

Description and Phylogenetic Relationships of a New Genus and Species of Lizard (Squamata, Gymnophthalmidae) from the Amazonian Rainforest of Northern Brazil

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ABSTRACT

Marinussaurus curupira, a new genus and species of Gymnophthalmidae lizard is described from Iranduba, state of Amazonas, Brazil. The genus is characterized by an elongate body; short and stout pentadactyl limbs; all digits clawed; single frontonasal; two prefrontals; absence of frontoparietals; interparietal and parietals forming a straight posterior margin, with interparietal shorter than parietals; distinctive ear opening and eyelid; few temporals; three pairs of chin shields; nasal divided; a distinct collar; smooth, mainly hexagonal, dorsal scales; smooth quadrangular ventral scales; two preloacal and three femoral pores on each side in males; pores between three or four scales. Parsimony (PAR) and partitioned Bayesian (BA) phylogenetic analyses with morphological and molecular data recovered the new genus as a member of the Eclepoderini radiation of the Cercosaurinae. A close relationship of the new genus with *Arthrosaura* is postulated.

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INTRODUCTION

Convergence in many morphological characters in different lineages of the lizard family Gymnophthalmidae, also broadly known as microteiids, has yielded a rather complicated taxonomy to the group. Characters such as head scales, degree of body elongation and limb development, presence or absence of eyelid, and external ear opening are commonly used to define many gymnophthalmid genera, but have proven to be convergent with the “way of life” of these lizards (Presch, 1980; Rodrigues et al., 2007). Although useful for systematic purposes, such characters should be carefully evaluated before conclusions on relationships could be made. On the other hand, difficulty in collecting some of the species, either because they are rare or secretive, limits the availability of material for detailed studies on morphology (e.g., hemipenis and osteology) and on molecular phylogenetics (tissues).

Recent molecular analyses have shed light on the relationships among gymnophthalmid genera and species, and on their evolution (Pellegrino et al., 2001; Castoe et al., 2004; Doan and Castoe 2005; Kohlsdorf and Wagner, 2006, Kohlsdorf et al., 2010). However, despite major improvements in the knowledge of relationships, geographic distribution, variation, ecology, and evolution of microteiids, several aspects of their systematics remain controversial. New species are still found on a regular basis (e.g., Ávila-Pires, 1995; Ávila-Pires and Vitt, 1998; Köhler et al., 2004; Kok, 2005, 2009; Rivas et al., 2005; Rodrigues and Ávila-Pires, 2005), whereas some are so peculiar that generic placement is not always an easy task (Harris and Rueda, 1985; Rodrigues et al., 2005; Kok, 2009). As a result, new genera are commonly described to accommodate single species (Myers and Donnelly, 2001; Kok, 2005, 2009; Rodrigues et al., 2005, 2007, 2009; Rodrigues and Santos, 2008), rendering a rather large number of monotypic taxa within the family.

During a revisionary study of the gymnophthalmid lizard *Ptychoglossus brevifrontalis* Boulenger, 1912, the senior author examined two misidentified specimens collected at Iranduba, state of Amazonas, Brazil. These specimens are superficially similar to *Anotosaura* and *Dryadosaura*, but we were unable to promptly identify or associate them to any of the microteiid genera currently recognized. After detailed examination and comparison with several microteiid genera, coupled with phylogenetic analyses of morphological and molecular data, we concluded that a new species and a new genus should be proposed to accommodate these specimens. Here, the new genus and species are named, described and associated with the Ecleopodini (sensu Pellegrino et al., 2001; Rodrigues et al., 2005, but see Rodrigues et al., 2009, for corrected spelling of “Ecleopini”).

MATERIAL AND METHODS

DESCRIPTIVE METHODS

Specimens used in the description or examined for comparison are housed in the following institutions: Instituto Nacional de Pesquisas da Amazônia, Amazonas, Brazil (INPA), Museu Paraense Emílio Goeldi, Pará, Brazil (MPEG), Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil (MZUSP), Smithsonian Institution, National Museum of Natural History, Washington, D.C. (USNM). List of the material examined is in appendix 1.

We measured **SVL** (snout-vent length; measured from the tip of the snout to vent); **TL** (tail length; from vent to the tip of the tail); **HL** (head length; from the tip of the snout to the anterior margin of the tympanum); **HW** (head width; measured on the widest portion of the head); **NL** (neck length; from posterior margin of tympanum to anterior margin of arm insertion); **FLL** (forelimb length; from arm insertion to tip of finger IV); **HLL** (hind limb length; from inguinal region to tip of toe IV); **DBM** (distance between members; from posterior margin of arm insertion to anterior margin of hind limb insertion). All measurements were taken with an electronic caliper under a stereomicroscope (to the nearest 0.1 mm), except for SVL, taken with naked eye, and TL, taken with a measuring tape (to the nearest 1.0 mm). Scale counts and general observations on scale morphology and shape were made with the aid of a stereomicroscope. Scale terminology follows Harris (1994) and Ávila-Pires (1995). Drawings were made with a drawing tube attached to a Zeiss stereomicroscope. Sex was determined by presence or absence of hemipenis, checked through a ventral incision at the base of the tail.

PHYLOGENETIC ANALYSES

In an attempt to retrieve the phylogenetic placement of the new taxon we studied members of selected taxa of most Gymnophthalmidae subfamilies and tribes as recognized by Pellegrino et al. (2001) and Rodrigues et al. (2005). We included several members of the Ecleopodini because we suspected, on the basis of morphological characters, that the new taxon is a member of that tribe. Terminals were the same used in Rodrigues et al. (2005), except for the absence of *Rhachisaurus brachylepis* Dixon, 1974 (Rhachisaurinae) and the addition of the Teiidae *Cnemidophorus ocellifer* (Spix, 1825), which was used as an outgroup. Because coding for morphological characters was not available for *Cnemidophorus*, two species of *Alopoglossus* were assigned as outgroups in the separate analysis of the morphological partition.

Sequences from three mitochondrial (12S, 16S, ND4: 1500 bp) and two nuclear (*c-mos* and 18S: 838 bp) gene regions were used to build the molecular data set. DNA sequences used were those of Pellegrino et al. (2001) with the addition of all sequences for the new taxon herein described (GenBank accession numbers JF690971–75). The molecular data set is composed of 2338 base pairs (bp) of aligned sequences. Minor adjustments on the original Rodrigues et al. (2005) alignments were performed manually on the reduced matrix used here to accommodate the new sequences and exclude unnecessary gaps. The morphological data set is the same used in Rodrigues et al. (2005), with minor adjustments, and is listed in appendices 2 (data matrix) and 3 (coding).

First we conducted separate analyses on the morphological and molecular partitions followed by a combined analysis under equally weighted parsimony (PAR) in PAUP* v4.0b10 (Swofford, 2002).

For a matrix of 37 morphological characters (appendix 2), with all character states coded as unordered and all transformations equally weighted, a search with the branch-and-bound algorithm was implemented. For the PAR analysis of the combined data sets (total of 2375 characters), a heuristic search with 10,000 replicates of random-addition sequences (RAS) and

tree-bisection and reconnection (TBR) branch swapping was implemented.

Nodal support was estimated by nonparametric bootstrapping (BS; Felsenstein, 1985) with 10,000 random stepwise additions per bootstrap pseudoreplicate, and TBR branch swapping, in both branch-and-bound (morphology) and heuristic (molecular only and combined data sets) searches. Bootstrap values greater than 70% were considered as strong support for a node (Hillis and Bull, 1993; with caveats). We also calculated total Goodman-Bremer support values (GBS; Goodman et al., 1982; Bremer, 1988; Grant and Kluge, 2008) for all nodes on the total evidence and morphology partitions using TreeRoot v. 2.0 (Sorenson, 1999).

Bayesian analyses (BA) were performed on the combined, molecular and morphological, partition. Best-fit models of nucleotide substitution for each molecular partition using hierarchical likelihood ratio tests were selected using MrModeltest v.2.2 (Nylander, 2004): 12S, 16S and ND4 (GTR+I+ Γ), 18S (JC) and c-mos (SYM+ Γ). The partitioned Bayesian analysis was implemented in MrBayes 3.1.1 (Huelsenbeck and Ronquist, 2001) under the models of substitution for each gene region and morphological data set as "standard." Two independent runs with 4,000,000 generations, four chains and trees sampled at intervals of 100 generations, were implemented. Trees prior to stationary (10,000 trees) were discarded as "burn-in" and a 50% majority-rule consensus tree was obtained from 39,900 data points. Nodes with posterior probability (PP values) ≥ 0.95 derived from both runs were considered as evidence of significant support for a given clade.

RESULTS

TAXONOMY

Marinussaurus, new genus

Gymnophthalmidae, Cercosaurinae, Ecleopodini

DIAGNOSIS: A medium-sized Gymnophthalmidae with robust head, elongate body, well-developed pentadactyl limbs, and tail distinctly longer than body. Frontonasal single; two prefrontals; frontal large; frontoparietals absent; interparietal and parietals present, forming an almost straight line posteriorly; nasals divided; loreal and frenocular present; few temporals; three pairs of chin shields, none reaching oral border. Dorsal scales hexagonal, longer than wide, with angulate to nearly round posterior margin, smooth, imbricate. Lateral scales narrower than dorsals, laterally imbricate, with round or straight posterior margin. Ventral scales quadrangular, slightly imbricate, smooth. Preloacal and femoral pores present in males (females unknown); pores between three or four small scales.

CONTENT: Currently monotypic, the only known species, *Marinussaurus curupira*, sp. nov., is described below and therefore designated type-species of the genus.

ETYMOLOGY: The generic name *Marinussaurus* is given in honor of Marinus S. Hoogmoed, for his great contribution to the knowledge of the Amazonian fauna, for his friendship, and eternal willingness to teach. The genus is male in gender.

Marinussaurus curupira, new species.

Figures 1-3, 4A; table 1

HOLOTYPE: INPA 19855 (Field Number, Ponte 73; fig. 1); adult male, collected at “Ramal km 27,” Iranduba, state of Amazonas, Brazil (no coordinates available), on August 30, 2007, by V.T. Carvalho.

PARATYPE: INPA 19856 (Field Number, Ponte 41; figs. 2, 3); adult male, collected at Sítio Bom Lugar (Renato Cintra), Iranduba, Amazonas, Brazil (3°07'00"S; 60°19'01"W), on August 27, 2007, by V.T. Carvalho.



FIG. 1. *Marinussaurus curupira*, in life, INPA 19856 (paratype). SVL = 56.2 mm. Photo by V.T. Carvalho.

DIAGNOSIS: The same as generic definition plus the following additions: Maximum SVL (considering the two known specimens) 56.2 mm. Limbs relatively short and robust; all digits clawed. Three supraoculars; interparietal shorter than parietals; five occipitals of nearly the same size; few temporals (5–6); loreal large, in contact with supralabials, frenocular small; third pair of chin shields with a short medial contact, almost totally separated by two enlarged preangular scales, and in contact with fourth and fifth infralabials. It is further characterized by having 29 transverse rows of hexagonal, slightly imbricate, smooth dorsal scales between interparietal and posterior level of hind limbs; 20 transverse rows of quadrangular, slightly imbricate, smooth ventrals

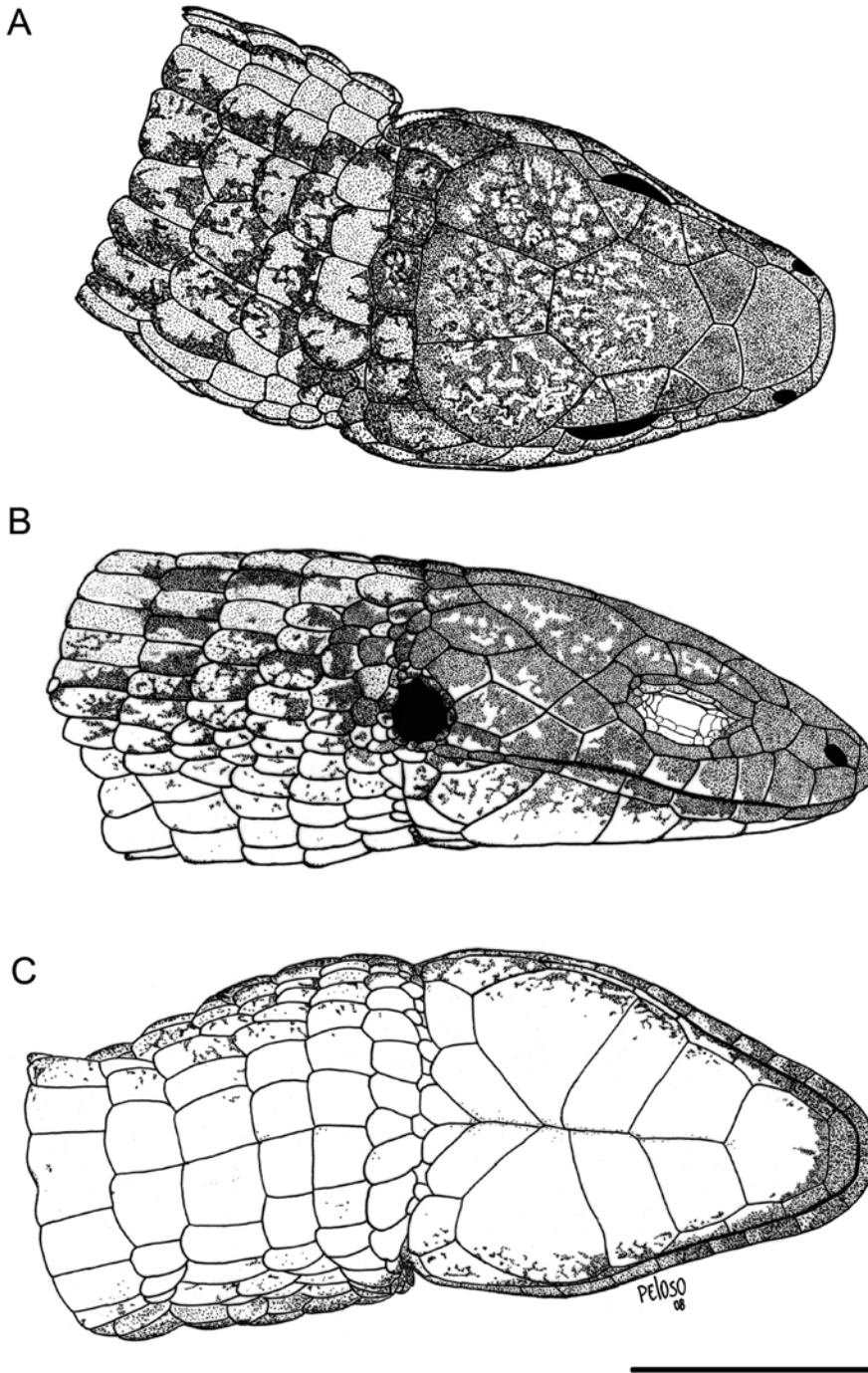


FIG. 2. *Marinussaurus curupira*, INPA 19855 (holotype). Drawings of A, dorsal, B, lateral, and C, ventral views of the head. Scale bar = 5 mm.

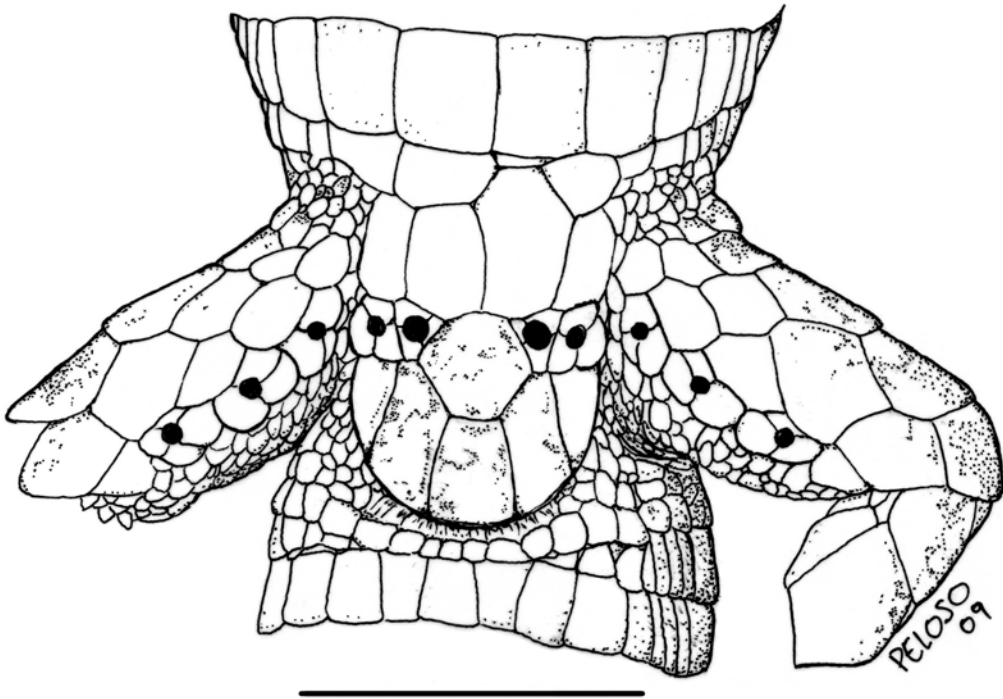


FIG. 3. *Marinussaurus curupira*, INPA 19856 (paratype). Drawing of the pericloacal region showing cloacal plate, preloacal and femoral pores. Scale bar = 5 mm.

between collar and preanals; 30–31 scales around midbody; three femoral pores and two preanal pores on each side in males (females unknown); preanal pores separated medially by the anterior preanal scale; preanal plate formed by an enlarged anterior, and five posterior scales; 7–8 lamellae under fourth finger, some divided, and 13 under fourth toe, all divided.

DESCRIPTION OF THE HOLOTYPE INPA 19855 [conspicuous differences observed in the paratype, INPA 19856, given between brackets]: A male, snout-vent length 52.1 mm [56.2 mm], tail length 60 mm [36 mm, of which 11 mm of original tail, the remaining 25 mm regenerated], round in cross section, tapering toward the tip; limbs well developed, but relatively small in relation to the body; neck as wide as body, which is slightly depressed. All measurements are given in table 1.

Rostral hexagonal, about 2.5 times as wide as high, in contact with first supralabials, nasals and frontonasal. Frontonasal pentagonal [heptagonal], slightly wider than long, in broad contact with rostral, nasals, and prefrontals, and in narrow contact with loreal. Prefrontals pentagonal, nearly as long as wide, in contact medially, with the frontonasal anteriorly, the loreal anterolaterally, the first supraocular posterolaterally, and the frontal posteriorly; the left prefrontal in point contact with the second supraocular, separating the first supraocular and the

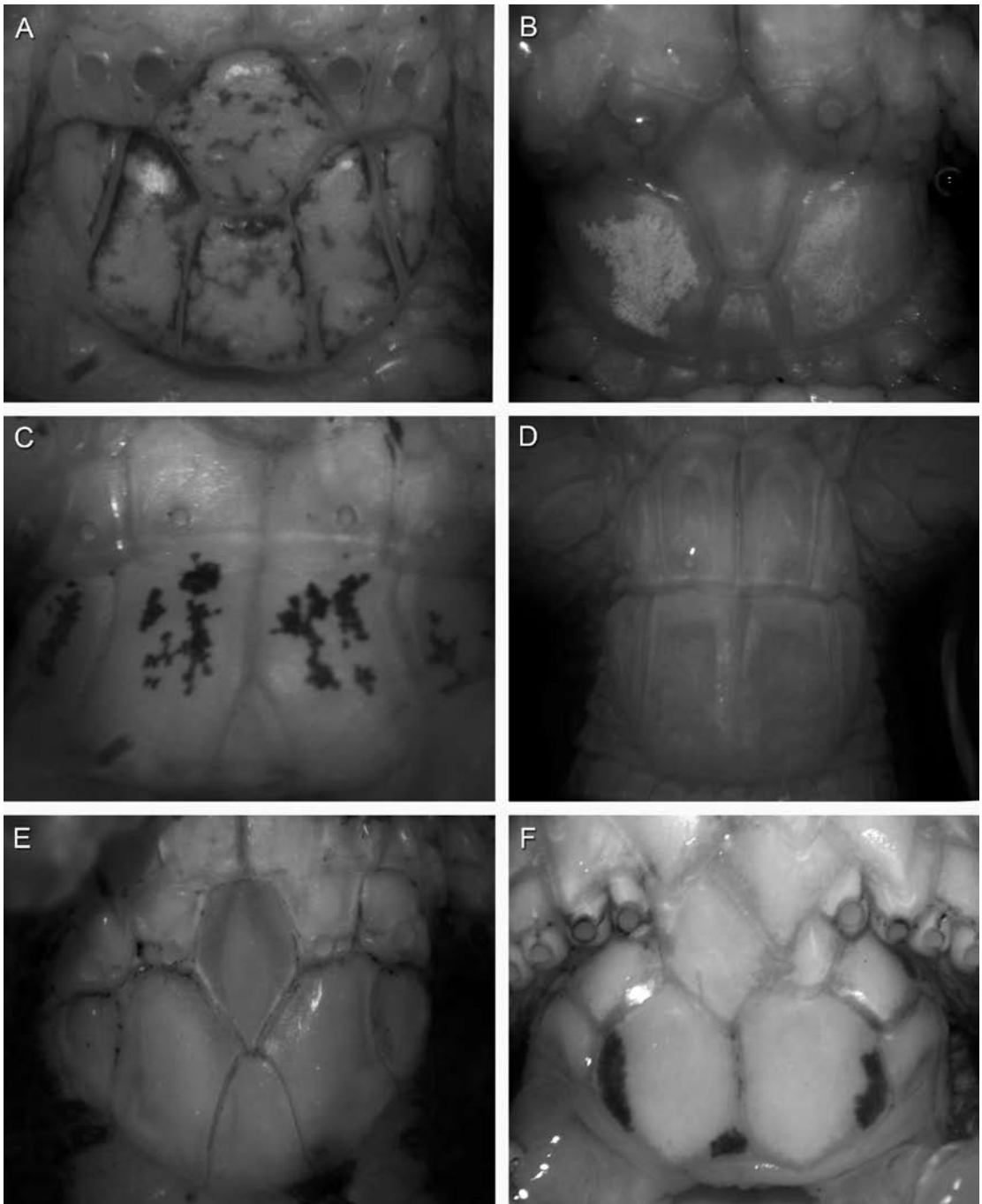


FIG. 4. Intergeneric variation of cloacal plate scales and precloacal pores: **A**, *Marimussaurus curupira*, INPA 19856; **B**, *Arthrosaura reticulata*, MPEG 19181; **C**, *Colobosauroides cearensis*, uncatalogued specimen from MPEG; **D**, *Dryadosaura nordestina*, MPEG 27738; **E**, *Amapasaurus tetradactylus*, MPEG 27370; **F**, *Alopoglossus angulatus*, MPEG 24372, a basal Gymnophthalmidae.

TABLE 1. Measurements and differences in scale counts in the two known specimens of *Marinussaurus curupira*^a

	<i>INPA 19855</i> (<i>Holotype</i>)	<i>INPA 19856</i> (<i>Paratype</i>)
Snout-vent length	52.1	56.2
Head length	9.3	10.1
Head width	7.1	7.6
Head height	5.4	5.5
Distance between members	26.6	31.7
Arm length	5.2	4.0
Forearm length	3.8	3.6
Hand length	4.8	4.4
Femur	5.4	6.0
Tibia length	5.5	5.7
Foot length	8.4	7.4
Supraciliaries	3/2	4/3
Temporals	5/6	6/6
Scales around midbody	30	31
Lamellae under fourth finger	8/8	7/7

^aDifferences in count within sides of the same specimen are given as left counts/right counts.

frontal, while on the right side these four scales touch each other [both prefrontals are in short contact with the second supraocular]. Medial contact between prefrontals shorter than that with loreal [about as wide as suture with loreal]. Frontal heptagonal, 1.1–1.2 times longer than wide, slightly wider posteriorly; in broad contact with second supraoculars and in narrow contact with third supraoculars (plus a point contact with first supraocular only on the right side of the holotype); posteriorly in contact with parietal and interparietals. Frontoparietals absent. Interparietal trapezoid, wider posteriorly. Parietals longer than interparietal, each in contact with frontal, third supraocular, postocular, two temporals and two occipitals. Interparietal and parietals form an almost straight line posteriorly, where they are in contact with five subequal occipitals (medial one slightly wider [not]).

Supraoculars three; first smallest, laterally in narrow contact with loreal and in contact with first supraciliary [left side in contact with first and second supraciliaries]; second supraocular largest, laterally in contact with first, second and third [second, third and fourth] (left side) or first and second [first, second and third] (right side) supraciliaries. Three [four] supraciliaries on the left side, two [three] on the right side; on both sides first supraciliary wider anteriorly and the longest, in broad contact with loreal [first supraciliary squarish on left side; elongate

and partially fused with loreal on right side]; posterior supraciliary also elongate, longer than second (when present), which is small. Nasal roughly rectangular, almost twice as long as high, divided medially by an oblique suture; in contact with rostral, frontonasal, loreal, and first and second supralabials; nostril on the lower half of the nasal suture. Loreal large, roughly pentagonal, as high as nasal, in contact with nasal, second and third supralabials, frenocular, a preocular, first supraciliary, first supraocular, prefrontal, and frontonasal. Frenocular small, quadrangular, slightly longer than high, in contact with third and fourth supralabials, anterior subocular, preocular, and loreal. It is followed posteriorly by a series of three suboculars; second longest, in contact ventrally with fourth, fifth, and sixth supralabials. A pentagonal, posteriorly pointed, postocular. Lower eyelid with a semitransparent, undivided disc. Seven supralabials, fifth below center of eye, second and sixth the highest, sixth and seventh [seventh] the longest. Five (left) or six (right) relatively large, polygonal temporals [six on both sides]. Three upper ones in contact dorsally with postocular (anterior one), parietal (the other two), and lateral occipital (posterior one). The remaining two or three temporals border the ear opening; the lowest border ventrally a small postinfralabial, which also reaches the ear-opening border. Tympanum shortly recessed.

Mental trapezoid, round anteriorly, wider than long. Postmental pentagonal, laterally in contact with first and second infralabials. Three pairs of enlarged chin shields, first and second in broad contact medially; third pair in narrow contact medially [separated by a short contact between second chin shields and pregonals]; all chin shields in contact with infralabials. Posterior chin shields in contact with three large scales, lateral and medial ones obliquely elongate, which are separated from gonals by a row of small irregularly shaped scales. Six infralabials of nearly the same length, suture between third and fourth approximately below center of eye; they are followed by two [one on the right side] smaller postinfralabials that reach the border of the ear opening. All scales on head smooth, juxtaposed, except for occipitals, which imbricate over postoccipitals.

Four roughly quadrangular, smooth, imbricate postoccipitals, slightly larger than occipitals. Posterior head scales become progressively longer than wide, grading into dorsals. Sides of neck with smooth, mostly rectangular, longer than wide, imbricate scales, in transverse rows that continues dorsally, with some extra scales in between some of the rows. Gonals in six well-defined transverse rows of rectangular (more rounded and irregular on the anterior row), imbricate, smooth scales, which become slightly larger posteriorly and wider medially. Posterior row of gonals forming a collar composed of seven scales, the medial one widest [not].

Dorsal scales imbricate, smooth, in 28/29 (because of a discontinuity on anterior rows) [29] transverse rows between interparietal and posterior level of hind limbs; anterior scales shorter, wider, roughly squared, becoming gradually longer, narrower, hexagonal, with angular to nearly round posterior margins. Toward the sides, scales become narrower and rectangular (except for small areas around arm insertion and near groin, where scales are small, flat, smooth, and juxtaposed). Ventrals smooth, slightly imbricate, in transverse rows; rectangular, only slightly longer than wide toward the midline, narrower toward the sides; lateralmost row as narrow as lateral dorsals and partially covered by them; in 20 transverse rows between collar and preanals, and 10 longitudinal rows. Thirty [31] scales around midbody. Two preanal and

three femoral pores on each side, each pore surrounded by 3-4 scales (figs. 3, 4A); preanal pores separated from femoral pores by a gap, and medially by the anterior scale of the preanal plate. Preanal plate with a hexagonal, large anterior scale and five posterior scales, medial widest.

Scales on tail rectangular, smaller than dorsals, smooth, slightly imbricate; they form complete rings around the tail, with ventral scales wider than dorsals.

Scales on forelimbs large, polygonal (mostly rhomboid on upper arms), smooth, imbricate in dorsal view, distinctly smaller in anterior view, and intermediate in size in posterior view. Scales on hind limbs variably polygonal, smooth, imbricate on ventral (except for pore scales), anterior and dorsal views of thigh and on lower leg; they are largest in anterior view of thigh. Scales small, imbricate, in posterior view of thigh. Carpal and tarsal scales large, imbricate; supradigital lamellae on digits smooth, imbricate. Palmar and plantar surfaces with smooth, small granules; most infradigital lamellae divided medially, eight [seven] on finger IV and 13 on toe IV on each side. Fingers and toes clawed, with the following relative sizes: finger $I < V < II < IV < III$; toe $I = V < II < III < IV$.

COLOR PATTERN IN PRESERVATIVE: Dorsal surface of INPA 19855 dark brown with lighter spots on top of head and four (two paravertebral, two dorsolateral) tan longitudinal bands on back (with irregular margins), and flanks predominantly tan, with irregular dark-brown spots. INPA 19856 predominantly dark brown dorsally, with only an inconspicuous dorsolateral red-brown band on back; ventralmost scales on flanks predominantly tan. Limbs predominantly dark brown dorsally in both specimens. Pattern of tail similar to dorsum, but the longitudinal bands in INPA 19855 become more irregular and turn into irregular spots at some distance from the base of the tail. Ventral region cream, except for palms, soles, and tip of tail, which are grey or brown, partially mottled with cream.

DISTRIBUTION: Known only from the type locality, located a few km W of the intersection of the Rio Negro and Rio Amazonas/Solimões (fig. 5).

ETYMOLOGY: The specific name is given after the Curupira, a mythological creature known from many regions in South America (e.g., Brazil, Argentina, Chile, Paraguay, and Uruguay). The most common versions of the legend regard the Curupira as an anthropomorphic creature of short height, with dark skin and with the feet pointed backward. The Curupira protects the forest and its inhabitants, severely punishing those who hunt for pleasure or who kill breeding females or defenseless juveniles. In the Amazonian region of Brazil the legend is vivid in the minds of people of riverside communities and the Curupira is sometimes much feared. The Curupira is also known as Curupi (in Argentina). For a comprehensive review of the Curupira legend we refer the reader to Pereira (1994).

COMPARISONS: In an attempt to properly place the new taxon among extant genera of the Gymnophthalmidae, we surveyed external morphological features of selected genera and species representing all major radiations of the family. General morphology of *Marinussaurus curupira* closely resembles that of *Anotosaura* spp., *Dryadosaura nordestina* Rodrigues et al., 2005, and to a lesser extent *Colobosauroides* spp. (all members of the tribe Ecleopodini, *sensu* Pellegrino et al., 2001; Rodrigues et al., 2005). Closer resemblance is found between the new taxon and *Dryadosaura*. Our phylogenetic analyses partially corroborate this view, recovering the new lizard



FIG. 5. Maps of northern Brazil showing the type locality (star) of *Marinussaurus curupira*.

within the Ecleopodini radiation, although a sister relationship with *Dryadosaura* is not supported. Therefore, we restrict our comparisons with the Ecleopodini and with few selected taxa of the Gymnophthalmidae that share some morphological features with the new species.

The new taxon is easily distinguished from *Anotosaura* by having a distinct ear opening (absent in *Anotosaura*). It is distinguished from *Colobosauroides* by the absence of frontoparietals (present in *Colobosauroides*), and by the size of the interparietal, shorter than parietals in *Marinussaurus* (as long as or longer than parietals in *Colobosauroides*). *Marinussaurus* differ from *Dryadosaura* by the presence of three pairs of chin shields (two pairs in *Dryadosaura*). The new genus also differs from *Anotosaura*, *Colobosauroides*, and *Dryadosaura* by having distinctive preloacal pore morphology. The preloacal pores of *Marinussaurus* (figs. 3 and 4A) are relatively large and arranged between three to four scales (pores relatively smaller and arranged in a single larger scale in *Anotosaura*, *Colobosauroides* [fig. 4C], and *Dryadosaura* [fig. 4D]).

Among the remaining ecleopodines, *Marinussaurus* differs from *Amapasaurus*,⁶ *Arthrosaura*, and *Leposoma* by the absence of frontoparietals (present in *Amapasaurus*, *Arthrosaura*,

and *Leposoma*), by having smooth ventrals (keeled in *Amapasaurus*, *Arthrosaura*, and *Leposoma*), and smooth head scales (usually ornamented by rugosities in *Amapasaurus* and *Leposoma*; smooth in *Arthrosaura*). From *Arthrosaura*, it can be distinguished by the absence of a frontoparietal (present in *Arthrosaura*), and by having smooth dorsal scales (keeled in *Arthrosaura*). From *Ecleopopus*, the new genus is distinguished by the absence of frontoparietals (present in *Ecleopopus*), in having smooth dorsals (keeled in *Ecleopopus*) and in the presence of femoral pores in males (absent in *Ecleopopus*). *Kaieteurosaurus*,⁶ and *Pantepuisaurus*⁶ were described based on single specimens (Kok, 2005, 2009, respectively), which we did not examine. On the basis of the original descriptions *Marinussaurus* is readily distinguished from both *Kaieteurosaurus* and *Pantepuisaurus* by the absence of frontoparietals (present in *Kaieteurosaurus* and *Pantepuisaurus*), smooth dorsals (keeled in *Kaieteurosaurus* and *Pantepuisaurus*), rectangular smooth ventrals (hexagonal, keeled in *Kaieteurosaurus* and *Pantepuisaurus*). A summary of diagnostic features among selected taxa within Ecleopodini is given in table 2.

Myers and Donnelly (2001) described the genus *Adercosaurus* based on a single specimen, for which Castoe et al. (2004) could not associate with any subfamilies, although they suggested the genus might be related to the Alopoglossinae, Cercosaurinae, or “Ecleopodinae” (considered here as Ecleopodini, a tribe of Cercosaurinae). Based on the original description of *Adercosaurus*, *Marinussaurus curupira* is distinguished from it by the absence of frontoparietals (present in *Adercosaurus*), posterior margins of parietals and interparietals forming a straight line (forming a “jagged line” in *Adercosaurus*), and dorsals smooth (sharply keeled in *Adercosaurus*).

Body scales and general body shape of *Marinussaurus* is similar to some species of *Ptychoglossus*, but head scales immediately distinguish the two genera. *Marinussaurus* lacks frontoparietal scales (present in all species of *Ptychoglossus*; Harris, 1994); and the interparietal is as nearly long as parietals in *Ptychoglossus* (visibly shorter in *Marinussaurus*). *Ptychoglossus* is a member of the basal Alopoglossinae (Castoe et al., 2004; Rodrigues et al., 2005) whereas *Marinussaurus* is a Cercosaurinae, tribe Ecleopodini (see our phylogenetic hypothesis below).

PHYLOGENETIC ANALYSES

We conducted both maximum parsimony (PAR) and Bayesian analyses (BA), but consider the topology obtained from PAR as our preferred hypothesis, and regard clade posterior probability (PP) values as support measure for clades. However, since the PAR topology is almost identical to the majority rule consensus tree of the BA (Clade-Bayes, sensu Wheeler and Pickett, 2008), the criterion chosen has little implication on the overall phylogenetic hypothesis presented herein. Arguments for the use of parsimony were given and discussed extensively in Farris (1983), Goloboff (2003), and Kluge and Grant (2006).

⁶ The inclusion of *Amapasaurus*, *Kaieteurosaurus* and *Pantepuisaurus* in the tribe Ecleopodini is based on preliminary phylogenetic analyses of molecular data (Pellegrino and Rodrigues, unpubl.).

TABLE 2. Diagnostic morphological features of *Marinusaurus curupira* and presumably closely related forms from the Eupleopodini, based on examined specimens and on literature.

	<i>Marinus-saurus</i>	<i>Amapa-saurus</i>	<i>Anotosaura</i>	<i>Arthrosaura</i>	<i>Colobo-sauroides</i>	<i>Dryadosaura</i>	<i>Eupleopus</i>	<i>Kateteuro-saurus^a</i>	<i>Leposoma</i>	<i>Pantepuisaurus^a</i>
External ear opening	present	present	absent	present	present	present	present	present	present	present
Frontoparietals	absent	present	absent	present	present	absent	present	present	present	present
Pairs of enlarged chinshields	three	three	three	three or two	three	two	three	two	three or four	three
Nasal	divided	partially divided	undivided	divided or undivided	undivided	undivided	undivided	divided	divided	undivided
Chinshield reach oral border	no	no	yes	no	no	no	no	no	no	no
Posterior dorsal scales	smooth	keeled	keeled	keeled	keeled	keeled	keeled	keeled	keeled	keeled
Predloacal pores	large	large	small	large	small	small	large	NA ^b	large	NA ^b

^aData taken from literature. Kok (2005) for *Kateteurosaurus*; Kok (2009) for *Pantepuisaurus*.

^bNA = not available. The description of the character is not sufficient to elucidate its state with certainty.

Separate and combined analyses of morphology and molecular data were performed to determine the phylogenetic placement of *Marinussaurus curupira* among major clades of Gymnophthalminae. First, a PAR analysis was conducted on the morphological partition of 37 characters (36 parsimony informative). The analysis recovered three equally most parsimonious trees. The strict consensus tree is shown in figure 6A (tree length, $L = 76$; consistency index, $CI = 0.684$; retention index, $RI = 0.784$). Subfamily ranks proposed by Pellegrino et al. (2001) were not recovered in this analysis, but most clades were recovered with low bootstrap and Goodman-Bremer support values. Cercosaurinae resulted as paraphyletic, with *Cercosaura ocellata* Wagler, 1830, curiously placed as the sister taxa of the remaining Cercosaurinae and Gymnophthalminae ($BS < 50$, $GBS = 1$). A Gymnophthalminae clade (*Colobosaura* (*Iphisa* (*Procellosaurinus* + *Micrablepharus*))) was recovered with low support ($BS = 67$, $GBS = 3$), but nested within a paraphyletic Cercosaurinae. A partially resolved relationship of *Marinussaurus curupira* with *Anotosaura*, *Colobosauroides*, and *Dryadosaura* was recovered with high support ($BS = 83$, $GBS = 3$).

The single most parsimonious tree obtained from the separate analyses of the molecular partition under PAR ($L = 2538$) was identical to that recovered from the combined morphology and molecular data sets, and will not be commented further. PAR analysis on the combined data resulted in a single most parsimonious tree shown in figure 6B (total of 2375 characters, 699 parsimony informative; $L = 2634$; $CI = 0.525$; $RI = 0.481$).

The partitioned Bayesian analyses (BA, not shown) on the combined data set resulted in a topology very similar to that obtained under PAR. The only incongruence was the placement of the highly supported sister relationship *Cercosaura* + *Bachia* ($BS = 87$, $GBS = 13$, $PP = 1.0$; fig. 6B). In the PAR analysis the clade *Cercosaura* + *Bachia* was weakly resolved as the sister group to the Ecleopodini (fig. 6B, Node X: $BS < 50$, $GBS = 4$), whereas in the BA analysis, this clade was highly supported as the sister clade to the Gymnophthalminae ($PP = 0.97$). The monophyly of Ecleopodini was well supported with *Ecleopus gaudichaudii* Duméril and Bibron, 1839, resolved as a basal taxon and sister to all remaining ecleopodines (fig. 6B, Node Y: $BS = 100$, $GBS = 31$, $PP = 1.0$). A clade including *Colobosauroides* + (*Anotosaura* + *Dryadosaura*) was recovered with high support ($BS = 100$, $GBS = 24$, $PP = 1.0$). Both PAR and BA analyses recovered *Marinussaurus* as a sister taxon of *Arthrosaura reticulata* (O'Shaughnessy, 1881), but with very distinct support indexes: low under PAR ($BS = 52$, $GBS = 3$; fig. 6B) and high under BA ($PP = 1.0$).

DISCUSSION

Systematics of lizards of the family Gymnophthalmidae has advanced quickly in the last two decades. Such advance is partially the result of cumulative efforts to reconstruct supraspecific phylogenetic relationships among microteiid taxa. Understanding of microteiid relationships has improved with the use of molecular (Pellegrino et al., 2001; Castoe et al., 2004; Doan and Castoe, 2005) or a combination of molecular and morphological approaches (Rodrigues et al., 2005, 2007, 2009). In the present study, we analyzed overall morphology of the new

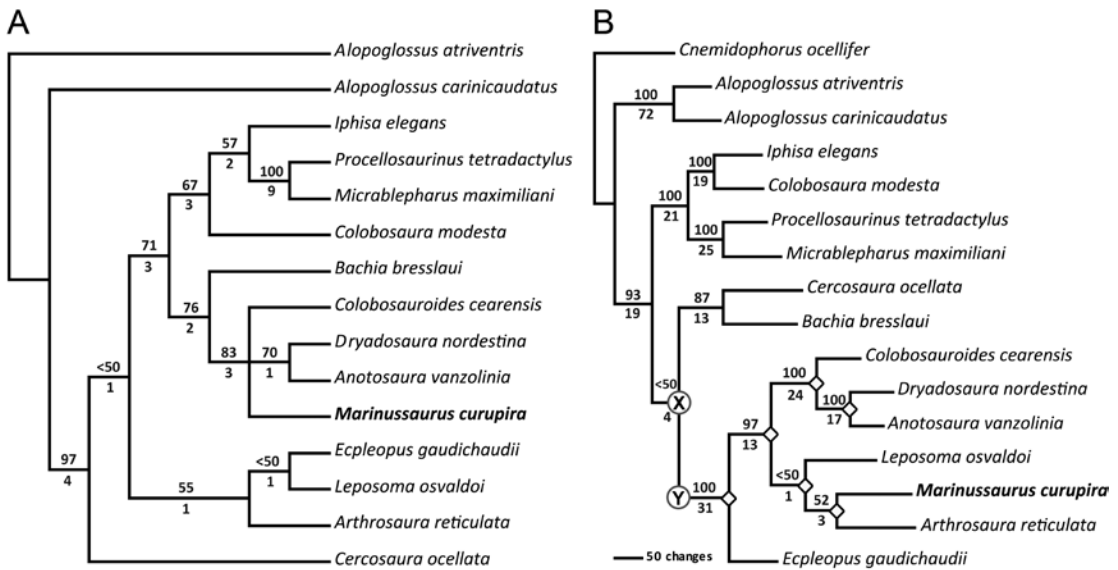


FIG. 6. Phylogenetic trees inferred from parsimony (PAR) analyses. **A**, Strict consensus of three equally parsimonious trees from the analysis of the morphological characters, ($L = 76$, $CI = 0.684$, $RI = 0.784$). **B**, Single most parsimonious tree based on combined analyses of morphology and molecular partitions ($L = 2634$, $CI = 0.525$, $RI = 0.481$). Numbers above branches are bootstrap support values (BS) and numbers below branches are total Goodman-Bremer support values (GBS). Open diamonds represent Bayesian posterior probability values of 1.0 (PP; only shown for the Ecleopodini clade). Node X represents incongruence among trees under PAR and Bayesian methods. Clades in node Y represent the tribe Ecleopodini, sensu Pellegrino et al. (2001) and Rodrigues et al. (2005).

taxon, described above, and conducted a phylogenetic analysis to determine the placement of the new genus and test its relationships with representatives of the Alopoglossinae, Gymnophthalminae, and Cercosaurinae (especially with those from the Ecleopodini tribe sensu Pellegrino et al., 2001).

The monophyly of the Ecleopodinae clade was reinforced here (fig. 6B, Node Y: BS = 100, GBS = 31, PP = 1.0). This clade was first reported by Pellegrino et al. (2001: 330), on the basis of molecular data only, as a tribe of the subfamily Cercosaurinae (Ecleopodini). Castoe et al. (2004) also used molecular data only but under a Bayesian framework recovered a monophyletic clade with the same content, though not related to the Cercosaurinae. In their analyses, the Ecleopodines formed a well-supported clade (PP = 1.0), sister to a more inclusive one containing members of the Gymnophthalminae and the Cercosaurinae. Castoe et al. (2004) gave the clade subfamily status Ecleopodinae (given by them as “Ecleopinae”; but see Rodrigues et al., 2009 for corrected spelling). Rodrigues et al. (2005) did not adopt the classification proposed by Castoe et al. (2004) on the basis of “preliminary evidence provided by an extensive morphological study of gymnophthalmids” and therefore retained Ecleopodini as a tribe of the Cercosaurinae. We found a conflicting result regarding the monophyly of Cercosaurinae (Node X in fig. 6B). Maximum parsimony analysis of combined morphology and molecular

data sets recovered *Cercosaura* + *Bachia* as a sister clade of the ecleopodines (BS < 50, GBS = 4), whereas the Bayesian analyses on the same data set resolved *Cercosaura* + *Bachia* as sister clade to the Gymnophthalminae, with a high support (PP = 0.97), resulting in a paraphyletic Cercosaurinae (if Ecleopodini is considered a tribe of it). Our experiment, however, was designed only to ascertain the position of *Marinussaurus* among the major clades of Gymnophthalmidae, and not to resolve this incongruence for which a much-improved taxonomic and character sampling is necessary.

The clade (*Leposoma* (*Arthrosaura* + *Marinussaurus*)) was poorly supported in the PAR analysis of combined morphology and molecular data sets, but well supported in the Bayesian analysis of the same data set (BS < 50, GBS = 1, PP = 1.0; fig. 6B). The relationship of *Marinussaurus* + *Arthrosaura* was recovered in both PAR and Bayesian analyses with the combined data set, but with very low support in the PAR analysis (BS, bootstrap = 52); however, that relationship was strongly supported under a Bayesian framework (PP = 1.0).

This relationship of *Marinussaurus* + *Arthrosaura* was not recovered in the PAR analysis of the morphology data set alone (fig. 6A). The clade containing (*Colobosauroides* (*Anotosaura* + *Dryadosaura*)) was recovered with high support in both analyses (PAR and BA) with the combined data set (BS = 100, GBS = 24, PP = 1.0). The same clade was recovered by Pellegrino et al. (2001) and Rodrigues et al. (2005). Castoe et al. (2004) recovered a slightly different topology under an exclusively Bayesian framework (*Dryadosaura* (*Anotosaura* + *Colobosauroides*)) (PP = 1.0), but with low support for the *Anotosaura* + *Colobosauroides* clade (PP = 0.51). The strict consensus tree from our analyses of the morphology partition recovered a relationship of (*Colobosauroides* + (*Anotosaura* + *Dryadosaura*) + *Marinussaurus*), with a significant support (BS = 83, GBS = 3; fig 6A).

In spite of the divergent results regarding analyses of the molecular and morphological data sets, it is clear that *Marinussaurus curupira* is part of the Ecleopodini radiation, and that it cannot be included in the genus *Dryadosaura*, nor in any of the other presently recognized Ecleopodini genera. Its relationships within the group remain uncertain.

DIVERSITY, MONOTYPIC GENERA, AND PHYLOGENETICS OF THE MICROTEIIDS

The high number of monotypic genera within the Gymnophthalmidae might raise some debates about the current classification of the family. For example, of the nine genera currently assigned to the Ecleopodini (*Amapasaurus*, *Anotosaura*, *Arthrosaura*, *Colobosauroides*, *Dryadosaura*, *Ecleopus*, *Kaieteurosaurus*, *Leposoma*, *Marinussaurus*, *Pantepuisaurus*), and presumably *Ardecosaurus*, over half are monotypic. As a result of the scarcity of material (especially tissue and additional specimens for osteological analyses), new monotypic microteiid genera are still being proposed and diagnosed solely on apomorphic external characters (Myers and Donnelly, 2001; Kok, 2005, 2009; Rodrigues and Santos, 2008). On the other hand, some of the more species-rich genera in the family may not be monophyletic (Pellegrino et al., 2001). Some species are still known only from their original description and/or type specimens, limiting

their inclusion in modern phylogenetic analysis. Monophyly has not been adequately assessed for most of the “speciose Gymnophthalmidae genera” (e.g., *Alopoglossus*, *Arthrosaura*, *Bachia*, *Euspondylus*, *Leposoma*, *Pholidobolus*, *Ptychoglossus*).

Because our data set is limited to a few important characters and taxa, a complete assessment of the supraspecific taxonomic reassessment of the Ecleopodini is not prudent at this time. No hemipenial, myological, and osteological studies were conducted, and only a single species of the species-rich genera *Arthrosaura* (*A. reticulata*) and *Leposoma* (*L. osvaldoi*) was sampled in this study. Our phylogenetic trees (fig. 6) and the current morphological knowledge within the family suggest no better solution than the erection of a new genus for the new species described herein. With the available data, two resolutions are possible. The first is to maintain current taxonomy of the Ecleopodini (one loaded with monotypic genera). The second is to cluster all species currently assembled in *Arthrosaura*, *Leposoma*, plus the new species into a single genus. This clustering is unacceptable, however, on account of the striking morphological differences between and within these genera. Therefore, we emphatically refuse to take this nomenclatural action regarding the already complicated taxonomy of the group. Moreover, such an action would reflect a poorly supported topology in our preferred analysis (PAR, fig. 6B). A similar position was adopted and discussed in Kok (2009: 55–58).

The current taxonomic scenario of the Gymnophthalmidae will continue to improve as more robust and complete phylogenetic experiments are designed and conducted. Increased taxon and character sampling (e.g., hemipenis, myology, behavior, additional molecular data enriched with several independent nuclear markers) within the Ecleopodini (e.g., *Amapasaurus*, *Arthrosaura* spp., *Kaieteurosaurus*, *Leposoma* spp., *Pantepuisaurus*), and presumed related genera (e.g., *Adercosaurus*), will help to resolve the current position of *Marinussaurus* among extant Gymnophthalmidae. A better knowledge on the dynamics of homoplastic characters within the microteiids is also needed. Nevertheless, understanding how morphological characters evolved in the highly specialized gymnophthalmids may be difficult to accomplish. Many characters are known or suspected products of convergent evolution (e.g., head scale arrangement, limb reduction, body elongation) and a reanalysis of a recent work reinforces the idea that some characters may reevolve after being lost (Kohldorf and Wagner, 2006; Kohldorf et al., 2010). For this reason, few unambiguous synapomorphies have been proposed to diagnose supraspecific groups within the Gymnophthalmidae. Among the Ecleopodini, the grouping of (*Anotosaura* + *Dryadosaura*) is apparently supported by a morphological synapomorphy (two pairs of sternal ribs), an apparent reduction from the ancestral three pairs, but this character has yet to be thoroughly surveyed even across all ecleopodines. We could not verify the state of this character on *Marinussaurus* from X-rays.

During the examination of specimens for this and additional studies, we noted that the morphology of precloacal and femoral pores might be a synapomorphic trait to the clade formed by (*Colobosauroides* (*Anotosaura* + *Dryadosaura*)). In those three genera precloacal pores are small and superficial, located in a single relatively large scale (fig. 4C, D), while pores are large and prominent and located in one or more small scales in all the remaining Ecleopodini examined (fig. 4A, B), and perhaps most other Gymnophthalmidae (fig. 4E, F). Detailed anatomical studies on the morphology of pores in squamates are rare (Antoniazzi et al., 1994;

Imparato et al., 2007), but should give some insights on the evolution of the organ and consequently on the phylogeny of the group. However, before we can use this kind of character for phylogenetic inference, more anatomical studies within and among the known clades of Gymnophthalmidae should be conducted. This would help us to understand how character evolution and variation is shaped among this highly diverse and interesting group of lizards.

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APPENDIX 1

ADDITIONAL SPECIMENS EXAMINED

Alopoglossus angulatus: MPEG 24272-73, Porto Trombetas, Oriximiná, Pará, Brazil. ***Amapasaurus tetradactylus***: MPEG 27370,, Serra do Acari, Estação Ecológica Grão-Pará, Oriximiná, Pará, Brazil. ***Anadia rhombifera***: USNM 285822-25, Pichincha, Ecuador. ***Anotosaura collaris***: MZUSP 788 (holotype), Villa Nova, Bahia, Brazil. ***Anotosaura vanzolinia***: MZUSP 45754, Reserva Biológica de Serra Negra, Inajá, Pernambuco, Brazil. ***Arhtosaura kockii***: MPEG 25991-96, Projeto Salobo, Barragem de Finos, Parauapebas, Pará, Brazil. ***Arthrosaura reticulata***: MPEG 17914–17, Melgaço, Pará, Brazil.; MPEG 19181, Serra do Navio, Amapá, Brazil. ***Bachia flavescens***: MPEG 27313, Estação Ecológica Grão-Pará, Oriximiná, Pará, Brazil. ***Bachia pyburni***: USNM 344820, Departamento Rio Negro, Territorio Federal Amazonas, Venezuela. ***Cercosaura ocellata***: MZUSP 82425–27 Juruena, Mato Grosso, Brazil; ***Colobosaura modesta***: MPEG 22452–53, Carajás, Pará, Brazil. ***Colobosauroides carvalhoi***: MZUSP 89453, Serra da Capivara, Piauí, Brazil; ***Colobosauroides cearensis***: MPEG 15574-75 (paratypes), Mulungu, Ceará, Brazil; MPEG 15577-78 (paratypes), Fortaleza, Ceará, Brazil. A specimen from MPEG with no available data, probably from Maranhão, was also examined (fig. 4C). ***Dryadosaura nordestina***: MZUSP 9931, MPEG 27738, Reserva Dois Irmãos, Recife, Pernambuco, Brazil; MZUSP 93219, 93222, Fazenda Bananeiras, Murici, Alagoas, Brazil. ***Ecleopus gaudichaudii***: MPEG 25072-73, Restinga de Setiba, Guarapari, Espírito Santo, Brazil. ***Heterodactylus imbricatus***: MPEG 14395, Rio de Janeiro, Rio de Janeiro, Brazil. ***Iphisa elegans***: MPEG 21545, Parque Nacional Serra da Cutia, Rondônia, Brazil. ***Leposoma osvaldoi***: MZUSP 82703-82737, Aripuanã, Mato Grosso, Brazil. ***Leposoma percarinatum***: MPEG 19252-53, Vitória do Xingu, Altamira, Pará, Brazil. ***Leposoma scincoides***: MPEG 27686, Jacarenema, Vila Velha, Espírito Santo, Brazil. ***Neusticurus rudis***: MPEG 15353, Cruz Alta, Oriximiná, Pará, Brazil. ***Placosoma cordylinum***: MPEG 1916, Parque Nacional da Serra dos Órgãos, Teresópolis, Rio de Janeiro Brazil. ***Ptychoglossus brevifrontalis***: USNM 196259, Rio Corrientes, Pastaza, Ecuador. ***Ptychoglossus kugleri***: MZUSP 7631, Pauji, Falem, Venezuela. ***Rachisaurus* cf. *brachylepis***: MPEG 21336, Canaã dos Carajás, Carajás, Pará, Brazil. ***Stenolepis ridleyi***: MPEG 16884-85, Sítio Santana, Ubajara, Ceará, Brazil.

APPENDIX 2: MATRIX OF MORPHOLOGICAL CHARACTERS

Characters are defined in appendix 3.

Species / Characters	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	32	33	34	35	36	37			
Outgroups																																								
<i>Alopoglossus atriventris</i>	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	2	0	0	?	1	0	?	2			
<i>Alopoglossus carinicaudatus</i>	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	2	0	0	?	1	0	?	2			
Ingroup																																								
<i>Anotosaura vanzolinia</i>	1	0	0	1	1	1	0	1	1	1	1	1	1	1	1	1	1	0	0	0	4	0	0	1	0	1	2	1	1	0	0	0	?	0	0	?	1			
<i>Arthrosaura reticulata</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	
<i>Bachia bresslaui</i>	1	0	0	1	1	0	1	1	1	0	0	1	0	0	2	1	0	0	1	0	0	1	0	0	0	0	0	0	1	0	0	0	1	0	0	1	1	1	2	
<i>Cercosaura ocellata</i>	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	2	0	0	0	0	0	0	0	0	0	2	0	0	0	0	
<i>Colobosaura modesta</i>	0	0	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	2	1	1	0	1	0	1	0	0	0	1	1	0	0	1	0	0	0	0	
<i>Colobosauroides cearensis</i>	0	0	0	0	0	1	0	0	0	1	1	1	1	1	1	1	1	0	0	0	4	0	0	0	0	0	0	2	1	1	0	0	0	?	0	0	?	1		
<i>Dryadosaura nordestina</i>	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	4	0	0	1	0	0	2	1	1	0	0	0	?	0	0	?	1			
<i>Ecpleopus gaudichaudii</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	
<i>Iphisa elegans</i>	0	0	0	0	0	1	0	2	0	1	1	2	0	2	0	0	0	0	0	0	2	1	1	0	1	0	0	0	1	1	0	0	0	1	0	0	1	0	0	0
<i>Leposoma osvaldoi</i>	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	
<i>Marinussaurus curupira</i>	0	0	0	0	1	1	0	0	1	1	1	1	1	1	1	1	1	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
<i>Micrablepharus maximiliani</i>	0	0	0	1	0	1	0	0	0	1	1	2	0	2	0	0	0	1	1	3	1	1	0	0	0	1	0	0	2	1	1	0	0	2	1	1	0	0	2	3
<i>Procellosaurinus tetradactylus</i>	0	0	0	0	0	1	0	0	0	1	1	2	0	2	0	0	0	1	1	3	1	1	0	0	0	1	0	0	1	0	0	0	1	1	2	0	0	2	3	

APPENDIX 3

MORPHOLOGICAL CHARACTERS AND CHARACTER STATES USED FOR THE
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: (0) lanceolate; (1) quadrangular or slightly mucronate; (2) cycloid.
13. Ventral scales: (0) strongly imbricate; (1) juxtaposed.
14. Flank scales: (0) lanceolate, imbricate; (1) quadrangular, juxtaposed; (2) cycloid.
15. Collar: (0) absent; (1) present.
16. Limbs: (0) normal, slender; (1) stout, compact; (2) reduced.
17. Body form: (0) normal; (1) elongate.
18. Eyelid: (0) present; (1) absent.
19. Position of nostril: (0) in nasal border; (1) in centre of nasal.
20. Number of toes: (0) five, without reduction; (1) less than five.

Osteology

21. 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 orientated; (4) a longitudinal rod-shaped element, lateral processes absent; (5) transversal, clavicular and sternal processes absent.
22. Sternal process of interclavicle: (0) long, reaching sternal fontanelle; (1) small, not reaching fontanelle.
23. Sternal fontanelle process: (0) absent; (1) present.
24. Number of sternal ribs: (0) three; (1) two; (2) one.
25. Glossohyal: (0) separated from basihyal; (1) fused to basihyal.
26. Second pair of ceratobranchials: (0) present; (1) absent.
27. Supratemporal fenestra: (0) almost closed; (1) opened; (2) opened only posteriorly.
28. Postorbital: (0) distinct; (1) fused to postfrontal.
29. Postorbital width: (0) narrow; (1) wide.
30. 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 premaxilla; (2) separated by contact between frontal and premaxillary.
31. Supratemporal fenestra: (0) closed by parietal and postorbital; (1) opened.

32. Clavicle: (0) wide, flattened anteriorly and enclosing a single fenestra; (1) simple, boomerang shaped, fenestra absent; (2) axe shaped anteriorly, fenestra absent.
33. Postfrontal: (0) irregular, posteriorly wider and longer leaving opened the supratemporal fenestra; (1) triangular; (2) boomerang shaped.
34. Supratemporal: (0) angulose, extremely curved at the end; (1) slightly curved.
35. Lateral expansions of parietal: (0) present; (1) absent.
36. Postorbital: (0) covers postfrontal; (1) covered by postfrontal; (2) contacts prefrontal without overlap.
37. Premaxillary dorsal lamina: (0) wide, posteriorly triangular; (1) wide, posteriorly straight; (2) sub-triangular with end pointed towards but not reaching frontal; (3) large, subretangular, contacting frontal.

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