

## Comparative myology of Leiosauridae (Squamata) and its bearing on their phylogenetic relationships

Virginia Abdala<sup>1\*</sup>; Adriana S. Manzano<sup>2</sup>, Lucrecia Nieto<sup>3</sup> & Rui Diogo<sup>4</sup>

<sup>1</sup> Instituto de Herpetología, Fundación Miguel Lillo-CONICET, Facultad de Ciencias Naturales (UNT) Miguel Lillo 251 4000 Tucumán, Argentina.

<sup>2</sup> CICyTTP-CONICET. UADER. Matteri y España (3105), Diamante, Entre Ríos. Argentina.

<sup>3</sup> Cátedra de Embriología, Facultad de Ciencias Naturales (UNT) Miguel Lillo 251 4000 Tucumán, Argentina.

<sup>4</sup> Anthropology Department, George Washington University, USA

Corresponding author : virginia@webmail.unt.edu.ar

**ABSTRACT.** We present a study of the musculature of the leiosaurids, an ecologically diverse family of lizards that inhabits southern South America. Our first goal is to contribute to a better understanding of the anatomical structures, and particularly the muscular features, of leiosaurids and the related polychrotids *Anolis* sp. and *Polychrus* sp. To study these myological features in a cladistic context, we added 162 new cranial and postcranial myological characters to the 82 morphological characters of FROST et al. (2001) and assembled a matrix including 20 taxa and 244 characters including all leiosaurid genera, and analyzed them cladistically (data set II). We combined and contrasted our own muscular data with the morphological data of FROST et al. (2001) in different data sets (I, II, III) in order to analyze the evidence provided by myology against that provided by osteological and external features. The Enyaliinae is paraphyletic in all our analysis. In our analyses of data sets II and III, the Leiosauridae appears as a monophyletic group. We recovered Leiosaurinae as monophyletic in the analysis of data set II, III, and in the supertree. *Leiosaurus* genus is monophyletic in all our analyses, except that based on our data set I. *Diplolaemus* genus is monophyletic in all our analyses. *Pristidactylus* genus is a clade in our analyses of data sets II and III, while *Enyalius* genus appears as monophyletic in our analyses of data sets I, II and III. *Anisolepis* and *Urostrophus* genera are monophyletic in our supertree.

**KEY WORDS :** muscles, Maximun Parsimony, *Anolis*, *Polychrus*, Squamata

### INTRODUCTION

The Leiosauridae (FROST et al., 2001) is an ecologically diverse group of South American lizards including arboreal taxa such as *Enyalius* sp. (Wagler, 1830) and *Urostrophus* sp. (Duméril & Bibron, 1837), and terrestrial ones, such as the pristidactylines. FROST et al. (2001) consider the Leiosauridae to be composed of the Leiosaurinae and Enyaliinae (but see SCHULTE et al., 2003). Leiosaurines (*Diplolaemus* sp. (Werner, 1898), *Leiosaurus* sp. (Duméril & Bibron, 1837) and *Pristidactylus* sp. (Fitzinger, 1843)) occur mainly in Argentina, although some *Pristidactylus* species are endemic to Chile. Enyaliines (*Anisolepis* Mocquard 1887, *Enyalius*, *Urostrophus*) are also found in Argentina, but *Enyalius* sp. inhabits mainly Brazilian regions. The taxonomy of the Argentinian species of leiosaurids was studied by GALLARDO (1961; 1964), DONOSO-BARROS & CEI (1969), CEI (1986), ETHERIDGE & WILLIAMS (1991), and more recently CEI et al. (2001; 2003), among others. Chilean species were partially examined by DONOSO-BARROS (1975), but leiosaurids remain less studied than any other iguanian lizards. The relatively small and slender lizards of the family Polychrotidae (sensu FROST & ETHERIDGE, 1989; subfamily Polychrinae sensu SCHULTE et al., 1998) are usually regarded as being closely related to the leiosaurids (FROST et al., 2001; CONRAD, 2008).

Morphological traits of leiosaurids were explored by FROST et al. (2001) in their phylogenetic analysis of the iguanian lizards. These authors included a total of 82 anatomical features in the analysis, which thus remains the

most comprehensive cladistic study of leiosaurids, and thus is used as the phylogenetic framework for this study. However, leiosaurid myological structures were not included in that analysis. The scarcity of information on myology imposes serious limitations on the effective discussion of the functional anatomy, ecomorphology, phylogeny and evolution of this ecologically diverse group of lizards.

One of the main goals of this paper is to increase the understanding of the anatomy, and particularly of the myology, of leiosaurids. Another goal is to examine the bearing of myological characters on leiosaurid phylogenetic relationships in a broader anatomical and evolutionary context. We add 162 new cranial and postcranial myological characters to those 82 already analyzed by FROST et al. (2001), and assemble a matrix of 48 taxa and 244 characters (resulting in the largest morphological data set published so far for this group of lizards). We also discuss certain myological features that were found in some of the taxa examined (e.g. *Urostrophus* sp.) and that have not been previously recorded.

### MATERIALS AND METHODS

We studied 75 specimens representing 16 leiosaurid species (including all genera and 50% of the described species insofar), 16 polychrotid species, and one corytophanid species (Appendix 1). All voucher specimens are deposited in the collection of the Instituto de Herpetología, Fundación Miguel Lillo, Tucumán, Argentina. Macroscopic observation of muscles was performed

using a binocular dissection microscope. The examined specimens include all of the leiosaurid genera of the FROST et al. (2001) analysis. Because of their scarcity in collections, it is difficult to obtain leiosaurid specimens for dissection; therefore the number of species we were able to study was constrained. However, whenever possible we also included morphological data obtained by other authors in our analysis, such as that provided by CEI et al. (2003) regarding *Diplolaemus sexcinctus* (CeI et al., 2003) and by CEI et al. (2001) concerning *Pristidactylus nigroiugulus* (CeI, Scolaro & Videla, 2001). We conducted two analyses: 1) one using only our 162 myological characters (data set I: 20 taxa x 162 characters), using *Polychrus* sp. (Cuvier, 1817) as an outgroup (Appendix 2; a detailed list of these myological characters, including hind-limb features that were not published previously, is given as Additional Data); 2) the other combining these characters with the 82 osteological and external characters of FROST et al. (2001) (data set II: 20 taxa x 244 characters). We also compiled and analyzed a data set III incorporating the 48 taxa surveyed by FROST et al. (2001) and including all 244 characters. Since we were unable to perform muscular dissections of all species analyzed by FROST et al. (2001) (48 taxa), in data set II we coded as missing entries the character states of those taxa we could not examine. Our discussion focuses on the result from the analysis of data set II, since it includes almost all the characters for all the 20 taxa considered.

As a way to keep our data set II analysis as similar as possible to that of FROST et al. (2001), we used not only *Polychrus* sp. and *Anolis* sp. (Daudin, 1802), but also corytophanids, Scleroglossa, Opluridae, and *Leiocephalus* sp. (Gray, 1825) as outgroups in the second data set, exactly as they were used in FROST et al. (2001). For this purpose, for the latter three taxa we used the osteological and external morphology characters provided by FROST et al. (2001). Regarding the corytophanid *Basiliscus vittatus*, we used the characters provided by FROST et al. (2001) plus the new myological data obtained by us. As stated above, our primary focus in this study was the leiosaurids, but we did include one of the *Anolis* species studied by FROST et al. (2001): *Anolis carolinensis*. Furthermore, we dissected other *Anolis* specimens, belonging to fourteen species, in order to evaluate anatomical variability among them, although we purposely did not include all of them in our data set, so as to keep our data set similar to that of FROST et al. (2001). Thus, we included 4 *Anolis* species, so our data set consisted of only 20 taxa. Our dissections revealed constancy of myological structures in *Anolis* specimens and we are thus confident that the characters used are an appropriate representation of the variation in the genus (see below). Of the 162 myological characters included in our phylogenetic analysis, 90 are informative (i.e. they provide evidence to enable inferences about relationships between the terminal taxa used) and 72 are uninformative because they are invariant. Although the latter do not provide direct information about relationships between terminal taxa, they are useful in documenting the distinctive attributes within these taxa. Thus, by including uninformative characters in a matrix, relevant anatomic information is being considered and documented (see e.g. DIOGO, 2004a). Muscular names for the hindlimb characters follow RUSSELL (1988; 1993).

All three data sets were analyzed using the TNT program (Tree Analysis using New Technology; GOLOBOFF et al., 2003a), with maximum parsimony as the optimality criterion. All three data set analyses were conducted by generating 500 Wagner trees and then submitting them to the tree bisection-reconnection branch-swapping method (TBR), as well as Nixon's ratchet method (NIXON, 1999). With this last method it is less likely to become trapped in islands of suboptimal trees. We used jackknifing and bootstrapping to estimate the support for the branches. Standard bootstrapping is influenced by uninformative characters (and by characters irrelevant to monophyly of a given group) (HOVENKAMP, 2004). Since our data set has many uninformative characters, we rather based our discussion on the jackknife support values. Bootstrap support values are given on Fig. 2, and jackknife support values in Appendix 3.

In order to evaluate the topological congruence between our morphological data set and the results for the molecular data of FROST et al. (2001), we calculated a semi-strict supertree (GOLOBOFF & POL, 2002) combining tree topologies with different taxon sets. We decided to use this methodology since we were unable to obtain the original molecular data set of FROST et al. (2001). We compared and contrasted all morphological data, ours and that of FROST et al. (2001), with the molecular data of FROST et al. (2001) in order to avoid analyzing their morphological data twice. Thus, tree topologies resulting from the molecular analysis of FROST et al. (2001) (21 taxa) and our data set II (20 taxa) were combined. A semi-strict supertree displays all the groups that are implied by at least some combination of input trees and contradicted by none (GOLOBOFF & POL, 2002). It should be noted that this amounts to producing a consensus tree, rather than an actual phylogenetic hypothesis.

## RESULTS AND DISCUSSION

The analysis of data set I (20 taxa x 162 char.) resulted in a single most parsimonious tree with 326 steps (Fig. 1), while the analysis of data set II (20 taxa x 244 char.) resulted in a single most parsimonious tree with 493 steps (Fig. 2). In both trees, three nodes are well supported (Appendix 3), with jackknife and bootstrap support values of 100% (*Anolis*, *Enyalius*, and *Diplolaemus* nodes), which suggest that the monophyly of these taxa is a sound hypothesis. Most of the nodes received similar values with both support measures, except nodes 29 and 32 that received no support with bootstrap. In general, deeper nodes have lower support values (e.g. leiosaurines have a jackknife value of 35%), although there are some exceptions, such as the Leiosauridae, which is supported by a jackknife value of 63% (Appendix 3). The analysis of the complete morphological data set of FROST et al. (2001) plus our data (data set III: 48 taxa x 244 char.), resulted in five most parsimonious trees, with 712 steps. The strict consensus of these five trees is shown in Fig. 3. By combining the tree topologies arising from the analysis of the molecular data of FROST et al. (2001) and the tree from our data set II, we obtained a semi-strict supertree (Fig. 4).

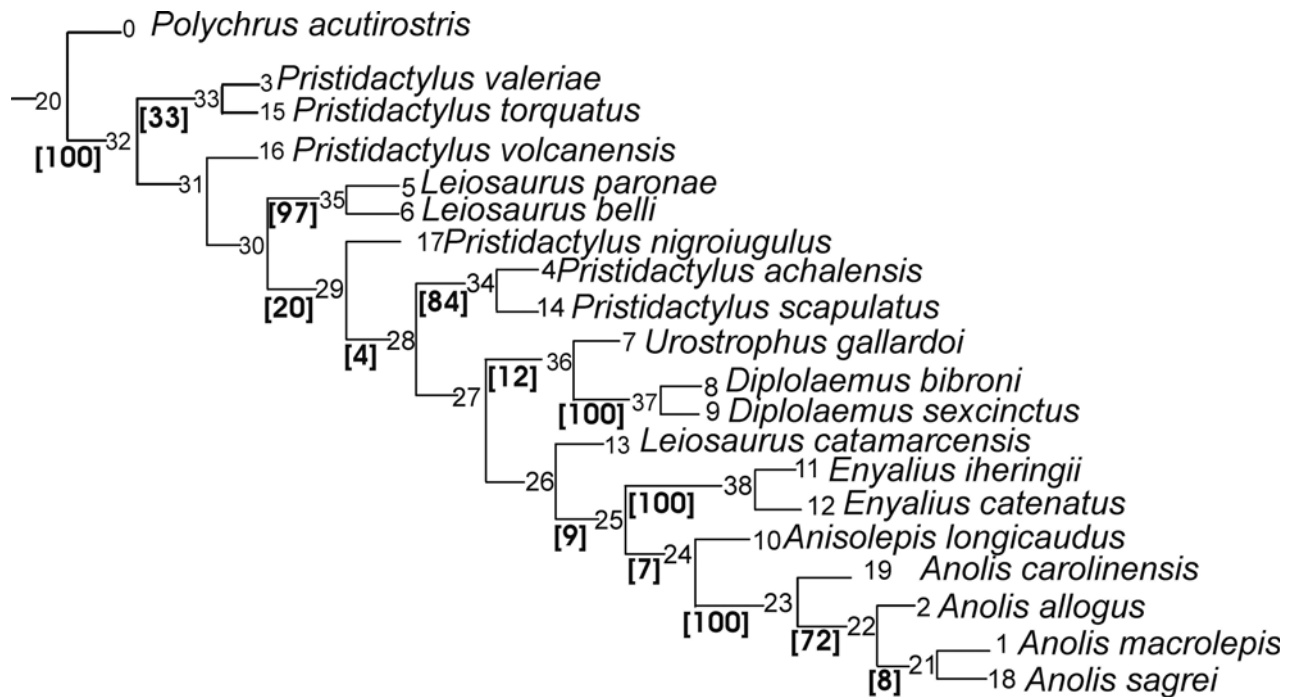


Fig. 1. – Tree generated from analyzing data set I (20 taxa x 162 all myological characters). Node numbers and bootstrap support values (in square brackets) are shown. Nodes without indicated values have no support.

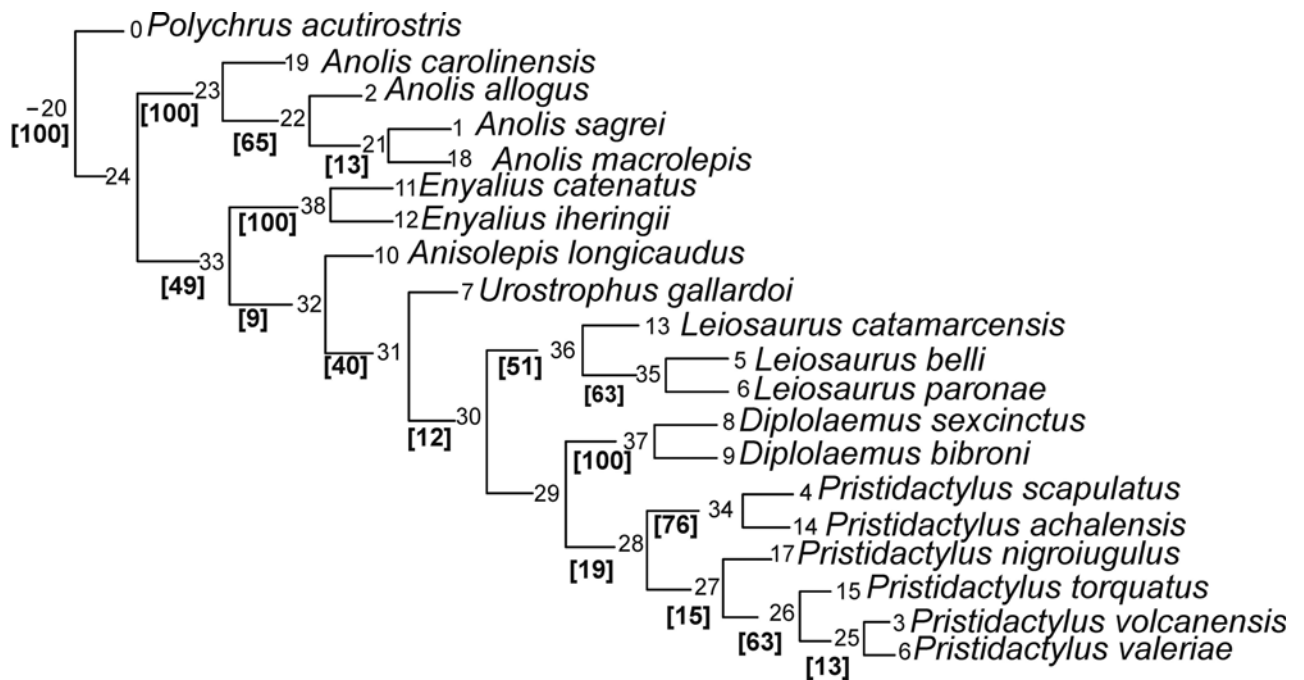


Fig. 2. – Tree generated from analyzing data set II: myological data plus morphological characters of FROST et al., 2001 (20 taxa x 244 characters). Node numbers and bootstrap support values (in square brackets) are shown. Nodes without indicated values have no support.

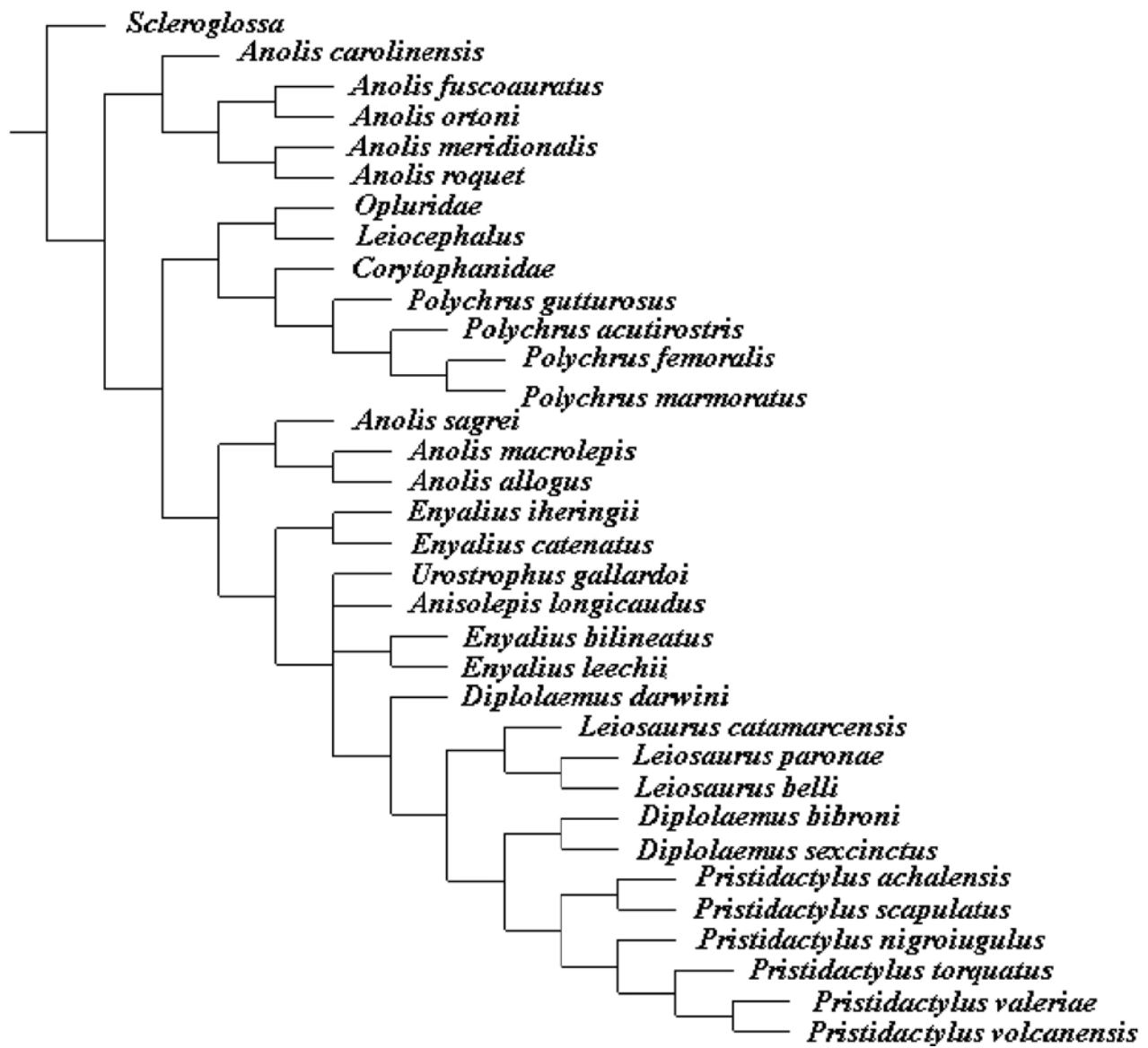


Fig. 3. – Strict consensus of 5 equally most-parsimonious trees generated from analyzing data set III using FROST et al.'s, (2001) morphological characters plus our myological characters (48 taxa x 244 characters).

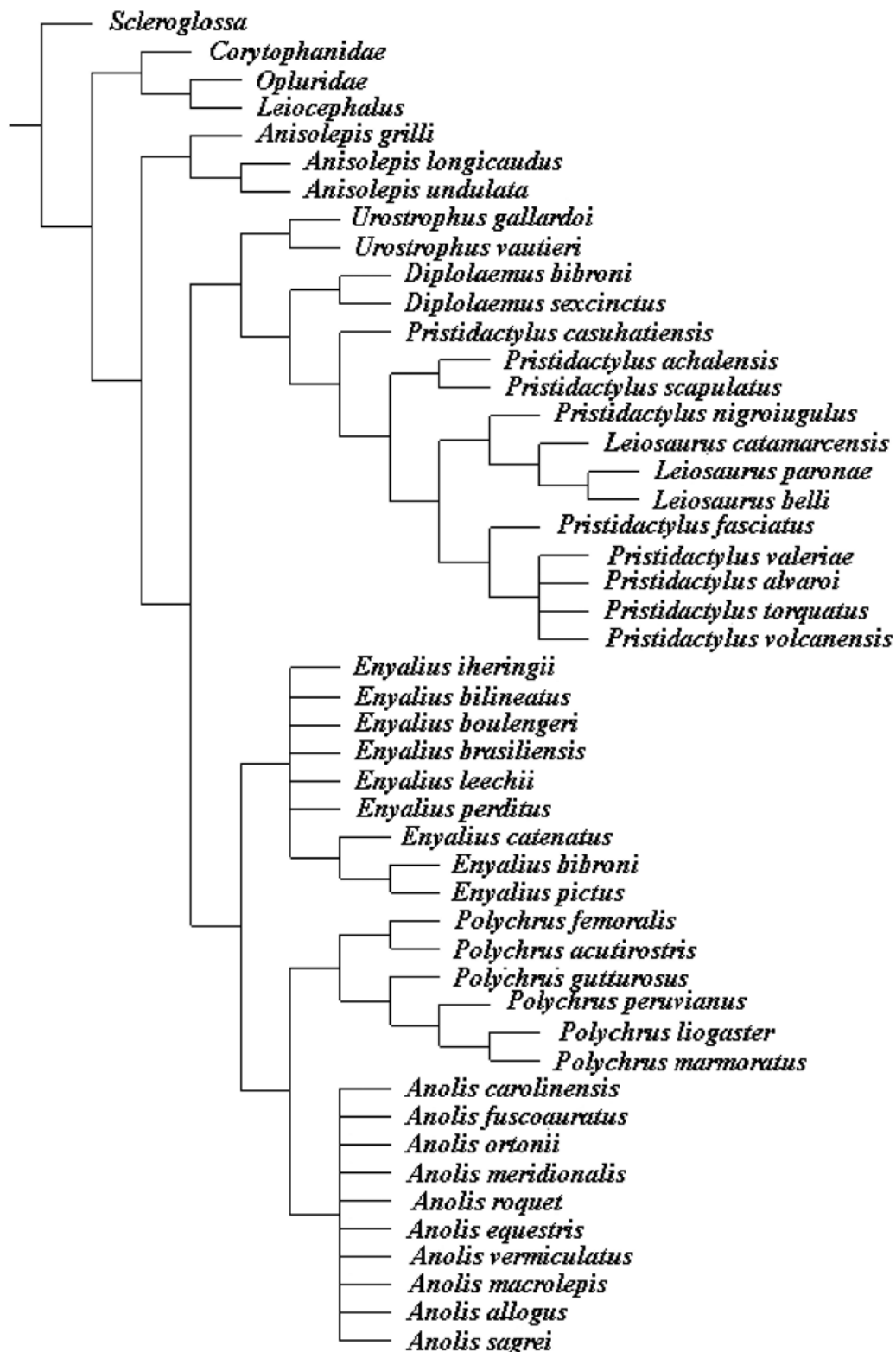


Fig. 4. – Semi-strict supertree, that results from combining tree topologies obtained from the molecular data set of FROST et al. 2001 analysis and from our data set II. Only two higher taxa are recovered as monophyletic groups: Polychrotidae and Leiosaurinae.

The results of our analysis of data set II indicate that, within the Leiosauridae, *Leiosaurus* genus is characterized by six unambiguous myological synapomorphies (Appendix 3), five of them associated with gular structures. Most of the derived characters of *L. catamarcensis* (Koslowsky, 1898) are highly homoplastic, i.e. they were independently acquired by other taxa (Appendix 3). Only eight of these derived characters are actually exclusively present in this species. Therefore, *L. catamarcensis* provides an interesting case of mosaic evolution (see e.g. GOULD, 2002; DIOGO, 2004a), combining peculiar autapomorphies with features that are also homoplastic found in other lizard species such as *Enyalius iheringi* (Boulenger, 1885). This is particularly interesting because these species apparently do not share similar locomotor modes, or microhabitat use, or any other ecological or ethological trait that could, in theory, be interpreted as constraining their morphology towards a homoplastic configuration. *Leiosaurus* sp. is a ground-dwelling lizard that inhabits mainly arid and semidesertic regions of Argentina (CEI, 1973). Lizards of the genus *Enyalius* are restricted to forested areas along the Atlantic Rainforest of eastern Brazil and the Brazilian Amazon forest, and are usually found using tree trunks, shrubs, fallen logs or leaves as perches (VAN SLUYS et al., 2004).

The enyaliine leiosaurid *Urostrophus* specimens analysed have a divided m. depressor mandibulae and a hypertrophied m. cervicomandibularis (Fig. 5a), almost twice the width of this muscle in e.g. *Anisolepis* (Boulenger, 1885) specimens (Fig. 5b). In general, the cranial musculature of *Urostrophus* specimens has a somewhat simplified configuration, many muscles being absent, e.g. the m. adductor posterior and m. mandibulohyoideus III. According to our phylogenetic analysis, in the case of the enyaliine taxon *Anisolepis*, 12 out of 30 character states are seemingly homoplastic parallelisms that are also found in closely related taxa (Appendix 3). Three of the six unique autapomorphies present in this taxon (Appendix 3) are modifications of upper limb muscles. One of these unique features is the absence of m. pronator teres, which is noteworthy considering that this muscle usually promotes the external rotation of the forearm. Another unique feature of *Anisolepis* genus concerns the m. pronator profundus, which occupies only half of the distal space between the radius and ulna, and not all this distal space, as seen in the other lizards analyzed. These peculiarities related to both the m. pronator teres and the m. pronator profundus make *Anisolepis* genus an interesting case study for conducting functional and ecomorphological studies on the relations between the seemingly pecu-

liar limb rotation movements displayed by this taxon and the type of environment in which it lives.

The clade composed by *Anolis* species is defined in our analysis by 11 unambiguous myological synapomorphies. Three of these synapomorphies are related to structures associated with the dewlap support (Appendix 3). In general, the cranial ventral musculature is modified in *Anolis* specimens, probably in association with the big size of the second ceratobranchials (Fig. 6). The ventral gular skin is adhered to this portion of the hyoid. In some specimens of *Anolis gundlachi* (Peters, 1876) examined by us (e.g. RT 144478), these hyoid structures reach the pelvic girdle in a resting position; in others (e.g. RT 14487, juvenile specimen) they reach the shoulder girdle. Dewlap size is known to vary ontogenetically and between sexes in many species of *Anolis* (FITCH & HILLIS, 1984; NICHOLSON et al., 2007); the difference in the length of the second ceratobranchials was already noted by FROST et al. (2001) in relation to the presence of dewlap (their char. 22). In *Anolis* specimens, the second ceratobranchials are partially covered ventrally by the m. constrictor colli (Fig. 6), which forms a continuous layer with the m. intermandibularis anterior and m. intermandibularis posterior. It is difficult to differentiate the m. constrictor colli from the m. intermandibularis posterior near their insertion on the mid-ventral fascia (Fig. 6). This ventral fascia formed by the two muscles reaches the most distal part of the head, covering the m. pterygomandibularis (Fig. 6).

In *Polychrus* specimens the second ceratobranchials are covered by the m. intermandibularis posterior, which is loosely attached to the skin (not shown). One main difference between the polychrotids and the leiosaurid type genus *Leiosaurus* concerns the position of the second ceratobranchial. In *Anolis* and *Polychrus* specimens, this bone is very superficial and does not have muscular fibers attached to it, while in *Leiosaurus* specimens it is deeply embedded in the muscular fibers of different hyobranchial muscles.

In the specimens of the leiosaurid *Anisolepis* the flexor plate with its palmar sesamoid is smaller than it is in taxa belonging to node 30 (e.g. *Leiosaurus* sp., Fig. 7a, b). The reduction in size of the palmar sesamoid is correlated with the independence of the flexor tendons, as is shown in *Anolis* specimens (Fig. 7c), which prevents the formation of a unique flexor plate. The presence of a palmar sesamoid embedded in the tendinous tissue probably prevents the complete closure of the manus because of its rigidity; that probably precludes, in turn, palmar flexion (pattern L of MORO & ABDALA, 2004).

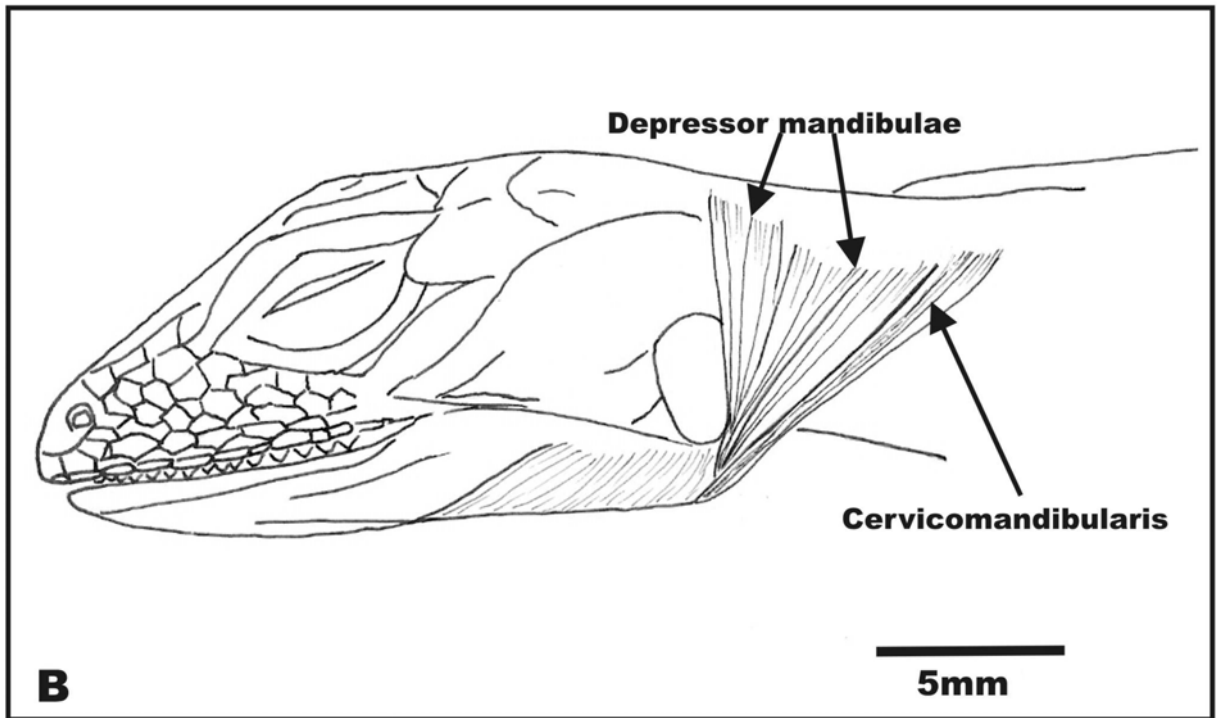
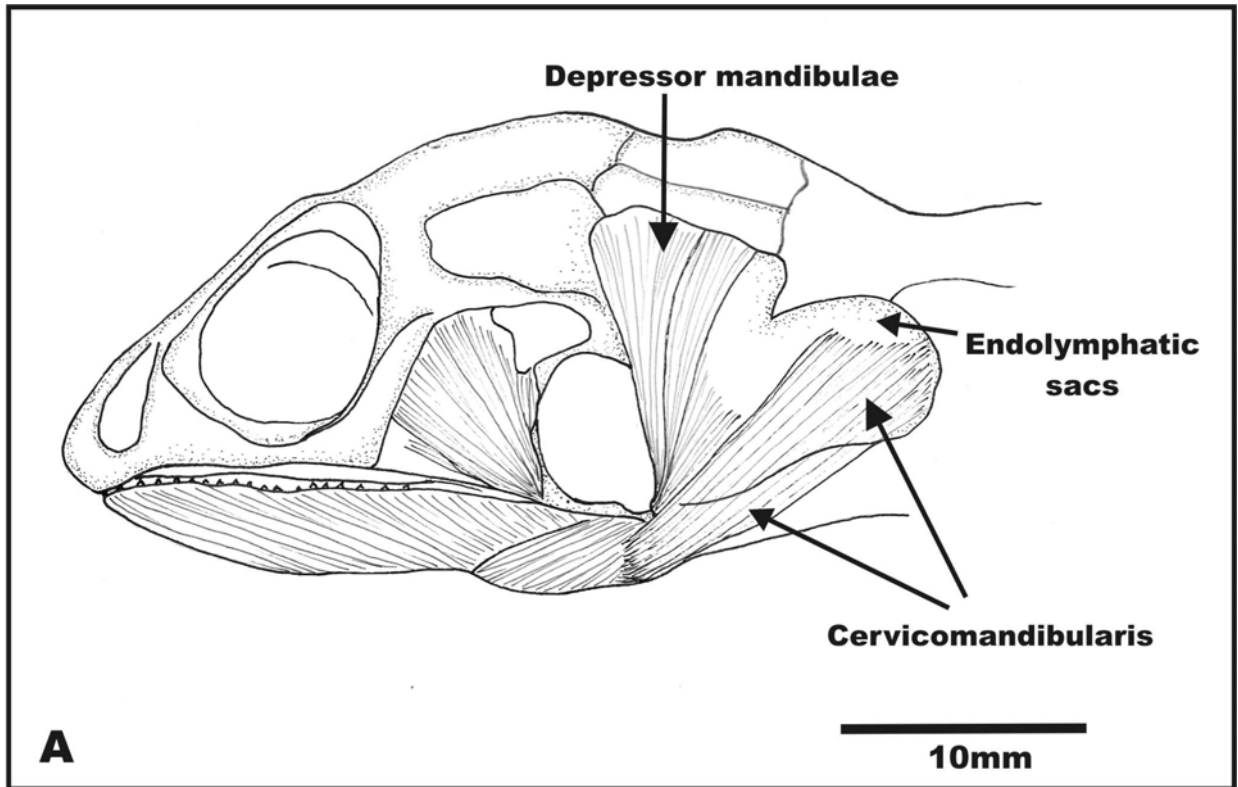


Fig. 5. – A. Lateral view of the cephalic musculature of *Urostrophus gallardoi*; note the hypertrophied m. cervicomandibularis covering the endolymphatic sacs. This is almost twice the width of this muscle in *Anisolepis longicaudus*. B. Lateral view of the cephalic musculature of *Anisolepis longicaudus*, with a normal m. cervicomandibularis.

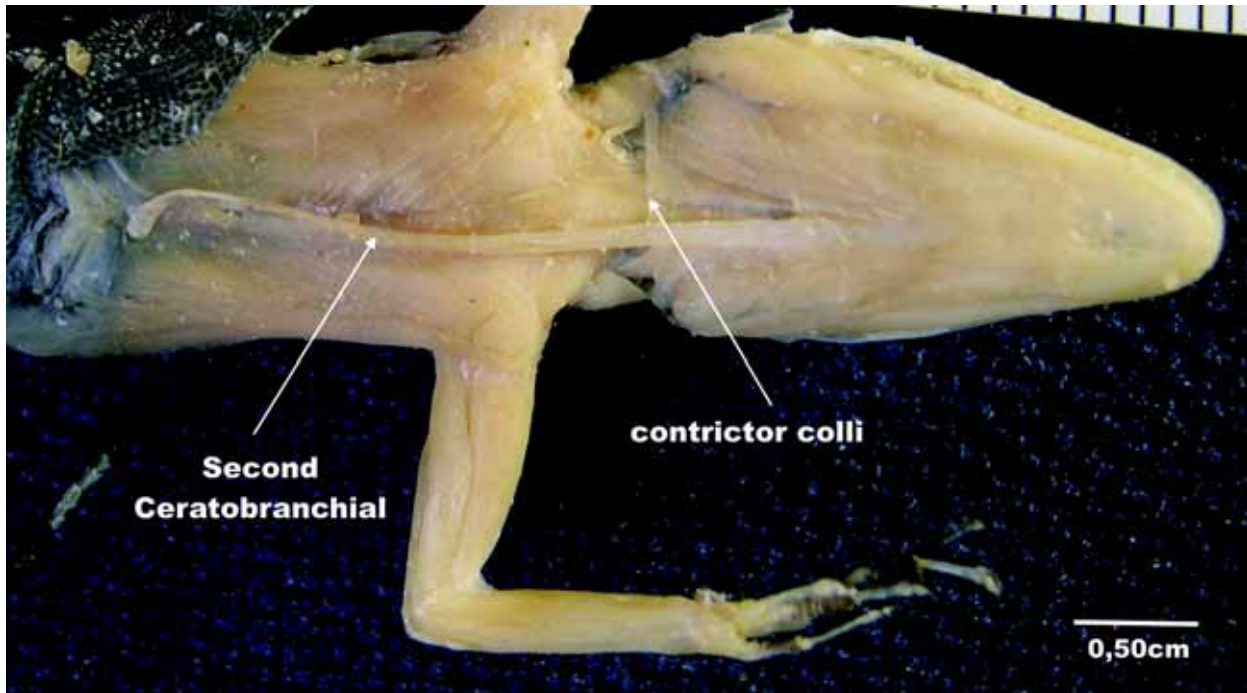


Fig. 6. – Photograph of the ventral view of the anterior region of *Anolis gundlachi*; note the very superficial location of the second ceratobranchials, partially covered by the m. constrictor colli.

#### Comparison among the different hypothesis.

The comparison of the tree topologies resulting from the combination of FROST et al. (2001) analysis and our own myological data reveals some interesting points that will be discussed below.

**DATA SET I.** The analysis of this data set, including only myological characters, results in a tree with most of the genera often recognized in the literature appearing as monophyletic clusters, except *Leiosaurus* and *Pristidactylus*, with most of the analyzed species belonging to this genera. This is particularly interesting, because some previous studies on a wide range of vertebrate taxa including lizards (e.g. MORO & ABDALA, 1998; ABDALA & MORO 1996; 2003; 2006) as well as bony fish, birds, and primates (see e.g. DIOGO, 2004b, for a recent review of this subject) have indicated that the analysis of muscular characters was more likely to reveal synapomorphies for higher taxa such as families and orders than for lower taxa such as species or genera. In fact, in the present study, the exclusive analysis of myological characters (data set I) did not recover any of the higher-level taxa (above the genus level) that are often recognized in the literature. RUSSELL (1988) stressed that myological fea-

tures should be approached and used with caution, especially at higher taxonomic levels because of homoplasy. All these contrasting results support the contention that myological data should be used with caution, indicating that the best option in morphological cladistic analysis thus continues to be trying to complement the evidence provided by hard tissues and that provided by soft structures, as well by other types of data (e.g. external features), i.e., to analyze all the anatomical data available.

**DATA SET II.** In fact, contrary to the analysis of our data set I, the analysis of data set II combining our own 162 myological characters with the 82 osteological characters of FROST et al. (2001) did recovered the monophyly of the family Leiosauridae, as well as of all its genera (Fig. 2). The family Polychrotidae and the subfamily Enyaliinae are recovered as paraphyletic taxa. In the consensus tree obtained from the morphological data set by FROST et al. (2001; see their Fig. 2), all enyaliine genera were grouped in a monophyletic unit, but their relationships appeared as unresolved. This group (Enyaliinae or Anisolepae sensu SCHULTE et al., 2003) should therefore be accepted with caution.



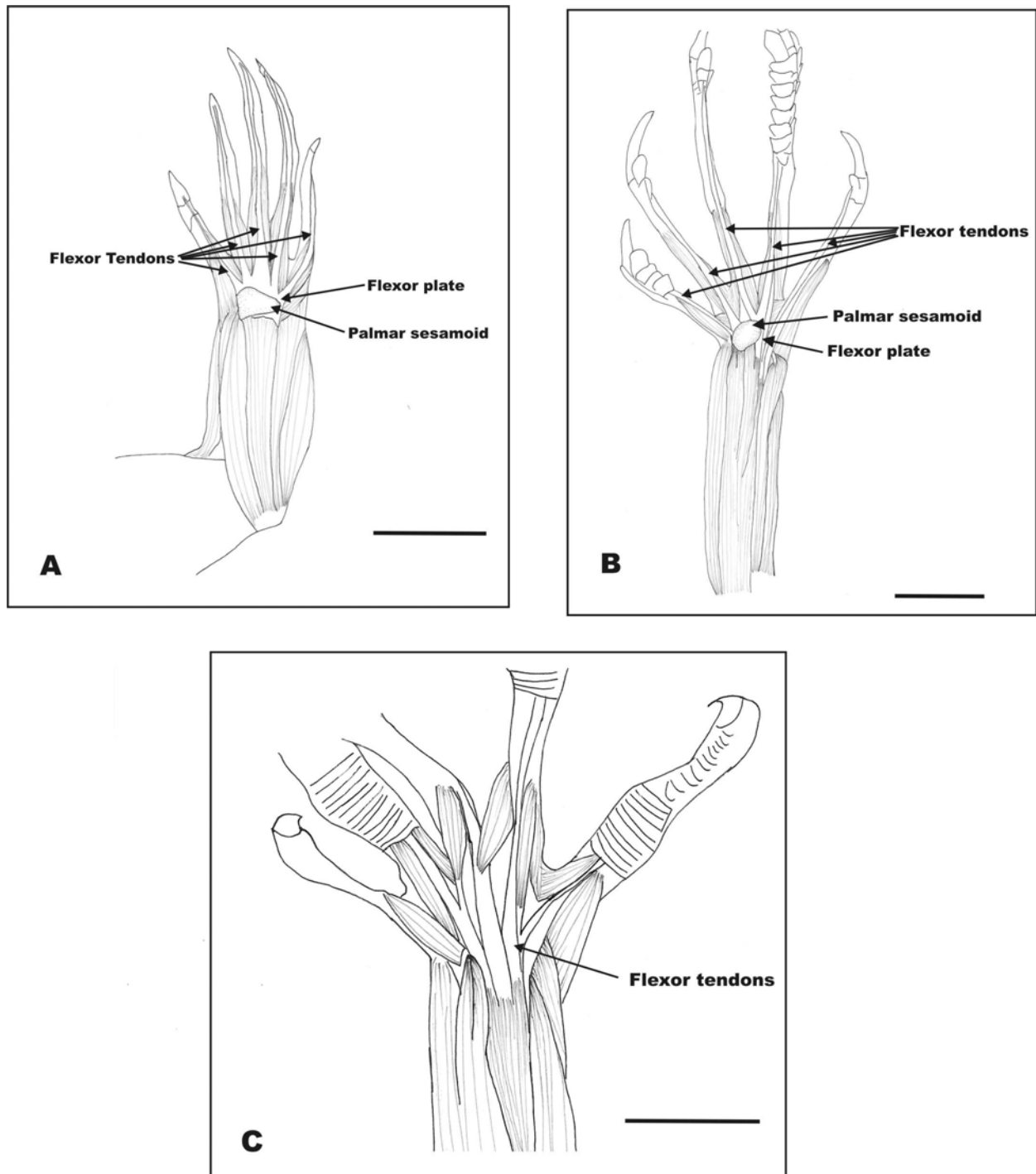


Fig. 7. – A. Ventral view of the manus of *Anisolepis longicaudus*; the flexor plate with its palmar sesamoid is smaller than it is in *Leiosaurus*. B. Ventral view of the manus of *Leiosaurus catamarcensis*; note the big palmar sesamoid, which probably prevents the flexion of the palm of the hand. C. Ventral view of the manus of *Anolis gundlachi*. There is no developed flexor plate.

In the analysis of data set II, *Leiosaurus* genus appears as monophyletic, with a 51% bootstrap support value. FROST et al.'s (2001) study for all data did recover this genus as a polytomy; the inclusion of myological characters on data set II has thus contributed to solve that polytomy (Appendix 3) with the synapomorphies commented above. Regarding the Pristidactylinae, although we recov-

ered it as monophyletic, this clade has essentially no support (bootstrap support 12%) in our analysis of data set II.

DATA SET III. Although the overall analysis of data set III recovers the family Polychrotidae as monophyletic, its unexpected phylogenetic position on the tree (Fig. 3, data set III) suggests that it is crucial to assemble more evi-

dence before the Polychrotidae - Leiosauridae relationships can be considered settled. When FROST et al. (2001) added molecular characters to their morphological data set, they obtained a more resolved consensus tree (see their Fig. 4). When we analyze the data set incorporating the 48 taxa surveyed by FROST et al. (2001) and including our own 162 myological characters and the 82 osteological characters of FROST et al. (2001) (data set III), monophyly of the Polychrotidae is again obtained, and the Leiosauridae and Enyaliinae appear as paraphyletic groups (Fig. 3). Only *Leiosaurus* and *Pristidactylus* appear as monophyletic within the Leiosauridae.

**SUPERTREE.** Only two higher taxa are recovered as monophyletic groups: Polychrotidae and Leiosaurinae. *Leiosaurus* genus is once again recovered as monophyletic. Leiosauridae, Enyaliinae and *Pristidactylus* genus appear as paraphyletic groups (Fig. 4).

**GENERAL COMMENTS.** The Enyaliinae appear as a paraphyletic group in all our analyses. The other taxa analyzed appear as paraphyletic in some analyses and monophyletic in others. Interestingly, in both FROST et al.'s (2001) and SCHULTE et al.'s (2003) studies and in our analyses of data sets II and III, the Leiosauridae appears as a monophyletic group. FROST et al. (2001) and SCHULTE et al. (2003) recovered the monophyly of Enyaliinae and Leiosaurinae, although SCHULTE et al. (2003) use different names for these clades. We recovered only Leiosaurinae as monophyletic in the analysis of data set II, III, and in the supertree. With respect to the lower taxa, *Leiosaurus* genus is recovered as monophyletic by FROST et al. (2001), using only morphological characters, by SCHULTE et al. (2003) and in all our analyses, except that based on our data set I. *Diplolaemus* genus is recovered as monophyletic by SCHULTE et al. (2003) and in all our analyses. *Pristidactylus* genus is recovered as a clade by FROST et al. (2001), and by our analyses of data sets II and III, while *Enyalius* genus appears as monophyletic in FROST et al. (2001) study, and in our analyses of data sets I, II and III. Lastly, *Anisolepis* and *Urostrophus* genera are monophyletic in FROST et al. (2001) study, and in our supertree.

In summary, of the taxa discussed in the present work, there are three taxa that consistently appear as monophyletic groups in at least some of the analyses made by both FROST et al. (2001), by SCHULTE et al. (2003), and by us: the Leiosauridae, Leiosaurinae, *Diplolaemus*, and the type genus of this family, *Leiosaurus*. Therefore, it can be said that in view of the data available, the monophyly of these four taxa is particularly well supported.

## ACKNOWLEDGEMENTS

Some of the specimens examined were generously made available by Richard Etheridge, Juan Daza, Felix Cruz, and Hussam Zaher. Claudia Szumick, Anthony Herrel, and Pablo Goloboff provided interesting comments and ideas. María José Tulli, Santiago, Tomás Calvo, and Agustina Arédez helped us with the cladogram figures. An early draft of the manuscript was read by Julián Faivovich. This project was funded by PIP 6347 (CONICET to VA).

## REFERENCES

- ABDALA V & MORO S (1996). Cranial musculature of South-American geckonids. *Journal of Morphology*, 229:59-70.
- ABDALA V & MORO S (2003). A cladistic analysis of ten lizard families (Reptilia: Squamata) based on cranial musculature. *Russian Journal of Herpetology*, 10:53-78.
- ABDALA V & MORO S (2006). Comparative myology of the forelimb of the *Liolaemus* sand lizards (Liolaemidae). *Acta Zoologica (Stockholm)*, 87:1-12.
- CEI JM (1973). Comentarios sobre algunos géneros de iguanidos: *Diplolaemus*, *Leiosaurus*, *Aperopristsis* y *Cupriganus*. *Physis*, 32(85):269-276.
- CEI JM (1986). Reptiles del centro, centro-oeste y sur de la Argentina. *Herpetofauna de las zonas áridas y semiáridas*. Museo Regionale di Scienze Naturali Monografie (Torino), 4: 527 pp.
- CEI JM, SCOLARO JA & VIDELA F (2001). The present status of argentinian Polychrotid species of the genus *Pristidactylus* and description of its southernmost taxon as a new species. *Journal of Herpetology*, 35(4):497-605.
- CEI JM, SCOLARO JA & VIDELA F (2003). A taxonomic revision of the recognized argentine species of the Leiosaurid genus *Diplolaemus* (Reptilia, Squamata, Leiosauridae). *FACENA*, 19:87-106.
- CONRAD JL (2008). Phylogeny and Systematics of Squamata (Reptilia) based on morphology. *Bulletin of the American Museum of Natural History*, 310:1-182.
- DIOGO R (2004a). Morphological evolution, adaptations, homoplasies, constraints, and evolutionary trends: catfishes as a case study on general phylogeny and macroevolution. Science Publishers, Enfield.
- DIOGO R (2004b). Muscles versus bones: catfishes as a case study for an analysis on the contribution of myological and osteological structures in phylogenetic reconstructions. *Animal Biology*, 54:373-391.
- DONOSO-BARROS R (1975). Nuevos Reptiles y Anfibios de Chile. *Boletín de la Sociedad de Biología de Concepción*, 47(1974):221.
- DONOSO-BARROS R & CEI JM (1969). Probable híbrido inter-específico entre *Diplolaemus darwini* y *Diplolaemus bibroni*. *Boletín de la Sociedad de Biología de Concepción*, 42:27-32.
- ETHERIDGE R & WILLIAMS EE (1991). A review of the South American lizard genera *Urostrophus* and *Anisolepis* (Squamata: Iguania: Polychrotidae). *Bulletin of the Museum of Comparative Zoology*, 152(5):317-361.
- FITCH H & HILLIS D (1984) The Anolis dewlap: interspecific variability and morphological associations with habitat. *Copeia*, 1984:315-325.
- FROST DR & ETHERIDGE R (1989). A phylogenetic analysis and taxonomy of iguanian lizards (Reptilia: Squamata). *Miscellaneous Publication Museum Natural History University of Kansas*, 81:1-65.
- FROST DR, ETHERIDGE R, JANIES D & TITUS TA (2001). Total evidence, sequence alignment, evolution of polychrotids lizards, and a reclassification of the Iguania (Squamata: Iguania). *American Museum Novitates*, 3343:1-38.
- GALLARDO JM (1961). Estudio zoogeográfico del género *Leiosaurus* (Reptilia, Sauria). *Physis*, 22(63):113-118.
- GALLARDO JM (1964). Los géneros *Urostrophus* D. et B. y *Cupriganus* gen. nov. (Sauria, Iguanidae) y sus especies. *Neotropica*, 10(33):125-136.
- GOLOBOFF P & POL D (2002). Semi-strict supertrees. *Cladistics*, 18:514-525.
- GOLOBOFF P, FARRIS J & NIXON K (2003a). Tree Analysis Using New Technologies. Available at <http://www.zmuc.dk/public/phylogeny/TNT/>.

- GOULD S J (2002). The structure of evolutionary theory. Belknap, Harvard.
- HOVENKAMP P (2004). A review of T.N.T. -Tree Analysis using New Technology. Version 1.0, by GOLOBOFF P, FARRIS JS & NIXON K. Available from the authors and from HYPERLINK "http://www.zmuc.dk/public/phylogeny/TNT/"http://www.zmuc.dk/public/phylogeny/TNT/. Cladistics 20(4):378-383.
- MORO S & ABDALA V (1998). Cranial myology of some species of *Liolaemus* and *Phymaturus* (Squamata: Tropicuridae: Liolaeminae). Amphibia-Reptilia, 19:171-192.
- MORO S & ABDALA V (2004). Análisis descriptivo de la miología flexora y extensora del miembro anterior de *Polychrus acutirostris* (Squamata, Polychrotidae). Papeis Avulsos de Zoologia, 44(5):81-90.
- NICHOLSON KE, HARMON LJ & LOSOS JB (2007). Evolution of *Anolis* lizard dewlap diversity. Plos One, 2(3): e274.
- NIXON CK (1999). The parsimony ratchet, a new method for rapid parsimony analysis. Cladistics, 15:407-414.
- RUSSELL AP (1988). Limb muscles in relation to lizard systematics: a reappraisal. In: ESTES R & PREGILL G, (eds), Phylogenetic relationships of lizard families: Essays commemorating Charles L. Camp Stanford Univ. Press: 119-281.
- RUSSELL AP (1993). The aponeurosis of Lacertilian ankle. Journal of Morphology, 218:65-84.
- SCHULTE II JA, MACEY JR, LARSON A & PAPPENFUSS TJ (1998). Molecular test of phylogenetic taxonomies: a general procedure and example using four subfamilies of the lizard family Iguanidae. Molecular Phylogenetics and Evolution, 10:367-376.
- SCHULTE II JA, VALLADARES JP & LARSON A (2003). Phylogenetic relationships within Iguanidae inferred using molecular and morphological data and a phylogenetic taxonomy of Iguanian lizards. Herpetologica, 59(3):399-419.
- VAN SLUYS M, FERREIRA VM & ROCHA CFD (2004). Natural history of the lizard *Enyalius brasiliensis* (Lesson, 1828) (Leiosauridae) from an atlantic forest of southeastern Brazil. Brazilian Journal of Biology, 64(2):353-356.

#### Appendix 1: Specimens analyzed

Acronyms: FBC, Félix Benjamin Cruz in Proyecto Tupinambis, Argentina; FML, Fundación Miguel Lillo (Argentina); MACN, Museo Argentino de Ciencias Naturales, Buenos Aires (Argentina); MNHN, Museum National d' Histoire Naturelle, Paris (France); MZUSP: Museu de Zoologia Universidade de São Paulo (Brazil); NMW, Naturhistorisches Museum, Wien (Austria); PT, Proyecto Tupinambis, Tucumán (Argentina); RT, private collection of Richard Thomas (Puerto Rico); SDSU, San Diego State University (USA); UNNEC: Universidad Nacional del Nordeste (Argentina); MMHN, Museo Municipal de Historia Natural, Mendoza, (Argentina).

#### Leiosaurinae

*Diplolaemus* sp. (3 specimens): FBC 53-55: 2/3/99. Río Negro, 67. 40° 26.955 S and 68° 22.613 W; (1 specimen) PT 4832: 21/2/99. Same data.

*Diplolaemus bibroni* (Bell, 1843) (1 specimen): MACN 35850 SN 43: 10/80. Santa Cruz, Argentina; (1 specimen) SN 29: 4/11/91. Forma alto patagónica. Somuncurá, Río Negro, Argentina.

*Diplolaemus sexinctus* (Ceí, Scolaro & Videla, 2003) (1 specimen): FML 16988. Puesto Rojas. Argentina.

*Leiosaurus paronae* (Peracca, 1897) (1 specimen): MACN 4386, no data.

*Leiosaurus belli* (Duméril & Bibron, 1837) (1 specimen): NMW 12976, no data; (2 specimens) PT 3998-3999: 4-9/12/98. Río Negro,

Argentina; (1 specimen) PT 4782: 2/2/99. 2 km Río Negro, Argentina; MMHN 403, 406-408. Mendoza, Argentina (4 specimens).

*Leiosaurus catamarcensis* (2 specimens): FBC 104-105: Santa María, Argentina. 26° 59.358 S and 66° 16.484 W; (1 specimen): FBC 145: 16/3/99. La Rioja, Argentina; (1 specimen): PT 3715: 1-2/11/98. La Rioja.

*Pristidactylus volcanensis* (Lamborot & Díaz, 1987) (2 specimens): MNHN: no number. El Volcán (Chile).

*Pristidactylus valeriae* (Veloso & Navarro, 1988) (1 specimen): FML no data.

*Pristidactylus torquatus* (Philippi, 1861) (2 specimens): NMW 18198, 18199, no data.

*Pristidactylus achalensis* (Gallardo, 1964) (1 specimen): MACN 32779: 1/83. Córdoba, Argentina. Stranech, Carrizo col.

*Pristidactylus scapulatus* (Burmeister, 1861) (1 specimen): MACN 35370: 3/93. San Juan, Argentina.

*Pristidactylus nigroiugulus* (Ceí, Scolaro & Videla, 2001) (1 specimen): FML s/n:7/3/03. Chubut. Scolaro, col.

#### Enyaliinae

*Enyalius iheringii* (1 specimen): MZUSP 74901: 19/11/91. Boracéia, FAG. Mello, Vanzo det.

*Enyalius catenatus pictus* (Jackson, 1978) (1 specimen): 16-28/II/86. Reserva Biológica Pau Brasil, Ba. M. Rodriguez 86.6024. M. Rodriguez det.

*Anisolepis longicauda* (Boulenger, 1891) (1 specimen): UNNEC: no data.

*Urostrophus gallardoii* (Etheridge & Williams, 1991) (3 specimens): FBC 127-129: Córdoba; (1 specimen) FBC 0036: 2/3/99. Córdoba, Argentina.

#### Polychrotidae

*Anolis olsseni* (1 specimen): SDSU 2164: 1953. Port au Prince, Haiti. R. Etheridge col.

*Anolis sagrei* (Duméril & Bibron, 1837) (1 specimen): SDSU 2175: 1953. Key West, Florida, USA. R. Etheridge col.

*Anolis lineatopus* (Gray, 1840) (1 specimen): SDSU 2157: 1953. Kingston, Jamaica. R. Etheridge col.

*Anolis cristatellus* (Duméril & Bibron, 1837) (1 specimen): SDSU 2145: 1953. San Juan, Puerto Rico. R. Etheridge col.

*Anolis coelestinus* (Cope, 1863) (1 specimen): SDSU 2148: 1953. Port au Prince, Haiti. R. Etheridge col.

*Anolis allogus* (Barbour & Ramsden, 1919) (1 specimen): SDSU 2136: US Bay Naval Base, Guantanamo, Cuba. R. Etheridge col.

*Anolis carolinensis* (2 specimens): FML no data.

*Anolis macrolepis* (Boulanger, 1911) (1 specimen): SDSU 2183: 24/7/68. Cano Decoraro, Chocó, Colombia. E.E. Williams col.

*Anolis notopholis* (Boulanger, 1896) (1 specimen): SDSU 2188: Cano Decoraro, Chocó, Colombia. E.E. Williams col.

*Anolis gundlachi* (9 specimens): RT 14476-14484: Bosque Carite, Puerto Rico.

*Anolis cuvieri* (Merrem, 1820) (1 specimen): RT 59694: Puerto Rico.

*Anolis* sp. (5 specimens): RT 14485-88, 14491: Reserva El Verde, Puerto Rico.

*Anolis krugi* (Peters, 1876) (2 specimens): RT 14489-90: Bosque Carite, Puerto Rico.

*Anolis stratulus* (Cope, 1861) (1 specimen): RT 14492: Reserva El Verde, Puerto Rico.

*Polychrus acutirostris* (Spix, 1825) (10 specimens): FML 00140: Jujuy, Argentina. MZUSP 08605, 08606, 08610, 08611: Pesqueira, Pe., Brazil. MZUSP 48166: Fazenda Babente, 13 Km E Exu, Pe., Brazil. MZUSP 48151, 48154, 48156: Exu, Pe., Brazil.

*Polychrus* sp. (1 specimen): MACN 7292: Paraguay.

#### Corytophanidae

*Basiliscus vittatus* (Wiegmann, 1828) (1 specimen): SDSU 02097 no data

**Appendix 2: Myological Data set, taxa and character codes (Polymorphism symbols:  
A=0 and 1; B=0 and 2; C=2 and 3; D=1 and 2; E=1 and 4; F=0 and 3; G=0 and 4; H=1 and 3; J=3 and 4)**

	1		2		3		4		5		6		7			
	01234	56789	01234	56789	01234	56789	01234	56789	01234	56789	01234	56789	01234	56789		
<i>Anolis allogus</i>	22002	00---	10102	10-12	1-220	-1102	02101	010-1	11011	0-000	11111	02001	0-1--	-1001	11022	2----
<i>Anolis macrolepis</i>	02000	00---	10102	10-12	1-220	-1102	02101	010-1	11011	0-000	11111	02001	0-1--	-1001	11022	2----
<i>Anolis sagrei</i>	02002	00---	10102	10-12	1-220	-1102	02101	010-1	11011	0-000	11111	02001	0-1--	-1001	11022	22---
<i>A. carolinensis</i>	22113	02---	00102	10-12	1-200	-1102	00101	01110	21011	0-000	01101	02001	0-1--	-1001	11022	22---
<i>U. gallardoi</i>	12100	02---	10112	10-12	0-200	-1101	020--	-10-1	22001	1-002	01110	02001	112-0	02001	11003	21110
<i>D. bibroni</i>	12100	02---	10112	10-12	0-200	-1101	02101	010-1	10001	0-000	11110	02020	1--1	01001	11003	11111
<i>D. sexcinctus</i>	12100	02---	10112	10-12	0-200	-1101	02101	010-1	10001	0-000	11110	02020	1--1	01001	11003	11111
<i>A. longicaudus</i>	22A03	1-01-	00102	11-12	12-00	-1102	0211-	010-1	01011	2-002	01111	02000	1--0	01001	G1003	21100
<i>E. iheringii</i>	22101	----1	00112	11-12	1-200	-1101	020--	-10-1	12001	0-000	11111	02000	1--0	01001	01002	11111
<i>E. catenatus</i>	22101	----1	00112	11-12	1-200	-1101	020--	-10-1	12001	0-000	11111	02000	1--0	01001	11002	11111
<i>P. scapulatus</i>	12002	02---	00112	11-12	0-200	-1100	02101	01111	10001	0-002	01011	02000	1--1	01001	00003	11111
<i>P. achalensis</i>	12002	02---	00112	10-12	0-200	-1100	02101	01111	00001	0-002	01011	02000	1--1	01001	00003	11111
<i>P. nigroingulus</i>	02100	02---	10102	11-11	2-201	01101	02101	01110	20000	0-002	01011	10000	111--	01001	00003	21111
<i>P. valeriae</i>	02100	02---	10102	10-12	1-001	01001	02101	01100	20010	0-002	01010	10101	111--	00--1	11002	1110-
<i>P. torquatus</i>	02100	02---	10102	10-12	1-301	01001	02101	01110	20010	0-002	01010	10101	111--	01101	21002	1110-
<i>P. volcanensis</i>	02100	1-0A-	10102	11112	1-B01	01A01	02101	011AA	20010	0-002	01010	10101	111--	01A0D	11002	2110-
<i>L. catamarcensis</i>	12100	02---	00110	11-12	0-200	-0101	02011	010-1	52000	1-000	01011	10100	----1	01002	01002	21111
<i>L. paronae</i>	01001	1--2	10102	11-12	0-101	01001	02101	01100	D2010	1-010	01010	10100	----1	0--1	11010	D111-
<i>L. belli</i>	02100	1-0A-	00102	11-12	0-F01	0100D	02101	01100	D2010	1-010	01010	10100	----1	01001	11010	D111-
<i>Polychrus</i>	02100	1--1	00112	11-12	11-01	01100	02100	01100	20010	0-002	01011	10101	110--	01001	11001	11100

	8		9		10		11		12		13		14		15		16
	01234	56789	01234	56789	01234	56789	01234	56789	01234	56789	01234	56789	01234	56789	01234	56789	01
<i>Anolis allogus</i>	--100	101-1	00011	20010	00121	10001	-0200	10021	00010	00101	01010	10000	11001	00000	00020	01011	11
<i>Anolis macrolepis</i>	--100	101-1	00011	20010	00121	10001	-0000	11021	00010	00101	01010	10000	11001	00000	00020	01011	11
<i>Anolis sagrei</i>	--100	101-1	00011	20010	00121	10001	-0000	11021	00010	00101	00000	00100	11001	00000	00020	01011	11
<i>A. carolinensis</i>	--100	101-1	00011	20010	00121	10001	-0000	11021	00010	00101	00000	00100	11001	00000	00020	01011	11
<i>U. gallardoi</i>	-0000	000-0	11100	00A10	00132	30041	-0001	001F0	00000	0A111	00000	10000	11011	00000	10000	10010	00
<i>D. bibroni</i>	-1001	001-0	02000	10010	0AADD	HA1J1	00F00	D0A01	000AA	B0A10	-0000	10000	11011	00001	10020	110-0	00
<i>D. sexcinctus</i>	-1001	001-0	02000	02000	0AADD	HA1J1	00F00	D0A01	000AA	B0A10	-0000	10000	11011	00001	10020	110-0	0
<i>A. longicaudus</i>	01100	002-1	A1000	20010	00121	30040	00000	10131	00010	100-0	-0000	10000	11101	11000	11000	01100	02
<i>E. iheringii</i>	-1000	100-1	00000	22110	01101	10041	00001	20101	10011	01121	10000	--000	11001	00001	10120	02022	02
<i>E. catenatus</i>	-1000	100-1	00000	22110	00101	10141	00001	00120	10011	01121	10000	10000	11001	00001	10120	02022	02
<i>P. scapulatus</i>	-1100	000-1	11100	----	----	----	----	----	----	----	----	----	----	----	----	----	--
<i>P. valeriae</i>	-1100	000-1	11100	20010	00122	30101	00100	00110	00010	10--1	00000	10000	11211	00001	10020	01010	00
<i>P. achalensis</i>	-1110	000-1	1-000	10010	00102	30101	00001	11001	00000	10111	00000	10000	11-11	00001	10020	01010	00
<i>P. nigroingulus</i>	-1110	000-0	12000	-0010	001-2	30101	00-0-	1-0-1	000-0	10111	00000	10000	11-11	00001	10020	01010	00
<i>P. torquatus</i>	-1110	000-0	11000	----	----	----	----	----	----	----	----	----	----	----	----	----	--
<i>P. volcanensis</i>	-1110	000-0	14000	----	----	----	----	----	----	----	----	----	----	----	----	----	--
<i>L. catamarcensis</i>	-1110	004-2	14100	20011	11002	30111	10201	20030	00010	00101	00000	01000	11111	20101	10120	00110	00
<i>L. paronae</i>	-1010	000-0	14000	00010	00102	30001	00000	10001	00000	10--0	-000-	0-100	11-11	00001	10000	00000	00
<i>L. belli</i>	-1110	000-2	1-000	10010	00002	30000	00000	10001	00000	10111	00000	1-200	11-10	00--1	----0	00000	00
<i>Polychrus</i>	-1100	001-0	0-000	11010	00A01	00000	00100	10101	00011	00100	-1010	10200	10001	00000	21-10	12120	00

**Appendix 3: List of synapomorphies of the main nodes with their jackknife support values  
(nodes as Fig. 2; Ja=Jackknifing; No=Node)**

No	Ja	Synapomorphies
21	42	<ul style="list-style-type: none"> <li>Adductor aponeurosis (character 0): very nacreous → not pigmented</li> </ul>
22	82	<ul style="list-style-type: none"> <li>Temporal fossa aponeurosis (character 2): pigmented → not pigmented</li> <li>Levator anguli oris insertion (character 10): with aponeurosis → without aponeurosis</li> <li>Temporal artery (character 23): visible → almost invisible</li> <li>Levator pterygoidei length (character 50): long → short</li> </ul>
23	100	<ul style="list-style-type: none"> <li>Tendinous system of the adductor mandibulae complex present (character 13): very developed → developed</li> <li>Adductor superficialis externus origin (character 16): extends on postorbital, squamosal and quadrate → extends on jugal, postorbital, squamosal, and quadrate</li> <li>Adductor mandibulae externus profundus origin (character 29): quadrate and prootic → quadrate, prootic, and parietal</li> <li>Depressor mandibulae anterior origin (character 60): does not include supraoccipital → includes supraoccipital</li> <li>Mandibulohyoideus (character 73): mid region of the dentary → posterior region of the dentary</li> <li>Omohyoideus (character 93): unique → divided</li> <li>Modified mandibulohyoideus II (character 94): absent → present</li> <li>Relative size of the extensores digiti brevis/dorsometacarpalis muscles (character 117): dorsometacarpalis = extensores digiti brevis → dorsometacarpalis bigger than extensores digiti brevis</li> <li>Larger muscle in dorsal view (character 118): extensor digitorum longus → extensor carpi radialis</li> <li>Tibialis anticus origin (character 159): all fibula length → half distal fibula length</li> <li>Tibialis anticus (character 160): unique → divided</li> <li>Digital pads (character 200): absent → present</li> <li>Sexual size dimorphism (character 207): females larger than males → males larger than females</li> <li>Coronoid lateral process (character 221): absent or short → large</li> <li>Splenial posterior extent (character 223): terminates posteriorly anterior to anterior edge of mandibular fossa → terminates posterior to anterior edge of mandibular fossa</li> <li>Angular (character 224): moderate to large → absent or reduced to splint</li> <li>Caudal autotomy fracture planes (character 241): absent → present</li> </ul>
25	33	<ul style="list-style-type: none"> <li>Scale organ of dorsum (character 204): spinules present → without spinules</li> <li>Dermal roof bone rugosities (character 215): strong rugosities that correspond to scale outlines extend over parietal and frontal and adjacent dermal skull bones → absent or weak, although indistinct rugosities may be present</li> </ul>
26	71	<ul style="list-style-type: none"> <li>Adductor mandibulae externus medialis insertion (character 27): coronoid and bodenaponeurosis → just bodenaponeurosis</li> <li>Pterygomandibularis origin (character 43): not divided → divided in two slips with tendon</li> <li>Intermandibularis anterior profundus – mandibulohyoideus II relation (character 57): both muscles attached → not attached</li> <li>Depressor mandibulae superficialis (character 59): undivided → divided</li> <li>Mandibulohyoideus I shape (character 74): rectangular → trapezoidal</li> <li>Mandibulohyoideus II relation (character 78): contralateral muscles joined → contralateral muscles separated</li> </ul>
27	27	<ul style="list-style-type: none"> <li>Adductor aponeurosis (character 0): pigmented → not pigmented</li> <li>Tendinous system present (character 13): very developed → developed</li> <li>Adductor mandibulae externus medialis (character 20): divided → undivided</li> <li>Position of the temporal artery (character 24): located over two muscles → located over one muscle</li> <li>Pseudotemporalis superficialis insertion extends over (character 39): both coronoid and bodenaponeurosis → bodenaponeurosis</li> <li>Pterygomandibularis volume (character 44): flattened → bulky</li> <li>Intermandibular anterior profundus aponeurosis (character 55): absent → present</li> <li>Intermandibular anterior profundus shape (character 56): rectangular → irregular</li> <li>Branchiohyoideus aponeurosis (character 83): absent → present</li> </ul>
28	35	<ul style="list-style-type: none"> <li>Pseudotemporalis superficialis origin (character 37): includes parietal and postorbital → does not include postorbital</li> <li>Flexor carpi radialis pattern (character 125): two branches → one branch</li> <li>Caudal annuli (character 192): irregular → regular</li> <li>Sexual size dimorphism (character 207): females larger than males → males larger than females</li> <li>Sexual dichromatism (character 208): absent → present</li> <li>Black antehumeral bar (character 209): absent → present</li> </ul>
29	16	<ul style="list-style-type: none"> <li>Pseudotemporalis profundus insertion (character 41): mandibular fossa and coronoid; mandibular fossa, coronoid and bodenaponeurosis → mandibular fossa</li> <li>Pterygomandibularis aponeurosis (character 45): scarcely pigmented → not pigmented</li> <li>Mandibulohyoideus I insertion (character 75): ceratobranchial I and epibranchial → ceratobranchial I</li> <li>Distal subdigital lamellae (character 199): not divided → longitudinally grooved or divided</li> <li>Caudal autotomy fracture planes (character 241): absent → present, although occasionally showing ventral fusion</li> </ul>
30	35	<ul style="list-style-type: none"> <li>Depressor mandibulae superficialis origin (character 64): parietal and spinalis capitis → parietal, spinalis capitis, and squamosal</li> <li>Mandibulohyoideus II insertion including ceratobranchial I (character 79): ceratobranchial I and basihial → ceratobranchial I</li> <li>Relative of the extensores digiti brevis/dorsometacarpalis muscles (character 117): dorsometacarpalis = extensores digiti brevis → dorsometacarpalis bigger than extensores digiti brevis</li> <li>Femorotibialis aponeurosis (character 149): fan shaped → rectangular</li> <li>Supradigital scale shape (character 194): not all supradigitals of third phalanx → all supradigitals at third phalanx as least twice as broad as postdigital of third phalanx</li> <li>Postdigital scales of third finger (character 196): single lateral row penetrating proximally to penultimate phalanx → triple postdigital row penetrating proximally to penultimate phalanx</li> </ul>

No	Ja	Synapomorphies
		<ul style="list-style-type: none"> <li>Osseus labyrinth (character 216): high elevation of the osseus labyrinth above the level of the opisthotic → superficial outline of osseus labyrinth distinctly above the level of the opisthotic</li> <li>Retroarticular fossa (character 227): well developed → reduced</li> <li>Marginal teeth (character 229): tricuspid → tapered blunt</li> </ul>
31	54	<ul style="list-style-type: none"> <li>Adductor aponeurosis (character 0): very nacreous → pigmented</li> <li>Adductor mandibulae externus medialis (character 20): undivided → divided</li> <li>Limb aponeurosis (character 95): not pigmented → lightly pigmented</li> <li>Extensor carpi radialis branch number (character 104): 2 → 3</li> <li>Palmar patella morphology (character 143): very small → big, flat</li> <li>Paravertebral scale shape (character 186): polygonal → rounded</li> <li>Ventral body scales (character 189): unicarinate → smooth</li> <li>Total caudal vertebrae (character 242-243): 46-64 → 33-44</li> </ul>
32	23	<ul style="list-style-type: none"> <li>Pterygomandibularis aponeurosis (character 45): not pigmented → scarcely pigmented</li> <li>Mandibulohyoideus I shape (character 74): trapezoidal → rectangular</li> <li>Sternohyoideus insertion (character 91): ceratobranchial I and basihyal → ceratobranchial I</li> <li>Extensor carpi radialis branch development (character 105): supinator+intermedia developed, profundus reduced → all three braches equally developed</li> <li>Nasal scale-postrostral scale contact (character 166): separated → in contact</li> <li>Frontal region (character 173): concave → flat or slightly convex</li> <li>Transverse processes of caudal vertebrae (character 240): do not extend beyond 16 → extend beyond 16</li> </ul>
33	63	<ul style="list-style-type: none"> <li>Depressor mandibulae superficialis (character 59): divided → undivided</li> <li>Omohyoideus origin (character 87): clavicular bar and interclavicle → clavicular bar</li> <li>Extensores digiti brevis pattern (character 108): origin on ulnar; insertion onto proximal extremity of the corresponding metacarpal → origin on ulnar; insertion onto distal end of each metacarpal</li> <li>Pronator profundus pattern (character 131): divided → undivided</li> <li>Mental scale (character 164): divided → undivided</li> <li>Head scale striae (character 174): linear rugosities present → linear rugosities absent</li> <li>Supraorbital semicircles (character 177): separated by a single row → separated by two or four rows</li> <li>Splenic anterior extent (character 222): extremely short or absent, not extending anteriorly more than 25% length of tooth row → extend anteriorly more than 25% length of tooth row</li> <li>Posterior mylohyoid foramen (character 226): on ventral or ventrolateral face of mandible → on medial face of mandible</li> <li>Sternum anterior extent (character 232): sternum approaches junction of lateral and posterior processes of interclavicle closely → sternum does not approach junction of lateral and posterior processes of interclavicle closely for more than 50% of length of anterior process anterior to the lateral horns of sternum</li> <li>Posterior coracoid fenestra (character 235): absent → present, marginal, and weak</li> <li>Sternal ribs (character 236-237): three, with posterior extremity of sternum not elongated to form parallel rods continuous with xiphisternal rods, and bearing third pair of ribs articulating via synovial joints → four</li> </ul>
34	87	<ul style="list-style-type: none"> <li>Levator anguli oris condition (character 4): wide triangular → narrow rectangular</li> <li>Adductor mandibulae externus profundus origin (character 29): quadrate and prootic → quadrate</li> <li>Sternohyoideus (character 92): absent → present</li> </ul>
35	71	<ul style="list-style-type: none"> <li>Adductor aponeurosis (character 0): pigmented → not pigmented</li> <li>Levator anguli oris origin (character 5): includes postorbital and jugal → does not include postorbital and jugal</li> <li>Tendinous system present (character 13): very developed → developed</li> <li>Position of the temporal artery (character 24): temporal artery located over two muscles → temporal artery located over one muscle</li> <li>Adductor mandibulae externus medialis insertion (character 27): coronoid and bodenaponeurosis → just bodenaponeurosis</li> <li>Pseudotemporalis superficialis origin (character 37): includes parietal and postorbital → does not include postorbital</li> <li>Pseudotemporalis superficialis insertion extends over (character 39): both coronoid and bodenaponeurosis → bodenaponeurosis</li> <li>Pterygomandibularis origin (character 43): not divided → divided in two slips with tendon</li> <li>Levator pterygoidei (character 48): well developed → reduced</li> <li>Mandibulohyoideus I origin (character 73): mid region of the dentary → posterior region of the dentary</li> <li>Flexor carpi radialis pattern (character 125): two branches → one branch</li> <li>Flexores brevis superficialis position (character 158): of the digits I, II, and III in the same superficial plane → of digits IV, III, II, and I in the same plane</li> </ul>
36	62	<ul style="list-style-type: none"> <li>Intermandibularis anterior profundus aponeurosis (character 55): absent → present</li> <li>Intermandibularis anterior profundus shape (character 56): rectangular → irregular</li> <li>Intermandibularis anterior profundus-Mandibulohyoideus II relation (character 57): attached → not attached</li> <li>Branchiohyoideus aponeurosis (character 83): absent → present</li> <li>Sternohyoideus insertion (character 91): ceratobranchial I → ceratobranchial I, basihyal, and ceratobranchial II</li> <li>Extensor digitorum longus branch number (character 103): Two or three branches → one branch</li> <li>Nasal scale-postrostral scale contact (character 166): in contact → separated</li> <li>Infralabial scale number (character 178-179): 7-7 or fewer → 8-8 to 12-12</li> <li>Middorsal scale row (character 185): absent → present but discontinuous</li> <li>Paravertebral scale surface (character 187): smooth → tuberculate</li> <li>Subdigital lamellae of toes (character 197): smooth → asymmetrical keels</li> <li>Dorsal color pattern (character 210): not fleur-de-lis → fleur-de-lis</li> </ul>
37	100	<ul style="list-style-type: none"> <li>Levator pterygoidei length (character 50): long → short</li> <li>Intermandibularis posterior insertion (character 58): joined with the contralateral muscle → joined with the contralateral muscle, and fibers joining the dorsal musculature</li> </ul>

No	Ja	Synapomorphies
		<ul style="list-style-type: none"> <li>• Branchiohyoideus origin (character 82): ceratobranchial I and epibranchial I → ceratobranchial I</li> <li>• Ceratohyoideus (character 84): absent → present</li> <li>• Omohyoideus origin (character 87): clavicular bar → clavicular bar and interclavicle</li> <li>• Sternohyoideus aponeurosis (character 90): not pigmented → pigmented</li> <li>• Sternohyoideus insertion (character 91): ceratobranchial I → ceratobranchial I, basihyal, and ceratobranchial II</li> <li>• Epitrochleoanconeus (character 129): present → absent</li> <li>• Extensor digitorum brevis section a origin (character 155): astragalo calcaneo by a tendon → metatarsal V fleshy</li> <li>• Hindlimb length (character 202): medium → short</li> <li>• Dermal roof bone rugosities (character 215): strong → absent or weak</li> <li>• Pterygoid teeth (character 228): present → absent</li> <li>• Transverse processes of caudal vertebrae (character 240): extend beyond 16 → do not extend beyond 16</li> </ul>
38	100	<ul style="list-style-type: none"> <li>• Levator anguli oris condition (character 4): wide triangular → narrow triangular</li> <li>• Adductor mandibulae posterior (character 32): present → absent</li> <li>• Levator pterygoidei length (character 50): long → short</li> <li>• Mandibulohyoideus II insertion including ceratobranchial I (character 79): ceratobranchial I and basihyal → ceratobranchial I</li> <li>• Branchiohyoideus origin (character 82): ceratobranchial I and epibranchial I → ceratobranchial I</li> <li>• Extensor digitorum longus origin (character 96): with short tendon → with long tendon</li> <li>• Extensor digitorum longus aponeurosis (character 97): present → absent</li> <li>• Extensor carpi radialis insertion (character 114): distal end of the radius → all radius length</li> <li>• Intermetacarpalis I surface (character 120): including almost all area between fingers → except space between digits 5 and 4, and 2 and 1</li> <li>• Pronator accesorius pattern (character 126): oblique between ulna and radius → parallel between ulna and radius</li> <li>• Epitrochleoanconeus pattern (character 130): origin on humerus → origin not on humerus</li> <li>• Femorotibialis aponeurosis (character 149): fan shaped → rectangular</li> <li>• Popliteus anticus (character 152): absent → present</li> <li>• Tibialis anticus origin (character 159): all tibia length → <math>\frac{3}{4}</math> distal length of the tibia</li> <li>• Snout orbit relative lengths (character 163): snout length greater than orbit diameter → orbital diameter greater than snout length</li> <li>• Supraocular scales (character 171): not carinate → strongly carinated</li> <li>• Mesoptychial scales (character 180): not conical → conical</li> <li>• Mid-dorsal scale row (character 185): absent → present</li> <li>• Paravertebral scale surface (character 187): unicarinate → tuberculate</li> <li>• Distal subdigital lamellae (character 199): not divided → divided</li> <li>• Hindlimb length (character 202): medium → long</li> <li>• Supratemporal bones (character 218): lateral side of supratemporal process of parietal → more-or-less equally on both sides of the supratemporal process of parietal</li> <li>• Sphenoccipital process (character 220): absent or short → long</li> <li>• Marginal teeth (character 229): tricuspid → tapered blunt</li> </ul>

*Received: January 17, 2008*

*Accepted: March 2, 2009*