

Phylogenetic relationships of a new genus and species of microteiid lizard from the Atlantic forest of north-eastern Brazil (Squamata, Gymnophthalmidae)

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A new genus and species of a short limbed and slightly elongate gymnophthalmid lizard is described from the Atlantic rain forests of north-eastern Brazil. The new genus is also characterized by short and stout pentadactyl limbs, presence of prefrontals, absence of frontoparietals, distinctive ear opening and eyelid, two pairs of genials, a distinct collar, smooth, quadrangular, dorsal scales, quadrangular ventrals, fused postfrontal and postorbital bones, and two pairs of sternal ribs. The geographical distribution of the new taxon extends from the state of Rio Grande do Norte to the northern bank of the Rio São Francisco in the state of Alagoas. All specimens were obtained in leaf litter, an observation which agrees with the fossorial habits suggested by the body shape and massive aspect of the head of this species. A phylogenetic analysis based on external morphology, osteology, and molecular data recovered the new lizard as the sister genus to *Anotosaura*, and *Colobosauroides* as the sister group to these two. © 2005 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2005, 144, 543–557.

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INTRODUCTION

The Brazilian Atlantic rain forests are one of the most endangered biodiversity hotspots in the world (Mittermeier *et al.*, 1999; Myers *et al.*, 2000; Rodrigues, Dixo & Accacio, 2002a). Formerly extending along the eastern coast of Brazil for about 5500 km, from the state of Rio Grande do Norte to the state of Rio Grande do Sul, most of the forest has now been cut down; the remainder does not exceed 6% of its original area, and most of this is located in south-eastern Brazil. In north-eastern Brazil, north to the mouth of Rio São Francisco,

the forest has been almost completely cleared for sugar cane farming and cattle ranching (Rodrigues *et al.*, 2002b). Only a few scattered and relatively small remnant patches remain, and these show different levels of disturbance. Nevertheless, several new species of reptiles and amphibians have been and continue to be described from these areas, some resulting from recent field work (Rodrigues & Borges, 1997; Rodrigues, 1997; Cruz, Caramaschi & Freire, 1999; Freire, 1999; Rodrigues *et al.*, 2002a, b; Caramaschi & Rodrigues, 2003; Peixoto, Caramaschi & Freire, 2003). Data on these new taxa are helpful to reconstruct the history of these forests by recovery of major biogeographical patterns (Carnaval, 2002; Mustrangi & Patton, 1997; Costa, 2003; Pellegrino *et al.*, 2005).

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About two decades ago one of us (MTR) collected specimens of a small microteiid lizard at João Pessoa, state of Paraíba, in the north-eastern Atlantic forest. These lizards were preliminarily associated with the earless genus *Anotosaura*, although characterized by a distinctive ear opening. They were subsequently collected in several localities and referred to as *Anotosaura* spn. in other publications (Rodrigues, 1990; Freire, 1996; Pellegrino *et al.*, 2001; Castoe, Doan & Parkinson, 2004). Description was deferred at that time due to the chaotic situation of microteiid systematics. The degree of body elongation, limb reduction, and absence or presence of eyelids and external ear openings characterizing different microteiid genera, and variation in presence or absence of several cephalic scutes within some genera, suggested extensive convergence, rendering impossible the proper generic allocation of the new form.

Only recently, with the use of molecular data, has the systematics of microteiid lizards advanced, especially regarding generic limits and intergeneric relationships. The first contribution was an extensive study of 26 of the 36 recognized genera of gymnophthalmids conducted by Pellegrino *et al.* (2001). They recognized four subfamilies: Alopoglossinae, Rhachisaurinae, Cercosaurinae (with two tribes, Cercosaurini and Ecleopini), and Gymnophthalminae (also with two tribes: Gymnophthalmini and Heterodactylini). Genera not represented in that study were tentatively allocated to the recognized clades on the basis of morphology.

More recently, Castoe *et al.* (2004) used four of the five genes explored by Pellegrino *et al.* (2001) and a slightly improved sampling design (12 new species and one new genus), to reanalyse the Pellegrino *et al.* data. Their results, based on partitioned Bayesian analyses, were generally consistent with those obtained by Pellegrino *et al.* (2001), but the following higher level taxonomic changes were proposed: (1) *Ptychoglossus* was included in Alopoglossinae; (2) Heterodactylini and Gymnophthalmini were combined in Gymnophthalminae without tribal divisions; (3) Ecleopini was raised to subfamily status, and (4) *Bachia* was allocated to the new tribe Bachini within the Cercosaurinae.

We fully agree with the first change proposed, because it was due to a swapping of taxon names between *Ptychoglossus* and *Neusticurus juruazensis* during the analysis of Pellegrino *et al.* (2001). However, we think that the other changes proposed by Castoe *et al.* (2004) are premature, considering the preliminary evidence provided by an extensive morphological study of gymnophthalmids we are conducting. We are developing a matrix of a limited number of unambiguous characters (i.e. those for which hypotheses of anatomical homology across taxa are clear, and that can be coded into discrete alternatives), following

the suggestion of Scotland, Olmstead & Bennett (2003) that these will be the easiest to evaluate against each other and in combination with molecular data, for taxonomic congruence. One example – the shape of the postorbital and its contact with the postfrontal, and the shape of the interclavicle – suggests a close relationship between the Ecleopini and the Cercosaurini. Similarly, the condition of the nasals – wide, divergent and in contact at midline in Heterodactylini, separated by contact between frontal and premaxillary in Gymnophthalmini, along with the shape of interclavicle – suggests that tribal status of these clades is appropriate.

Because the taxonomic and character sampling of Cercosaurini is still limited, and much additional work is needed in order to better characterize its diversity and relationships, we prefer not to adopt the molecular-based Bachini proposed by Castoe *et al.* (2004). The morphological distinctiveness of *Bachia* is based primarily on highly homoplastic character complexes (body elongation, limb reduction and earlessness), but there are no other independent morphological data distinguishing this genus from all other Cercosaurini. Here again we prefer to follow the classification proposed by Pellegrino *et al.* (2001) for the Gymnophthalmidae, at least until extensive character and taxon sampling has been completed.

Molecular and morphological evidence suggests that the lizard described herein is a new genus of the radiation Ecleopini, as recovered from phylogenetic analyses designed to test the placement of this new genus relative to other Ecleopini and the major clades of Gymnophthalmidae. Considering that neither the Pellegrino *et al.* nor the Castoe *et al.* studies of the Gymnophthalmidae included any morphological data, the availability of these characters for some taxa allows us to (1) evaluate the relative contributions of molecular and morphological data to the resolution and/or degree of support for phylogenetic placement of the new genus, and (2) assess, at a more limited level, the potential for both character sets to resolve placement of the major groups of gymnophthalmids recognized by Pellegrino *et al.* (2001) and Castoe *et al.* (2004).

MATERIAL AND METHODS

Snout–vent length was measured to the nearest millimetre with a ruler. Scale counts and osteological data (on cleared specimens, Appendix 1) were taken with the aid of a stereomicroscope. Scale counts and nomenclature follow Rodrigues & Borges (1997), while osteological nomenclature follows Presch (1980) and Estes, de Queiroz & Gauthier (1988). Sex was determined by the presence/absence of femoral pores and confirmed by dissection of previously examined specimens. All morphological data were taken from preserved speci-

mens housed in the following institutions: MNRJ (Museu Nacional do Rio de Janeiro), MZUSP (Museu de Zoologia, Universidade de São Paulo), and MUFAL (Museu de História Natural, Universidade Federal de Alagoas). Fifteen species, assigned to 14 genera of Gymnophthalmidae (including the new one herein described) were used in the present study (Table 1). The DNA sequences used were those from Pellegrino *et al.* (2001), with the present molecular partition composed of 2359 of aligned bases from regions of three mitochondrial and two nuclear genes. Minor adjustments of the original Pellegrino *et al.* (2001) alignments for the ribosomal 12S, 16S, and 18S regions were made manually on the reduced matrix used in this study to exclude unnecessary gaps.

Phylogenetic inference was first conducted on the separate morphological partition followed by combined analyses with the molecular partitions under equally weighted parsimony (MP) in PAUP* v. 4.0b10 (Swofford, 2002). For a matrix of 37 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 a MP heuristic search with 1000 replicates of random stepwise addition and TBR branch-swapping.

Nodal support was assessed by bootstrap analysis (BS; Felsenstein, 1985) with a 1000 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 & Bull, 1993) were interpreted as strong support for a node. Total and partitioned Bremer support (PBS) indexes (Baker & 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).

Two species of *Alopoglossus*, constrained to monophyly, were used as the outgroup, based on the placement of this clade in the studies of Pellegrino *et al.* (2001) and Castoe *et al.* (2004). *Rachisaurus brachylepis* and selected taxa from Heterodactylini, Gymnophthalmini and Cercosaurinii (*sensu* Pellegrino *et al.*, 2001) were used as part of the ingroup to test placement of the new form (Table 1).

RESULTS

DRYADOSAURA GEN. NOV.

Definition: Small gymnophthalmid with a robust and short head, elongate body and short, stout, pentadactyl limbs. Collar fold, ear opening and eyelid present.

Table 1. Matrix of morphological character (numbers in bold are the characters 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 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 | 31 | 32 | 33 | 34 | 35 | 36 | 37 | | | |
|---------------------------------------|---|---|---|---|---|---|---|---|---|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|---|---|---|
| Ingroup | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | | |
| <i>Dryadosaura nordestina</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | | |
| <i>Anotosaura vanzolinia</i> | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 4 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | |
| <i>Colobosauroides cearensis</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | |
| <i>Epleopus gaudichaudii</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | |
| <i>Arthrosaura reticulata</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 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 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | |
| <i>Rachisaurus brachylepis</i> | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 3 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Iphisa elegans</i> | 0 | 0 | 0 | 0 | 1 | 0 | 2 | 0 | 1 | 1 | 2 | 0 | 2 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Colobosaura modesta</i> | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Procellosaurinus tetradactylus</i> | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 2 | 0 | 2 | 0 | 2 | 0 | 0 | 0 | 0 | 1 | 3 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Micrablepharus maximiliani</i> | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 2 | 0 | 2 | 0 | 2 | 0 | 0 | 0 | 0 | 1 | 3 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Cercosaura ocellata</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Bachia bresslaui</i> | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Outgroup | 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 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | |
| <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 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | |
| <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 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | |

Frontonasal single; prefrontals, parietals and interparietals present; frontoparietals absent. Two pairs of chin shields and three supraoculars. Dorsal scales in transverse rows; anteriorly smooth, imbricate, rounded in the occipital region, becoming narrower, elongate and rectangular at the arm level; posterior to the arm, dorsal scales become progressively and irregularly mucronate, with lateral sides almost juxtaposed, keeled. Lateral scales of body about the same size as dorsals, smooth, rectangular, and laterally imbricate. Ventral scales smooth, juxtaposed or slightly imbricate, rectangular. Males with preanal and femoral pores; only preanal pores in females.

Content: *Dryadosaura nordestina* sp. nov.; monotypic.

Etymology: From the Greek *Dryades*, meaning 'woodland nymph'. This was the first name proposed (by Carl Philipp von Martius) for the biogeographical province of the Atlantic Forest.

Considering the multiple origins of character complexes related to fossoriality in gymnophthalmid lizards and their chaotic taxonomy, until recently based only on external attributes, we emphasize morphological comparisons of *Dryadosaura* with *Anotosaura* and *Colobosauroides*, their closest relatives according to the molecular phylogenetic analyses of Pellegrino *et al.* (2001) and Castoe *et al.* (2004). In those papers, *Dryadosaura* (referred to as *Anotosaura* spn.), *Anotosaura vanzolinia*, and *Colobosauroides cearensis* were recovered as a strongly supported monophyletic group. However, Pellegrino *et al.* (2001) emphasized that the status of *Anotosaura* spn. was tentative, pending correct generic allocation. The pronounced morphological gap between *Dryadosaura* and its close relatives, in characters as number of sternal ribs, presence of an external ear opening, body shape and pholidosis, among other characters presented below, support the generic status here proposed.

Only two species (*Anotosaura vanzolinia* and *A. collaris*) are currently recognized in the genus *Anotosaura*. *Anotosaura brachylepis*, formerly included in *Anotosaura* due to the absence of an external ear opening, is now allocated to *Rhachisaurus*, a monotypic genus of the new subfamily Rhachisaurinae (Pellegrino *et al.*, 2001). *Rhachisaurus* is characterized by the absence of an external ear opening, the presence of four digits on the front and hind limbs, a high number of short, narrow and smooth dorsal scales (57–60), absence of collar, a tail that is more than twice body length, a large number of temporals, ten rows of gulars, three pairs of chinshields, four supraoculars, six superciliaries, squared ventrals and rounded scales in the lateral sides of the neck.

Dryadosaura differs from *Anotosaura* and *Colobosauroides* by its larger size (maximum SVL, respectively: 57 mm, 43 mm, and 35 mm), robust body and

massive fore limbs (more slender in both of the other genera). *Dryadosaura* also differs from *Anotosaura* by the presence of an external ear opening (absent in *Anotosaura*), two pairs of chinshields (three in all other Eupleopini) and dorsal scales keeled posteriorly (vs. smooth in the others). It further differs from *A. vanzolinia* by the presence of a pair of prefrontals (vs. absence); prefrontals are present in *A. collaris*. Two very similar species of *Colobosauroides* are currently recognized: *C. cearensis* and *C. carvalhoi*. From them *Dryadosaura* can be externally distinguished by the absence of frontoparietals (present in *Colobosauroides*), by having only two pairs of chinshields (vs. three), an interparietal scale shorter than parietal (vs. longer), and four temporal scales (vs. six). *Dryadosaura* further differs from *Colobosauroides* by the presence of two pairs of sternal ribs (vs. three).

Other Gymnophthalmidae having two pairs of genials are the clades Gymnophthalmini (*Gymnophthalmus*, *Psilophthalmus*, *Nothobachia*, *Calyptommatus*), Heterodactylini (*Colobosaura*, *Stenolepis*, *Colobodactylus*, *Heterodactylus*), and some species of the Cercosaurini (*Bachia*). Among other characters, *Dryadosaura* differs from the first group by having an eyelid (absent in the referred Gymnophthalmini), from the Heterodactylini by having small and superficial preanal and femoral pores separated by a gap (large, prominent, and continuous), and short and stout fore limbs (vs. long and slender), and from *Bachia* by the presence of a distinctive ear opening (absent). As discussed below, the sister group of *Dryadosaura* is *Anotosaura*. The absence of an external ear opening and a longer body in *Anotosaura*, compared to the shorter and stout body and the presence of a distinct ear opening in *Dryadosaura* suggest different adaptation processes for these two radiations.

***DRYADOSAURA NORDESTINA* SP. NOV.**

(FIGS 1–4)

Holotype: MZUSP 60635, an adult male from João Pessoa (07°07'S, 34°52'W): state of Paraíba: Brazil, collected by Miguel T. Rodrigues 6 September 1983.

Paratypes: MZUSP 60334, 60336–60339, 61132, 65983, 65984, 65987, 65988, from João Pessoa, state of Paraíba; MZUSP 66352, 87709–87719, from Serra dos Cavalos, state of Pernambuco; MNRJ 9931, from Recife (Parque Dois Irmãos), state of Pernambuco; MZUSP 93218–93222, and MUFAL 1537, 1540–1546, Murici (Fazenda Bananeiras); MUFAL 293–296, Pontal do Peba, Piaçabuçu, State of Alagoas; MUFAL 1547, from Mata do Catolé, Maceió, state of Alagoas; MUFAL 1534–1536, 1538, 1539, Mata do Cedro, Rio Largo, state of Alagoas; MUFAL 055, from Natal (Parque Estadual das Dunas), state of Rio Grande do

Norte; MUFAL 007, Praia de Cutuvelo, Parnamirim, state of Rio Grande do Norte; MUFAL 052, Tibaú do Sul, State of Rio Grande do Norte.

Etymology: Nordestina refers to north-eastern Brazil, the geographical region where the species occurs.

Diagnosis: Microteiid characterized by an elongate body, five toes and fingers, and short stout limbs. Collar fold, ear opening, and eyelid present. Frontonasal single; prefrontals, parietals and interparietals present; frontoparietals absent. Two pairs of chin shields; three supraoculars. Dorsal scales in 23–25 regular transversal rows; anteriorly smooth, becoming progressively hexagonal and mucronate; keeled at rump level. Lateral scales similar to dorsals, smooth, rectangular, laterally imbricate. Ventral scales smooth, juxtaposed or slightly imbricate, rectangular, in 15–17 rows; 26–33 scales around midbody. Infradigital lamellae mostly divided 6–9 in finger IV, and 13–16 in toe IV. Preanal and femoral pores number four and six, respectively, in males; 2–4 preanal pores in females.

Description of holotype (Fig. 1A–C): Rostral broad, wider than high, contacting first supralabial, nasal and frontonasal. Frontonasal pentagonal, wider than long, contacting rostral, nasal, loreal and prefrontals. Prefrontals pentagonal, almost as long as wide, in broad contact at midline; midline suture shorter than suture with frontonasal. Frontal heptagonal, slightly longer than wide, wider posteriorly; anterior margin angulose, indenting prefrontals, lateral margins almost parallel, slightly divergent posteriorly, contacting second and third supraoculars, posterior margins diagonally contacting parietals and in straight contact with interparietal. Frontoparietals absent. Interparietal subrectangular, longer than wide, as long as or slightly longer than, and narrower than frontal, narrower than parietals. Lateral margins of interparietal slightly diverging posteriorly; left suture of the scale incomplete posteriorly. A pair of very large irregularly hexagonal parietals in straight lateral contact with interparietal and also anteriorly contacting the frontal, and laterally contacting third supraocular and postocular; posterior part of parietals almost rounded and contacting two large temporal and two smaller occipital scales.

Three supraoculars, first slightly smaller than third, second the largest, as large as prefrontal; first supraocular contacting prefrontal, second supraocular in broad contact with frontal, third supraocular in broad contact with parietal. Nasal mostly above first supralabial, and also contacting second infralabial, loreal, frontonasal and rostral, large, longer than high, with nostril centrally placed in the lower part of scale, and slightly indenting suture with first labial. Loreal posterior to nasal, narrower and diagonally

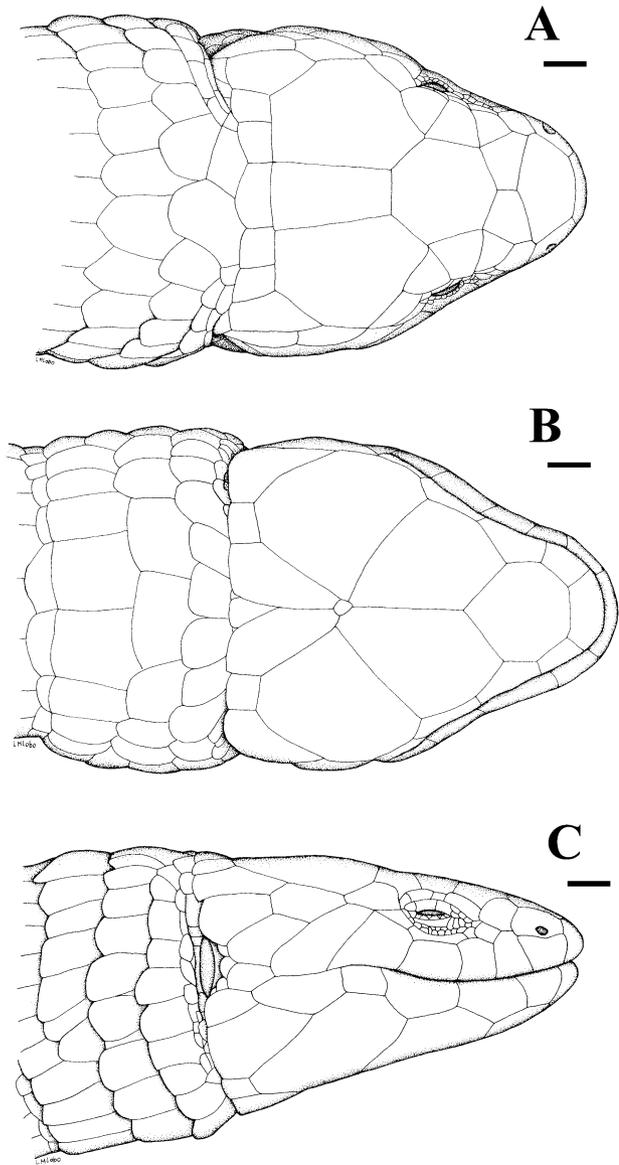


Figure 1. Dorsal (A), ventral (B), and lateral (C) view of the head of the holotype of *Dryadosaura nordestina* (MZUSP 60635). Scale bars = 1 mm.

orientated; contacting frontonasal, prefrontal, first supraocular, a small frenocular, and second supralabial. Frenocular small, longer than high, followed posteriorly by two suboculars, the second the largest. Six supralabials; fourth under the eye, fifth and sixth the highest, fourth and sixth the largest, first and second subequal, smaller. Fourth supralabial separated from the eye by a large subocular posteriorly followed by a scale which contacts fifth supralabial and a postocular inserted between third supraocular and parietal. Sixth supralabial followed posteriorly by an elongate granule which contacts anterior margin of ear. Four

superciliaries, second smallest, first the largest, wider anteriorly, longer than first supraocular, contacting 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 and irregularly shaped smooth granules. Lower eyelid with 8-9 strongly pigmented palpebrals. Temporal region with four large, smooth and juxtaposed scales between parietal, sixth supralabial, and the ear, two of them diagonally contacting the sixth labial. Ear opening surrounded by a series of small and juxtaposed granules contacting anteriorly two large temporals, and two much smaller elongate and juxtaposed flat granules; external auditory meatus small, tympanum distinct, subovoid with anterior margin rounded. Lateral surface of neck with smooth scales, irregular in size and shape, varying from juxtaposed to slightly imbricate, and arranged in irregular transverse series between ear and shoulder. All head scales smooth and juxtaposed with scattered sensorial organs.

Mental broad, wider than high. Postmental heptagonal, longer than wide. Two pairs of genials, both contacting infralabials; the first smaller and in broad contact at midline, the second separated by an enlarged pair of flat and elongate pregenials, which contact at midline, preventing contact between second pair of chin shields. Five infralabials, first smallest, all others subequal. Gulars smooth, imbricate, quadrangular, juxtaposed to slightly imbricate, irregular in size, in five transverse rows. Gulars followed by a distinct interbrachial region with eight larger and elongate scales. A distinct collar fold characterized by some granules and reduced scales in the second row of gulars preceding the interbrachial row.

Dorsal scales disposed in regular transversal rows, anteriorly smooth, imbricate, rounded in the occipital region, becoming progressively narrower, more elongate and rectangular towards the arm level, and then progressively hexagonal, with lateral sides almost juxtaposed, keeled at rump level. Twenty-five transverse rows of dorsals between interparietal and the posterior level of hind limbs. Lateral scales about the same size as dorsals but smooth, rectangular, imbricate laterally, not acuminate and more diagonally orientated than dorsals; those closer to ventrals larger. A series of transversally arranged granules in the skin separating transverse series of lateral scales. A distinctive area with granular scales surrounds the area of arm insertion. Scales around midbody 28. Ventral scales smooth, laterally juxtaposed, slightly imbricate anteroposteriorly, rectangular, about twice as long as wide; 15 transverse rows from interbrachials (excluded) to preanals. Four scales in precloacal region, the central ones the largest. Ten pores (four preanal, six femoral).

Tail scales shorter and more imbricate anteroposteriorly than midbody dorsals, otherwise identical to them, keeled, lanceolate; those from ventral part of tail base wider than those of dorsal part, becoming gradually identical in size towards tip of tail. Tail regenerated with rectangular and smooth scales.

Fore limbs extremely robust with large, smooth and imbricate scales, larger and flat dorsally; those from ventral part of brachium smaller. Forearm as long as thick. Anterior and ventral parts of hind limbs with irregularly large, smooth and imbricate scales, largest scales ventrally. Posterior part of hind limbs with granular and juxtaposed scales. Dorsal part of tibia and femur with keeled, imbricate scales. Carpal and tarsal scales large, imbricate; supradigital lamellae smooth, imbricate. Palmar and plantar surfaces with smooth, small granules; infradigital lamellae mostly divided, seven on finger IV and 15 on toe IV. Fingers and toes clawed, respectively, with the following relative sizes: $1 < 2 = 5 < 4 < 3$ and $1 < 5 < 2 < 3 < 4$.

Dorsal surfaces of body and tail and lateral part of tail dark brown with an irregularly distributed yellowish reticulate or interrupted pattern. Yellow pigment is concentrated in parietal area of head and along dorsolateral part of body where irregular and enlarged spots occupy the central part of scales, delimiting a discontinuous pale line. Flanks predominantly yellowish to cream, as the ventral parts of body and tail, but strongly mottled with an irregular dark brown pattern. Lateral parts of head predominantly dark brown with scattered yellow spots concentrated in the suture region of posterior labials; ventral part of the head creamy yellow, immaculate, except for infralabials and scattered and irregular dark brown pigmentation on the posterior part of last pair of genials. Ventral parts of body and tail creamy yellow, immaculate. Ventral part of tail becomes gradually darker distally. Limbs dark brown, irregularly mottled with yellow dorsally, creamy yellow and immaculate ventrally. Palmar and plantar surfaces greyish.

Measurements of holotype: SVL 54 mm; tail length 31 mm, regenerated.

Variation: Regardless of sex, range variation in scale counts are as follows: 23–25 dorsal, 15–17 ventral, 23–33 around the body; 6–9 lamellae in finger IV, and 13–16 lamellae in toe IV. Apart from differences in scale counts there is little variation in scalation in the type series. The shape of the lateral margins of the interparietal varies from straight to slightly divergent, as does the condition of the second pair of genials; these are in contact at midline in most specimens, although the extent of contact varies. Although in most specimens prefrontals are in broad contact, in two specimens (MUFAL 007, 293) the frontonasal and frontal

are in slight contact, preventing contact between prefrontals. Number of supra- and infralabials is fairly constant, but some variation also occurs. In two specimens (MZUSP 60638, 60636) sutures between supralabials are incomplete between 4th and 5th supralabials; in two specimens there are seven (MZUSP 60637) or four (MUFAL 1536) supralabials in one side, instead of six. As in the holotype, most of specimens have five infralabials, but some have four due to a fusion between an infralabial and the second pair of genials. Some specimens show only two superciliaries due to a fusion between first and second.

All adult males have a total of ten pores, four preanal plus six femoral; these are also observed in juveniles but are not so conspicuous. Most adult females have two rather inconspicuous preanal pores (exceptionally four); femoral pores are absent in females. Males are slightly larger than females (maximum SVL, respectively, 57 mm and 52 mm) and have a massive musculature in the temporal region (less developed in females). Tail length varies between 1.14 and 1.45 SVL. There is little variation in colour pattern except for the brown pigmentation on the lateral part of the head, which can be more or less extensive, and the ventral colour of live adult males, which is more

reddish compared with the creamy venter of adult females.

Hemipenis (Fig. 2): The hemipenis of four specimens (MZUSP 65983, 87711, 87712, 87718) although without the apex totally everted, shows distinctive bilobation. The sulcate face of the organ lacks ornamentation and is characterized by a conspicuous sulcus spermaticus, which bifurcates centripetally towards the apex of each lobe. The opposite face has two longitudinally aligned series of 4–5 large spines, separated by naked intervals of about the same size as the spines, which converge at the base of the organ. The right and left lobes are symmetrical, with two longitudinal series of about 20 frounces with evident comb-like spines separated by areas without ornamentation.

Osteology (Figs 3A, B, 4A–D): The following description is based on three alizarin prepared skeletons (MZUSP 66230, 93422, 93423). Premaxillary broader than long, touching but not articulating laterally the maxillary, its posterior border straight, covering the anterior part of nasals; 11 premaxillary conical teeth. Nasals large, longer than wide, wider anteriorly, in broad contact at midline and covering the anterior

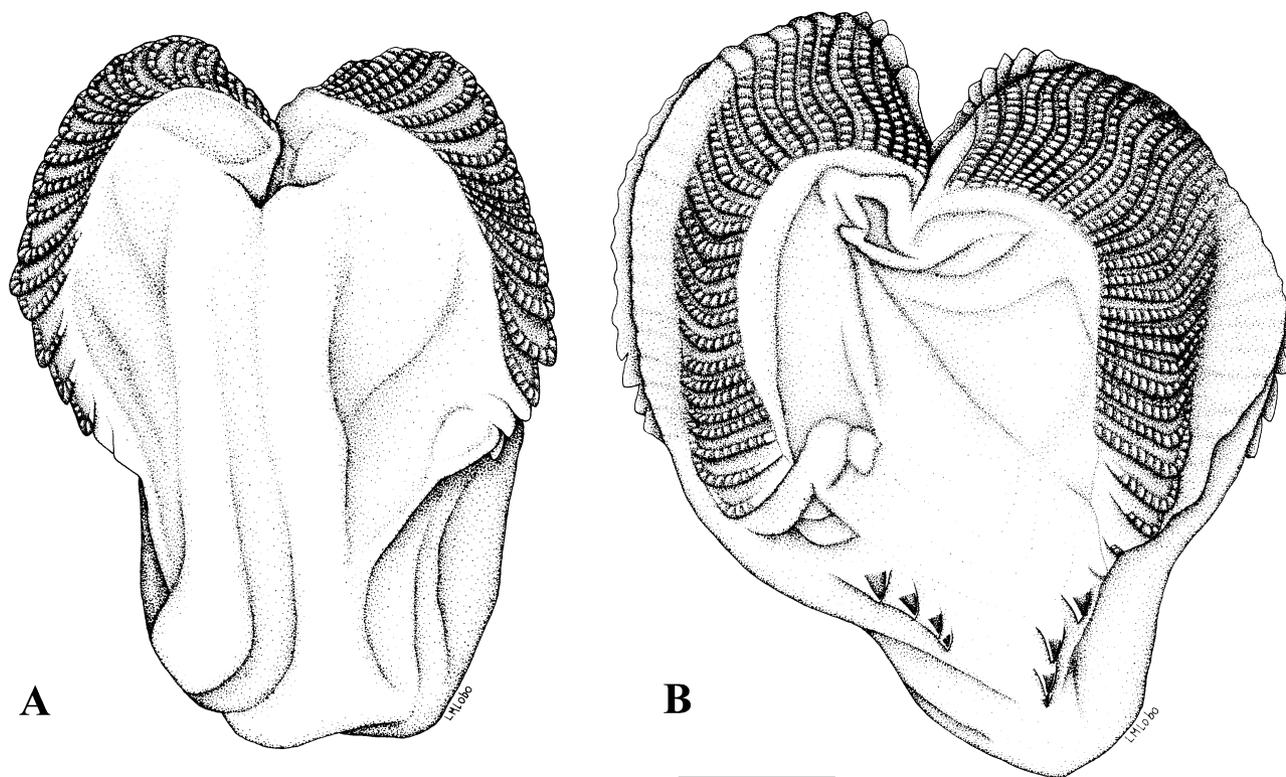


Figure 2. Sulcate (A) and asulcate (B) face of the right hemipenis of *Dryadosaura nordestina* (MZUSP 65983). Scale bars = 1 mm.

margin of the frontal. Frontal as long as wide, wider posteriorly, covering parietal by a pair of frontoparietal tabs. Parietal longer than wide, wider posteriorly and covering the lateral margin of the occipital region. Epipterygoid wider above, contacting externally the descending epipterygoid process of the parietal. Maxillary contacting nasal dorsally, almost without overlapping, covering extensively the prefrontal and posteriorly contacting the jugal; 12–13 maxillary teeth.

Prefrontal large, posterior process long, in broad contact with frontal and forming the major part of the dorsal part of the orbital region. Lacrimal absent, apparently fused to the prefrontal and forming a slight median protuberance at the anterior part of the orbita. Postfrontal and postorbital fused in an anteriorly very wide postorbitofrontal, closing posteriorly the orbita and contacting dorsally the frontal and parietal, ventrally the jugal, and externally and posteriorly the squamosal. Squamosal posteriorly curved, fitting at the top of the quadrate. Supratemporal fenestra opened, but constrained anteriorly by the parietal and postorbitofrontal, and posteriorly by the parietal. Supratemporal present, in straight contact with posterior part of parietal. Thirteen scleral ossicles in the eye. Vomer, palatine, pterygoid and ectopterygoid present. Vomer, palatine, premaxillary and

maxillary in contact, restricting the fenestra exocoanalis. Infraorbital fenestra large, bordered posteriorly by the ectopterygoid. Stapes rod-like, wider at the base. Sutures between the supraoccipital, exoccipital, basioccipital and otic area of the skull are not as visible as those between the basioccipital and basisphenoid. Processes basipterygoides and parashynoidales are well developed.

In the lower jaw the dentary, articular, splenial, angular, and supra-angular are distinct; there are 14–15 dentary teeth, conical anteriorly, bicuspid or tricuspid posteriorly.

Glossohyal long, separated from basihyal. First ceratobranchial curved and wider posteriorly; hypohyal and ceratohyal present.

Anterior part of clavicle flattened, enlarged, enclosing a fenestra. Interclavicle long, elongate, with lateral processes extremely reduced, reaching the posterior part of sternal fenestra. Coracoid, scapular, and scapulocoracoid fenestrae present in the scapulocoracoid; suprascapula present. Sternum with a large fenestra, two sternal ribs and a xiphisternum receiving two inscriptional ribs. Ilium, ischium and pubis present, the latter with a conspicuous pectinate apophysis. Hypoischium long, almost reaching the preanal border; a small preischium present.

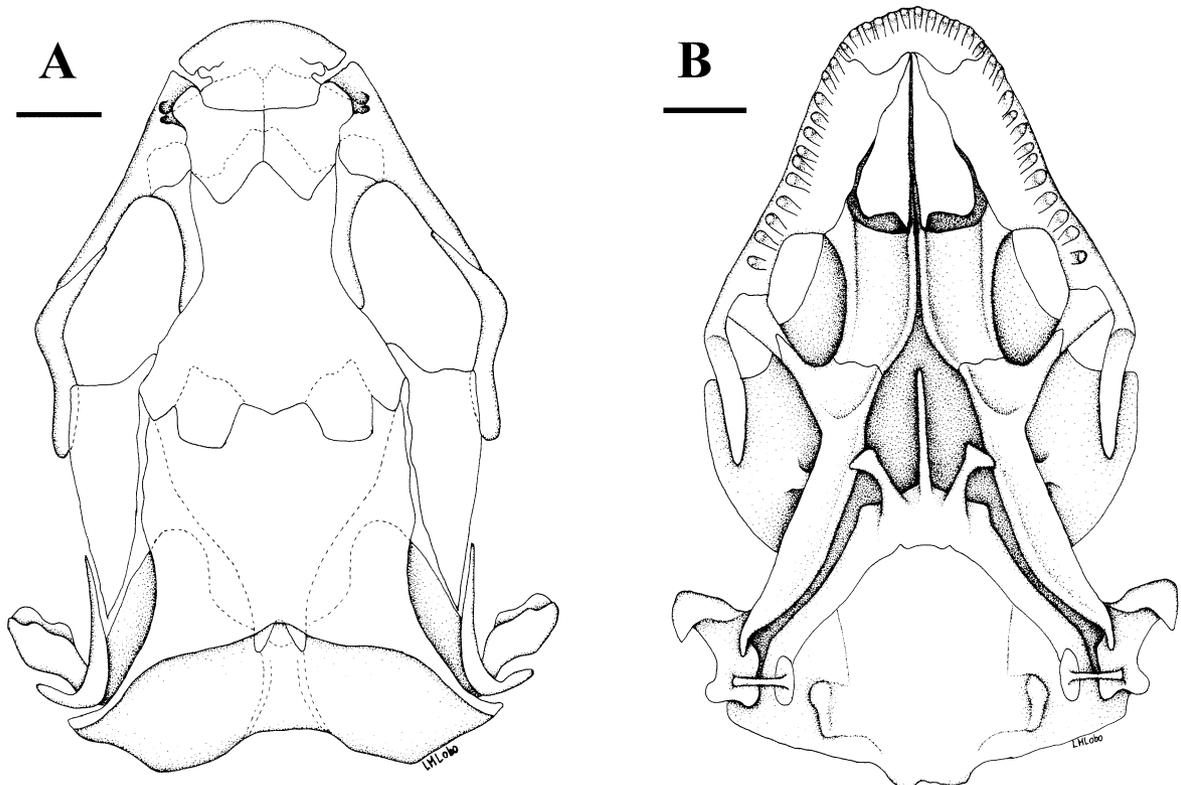


Figure 3. Dorsal (A) and ventral (B) view of the skull of *Dryadosaura nordestina* (MZUSP 93422). Scale bars = 1 mm.

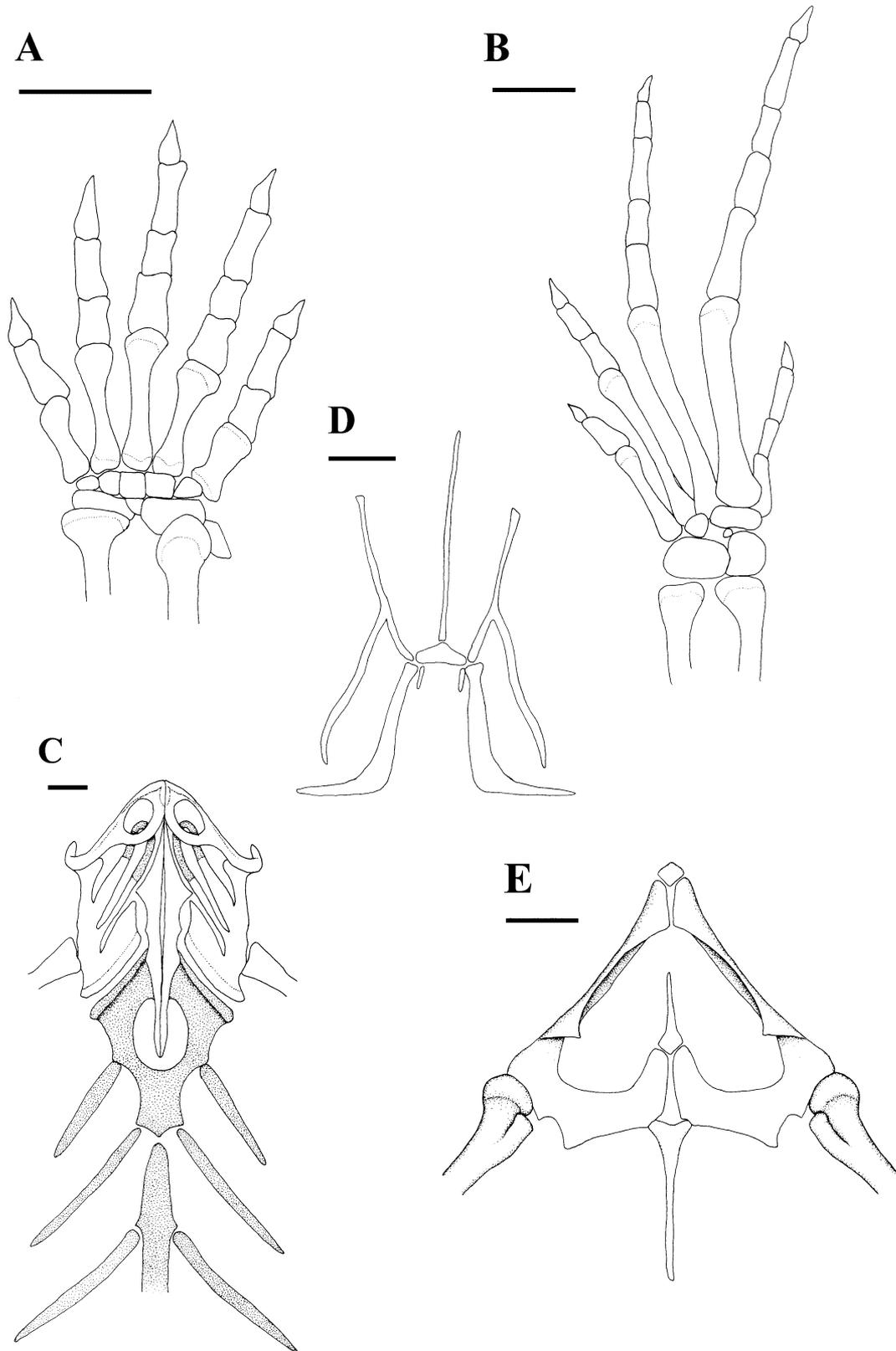


Figure 4. Right hand (A), right foot (B), shoulder girdle (C), hyoid (D), and pelvic girdle (E) of *Dryadosaura nordestina* (MZUSP 93422). Scale bars = 1 mm.

Twenty-five procoelous presacral vertebrae, neural spines low, higher anteriorly; hypopophyses present in the first six vertebrae; zygantrum-zygosphene present. Last presacral vertebra lacking ribs. Two sacral vertebrae.

Humerus and femur slightly larger than radius and ulna and tibia and fibula. Remaining elements of fore and hind limbs as in Figure 4A, B.

Ecology and distribution: *Dryadosaura nordestina* occurs in the remnant patches of Atlantic Forest domain (Ab'Saber, 1977) from the state of Rio Grande do Norte to the northern bank of Rio São Francisco in the state of Alagoas. All specimens were collected on the forest floor, either by hand under logs, or searching leaf litter, or with pitfall trap; we never saw active individuals except for one specimen crossing a trail at Mata da Salva (municipality of Rio Largo, state of Alagoas) at 16.00 hrs. We suggest that their massive head and forelimb musculature might be associated with fossorial and digging habitats. *Dryadosaura nordestina* is apparently restricted to the Atlantic forests near the coast and does not extend inland to the isolated forest islands of the open semiarid *Caatingas* of north-eastern Brazil. These forest remnants are relicts from times when the Atlantic forest covered a larger area in the semiarid *Caatingas* (Vanzolini, 1981; Rodrigues, 2003). The westernmost record for *D. nordestina* is Serra dos Cavalos, a forested mountain near the Atlantic forest/*Caatinga* transition in the state of Pernambuco.

Phylogenetic analyses

Parsimony analysis to determine the phylogenetic placement of *Dryadosaura* based on 37 morphological characters (all informative, Table 1) with all states coded as unordered, produced a single most parsimonious tree of 86 steps (CI = 0.60, RI = 0.72) (Fig. 5A). (*Colobosauroides cearensis* (*Anotosaura vanzolinia* + *Dryadosaura nordestina*)) are recovered in a well supported clade (BS = 88; Bremer value = 5.0), with the (*D. nordestina* + *A. vanzolinia*) clade supported at a level of BS = 76 and Bremer value = 1.0. The Ecleopini clade was not recovered by the morphological partition alone, but there is no support (BS < 50%; Bremer value = 1.0) for the large clade that includes the ecleopines *C. cearensis*, *A. vanzolinia*, *D. nordestina*, *Arthrosaura reticulata*, *Ecleopus gaudichaudii*, *Leposoma osvaldoi*, plus the cercosaurinae *Bachia bresslaui* and the heterodactylines *Iphisa elegans* and *Colobosaura modesta* (Fig. 5A).

Combined analyses of the morphological and molecular partitions resulted in a single most parsimonious tree of 2413 steps and 632 parsimony-informative characters (CI = 0.54, RI = 0.44) (Fig. 5B). The ecle-

opines are recovered as a strongly supported clade (node 1: BS = 90; Bremer value = 9; Table 2) related to Cercosaurini, with higher nodal support both for the (*Colobosauroides* (*Anotosaura* + *Dryadosaura nordestina*)) clade (node 4: BS = 100; Bremer value = 29), than the nested (*D. nordestina* + *A. vanzolinia*) clade (node 5: BS = 84; Bremer value = 8).

These analyses also recovered the sister-group relationship between Heterodactylini and Gymnophthalmini (node 11: BS = 98; Bremer value = 14) as well the monophyly of each (node 10: BS = 100; Bremer value = 17 and node 12: BS = 100; Bremer value = 21, respectively; Table 2). The monophyly of Cercosaurini was not recovered, but support for the alternative topology ((*Rhachisaurus* + *Bachia*) *Cercosaura*) was very low (node 7: BS < 50; Bremer value = 6 and node 8: BS < 50; Bremer value = 3). Although the Ecleopini was recovered as a highly supported monophyletic group (node 1), this was not the case for its sister group when assembling the taxa included in node 9 (BS < 50; Bremer value = 3; Fig. 5B).

DISCUSSION

Considering that many species and genera of Gymnophthalmidae are still unknown beyond their original descriptions, and that new genera are still being discovered on a regular basis (at least five new genera have been recently described, see Rodrigues & Juncá, 2002), we are still far from having a broad survey of morphological characters for a significant number of taxa. As a comprehensive assembling of morphological data for all genera will require a huge effort, we suggest that the presentation of morphological information for selected groups, targeting specific questions that can be addressed by combining molecular and morphological data, will be useful to refine published hypotheses and extend our knowledge of the evolution of this clade on an incremental basis.

The morphological data set used in this study recovered a sister group relationship between *Dryadosaura nordestina* and *Anotosaura vanzolinia* (BS = 76; Bremer value = 1.0) as well as *Colobosauroides cearensis* as their sister taxon (BS = 88; Bremer value = 5.0; Fig. 5A). These relationships were also recovered by the combined analyses, but with much higher support indexes (nodes 4 and 5; Fig. 5B). The partitioned Bremer indexes (Table 2) show the relevant contribution of the morphology to improving support for both of these nodes. Of the six data sets combined in a single character matrix, the morphological set is the second in influence in the support of node 5 [the (*Dryadosaura* + *Anotosaura*) clade], and first for node 4 [(*Colobosauroides*(*Dryadosaura* + *Anotosaura*); see Table 2].

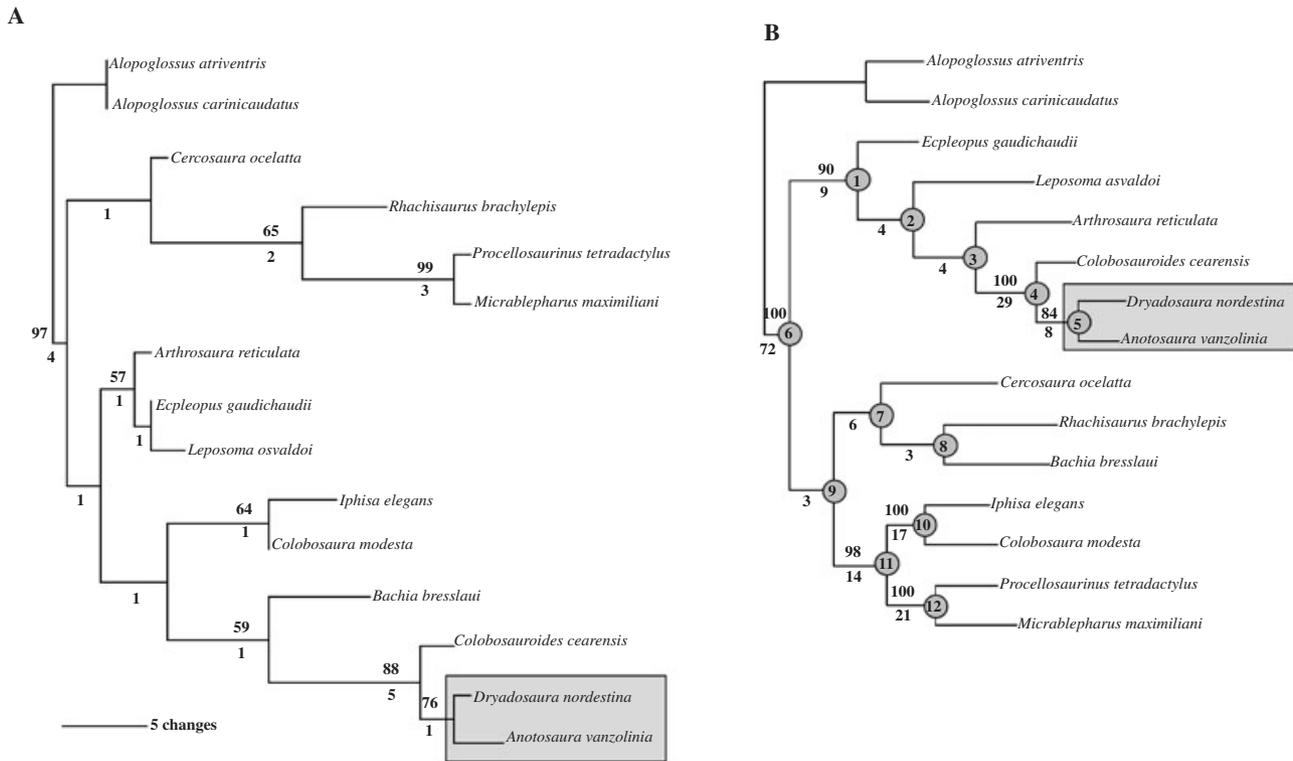


Figure 5. Single most parsimonious tree recovered from analyses of: (A) morphology (L = 86, CI = 0.60, RI = 0.72) and (B) combined morphology and molecular partitions (L = 2413, CI = 0.54, RI = 0.44). Numbers above and below branches represent bootstrap (> 50%) and total Bremer indexes, respectively. The internal nodes are numbered (circles) and support indexes are listed in detail for each node (Table 2). The inset includes *Dryadosaura nordestina* and its sister taxon.

Table 2. Measures of support for all internal nodes of the most parsimonious tree recovered from the combined analysis of morphology (morph) and molecular partitions (Fig. 5B). Columns present the bootstrap proportions, total and partitioned Bremer. 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 & DeSalle, 1997; Gatesy & Arctander, 2000). Node # 5, highlighted in bold, presents the support for the relationship between *Dryadosaura nordestina* and its sister taxon (see Fig. 5B)

| Node # | Bootstrap support | Bremer support | Partitioned Bremer | | | | | |
|----------|-------------------|----------------|--------------------|-------------|-------------|------------|------------|------------|
| | | | 12S | 16S | ND4 | 18S | c-mos | morph |
| 1 | 90 | 9 | -6.0 | 2.5 | 9.5 | -1.0 | 2.0 | 2.0 |
| 2 | <50 | 4.0 | -7.0 | -2.0 | 12.0 | 0.0 | 0.0 | 1.0 |
| 3 | <50 | 4.0 | -7.0 | -2.0 | 12.0 | 0.0 | 0.0 | 1.0 |
| 4 | 100 | 29.0 | 5.0 | -1.0 | 11.0 | 0.0 | 0.0 | 12 |
| 5 | 84 | 8.0 | -7.0 | -2.0 | 12.0 | 0.5 | 0.0 | 4.5 |
| 6 | 100 | 72 | 0.0 | 16.0 | 20.0 | 2.0 | 28.0 | 6.0 |
| 7 | <50 | 6.0 | -9.0 | 1.0 | 12.0 | -2.0 | 2.0 | 2.0 |
| 8 | <50 | 3.0 | 0.0 | 2.0 | -4.0 | -2.0 | 1.0 | 6.0 |
| 9 | <50 | 3.0 | -1.0 | 3.0 | 1.0 | 1.0 | 0.0 | -1.0 |
| 10 | 100 | 17.0 | 3.0 | 0.0 | 10.0 | 0.0 | 5.0 | -1.0 |
| 11 | 98 | 14.0 | -1.0 | 6.0 | 0.0 | -2.0 | 8.0 | 3.0 |
| 12 | 100 | 21.0 | 2.0 | 2.0 | 3.5 | -1.0 | 11.0 | 3.5 |

The molecular analyses for the Gymnophthalmidae performed by Castoe *et al.* (2004) under a Bayesian framework recovered an alternative topology that places *A. vanzolinia* and *C. cearensis* as sister taxa, but with very low support (posterior probability = 0.51), with a well supported *Dryadosaura* (referred to by Castoe *et al.* as *Anotosaura* spn.) as their sister taxon [(*Dryadosaura*(*Anotosaura vanzolinia* + *Colobosauroides*)); posterior probability = 1.0]. Our topology is supported by four morphological characters, including absence of frontoparietal scales, number of temporal scales, size of the interparietal scale, and number of sternal ribs (congruence of characters 5, 7, 9, 24, respectively; Appendix 1). It is worth pointing out here that *Colobosauroides* was always thought to be related to *Colobosaura* based on external similarity, but never with *Anotosaura* (Cunha, Lima-Verde & Lima, 1991; Soares & Caramaschi, 1998).

Although the taxonomic sampling here is limited with regard to total microteiid diversity, and was mainly orientated to test the relationships of *Dryadosaura*, our analysis recovered several monophyletic groups of Gymnophthalmidae originally recognized by Pellegrino *et al.* (2001). The morphological partition confirms the distinctiveness of *Rhachisaurus*; it is unrelated to *Anotosaura* (as previously thought), and it is recovered as the sister group of the (*Procellosaurinus* + *Micrablepharus*) clade (Fig. 5A), but as the sister taxon to *Bachia* in the combined analysis (Fig. 5B). Both positions are only weakly supported and cannot be resolved with our data.

Our combined analyses of morphological and molecular characters recovered the ecleopines as a monophyletic group unrelated to the Cercosaurini (node 1, Fig. 5B), in agreement with Castoe *et al.* (2004), who raised this clade to subfamilial status. Our combined data hypothesis (Fig. 5B) recovered the following ecleopine topology: (*Ecleopus* (*Leposoma* (*Arthrosaura* (*Colobosauroides* (*Dryadosaura* + *Anotosaura*))))), whereas the topology of Pellegrino *et al.* (2001) recovered the same basal genera to the referred clade but in a different sequence: (*Arthrosaura* (*Leposoma* (*Ecleopus* (*Colobosauroides* (*Dryadosaura* + *Anotosaura*))))).

A very different topology for the Ecleopinae was presented by Castoe *et al.* (2004): *Ecleopus* was recovered as the sister taxon of all other ecleopines which were represented by two monophyletic assemblages: (*Ecleopus* (*Dryadosaura* (*Anotosaura* + *Colobosauroides*)) + (*Arthrosaura* + *Leposoma*)). Support for placement of the basal genera is weak for all of these topologies, but all of the nodes supporting ecleopines (1–5) in Figure 5B are supported by at least two independent data partitions (mtDNA + nuclear, mtDNA + morphology, or nuclear + morphology; Table 2), and this is the strongest possible support

when traditional measures of nodal support (i.e. bootstrap or decay values) are low (Flores-Villela *et al.*, 2000). Considering the contribution of the morphological characters to this topology (all five nodes; Table 2), we accept this topology as the best working hypothesis of relationships within this clade, pending additional studies.

A weakly supported sister-group relationship between the Gymnophthaminae and a (*Rhachisaurus* + *Bachia*) *Cercosaura*) clade was recovered by our combined analysis (node 9), and although taxon sampling is extremely limited, this same analysis recovered strongly supported clades Gymnophthaminae (node 11), Heterodactylini (node 10) and Gymnophthalmini (node 12; Fig. 5B). Two of these are supported with a significant contribution from the morphological data set (nodes 11 and 12; Table 2). This result reinforces the previous tribal allocations in Gymnophthaminae suggested by Pellegrino *et al.* (2001), in contrast with the Castoe *et al.* hypothesis for a paraphyletic Heterodactylini, and removal of the tribal division within Gymnophthaminae. We will return to this issue in another paper devoted to the discussion of the Heterodactylini relationships.

Both Pellegrino *et al.* (2001) and Castoe *et al.* (2004) recovered the Rhachisaurinae as the sister clade of Gymnophthaminae. The partitioned Bremer indexes clearly revealed that morphology represents the major contribution to the support of the sister relationship between *Rhachisaurus* and *Bachia* (node 8; Table 2), and this comes from characters classically subject to convergence (i.e. limb reduction, body elongation, earlessness; Appendix 1). Finally, although our taxonomic sampling of Cercosaurini is limited (of the 13 genera now accepted [Doan, 2003] only *Bachia* and *Cercosaura* are represented here), our combined analysis does suggest that morphological data are phylogenetically informative within the Gymnophthalmidae. Despite the potential for convergence or parallelism in some character complexes (which can be explained in the context of a best-supported phylogeny inferred from molecular and other morphological data; Scotland *et al.*, 2003), future studies will need to include morphological characters from many more taxa and involve the collection of data from many unlinked nuclear genes.

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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*: (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) subtriangular with end pointed towards but not reaching frontal; (3) large, subretangular, contacting frontal

APPENDIX 2

ADDITIONAL SPECIMENS EXAMINED

Stored in alcohol

Alopoglossus atriventris: MZUSP 13922–13924. Estiron, Rio Ampiyacu, Peru. *Alopoglossus carinicaudatus*: MZUSP 53683–53684. Cachoeira do Limão, Rio Tapajós, Pará. *Anotosaura collaris*: MZUSP 788, holotype, Villa Nova, Bahia. *Anotosaura vanzolinia*: MZUSP 47754, Serra Negra, Inajá, Pernambuco; MZUSP 60773, 60775–60777, 60780–60785, Cabaceiras, Paraíba; MZUSP 80151, Xingó, Alagoas. *Arthrosaura reticulata*: MZUSP 82644–82646 Aripuanã, Mato Grosso. *Bachia bresslaui*: MZUSP 10300. Utiariti, Mato Grosso. *Cercosaura ocellata*: MZUSP 82425–82427 Juruena, Mato Grosso. *Colobosaura modesta*: MZUSP 81346–81362. Caldas Novas, Goiás. *Colobosauroides carvalhoi*: MZUSP 89453, Parque Nacional da Serra da Capivara, Piauí. *Colobosauroides cearensis*: 87580–87583, Mulungú, Ceará. *Eupleopus gaudichaudii*: MZUSP 78975, 79559 Caraguatatuba, and MZUSP 81401 Ariri, São Paulo. *Iphisa elegans*: MZUSP 82654–82676, Aripuanã, Mato Grosso. *Leposoma osvaldoi* MZUSP 82703–82737, Aripuanã, Mato Grosso. *Micrablepharus maximiliani*: MZUSP 50172–50174. Exú, Pernambuco. *Procellosaurinus tetradactylus*: MZUSP 71598–71604. Alagoado, Bahia. *Rhachisaurus brachylepis*:

MZUSP 54897, 54898, 55533, Serra do Cipó, Minas Gerais.

Cleared and stained

Alopoglossus atriventris: MZUSP 132922. *Alopoglossus carinicaudatus*: MZUSP 67488, 79544. *Anotosaura vanzolinia*: MZUSP 60772, 93417, 93418, Cabaceiras, Paraíba. *Arthrosaura kocki*: MZUSP 82951 Vila Rica, Mato Grosso. *Arthrosaura reticulata*: MZUSP 52504. *Bachia bresslaui*: MZUSP 93419, Brasília, Distrito Federal. *Cercosaura ocellata*: MZUSP 79556, Chapada dos Guimarães, Mato Grosso. *Colobosaura mentalis*: MZUSP 79557, Maracás Bahia. *Colobosaura modesta*: MZUSP 93420, Serra da Mesa, Goiás. *Colobosauroides cearensis*: MZUSP 79595, 93421, Serra de Baturité, Ceará. *Dryadosaura nordestina*: MZUSP 66230, 93422, 93423. *Eupleopus gaudichaudii*: MZUSP 79558–79559, 93424, 93425. *Iphisa elegans*: MZUSP 82654, 82658, Aripuanã, Mato Grosso. *Leposoma osvaldoi*: MZUSP 93426, UHE Samuel, Rondônia. *Leposoma scincoides*: MZUSP 79564–79565. *Micrablepharus maximiliani*: MZUSP 66233, João Pessoa, Paraíba, and MZUSP 79689–79691. *Procellosaurinus erythrocerus*: MZUSP 74935, 74942, Ibiraba, Bahia. *Rhachisaurus brachylepis*: MZUSP 55533, Serra do Cipó, Minas Gerais.