (1) opened; (2) opened only posteriorly
32. Postorbital: (0) distinct; (1) fused to postfrontal
33. Postorbital width: (0) narrow; (1) wide
34. Nasals: (0) wide, almost parallel, in broad contact under and with premaxillary; (1) wide, divergent and in contact at midline but broadly separated anteriorly by the subtriangular lamina of premaxillary, in slight contact with premaxila; (2) separated by contact between frontal and premaxillary.
35. Supratemporal fenestra: (0) closed by parietal and postorbital; (1) opened
36. Clavicle: (0) wide, flattened anteriorly and enclosing a single fenestra; (1) simple, boomerang shaped, fenestra absent; (2) axe shaped anteriorly, fenestra absent
37. Postfrontal: (0) irregular, posteriorly wider and longer leaving opened the supratemporal fenestra; (1) triangular; (2) boomerang-shaped
38. Supratemporal: (0) angulose, extremely curved at the end; (1) slightly curved
39. Lateral expansions of parietal: (0) present; (1) absent.
40. Postorbital: (0) covers postfrontal; (1) covered by postfrontal; (2) contacts postfrontal without overlap
41. Premaxillary dorsal lamina: (0) wide, posteriorly triangular; (1) wide, posteriorly straight; (2) sub-triangular with end pointed toward but not reaching frontal; (3) large, subrectangular, contacting frontal.
42. Frontal: (0) normal; (1) anteriorly divided.

APPENDIX 2

Matrix of Morphological Characters

(Characters 1–42 are defined in appendix 1)

Species/Characters	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
Ingroup																					
Alexandresaurus camacan	0	0	0	0	0	1	0	1	0	1	0	0	0	1	0	0	0	0	1	0	0
Colobodactylus taunayi	0	0	0	1	0	1	0	1	0	1	0	0	0	0	0	0	1	0	1	0	1
Colobosaura mentalis	0	0	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	0	1	0	0
Colobosaura modesta	0	0	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	1	0	0
Heterodactylus imbricatus	1	0	0	1	1	1	0	1	?	1	0	0	0	0	0	0	1	0	1	0	1
Iphisa elegans	0	0	0	0	0	1	0	2	0	1	1	2	0	3	0	0	0	0	1	0	0
Stenolepis ridleyi	0	0	0	1	0	1	0	1	0	1	0	0	0	1	0	0	0	0	1	0	0
Selected taxa																					
Anotosaura vanzolinia	1	0	0	1	1	1	1	0	1	1	1	1	1	2	1	1	1	0	1	0	0
Arthrosaura reticulata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0
Bachia bresslaui	1	0	0	1	1	1	0	1	1	1	0	0	1	0	0	2	1	0	1	0	1
Cercosaura ocellata	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0
Colobosauroides cearensis	0	0	0	0	0	1	0	0	0	1	1	1	1	2	1	1	1	0	1	0	0
Ecpleopus gaudichaudii	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Leposoma osvaldoi	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Micrablepharus maximiliani	0	0	0	1	0	1	0	0	0	1	1	2	0	3	0	0	0	1	–	1	1
Procellosaurinus tetradactylus	0	0	0	0	0	1	0	0	0	1	1	2	0	3	0	0	0	1	–	1	1
Rhachisaurus brachylepis	1	0	0	0	1	0	0	0	0	1	1	1	1	2	0	0	1	0	1	1	1
Outgroup																					
Alopoglossus atriventris	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Alopoglossus carinicaudatus	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0

APPENDIX 2
(Continued)

Species/characters	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42
Ingroup																					
Alexandresaurus camacan	0	0	0	2	1	1	0	1	0	0	0	1	1	0	0	1	0	0	0	0	0
Colobodactylus taunayi	0	1	1	2	1	1	0	1	0	1	0	0	1	1	0	0	0	1	0	0	0
Colobosaura mentalis	0	0	1	2	1	1	0	1	0	0	0	1	1	0	0	1	0	0	0	0	1
Colobosaura modesta	0	0	1	2	1	1	0	1	0	0	0	1	1	0	0	1	0	0	0	0	0
Heterodactylus imbricatus	1	1	1	2	1	1	0	1	0	1	0	0	1	1	0	0	0	1	0	0	0
Iphisa elegans	0	0	1	2	1	1	0	1	0	0	0	1	1	0	0	1	0	0	0	0	0
Stenolepis ridleyi	0	0	1	2	1	1	0	1	0	0	0	1	1	0	0	1	0	0	0	0	0
Selected taxa																					
Anotosaura vanzolinia	0	0	0	4	0	0	1	0	1	2	1	1	0	0	0	?	0	0	?	1	0
Arthrosaura reticulata	0	0	0	1	0	0	0	0	1	0	0	1	0	0	0	1	0	0	1	0	0
Bachia bresslaui	0	0	0	0	0	0	2	0	0	0	0	1	0	0	2	2	0	0	1	0	0
Cercosaura ocellata	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	1	1	1	2	0
Colobosauroides cearensis	0	0	0	4	0	0	0	0	0	2	1	1	0	0	0	?	0	0	?	1	0
Ecpleopus gaudichaudii	0	0	0	1	0	0	0	0	1	0	0	1	0	0	0	1	0	0	1	1	0
Leposoma osvaldoi	0	0	0	1	0	0	0	0	1	0	0	1	0	0	0	1	1	0	1	1	0
Micrablepharus maximiliani	0	0	0	3	1	1	0	0	0	1	0	0	2	1	1	1	0	0	2	3	0
Procellosaurinus tetradactylus	0	0	0	3	1	1	0	0	0	1	0	0	2	1	1	2	0	0	2	3	0
Rhachisaurus brachylepis	0	0	0	3	1	1	0	0	0	1	0	0	0	1	2	1	1	1	0	2	0
Outgroup																					
Alopoglossus atriventris	0	0	0	0	0	0	0	0	0	0	1	1	2	0	0	?	1	0	?	2	0
Alopoglossus carinicaudatus	0	0	0	0	0	0	0	0	0	0	1	1	2	0	0	?	1	0	?	2	0

APPENDIX 3

Additional Specimens Examined

Alcohol. *Alopoglossus atriventris*: MZUSP 13922–24. Estiron, Rio Ampiyacu, Peru. *Alopoglossus carinicaudatus*: MZUSP 53683–84. Cachoeira do Limão, Rio Tapajós, Pará. *Anotosaura vanzolinia*: MZUSP 47754, Serra Negra, Inajá, Pernambuco; MZUSP 60773, 60775–77, 60780–85, Cabaceiras, Paraiba; MZUSP 80151, Xingó, Alagoas. *Arthrosaura reticulata*: MZUSP 82644–46 Aripuanã, Mato Grosso. *Bachia bresslaui*: MZUSP 10300. Utiarití, Mato Grosso. *Cercosaura ocellata*: MZUSP 82425–27 Juruena, Mato Grosso. *Colobodactylus taunayi*: MZUSP 91446–48 Pinhalão, Paraná. *Colobosaura mentalis*: MZUSP 56933, Grão Mogol, Minas Gerais. *Colobosaura modesta*: MZUSP 81346–62, Caldas Novas, Goiás. *Colobosauroides carvalhoi*: MZUSP 89453, Parque Nacional da Serra da Capivara, Piauí. *Colobosauroides cearensis*: 87580–83, Mulungú, Ceará. *Ecpleopus gaudichaudii*: MZUSP 78975, 79559, Caraguatatuba, and MZUSP 81401, Ariri, São Paulo. *Heterodactylus imbricatus*: MZUSP 89185–86, Parque Estadual da Cantareira (Núcleo Pedra Grande), São Paulo; MZUSP 3309 Santa Bárbara, Serra do Caraça, Minas Gerais. *Iphisa elegans*: MZUSP 82654–76, Aripuanã, Mato Grosso. *Leposoma osvaldoi*: MZUSP 8270–37, Aripuanã, Mato Grosso. *Micrablepharus maximiliani*: MZUSP 50172–74, Exú, Pernambuco. *Procellosaurinus tetradactylus*: MZUSP 71598–604, Alagoado, Bahia. *Rhachisaurus brachylepis*: MZUSP 54897, 54898, Serra do Cipó, Minas Gerais. *Stenolepis ridleyi*: MZUSP 78724, Mulungú (Sitio Lorena), Ceará.

Cleared and stained. *Alopoglossus atriventris*: MZUSP 13922, Peru, Loreto, Rio Ampiyacu. *Alopoglossus carinicaudatus*: MZUSP 67488, 79544, no further data. *Anotosaura vanzolinia*: MZUSP 60772, 93417, 93418, Cabaceiras, Paraíba. *Arthrosaura kocki*: MZUSP 82951 Vila Rica, Mato Grosso. *Arthrosaura reticulata*: MZUSP 52504, no further data. *Bachia bresslaui*: MZUSP 93419, Brasília, Distrito Federal. *Cercosaura ocellata*: MZUSP 79556, Chapada dos Guimarães, Mato Grosso. *Colobodactylus taunayi*: MZUSP 94254, Salesópolis, São Paulo. *Colobosaura mentalis*: MZUSP 79557, Maracás Bahia; MZUSP 66231, Cabaceiras, Paraíba; MNRJ 9968, no further data. *Colobosaura modesta*: MZUSP 93420, Serra da Mesa, Goiás. *Colobosauroides cearensis*: MZUSP 79595, 93421, Serra de Baturité, Ceará. *Ecpleopus gaudichaudii*: MZUSP 79558–59, 93424, 93425, no further data. *Heterodactylus imbricatus*: MZUSP 79562, no further data; MZUSP 94255, Caucaia, Ibiúna, São Paulo. *Iphisa elegans*: MZUSP 82654, 82658, Aripuanã, Mato Grosso. *Leposoma osvaldoi*: MZUSP 93426, UHE Samuel, Rondônia. *Leposoma scincoides*: MZUSP 79564-65, no further data. *Micrablepharus maximiliani*: MZUSP 66233, João Pessoa, Paraíba; MZUSP 79589-91, no further data. *Procellosaurinus erythrocercus*: MZUSP 74935, 74942, Ibiraba, Bahia. *Rhachisaurus brachylepis*: MZUSP 55533, Serra do Cipó, Minas Gerais. *Stenolepis ridleyi*: MZUSP 66049, Serra dos Cavalos, Pernambuco.

APPENDIX 4

MEASURES OF SUPPORT FOR ALL INTERNAL NODES OF MOST PARSIMONIOUS TREE RECOVERED FROM COMBINED ANALYSIS OF MORPHOLOGY (MORPH) AND MOLECULAR PARTITIONS (fig. 6)

Columns present the bootstraps proportions, total and partitioned Bremer values; positive and negative partitioned values indicate support for a given relationship in the combined analysis over the alternative relationship in separate analyses, and contradictory evidence for a particular relationship in the combined analysis, respectively. Zero score indicates the indifference of a given data set at a specific node (Baker and DeSalle, 1997; Gatesy and Arctander, 2000). Node # 5, highlighted in bold, present the support for the relationship between *Alexandresaurus camacan* and its closest relatives (see fig. 6).

Node #	Bootstrap support	Bremer support	Partitioned Bremer					
			12S	16S	ND4	18S	c–mos	morph
1	< 50	1	1.5	0.5	−5.0	−2.0	1.0	5.0
2	< 50	6	−0.8	4.2	2.2	−1.5	1.8	0.0
3	99	13	1.3	4.0	−0.3	0.0	3.0	5.0
4	< 50	1	3.0	−0.5	−3.5	−1.0	0.5	2.5
5	**< 50**	**2**	**2.0**	**0.5**	**−2.5**	**−1.0**	**0.5**	**2.5**
6	100	18	7.0	1.0	6.0	1.0	3.0	0.0
7	75	5	−3.0	−1.0	3.0	0.0	3.0	3.0
8	92	11	1.0	0.5	5.0	−1.0	−1.0	6.5
9	100	28	2.5	3.0	6.5	−2.0	12	6.0
10	96	11	1.0	5.3	−5.3	−1.7	7.7	4.0
11	50	6	0.0	2.5	1.0	−0.5	1.5	1.5
12	100	32	7.0	4.0	4.0	−2.0	1.0	18
13	62	8	−8.0	−1.0	14.8	−1.5	0.8	3.0
14	64	8	−8.0	−1.0	14.8	−1.5	0.8	3.0
15	92	11	−6.0	0.5	13	−1.0	2.0	2.5
16	100	73	0.0	16	20	2.0	28	7.0

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