

A CLADISTIC ANALYSIS OF TEN LIZARD FAMILIES (REPTILIA: SQUAMATA) BASED ON CRANIAL MUSCULATURE

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The cranial musculature of species of ten families of lizards (Gekkonidae, Teiidae, Gymnophthalmidae, Anguidae, Scincidae, Lacertidae, Tropiduridae, Liolaemidae, Leiosauridae, and Polychrotidae) was analyzed. Using 93 myological cranial characters, a cladistic analysis was performed. To root the trees, data of *Sphenodon* were added to the matrix. The cladistic analysis yielded 129 equally parsimonious trees with a fit of 426.0 (39%) and 467 steps. In the consensus tree we observed only five nodes congruent with traditional phylogenetic hypothesis of the groups analyzed: teiids + gymnophthalmids (node 128); geckos (node 136); liolaemids (node 116); genus *Liolaemus* (node 115); and genus *Phymaturus* (node 92). Thus in these groups, phylogeny seems to be better predictor of muscle morphology than ecology or diet.

They are many problematic groups whose monophyly requires further analysis (tropidurids, polychrotids, and scincids). In no case we were able to recognize differences that could be attributed to functional features.

Key words: Cranial musculature, Lizards, Phylogeny, Cladistic analysis.

INTRODUCTION

Since XIX century it is possible to recognize some fundamental subjects in relation to the muscular system in vertebrates: the association between muscles and skeleton (Mivart, 1870; Adams, 1919; Lubosch, 1938); the muscles and its nerve supply (Mivart, 1870; Lakjer, 1926; Haines, 1935, 1939; Howell, 1938; Kesteven, 1944); the relation muscles — function or muscles — habits (Gnanamuthu, 1937; Ostrom, 1962; Iordansky, 1964, 1970; Gorniak et al., 1982; Gans et al., 1985; Gans and de Vree, 1987; Wainwright et al., 1991; Wainwright and Bennett, 1992); there are also cases in which the muscles were used in a typical descriptive context (Mivart, 1867; Sanders, 1870, 1872, 1874; Oelrich, 1956; Haas, 1960); and the possibilities of muscles to recover phylogenetic information (Camp, 1923; Howell, 1938; Romer, 1942; Haas, 1960; Avery and Tanner, 1964; Fischer and Tanner 1970; Iordansky,

1970; Fanghella et al., 1975; Raikow, 1977; Rieppel, 1980, 1984; Russell, 1988; Raikow et al., 1990; Abdala and Moro 1996; Moro and Abdala, 1998, 2000). This last subject implies the question about muscles variability. In relation to that, at least two completely different conceptions could be observed in the literature:

The Bauplan conception:

This conception implies the interpretation of the muscles as stable structures conforming patterns that could be assigned to some taxonomic group.

Among many of the previously mentioned authors, considering the muscular system as reflecting anatomical general pattern was a common place (Adams, 1919; Howell, 1938; Lubosch, 1938; Poglayen-Neuwall, 1954; Fanghella et al., 1975; Abdala and Moro, 1996; Moro and Abdala, 1998, 2000). Some of them used the term “Bauplan” or “plan” to express general anatomical pattern (Brock, 1939; Lubosch, 1938; Iordansky, 1964; Abdala and Moro, 1996). This is a problematic term among the systematics, as it is associated with metaphysical concepts of the pre-darwinian anatomists. However, it has a rather general use among the morphologists. In any case,

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Bauplan is only a word with the additional value of to immediately suggest “anatomical general pattern.”

Adams (1919) states: “since with few exceptions the arrangements of the jaw muscles are remarkable constant in fundamental characters in each of the vertebrate classes...”. And also Lubosch (1938) in reference to urodeles and sauropsids: “...wir erkennen den gleichen Bauplan...”. Both of them express clearly the conception of stability and invariability of the muscles (see also Poglayen-Neuwall, 1953, p. 113).

The conception of muscles being plastic structures:

This point of view minimizes the possibilities of these characters to recover the phylogenetic history of the groups because of its great variability. Brock (1939) states: “Muscles are notoriously difficult to reduce to a coherent comparative scheme, since they are the most adaptable and changeable of morphologic structures, responding to a new functional demands upon them with a readiness to migrate, to subdivide, or not to divide...”. Iordansky (1970) agrees with Brock (op. cit.) that muscles are very plastic structures which are easily rebuilt in accordance with new functional requirements (p. 385).

Romer (1942) states: “...Lack of embriological investigation appears to have been due to the general belief that little of value could be obtained from the early history of such plastic material as limb muscles tissues...”.

Russell (1988) and Kluge (1989) also consider muscles as very plastic structures.

As can be seen from the literature, both conceptions are coexisting in the myological and phylogenetical studies of nowadays.

No matter what conception is taken, the myological characters were no often used in the majority of data sets analyzed to obtain the phylogenetic hypothesis of lizards or Squamata published until now (or in few cases, e.g. Estes et al., 1988, 5 of 148 characters were myological; see also Gauthier et al., 1988, 4 of 171 characters were myological; Caldwell, 1999, 1 of 97). This situation determines a gap among osteology and external anatomy by one side, and myology by the other, considering their use in cladistic analysis.

The question remains: “Can we use the muscles as source of phylogenetic information?” In other words: “Do the muscular characters recover the phylogenetic history of the lizards groups?” In previous works (Abdala and Moro, 1996; Moro and Abdala, 1998, 2000) we used these myological characters, and performed cladistic analysis with different liz-

ards groups. Our results show different situations. We recovered some traditionally groups (geckos, teiids, liolaemins), but in minor level of analysis (e.g., genus relations) we obtained many rather bizarre clades. So, after that analysis of isolated groups we decide to perform an analysis with a more complex data set to see the relationships as suggested by myological cranial characters in a broader group context. How do the characters behave in larger data sets?, do we recover the same groups as when analyze them isolated?, do we recover groups congruent with the usually recognized clades?.

In this work, we made a data set with 74 lizard taxa, considering 93 cranial myological characters and perform a cladistic analysis. Our objectives are, by one side, to add more information about myological characters, helping to fill the gap with other systems. By the other side, to compare the groups obtained with this larger data set with those previously obtained by ourselves; to compare, through congruence, those groups proposed from other systems, and to analyze the possibilities of the myological character as source of phylogenetic information.

MATERIAL AND METHODS

Two hundred specimens belonging to ten families of Squamata were analyzed: 15 Gekkonidae, 51 Teiidae, 11 Gymnophthalmidae, 1 Anguinae, 4 Scincidae, 1 Lacertidae, 65 Liolaemidae, 41 Tropicuridae, 9 Polychrotidae, and 2 Leiosauridae (Appendix I). Voucher specimens are housed in the collection of the Instituto de Herpetología, Fundación Miguel Lillo, Tucumán, Argentina. Macroscopic observation of muscles was performed under binocular dissection microscope. Some specimens were double stained with Alizarine Red S (for bone) and Alcian Blue (86x) (for cartilage) (Wassersug, 1976) in order to determine muscle origins and insertions. Outline drawings were made.

Although we re-analyze three of our previous data set (all together), we add 22 more taxa, recode 12 of our previous characters, and add 13 new characters. A brief description of the muscles not considered in those works (Abdala and Moro, 1996; Moro and Abdala, 1998, 2000) is given.

The terminology and classification of muscles proposed by Haas (1973) is adopted.

Parsimony analysis was performed using the Pee-Wee program (Goloboff, 1993a). PeeWee finds the

most parsimonious trees under predefined weights (for a fundamental of weighting see Goloboff, 1993b). Due to the high number of taxa implied we could only perform an heuristic search of optimal trees. The search strategy included 300 ratchet iterations (factor default 20%) (Nixon, 1999) saving one tree by iteration. Additional trees were found using TBR (tree bisection-reconnection branch swapping). To root the tree, data for *Sphenodon* from the literature (Haas, 1973; Lakjer, 1926) were added to the matrix. Since many of the sample groups analyzed are scarce, we consider all the clades and their proposed synapomorphies as putatives clades. Rooting the cladogram at the outgroup established polarity for all characters on the cladogram (Nixon and Carpenter, 1993). Only unambiguous changes are considered as synapomorphies for groups. The results of the analysis are summarized by means of a strict consensus tree. The list of synapomorphies for clades occurring in the strict consensus was produced by optimizing individual (dichotomous) trees, which constitute equally parsimonious resolutions (command apo-) (Goloboff, 1995). The list of the synapomorphies presented, therefore, does not correspond to a single most parsimonious optimization, but instead shows what is common to several optimizations (corresponding to different trees).

Since many of the multistate characters could be arranged in a logical series, we scored them as additives (cc+). In some cases (characters 5 to 9; 12 and 13) splitting the character allowed us to propose additional logical series that remain confused in too many options of one character. For example, in the case of character 6 (m. *levator anguli oris* origin), it implies an increasing origin surface, while character 8 could be interpreted as a logical series of a decreasing surface (Fig. 3). This make also easier to have a mental graphical scheme of some variations. Please note that these characters provide no redundant information, since the groups that they sustain, are generally not congruent (in analyzing this point we used the Win Clada program by Nixon, 1999).

The characters 36, 48, 56, 63, 70, 72, and 74 are considered non additives (cc-).

Node support was estimated by Bremer relative support value (Goloboff and Farris, 2001).

RESULTS

1. Character Descriptions and List of Characters

1.1. *Adductor mandibulae*

1.1.1. *Adductor mandibulae externus*

Character 0: *Adductor* aponeurosis: (0) not pigmented; (1) pigmented (Moro and Abdala, 1998).

Character 1: *Adductor* aponeurosis condition (Fig. 1): (0) very narrow; (1) narrow; (2) wide (Moro and Abdala, 2000).

Character 2: Temporal fossa aponeurosis: (0) not pigmented; (1) pigmented.

Character 3: *Levator anguli oris*: (0) present; (1) absent (Moro and Abdala, 1998).

Character 4: *Levator anguli oris* condition: (0) wide triangular; (1) narrow triangular; (2) narrow rectangular (Moro and Abdala, 2000).

Character 5: *Levator anguli oris* origin: (0) includes postorbital and jugal; (1) does not include postorbital and jugal (Moro and Abdala, 2000).

Character 6: *Levator anguli oris* origin including postorbital and jugal (Fig. 2): (0) jugal and postorbital; (1) jugal, postorbital, and squamosal; (2) jugal, postorbital, squamosal, and quadrate (Moro and Abdala, 2000).

Character 7: *Levator anguli oris* origin not including postorbital: (0) includes quadrate; (1) does not include quadrate (Moro and Abdala, 2000).

Character 8: *Levator anguli oris* origin not including postorbital but including quadrate (Fig. 3): (0) includes jugal, squamosal, and quadrate; (1) includes squamosal and quadrate; (2) includes just quadrate (Moro and Abdala, 2000).

Character 9: *Levator anguli oris* origin not including jugal (Fig. 4): (0) includes just postorbital; (1) includes both postorbital and squamosal; (2) includes postorbital, squamosal, and quadrate (Moro and Abdala, 2000).

Character 10: *Levator anguli oris* insertion: (0) with aponeurosis; (1) without aponeurosis (Moro and Abdala, 1998).

Character 11: *Retractor anguli oris*: (0) absent; (1) present (Moro and Abdala, 2000).

Character 12: Tendinous system: (0) absent; (1) present.

Character 13: Tendinous system present: (0) developed; (1) very developed (Moro and Abdala, 2000).

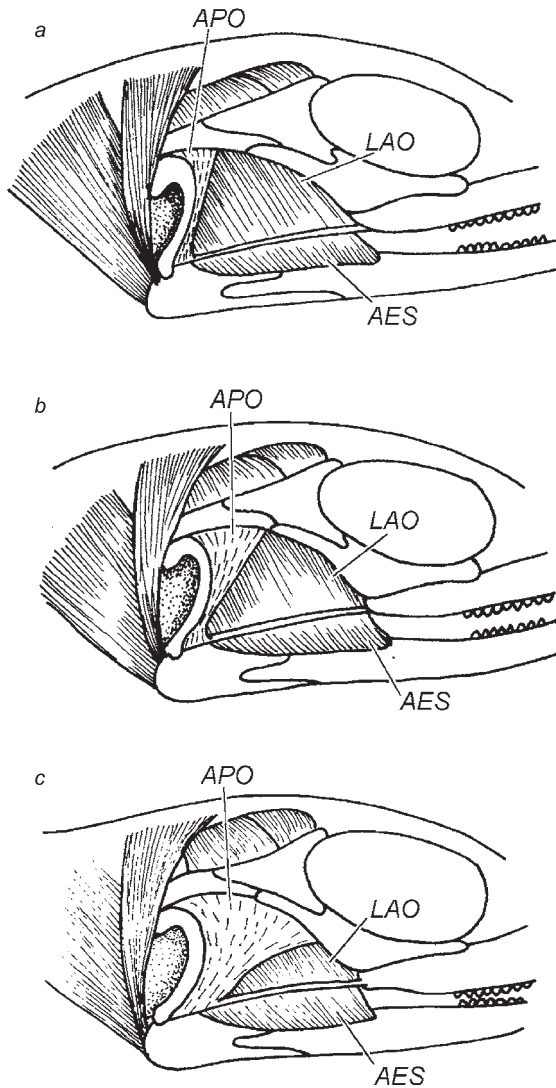


Fig. 1. Adductor aponeurosis condition (character 1). *a*) Aponeurosis very narrow (*Kentropyx lagartija*). *b*) Aponeurosis narrow (*Tropidurus etheridgei*). *c*) Aponeurosis wide (*Tropidurus oreadicus*). Abbreviations: AES, m. adductor mandibulae externus superficialis; APO, adductor aponeurosis; LAO, m. levator anguli oris.

Character 14: Adductor mandibulae externus: (0) not divided; (1) partially divided; (2) completely divided (Moro and Abdala, 1998).

Character 15: Adductor mandibulae externus superficialis origin: (0) includes parietal; (1) does not include parietal (Moro and Abdala, 2000).

Character 16: Adductor mandibulae externus superficialis origin not including parietal, but including postorbital: (0) extends on jugal, postorbital,

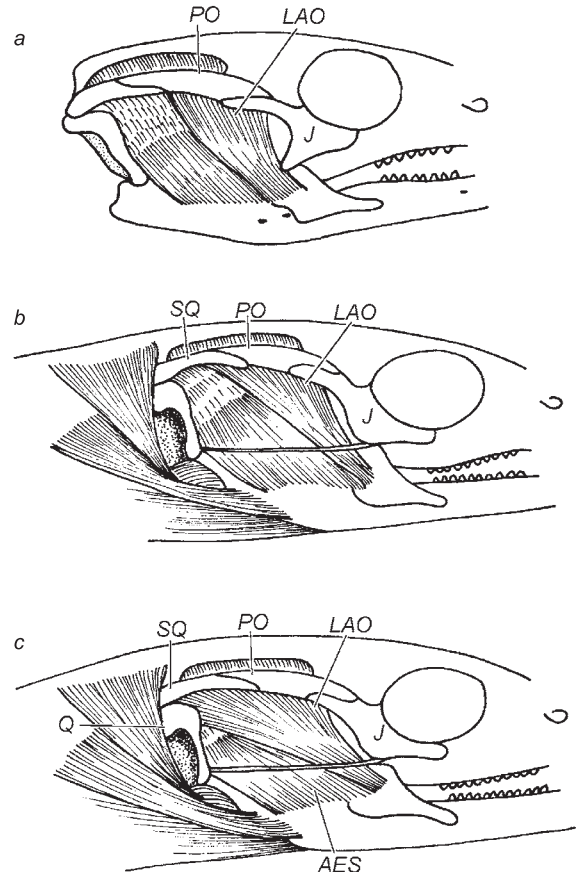


Fig. 2. M. levator anguli oris origin (character 6). *a*) Origin of the m. levator anguli oris on the jugal and postorbital (*Echinosaura horrida*). *b*) Origin of the m. levator anguli oris on the jugal, postorbital, and squamosal (*Kentropyx lagartija*). *c*) Origin of the m. levator anguli oris on the jugal, postorbital, squamosal, and quadrate (*Tupinambis rufescens*). Abbreviations: AES, m. adductor mandibulae externus superficialis; J, jugal; LAO, m. levator anguli oris; PO, postorbital; Q, quadrate; SQ, squamosal.

squamosal, and quadrate; (1) extends on postorbital, squamosal, and quadrate; (2) extends on postorbital and squamosal (Moro and Abdala, 2000).

Character 17: Adductor mandibulae externus superficialis origin not including parietal and not including postorbital: (0) extends on jugal, squamosal, and quadrate; (1) extends on squamosal and quadrate (Moro and Abdala, 2000).

Character 18: Adductor mandibulae externus superficialis insertion: (0) does not include coronoid; (1) includes coronoid (Moro and Abdala, 2000).

Character 19: Adductor mandibulae externus superficialis insertion including coronoid: (0) extends on coronoid; (1) extends on coronoid, boden-

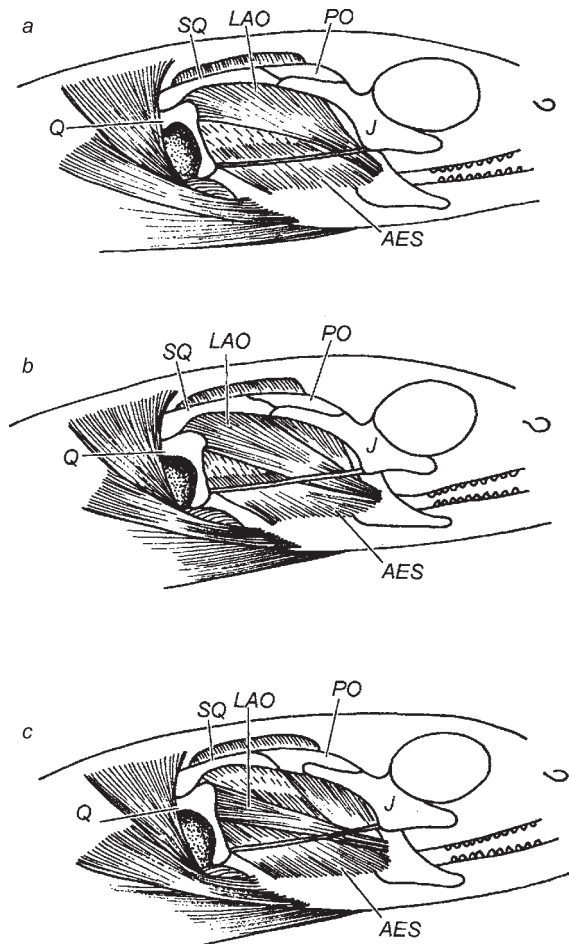


Fig. 3. *M. levator anguli oris* origin (character 8). a) Origin of the *m. levator anguli oris* on the jugal, squamosal, and quadrate (*Teius teyou*). b) Origin of the *m. levator anguli oris* on the squamosal and quadrate (*Cnemidophorus ocellifer*). c) Origin of the *m. levator anguli oris* on the quadrate (*Dracaena paraguayensis*). Abbreviations: AES, *m. adductor mandibulae externus superficialis*; J, jugal; LAO, *m. levator anguli oris*; PO, postorbital; Q, quadrate; SQ, squamosal.

aponeurosis, and articular; (2) extends on coronoid, bodenaponeurosis, articular, and angular (Moro and Abdala, 2000).

Character 20: *Adductor mandibulae externus medialis*: (0) divided; (1) undivided (Moro and Abdala, 2000).

Character 21: *Adductor mandibulae externus medialis* origin not including parietal extends over: (0) prootic; (1) prootic and squamosal (Moro and Abdala, 2000).

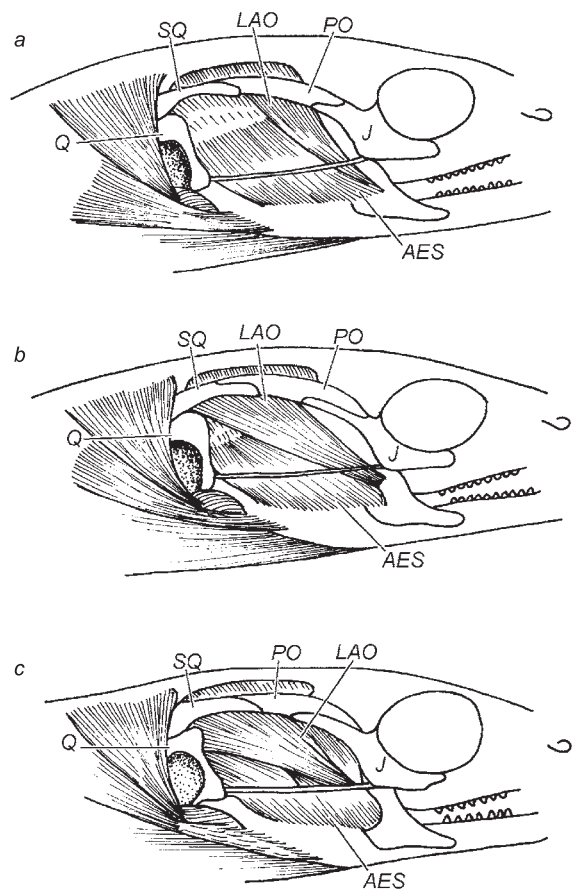


Fig. 4. *M. levator anguli oris* origin (character 9). a) Origin of the *m. levator anguli oris* on the postorbital (*Sphenodon punctatus*). b) Origin of the *m. levator anguli oris* on the postorbital and quadrate (*Crocodilurus lacertinus*). c) Origin of the *m. levator anguli oris* on the postorbital, squamosal, and quadrate (*Stenocercus caducus*). Abbreviations: AES, *m. adductor mandibulae externus superficialis*; J, jugal; LAO, *m. levator anguli oris*; PO, postorbital; Q, quadrate; SQ, squamosal.

Character 22: *Adductor mandibulae externus medialis* origin including parietal extends over (Fig. 5): (0) parietal and prootic; (1) parietal, prootic, and quadrate; (2) parietal, prootic, quadrate, squamosal, and postorbital; (3) parietal, prootic, and squamosal; (4) parietal and squamosal (Moro and Abdala, 2000).

Character 23: Temporal artery: (0) temporal artery visible; (1) temporal artery not visible.

Character 24: Position of the temporal artery: (0) temporal artery located over two muscles; (1) temporal artery located over one muscle.

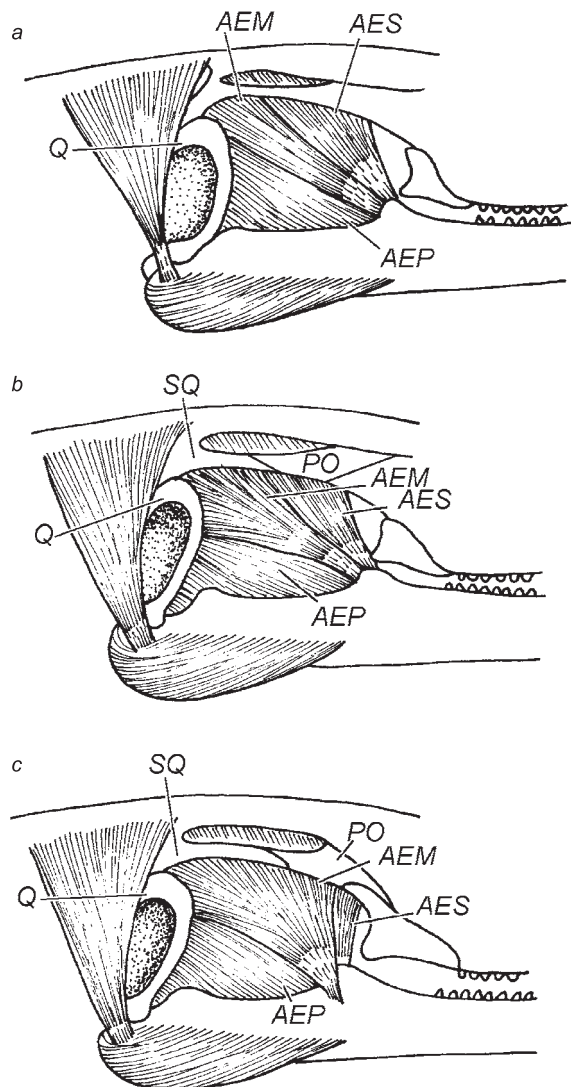


Fig. 5. Origin of the *m. adductor mandibulae externus medialis* (character 22). *a*) Origin of the *m. adductor mandibulae externus medialis* on the parietal and prootic (*Liolaemus cuyanus*). *b*) Origin of the *m. adductor mandibulae externus medialis* on the parietal, prootic, and quadrate (*Cnemidophorus ocellifer*). *c*) Origin of the *m. adductor mandibulae externus medialis* on the parietal, prootic, quadrate, squamosal, and postorbital (*Podarcis sicula*). Abbreviations: AEM, *m. adductor mandibulae externus medialis*; AEP, *m. adductor mandibulae externus profundus*; AES, *m. adductor mandibulae externus superficialis*; PO, postorbital; Q, quadrate; SQ, squamosal.

Character 25: Position of the temporal artery over one muscle: (0) temporal artery located over *m. pseudotemporalis superficialis*; (1) temporal artery located over *m. adductor mandibulae externus medialis* (Moro and Abdala, 2000).

Character 26: *Adductor mandibulae externus medialis* — *pseudotemporalis superficialis* relation: (0) *m. adductor mandibulae externus medialis* fully covers *m. pseudotemporalis superficialis*; (1) *m. adductor mandibulae externus medialis* located back to *m. pseudotemporalis superficialis* (Moro and Abdala, 1998).

Character 27: *Adductor mandibulae externus medialis* insertion extends over: (0) just bodenaponeurosis; (1) both coronoid and bodenaponeurosis (Moro and Abdala, 1998).

Character 28: *Adductor mandibulae externus profundus* origin includes: (0) quadrate; (1) parietal and prootic (Moro and Abdala, 2000).

Character 29: *Adductor mandibulae externus profundus* origin including quadrate, extends over: (0) quadrate; (1) quadrate and prootic; (2) quadrate, prootic, and parietal (Moro and Abdala, 2000).

Character 30: *Adductor mandibulae externus profundus* insertion: (0) including mandibular fossa; (1) only on bodenaponeurosis (Moro and Abdala, 2000).

Character 31: *Adductor mandibulae externus profundus* insertion including mandibular fossa, extends over (Fig. 6): (0) just mandibular fossa; (1) mandibular fossa and coronoid; (2) mandibular fossa, coronoid, and bodenaponeurosis (Moro and Abdala, 2000).

Character 32: *Adductor mandibulae posterior*: (0) absent; (1) present (Moro and Abdala, 2000).

Character 33: *Adductor mandibulae posterior* origin: (0) with tendon; (1) without tendon (Moro and Abdala, 2000).

Character 34: *Adductor mandibulae posterior* tendon: (0) tendon length is the half of quadrate length; (1) tendon length is the same of quadrate length (Moro and Abdala, 1998).

Character 35: *Adductor mandibulae posterior* insertion extends over: (0) just the mandibular fossa; (1) both the mandibular fossa and Meckel's canal (Moro and Abdala, 2000).

1.1.2. *Adductor mandibulae internus*

Character 36: *Pseudotemporalis superficialis*: (0) absent; (1) present (Moro and Abdala, 1998).

Character 37: *Pseudotemporalis superficialis* origin: (0) includes parietal and postorbital; (1) does not include postorbital (Moro and Abdala, 2000).

Character 38: *Pseudotemporalis superficialis* origin not including postorbital, extends over: (0) parietal; (1) parietal and prootic *crista alaris*; (2) pari-

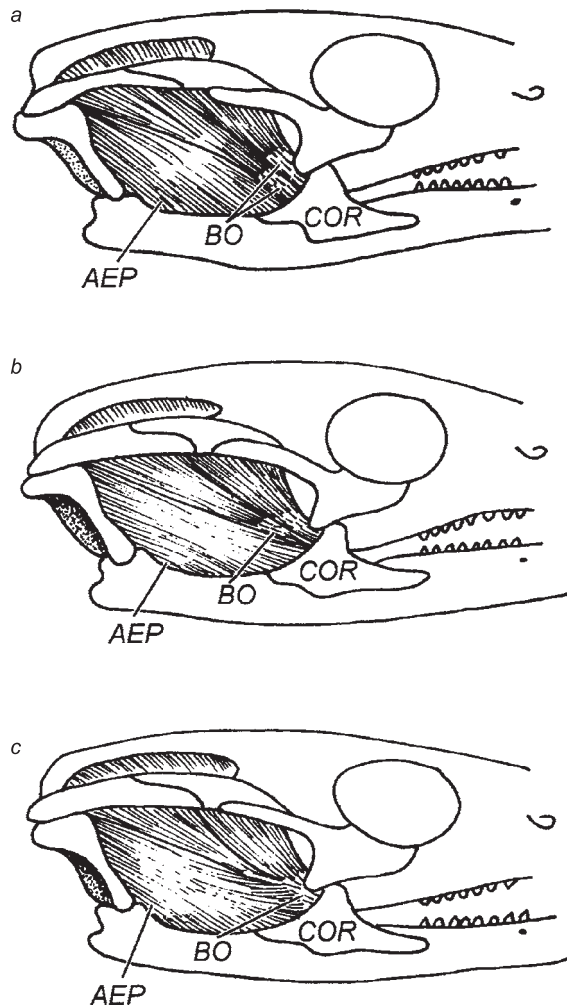


Fig. 6. Insertion of the *m. adductor mandibulae externus profundus* (character 31). *a*) On the mandibular fossa (*Echinosaura horrida*). *b*) On the mandibular fossa and coronoid (*Chalcides chalcides*). *c*) On the mandibular fossa, coronoid, and bodenaponeurosis (*Cnemidophorus ocellifer*). Abbreviations: AEP, *m. adductor mandibulae externus profundus*; BO, bodenaponeurosis; COR, coronoid.

etal, *crista alaris*, and squamosal (Moro and Abdala, 2000).

Character 39: *Pseudotemporalis superficialis* insertion extends over: (0) bodenaponeurosis; (1) both coronoid and bodenaponeurosis (Moro and Abdala, 1998).

Character 40: *Pseudotemporalis profundus* origin extends over (Fig. 7): (0) epipterygoid; (1) epipterygoid and *crista alaris*; (2) epipterygoid, *crista alaris*, and parietal; (3) epipterygoid, *crista*

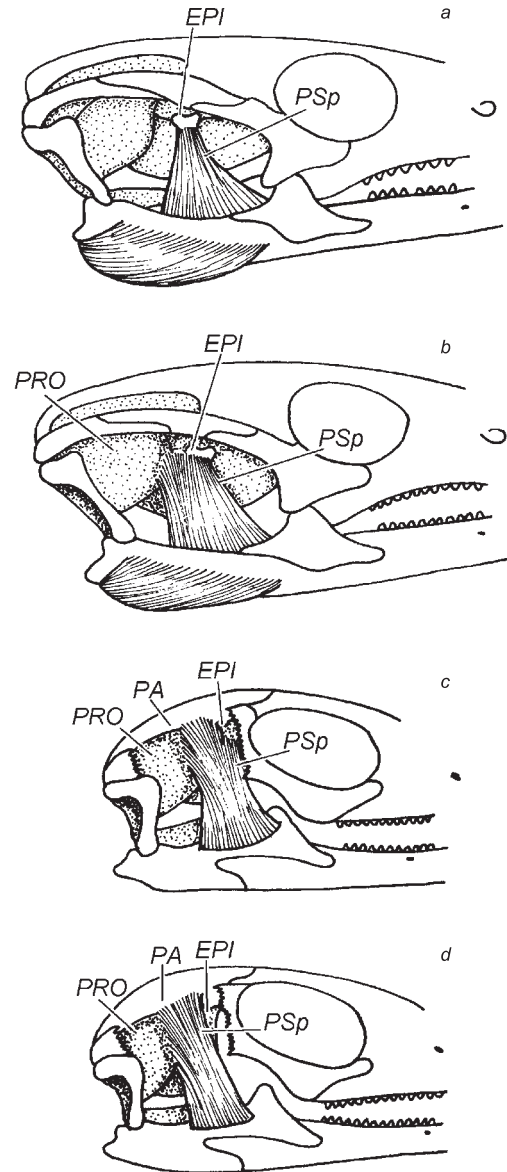


Fig. 7. *a*) Origin of the *m. pseudotemporalis profundus* (character 40): *a*) Origin on the epipterygoid (*Tropidurus etheridgei*). *b*) Origin on the epipterygoid and *crista alaris* (*Phymaturus punae*). *c*) Origin on the epipterygoid, *crista alaris*, and parietal (*Liolaemus scapularis*). *d*) Origin on the *crista alaris* and parietal (*Calyptommatum leiolepis*). In *c* and *d* the temporal arch was removed. Abbreviations: EPI, epipterygoid; PA, parietal; PRO, prootic; PSp, *m. pseudotemporalis profundus*.

alis, parietal, and frontal; (4) *crista alaris* and parietal; (5) epipterygoid, parietal, and membranous wall of the braincase; (6) epipterygoid and parietal (Moro and Abdala, 2000; with modifications in this work).

Character 41: *Pseudotemporalis profundus* insertion extends over: (0) mandibular fossa; (1) mandibular fossa and coronoid; (2) mandibular fossa, coronoid, and bodenaponeurosis (Moro and Abdala, 1998).

Character 42: *Pseudotemporalis profundus* expansion: (0) scarcely expanded; (1) very expanded (Moro and Abdala, 2000).

Character 43: *Pterygomandibularis* origin: (0) not divided; (1) divided in two slips with tendon; (2) divided in two slips without tendon; (3) divided in four slips without tendon (Moro and Abdala, 2000; with modifications in this work).

Character 44: *Pterygomandibularis* volume: (0) bulky; (1) flattened (Moro and Abdala, 2000).

Character 45: *Pterygomandibularis* aponeurosis: (0) not pigmented; (1) scarcely pigmented; (2) very pigmented (Moro and Abdala, 1998).

Character 46: Sexual dimorphism in the *pterygomandibularis* (muscle more developed in males): (0) absent; (1) present (Moro and Abdala, 2000).

Character 47: *Pterygomandibularis atypicus*: (0) absent; (1) present (Moro and Abdala, 2000).

1.2. Constrictor internus

1.2.1. *Constrictor internus dorsalis*

Character 48: *Levator pterygoidei*: (0) well developed; (1) reduced.

Character 49: *Levator pterygoidei* shape: (0) triangular; (1) trapezoidal; (2) rectangular (Moro and Abdala, 2000; with modifications in this work).

Character 50: *Levator pterygoidei* length: (0) long; (1) short (Moro and Abdala, 2000).

Character 51: *Protractor pterygoidei*: (0) absent; (1) present (Moro and Abdala, 2000).

Character 52: *Protractor pterygoidei* origin: (0) basisphenoid; (1) basisphenoid and prootic; (2) prootic (Moro and Abdala, 1998, with modifications in this work).

Character 53: *Retractor pterygoidei*: (0) present; (1) absent (Moro and Abdala, 2000).

1.2.2. *Constrictor internus ventralis*

Character 54: *Intermandibularis anterior superficialis*: (0) absent; (1) present (Moro and Abdala, 1998). **Character 55:** *Intermandibularis anterior profundus* aponeurosis: (0) absent; (1) present (Moro and Abdala, 1998).

Character 56: *Intermandibularis anterior profundus* shape: (0) irregular; (1) fan-shaped; (2) rect-

angular (Moro and Abdala, 1998; with modifications in this work).

Character 57: *Intermandibularis anterior profundus — mandibulohyoideus II* relation: (0) both muscles are attached; (1) both muscles are not attached (Moro and Abdala, 1998).

Character 58: *Intermandibularis posterior* insertion: (0) joined with the contralateral muscle; (1) joined with the contralateral muscle and with the m. *genioglossus* (Moro and Abdala, 1998).

1.3. Constrictor of the neck and throat

The m. *depressor mandibulae* could be single or divided, in a superficial (m. *depressor mandibulae superficialis*) and a deep (m. *depressor mandibulae profundus*) layer. Moreover, the superficial layer could be divided in an anterior and a posterior part.

Character 59: *Depressor mandibulae superficialis* (Fig. 8a): (0) undivided; (1) divided (Moro and Abdala, 2000).

Character 60: *Depressor mandibulae superficialis* anterior origin: (0) includes supraoccipital; (1) does not include supraoccipital.

Character 61: *Depressor mandibulae superficialis* anterior origin not including supraoccipital, extends over (Fig. 8b): (0) parietal; (1) parietal and m. *spinalis capitis*; (2) parietal, m. *spinalis capitis*, and surface of the mm. *adductores*.

Character 62: *Depressor mandibulae superficialis* posterior insertion extends over: (0) retroarticular process; (1) retroarticular process and *depressor mandibulae superficialis* anterior tendon; (2) *depressor mandibulae superficialis* anterior tendon (Moro and Abdala, 2000).

Character 63: Undivided m. *depressor mandibulae superficialis* origin without including parietal: (0) m. *spinalis capitis*; (1) supraoccipital and m. *spinalis capitis*.

Character 64: *Depressor mandibulae superficialis* origin including parietal: (0) parietal and m. *spinalis capitis*; (1) parietal, m. *spinalis capitis*, and squamosal; (2) parietal, squamosal, posterior arcade, and *ligamentum nuchae* (Moro and Abdala, 2000; with modifications in this work).

Character 65: *Depressor mandibulae profundus*: (0) absent; (1) present (Moro and Abdala, 2000).

Character 66: *Cervicomandibularis*: (0) absent; (1) present.

Character 67: *Cervicomandibularis* extension: (0) narrow and partially covers the m. *pterygomandibularis*; (1) wide and partially covers the m. *pterygo-*

mandibularis; (2) wide and completely covers the m. *pterygomandibularis* (Moro and Abdala, 2000).

Character 68: *Cervicomandibularis* insertion: (0) undivided; (1) divided (Moro and Abdala, 2000).

1.4. Tongue muscles

Character 69: *Hyoglossus* origin: (0) ceratobranchial I and basihyal; (1) ceratobranchial I; (2) ceratobranchial I and epibranchial I (Moro and Abdala, 1998).

Character 70: *Genioglossus* contact: (0) without contact with the contralateral muscle; (1) with contact only at the origin end; (2) with contact along all the mid-ventral line; (3) with contact along the mid-ventral line, but not including the origin end (Moro and Abdala, 1998; states were re-ordered in this work).

Character 71: *Genioglossus* shape: (0) triangular; (1) rectangular (Moro and Abdala, 1998).

Character 72: *Genioglossus* aponeurosis: (0) absent; (1) present (Moro and Abdala, 1998).

1.5. Hyoid muscles

Character 73: *Mandibulohyoideus* I origin: (0) mid region of the dentary; (1) posterior region of the dentary.

Character 74: *Mandibulohyoideus* I shape: (0) irregular; (1) triangular; (2) trapezoidal; (3) rectangular (Moro and Abdala, 2000; with modifications in this work).

Character 75: *Mandibulohyoideus* I insertion: (0) ceratobranchial I and basihyal; (1) ceratobranchial I; (2) ceratobranchial I and epibranchial I; (3) ceratobranchial I, basihyal, and epibranchial I.

Character 76: *Mandibulohyoideus* II: (0) absent; (1) present (Moro and Abdala, 1998).

Character 77: Division of the *mandibulohyoideus* II: (0) divided; (1) undivided (Moro and Abdala, 2000).

Character 78: *Mandibulohyoideus* II relation: (0) contralateral muscles separated; (1) contralateral muscles joined.

Character 79: *Mandibulohyoideus* II insertion including ceratobranchial I: (0) ceratobranchial I and basihyal; (1) ceratobranchial I.

Character 80: *Mandibulohyoideus* II insertion including entoglossal process: (0) basihyal and entoglossal process; (1) basihyal (Moro and Abdala, 2000; with modifications in this work).

Character 81: *Mandibulohyoideus* III: (0) absent; (1) present (Moro and Abdala, 1998).

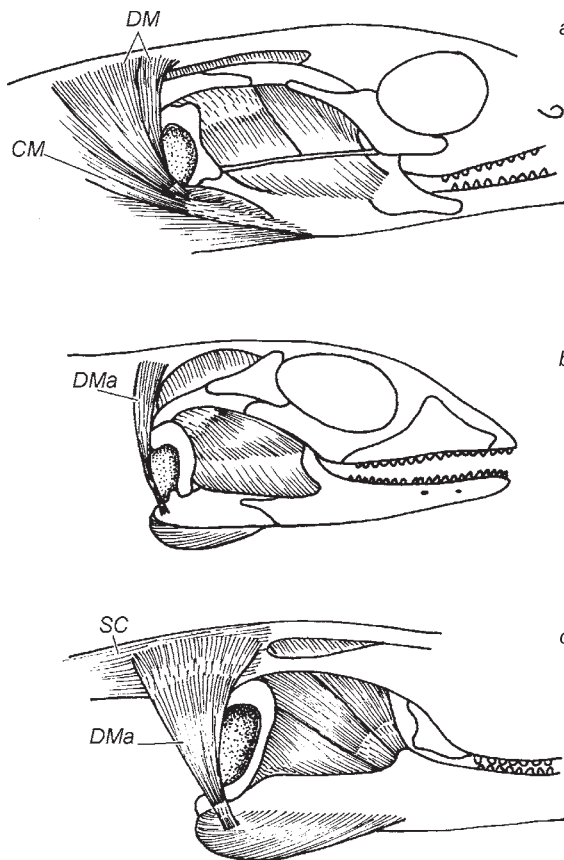


Fig. 8. a) *M. depressor mandibulae superficialis* (character 59): divided (*Liolaemus cuyanus*). b) Origin of the m. *depressor mandibulae superficialis* anterior on the parietal (character 61) (*L. cuyanus*). c) Origin of the m. *depressor mandibulae superficialis* anterior on the parietal and mm. *spinalis capitis* (character 61) (*Cnemidophorus ocellifer*). Abbreviations: CM, m. *cervicomandibularis*; DM, m. *depressor mandibulae superficialis*; DMA, m. *depressor mandibulae superficialis* anterior; SC, m. *spinalis capitis*.

Character 82: *Branchiohyoideus* origin: (0) ceratobranchial I; (1) ceratobranchial I and epibranchial I (Abdala and Moro, 1996).

Character 83: *Branchiohyoideus* aponeurosis: (0) absent; (1) present (Moro and Abdala, 1998).

Character 84: *Ceratohyoideus*: (0) absent; (1) present (Moro and Abdala, 2000).

Character 85: *Geniohipohyoideus*: (0) absent; (1) present (Moro and Abdala, 2000).

Character 86: Muscle X: (0) absent; (1) present (Moro and Abdala, 2000).

Character 87: *Omohyoideus* origin: (0) clavicular bar; (1) clavicular bar and interclavicle; (2) clavicular bar and sternum; (3) clavicular bar, sternum,

and interclavicle; (4) clavicular bar, interclavicle, and suprascapula (Moro and Abdala, 2000).

Character 88: *Omohyoideus* insertion not including basihyal: (0) ceratobranchial I; (1) ceratobranchial I and ceratobranchial II; (2) ceratobranchial I and II, and epibranchial I (Moro and Abdala, 2000; with modifications in this work).

Character 89: *Omohyoideus* insertion including basihyal: (0) ceratobranchial I, ceratobranchial II, and basihyal; (1) ceratobranchial I and basihyal; (2) ceratobranchial II, epibranchial I, and basihyal (Moro and Abdala, 2000; with modifications in this work).

Character 90: *Sternohyoideus* aponeurosis: (0) pigmented; (1) not pigmented (Moro and Abdala, 1998).

Character 91: *Sternohyoideus* insertion: (0) ceratobranchial I and basihyal; (1) ceratobranchial I; (2) ceratobranchial I, epibranchial I, and basihyal; (3) ceratobranchial I and epibranchial I; (4) ceratobranchial I, basihyal, and ceratobranchial II (Moro and Abdala, 2000; with modifications in this work).

Character 92: *Sternothyroideus*: (0) absent; (1) present (Moro and Abdala, 1998).

2. Cladistic Analysis

The cladistic analysis yielded 129 equally parsimonious trees with a fit of 426.0 (39%), and 467 steps. The strict consensus tree is shown in Fig. 9. This tree shows two main clades: Teiidae + Gymnophthalmidae + *Podarcis* (node 128); and the rest of the taxa analyzed (node 146). Gymnophthalmidae is well defined (node 81), even though Teiidae are paraphyletic, and *Pantodactylus schreibersii* is excluded from this clade.

The topology of the clade specified by node 146 differs radically from the relationships of these taxa that have been proposed by other authors. For example, node 77 shows a polychrotid species as the sister taxon to two scincids. Node 96 shows the anguid genus *Ophiodes* as sister taxon to two polychrotid species. All of the tropidurid and liolaemids species are included in node 143, but one scincid and all of the gekkonids are also nested within them, i.e., node 138 shows *Tropidurus hispidus* as the sister taxon to a clade composed of one scincid genus, *Feylinia*, and 10 gekkonid species. Except for *Thecadactylus*, the relationships inside Geckos are totally unresolved.

Node 116 represents all the taxa of Liolaemidae analyzed and it is well defined. Two species of

Phymaturus are grouped in a clade (node 92) and all the species of *Liolaemus* are grouped in another clade (node 115), almost totally unresolved.

Support values. It is difficult to make a decision about what group should be considered reliable. However it should be kept in mind that the best hypothesis is that which used some criteria of maximality (higher fit of the tree in this case).

The support values (Fig. 10) are especially high in node 136 (geckos), 85%; node 137 (*Feylinia* + geckos), 80%; node 92 (*Phymaturus punae* + *Ph. palluma*) 84%, and nodes 106 and 93 corresponding to species of *Liolaemus*, both with 80% of node support. All teiioidea group (node 128) has 33% of support, very low compared with other groups (e.g., geckos). Only node 83 (*Tupinambis* + *Cnemidophorus longicaudus*) has, inside of teiid group, 60% of node support.

The great node 146 has 46% of node support. Some nodes, inside of node 145, have a very low support, but some others are well supported.

Analysis of the characters. In the matrix (Appendix II) we include several kind of characters: presence/absence characters (e.g., character 12: tendinous system); branche division characters (e.g., character 59: m. *depressor mandibulae superficialis*); form characters (e.g., character 49: m. *levator pterygoidei* shape); etc. There are also characters that describe very slight variations in the origin or insertion of the muscles (e.g., character 69: m. *hyoglossus* origin). When the fit of these characters is considered (Table 1), we observe that there are twelve characters with maximal fit (10.0). Of these maximal fit characters, only three (21, 60, and 80), are defined in relation to origin or insertion. When we analyzed the characters with minimal fit (arbitrarily defined here as those characters with fit < 3), we observed that 10 of 16 characters are characters with a "slight variation." In a previous work (Moro and Abdala, 1998) we stressed that "Many of the myological characters are very slight variations in the origin or insertion points of muscles, and also in the shape of muscles. We used this variation because we felt we could score it confidently, but we admit that these characters are easily arguable, and we prefer to regard the nodes sustained by this type of characters as poorly supported..." This is to say that they are very homoplastic and, hence, that the groupings they conform are usually not reliable. This interpretation of certain myological characters appears also in Pöglayen-Neuwall (1954): "Innerhalb der Eidechsen verhält sich die

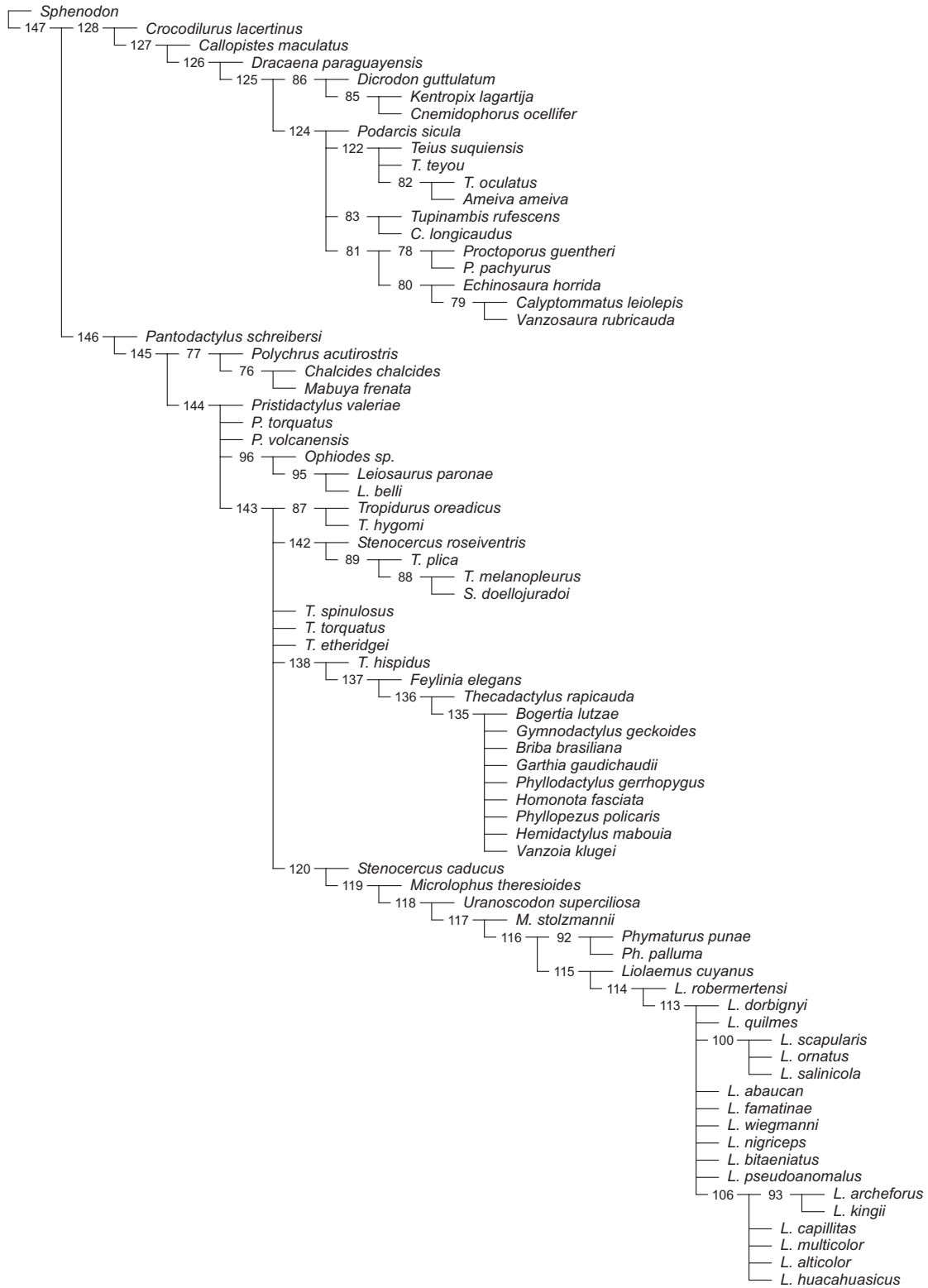


Fig. 9. Strict consensus tree, obtained from the analysis with PIWE program (Goloboff, 1993a).

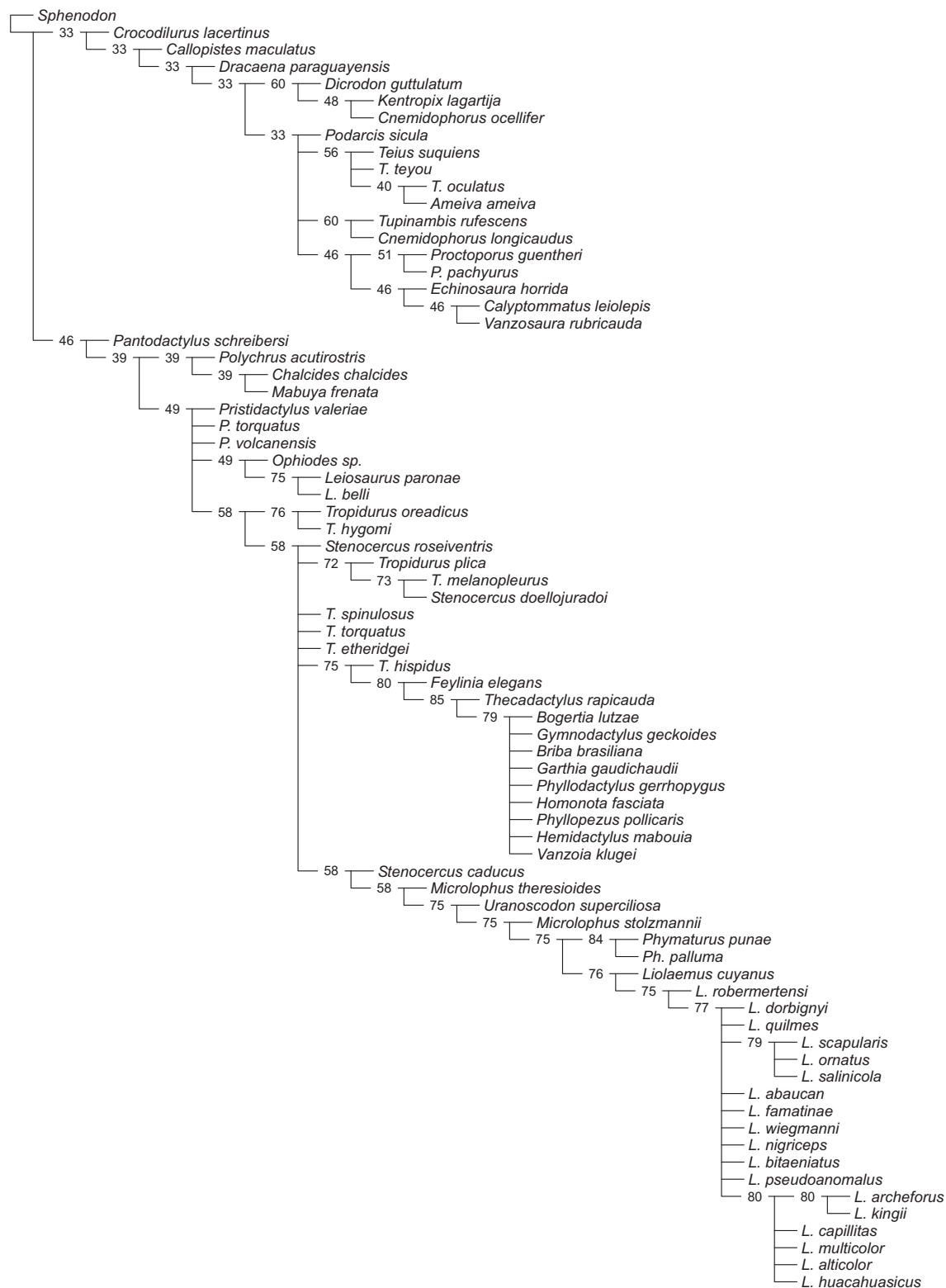


Fig. 10. Cladogram that shows the Bremer relative support values.

Muskulatur konstant, wenn man von zahlreichen geringen Variationen in Ursprung und Ansatz und verschiedenen shennigen Differenzierungen absieht...".

We think that our previous interpretation could also be sustained in the present work. However, we would like to point out that the fit function that we used gives low weight to these highly homoplastic characters.

We also use 17 uninformative characters. We left these characters in the data set because they exhibit interesting anatomical characteristics of the groups.

DISCUSSION

It is normally considered that the cladistic analysis should be done with so many characters of so many sources as possible. However, considering only one source could be usefully to evaluate what is going on with these characters without any noise. We will analyze in the first place, our nodes and their synapomorphies, and then we will compare them with our previous hypothesis, and the current hypothesis published for these taxa.

Among the synapomorphies of the large node 147 (Fig. 9) are the absence of three muscles in lizards in general, and present in *Sphenodon*: *m. retractor anguli oris*, *m. pterygomandibularis atypicus*, and *m. retractor pterygoidei*. Their presence in *Sphenodon* has been considered as a primitive character by Haas (1973). Haas (op. cit.) has also considered that

the partially fused condition of certain muscles represents a more primitive level of differentiation in *Sphenodon* (compared with lizards). The presence in *Sphenodon* of the *constrictor dorsalis* group is also striking, since its skull has been considered as highly akinetic (Versluys, 1912; Lakjer, 1926 in Ostrom, 1962). It seems that to imply a direct relationship between the *constrictor dorsalis* muscles and cranial kinesis as in Brock (1939), or Haas (1973) result a little risky.

In relation to the myological cranial characters of lizards, we could recover a few groups that in the consensus cladogram (Fig. 9) are congruent with previous proposed phylogenies:

a) Node 128 is supported by two synapomorphies (see Table 2). Both (characters 35 and 42), were proposed by Rieppel (1980) as synapomorphies of Teiidae shared with Lacertidae. MacLean (1974), Presch (1974), and Rieppel (1980) consider Teiidae as composed of two groups: macro- and microteiids. Our results disagree with their statements, because Gymnophthalmidae appears within of the broader teiid node (128). In a previous analysis (Moro and Abdala, 2000), we hypothesized teiids as a monophyletic group, and gymnophthalmids paraphyletic. The present results are not congruent with those. It must be considered, that the present matrix is larger than the first that we analyzed. Although there are groups whose relationships are not modified when more taxa and characters are added, these usually have high support values (e.g., geckos and Liolaemidae are, in the present work, monophyletic groups as they were in the previous analyses: Abdala and Moro, 1996; Moro and Abdala, 1998). *Pantodactylus* is excluded from node 128, because it does not have the synapomorphies that characterize this node, and that clearly describe the "Teiidae – Gymnophthalmidae pattern." Caldwell (1999) considers Gymnophthalmidae, Teiidae, and Lacertidae to be closely related groups. Interpreting this relation from the cranial muscular anatomy, it allows us to postulate a myological cranial pattern, or bauplan, shared for the taxa of node 128. This clade could be considered equivalent to Lacertiformes group defined by Estes et al. (1988).

b) The clade of geckos (136) is one of the best supported (85%), with six synapomorphies (tendinous system absent; *m. adductor mandibulae externus* not divided; *m. depressor mandibulae superficialis* divided; *m. cervicomandibularis* absent; *m. genio-glossus* triangular; *m. mandibulohyoideus II* absent). Among the characters sustaining the clade there are

TABLE 1. Command ics for Each Character (Fit)

0	1	2	3	4	5	6	7	8	9
5.0	2.0	7.5	4.2	3.3	7.5	—	5.0	—	10.0
10	11	12	13	14	15	16	17	18	19
7.5	5.0	10.0	—	5.0	6.0	—	6.0	10.0	1.1
20	21	22	23	24	25	26	27	28	29
7.5	—	7.5	10.0	3.7	—	5.0	5.0	3.7	—
30	31	32	33	34	35	36	37	38	39
6.0	7.5	10.0	—	2.0	7.5	2.7	1.5	7.5	7.5
40	41	42	43	44	45	46	47	48	49
5.0	6.0	10.0	1.5	6.0	2.1	3.7	3.3	3.7	10.0
50	51	52	53	54	55	56	57	58	59
7.5	2.5	10.0	7.5	4.2	—	7.5	2.0	2.7	2.0
60	61	62	63	64	65	66	67	68	69
7.5	10.0	1.8	2.3	3.0	2.3	2.0	6.0	6.0	3.7
70	71	72	73	74	75	76	77	78	79
1.7	—	5.0	3.7	2.3	4.2	7.5	7.5	6.0	6.0
80	81	82	83	84	85	86	87	88	89
7.5	—	—	7.5	5.0	10.0	10.0	—	7.5	—
90	91	92							
10.0	—	10.0							

only two with a low fit: 59 (fit = 3) and 76 (fit = 3). The general pattern of geckos is basically defined by absences. Iordansky (1994) hypothesizes that the Ophidia aponeurotic pattern could be derived from that present in Gekkota. Both groups have the tendinous structures of jaw muscles reduced. Rieppel (1983) interprets the absence of *m. pseudotemporalis superficialis* as a consequence of a pedomorphic process in that group. In our experience (see also Abdala and Moro, 1996), the myological cranial pattern of geckos could be described as the simplest among all lizards. In this case we do not obtained resolution for the internal nodes of geckos as in a previous work (Abdala and Moro, 1996).

The *m. levator anguli oris* is lacked both in geckos and scincid, *Gymnophthalmus* and *Proctoporus*, although in our hypothesis, all these are independent events. In these families, the reduced rictal plates attach directly to the surface of the anterior head of the *superficialis* muscle and are operated by this muscle rather than a separate sheet (Costelli, 1973). It must be noted, however, that Rieppel (1980) observed this muscle in some scincids.

c) Node 116 corresponds to family Liolaemidae. It is defined by four synapomorphies: *adductor* aponeurosis wide; *m. levator anguli oris* wide and triangular; *m. cervicomandibularis* narrow and partially covering the *m. pterygomandibularis*; and with contact between both mm. *genioglossus*.

Within this node, all the species of *Liolaemus* are grouped in a well supported clade (node 115, 76% node support), also sustained by four synapomorphies: *m. levator anguli oris* origin not including postorbital but including quadrate, extends over squamosal and quadrate; *m. levator anguli oris* inserts with an aponeurosis; *m. adductor mandibulae externus medialis* origin including parietal, extends over parietal and prootic; presence of *m. intermandibularis anterior profundus* aponeurosis. However, the relationships among the species of this genus are partially unresolved.

d) *Phymaturus* appears as the sister group of *Liolaemus*. The monophyly of *Phymaturus* is very well sustained (node 92, 84% node support). This node has the highest number of synapomorphies of any nodes (12) (except node 147). Its anatomical particularities are exceptionally well recovered by the cladistic analysis, in a way only comparable with geckos. One of its features is *m. adductor externus medialis* wich fully covers the *m. pseudotemporalis superficialis*. This implies that *m. pseudotemporalis*

superficialis is excluded from the supratemporal fossa. Costelli (1973) hypothesizes that there may be greater efficiency in the simpler, one muscle set up and this may contribute to the strength of the jaw apparatus.

This node 116 plus *Microlophus stolzmanni* is totally congruent with our previous hypothesis (Moro and Abdala, 1998).

In our experience, the cranial myology of [Teiidae + Gymnophthalmidae + Lacertidae]; geckos; Liolaemidae; *Phymaturus*, and *Liolaemus* are expressed in the cladistic pattern obtained in a very reliable fashion. This can be seen in the congruence with standard phylogenetic hypothesis, and in support for these nodes (except teiids with 33%). We postulate that each cladistic pattern and its synapomorphies represent the bauplan, the myological pattern correspondent to each group.

On the contrary, our arrangement of the species of *Tropidurus* is incongruent with those of Etheridge and De Queiroz (1988), Frost (1992), Schulte et al. (1999), Harvey and Gutberlet (2000), and Frost et al. (2001). In our analysis *Tropidurus* is paraphyletic in relation to *Stenocercus*, *Microlophus*, *Uranoscodon*, liolaemids, and also in relation to geckos and scincids. Moreover, we show that *Microlophus* and *Uranoscodon* are more closely related to liolaemids than to other tropidurines as proposed by Frost (1992), Harvey and Gutberlet (2000), and Frost et al. (2001). It must be noted, however, that any of those authors makes the analysis considering liolaemids in the data set.

Our hypothesis is also not congruent with those available for *Liolaemus* (Etheridge, 1995; Halloy et al., 1998; Lobo, 2001). The broader node 146 express many very bizarre relationships. Its support is rather low (46%), although it is not the lowest supported group. This node is characterized by a developed tendinous system. Iordansky (1994) hypothesizes that the ancestral forms had no developed tendinous system and muscular masses. In our hypothesis, it is more parsimonious to consider the state "very developed" as the ancestral state. *Sphenodon* has a tendinous system very developed (Haas, 1973), that is conserved in node 128 (except for *Echinosaura*), and change to developed state in all taxa of node 146 (except for *Polychrus* and geckos which suffer a reversion to a very developed state at node 128 and node 136).

Frost et al. (2001) found *Pristidactylus* to be monophyletic; however in our analysis the relationships of the species of *Pristidactylus* are unresolved.

In the other minor levels, we could not recognize groups congruent with current phylogenetic hypothesis.

Myological characters seems to be reliable as phylogeny descriptors only for a few groups. So, they should be used with caution, specially at minor taxonomic level (but see Russell, 1988).

In no case can we recognize differences that could be attributed to functional features. We analyzed specimens with many different diets (e.g., *Dracaena* is a molluscivorous teiid; *Tupinambis* is an omnivorous teiid; etc.), and their jaw musculature had no differences (Dalrympe, 1979; Abdala and Moro, 1996). This lack of differentiation in the myology of the jaws, is very common among lizards. For instance, in chameleons there are many variations in the kinematic of prey capture, or in the motor pattern used during prey capture, even individual variations (Wainwright et al., 1991), but the muscular pattern is the same. Costelli (1973) analyzed the function of the gape, or length of the jaw anterior to the *adductor* musculature in estimating the force of contraction present at the tip of the jaws. He states "If lizards A and B *both have identical musculature*, but A has a gape 20% longer than B, the laws of physics tell us that A will exert a lesser force at the tips of its mandible than B will" (our italics). These features could easily explain differences in possibilities of feeding, with no differences in the architecture of the muscles implied. In fact Costelli (op. cit.) postulate a close correlation between the length of the gape and the type of diet preferred by iguanid lizards.

The versatility of the mouth functions seems to be more related to other plastic structures, e.g., teeth. *Dracaena* has a typical teiid pattern in the cranial muscles (Dalrympe, 1979; Moro and Abdala, 2000); but the main differences are in its very distinctive bunodont teeth, that obviously facilitate crushing hard shells [*Hemisphaeriodon*, a scincid, has a dentition specially modified for durophagy (Edmund, 1969)]. Costelli (1973) suggests, in relation to the iguanids: "There seems to be no features in the musculature that one can point to as herbivorous specializations. The major adaptations seems to be in the serrate dentition which is necessary for shearing and grasping plant material."

Once again we see that myological cranial patterns seem to be flexible enough to permit those

variations in function without necessity of major changes. Adams (1919) arrived at the more general conclusion that "with a few exceptions the arrangements of the jaw muscles are remarkably constant in fundamental characters in each of the vertebrate classes." Also, Schwenk (1988) referring to the lizard tongue, stated that "One might expect the tongue to vary with factors such as diet, and/or body type... as a rule tongue morphology has evolved independent of ecological radiation within a family. Hence, phylogeny is a better predictor of tongue morphology than ecology..." Exactly the same statement we make for cranial musculature in some groups of lizards, e.g., geckos, liolemids [see also Cundall (1987) in relation to snakes]. But in many other groups, e.g., tropidurids, polychrotids, we can not even relate muscles and phylogeny.

Although it seems contradictory to propose a similar cranial musculature for so many groups, and at the same time also present 93 cranial myological characters, it must be noted that, except the absence/presence characters, they express features of structures, present in all taxa (e.g., *depressor mandibulae* muscle). Having these coupled structures (e.g., *constrictor dorsalis* muscles + *adductores mandibulae* muscles, etc.) is what conform the common pattern. This pattern would be very plesiomorphic indeed, because it express itself in having muscles to open the mouth, to swallow or chewing. The characters represent then, variation on this theme, or general pattern, and are used as any other type of character to recover the phylogenetic history of a group.

CONCLUSIONS

- The study of the cranial myology of lizards allow us to provide 93 characters for phylogenetic analysis.
- The characters that describe slight variations of origin or insertion points of muscles have a tendency to be very homoplastic and to support groups not very reliable. Thus, they are not very useful in recovering phylogenies.
- Using cranial myological characters, we obtained only five nodes congruent with traditional phylogenetic hypothesis of the group analyzed: node 128: teiids + gymnophthalmids; node 136: geckos; node 116: liolaemids; node 115: *Liolaemus*; and node 92: *Phymaturus*. In these groups phylogeny seems to be better predictor of muscle morphology than ecology or diet.

- We see problematic groups, as they have no congruence at all with the traditional phylogenetic hypothesis. These could be considered hot groups, whose monophyly requires further analysis: tropidurids, polychrotids, and scincids.
- In no case are we able to recognize differences that could be attributed to functional features.

Myological cranial patterns seems to be flexible enough to allow variations in function without necessity of major anatomical changes.

Acknowledgments. Early drafts of the manuscript were read by Ueso Montero and Pablo Goloboff. Richard Etheridge and Marissa Fabrezi helped us considerably.

TABLE 2. Synapomorphies of the Main Nodes of the Cladogram, with the Relative Branch Support of Each One

Node	Relative branch support, %	Synapomorphies
Node 76	39	<i>Levator anguli oris</i> (character 3): present → absent <i>Adductor mandibulae externus profundus</i> insertion including mandibular fossa, extends over (character 31): mandibular fossa, coronoid and bodenaponeurosis → mandibular fossa and coronoid <i>Depressor mandibulae profundus</i> (character 65): absent → present <i>Genioglossus</i> contact (character 70): with contact only at the origin end → without contact with the contralateral muscle <i>Mandibulohyoideus</i> III (character 81): present → absent <i>Geniohipohyoideus</i> (character 85): absent → present * <i>Branchiohyoideus</i> origin (character 82): ceratobranchial I and epibranchial I → ceratobranchial I
Node 77	39	<i>Adductor mandibulae externus profundus</i> origin including quadrate, extends over (character 29): quadrate and prootic → quadrate <i>Depressor mandibulae superficialis</i> posterior insertion, extends over (character 62): retroarticular process and <i>depressor mandibulae superficialis</i> anterior tendon → retroarticular process <i>Omohyoideus</i> origin (character 87): clavicular bar → clavicular bar and interclavicle
Node 78	51	<i>Adductor mandibulae externus superficialis</i> origin not including parietal, but including postorbital (character 16): postorbital, squamosal and quadrate → jugal, postorbital, squamosal and quadrate <i>Pseudotemporalis superficialis</i> origin not including postorbital, extends over (character 38): parietal and prootic <i>crista alaris</i> → parietal <i>Levator pterygoidei</i> length (character 50): short → long <i>Depressor mandibulae superficialis</i> (character 59): undivided → divided <i>Mandibulohyoideus</i> I shape (character 74): trapezoidal → rectangular <i>Branchiohyoideus</i> origin (character 82): ceratobranchial I and epibranchial I → ceratobranchial I
Node 79	46	<i>Levator anguli oris</i> origin (character 5): includes postorbital and jugal → does not include postorbital and jugal <i>Pterygomandibularis</i> shape (character 44): bulky → flattened <i>Mandibulohyoideus</i> I origin (character 73): mid region of the dentary → posterior region of the dentary
Node 80	46	<i>Adductor aponeurosis</i> extension (character 1): wide → very narrow <i>Mandibulohyoideus</i> II (character 76): present → absent <i>Sternohyoideus aponeurosis</i> (character 90): pigmented → not pigmented * <i>Sternohyoideus</i> insertion (character 91): ceratobranchial I → ceratobranchial I and basihyal
Node 81	46	<i>Levator anguli oris</i> origin including postorbital and jugal (character 6): jugal, postorbital and squamosal → postorbital and jugal * <i>Adductor mandibulae externus profundus</i> insertion including mandibular fossa, extends over (character 31): mandibular fossa, coronoid and bodenaponeurosis → just mandibular fossa
Node 82	40	<i>Protractor pterygoidei</i> origin (character 52): basisphenoid → basisphenoid and prootic <i>Intermandibularis anterior profundus</i> shape (character 56): irregular → fan-shaped
Node 83	60	<i>Adductor externus mandibulae profundus</i> insertion (character 30): including mandibular fossa → only on bodenaponeurosis <i>Hyoglossus</i> origin (character 69): ceratobranchial I → ceratobranchial I and epibranchial I * <i>Levator anguli oris</i> origin including postorbital and jugal (character 6): jugal, postorbital and squamosal → jugal, postorbital, squamosal and quadrate
Node 85	48	<i>Geniohipohyoideus</i> (character 85): absent → present
Node 86	60	<i>Adductor aponeurosis</i> extension (character 1): wide → very narrow <i>Adductor externus mandibulae profundus</i> insertion (character 30): including mandibular fossa → only on bodenaponeurosis <i>Mandibulohyoideus</i> I insertion (character 75): ceratobranchial I → ceratobranchial I and epibranchial I

TABLE 2 (continued)

Node	Relative branch support, %	Synapomorphies
Node 87	76	<i>Levator anguli oris</i> insertion (character 10): without aponeurosis → with aponeurosis * <i>Levator anguli oris</i> origin (character 5): does not include postorbital and jugal → includes postorbital and jugal * <i>Adductor externus mandibulae medialis</i> origin including parietal, extends over (character 22): parietal, prootic and quadrate → parietal, prootic, quadrate, squamosal and postorbital * <i>Intermandibularis anterior superficialis</i> (character 54): absent → present
Node 88	73	<i>Adductor externus mandibulae profundus</i> origin including quadrate, extends over (character 29): quadrate and prootic → quadrate, prootic and parietal <i>Pseudotemporalis profundus</i> insertion, extends over (character 41): mandibular fossa → mandibular fossa, coronoid and bodenaponeurosis <i>Branchiohyoideus</i> origin (character 82): ceratobranchial I → ceratobranchial I and epibranchial I * <i>Levator pterygoidei</i> shape (character 49): triangular → trapezoidal
Node 89	72	<i>Pseudotemporalis profundus</i> origin extends over (character 40): epipterygoid → epipterygoid, crista alaris and parietal * <i>Pseudotemporalis superficialis</i> insertion extends over (character 39): bodenaponeurosis → both coronoid and bodenaponeurosis * <i>Intermandibularis anterior superficialis</i> (character 54): present → absent * <i>Genioglossus</i> contact (character 70): with contact only at the origin end → with contact along all the mid-ventral line
Node 92	84	<i>Adductor mandibulae externus superficialis</i> insertion including coronoid (character 19): extends on coronoid, bodenaponeurosis and articular → extends on coronoid <i>Adductor mandibulae externus medialis</i> origin including parietal, extends over (character 22): [parietal, prootic, and quadrate] [parietal, prootic, quadrate, squamosal, and postorbital] [parietal, prootic, and squamosal] → parietal and squamosal <i>Adductor mandibulae externus medialis</i> — <i>pseudotemporalis superficialis</i> relation (character 26): <i>adductor mandibulae externus medialis</i> fully covers <i>pseudotemporalis superficialis</i> → <i>adductor mandibulae externus medialis</i> fully covers <i>pseudotemporalis superficialis</i> <i>Adductor mandibulae externus medialis</i> insertion, extends over (character 27): just bodenaponeurosis → both coronoid and bodenaponeurosis <i>Adductor mandibulae externus profundus</i> origin including quadrate, extends over (character 29): quadrate and prootic → quadrate, prootic, and parietal <i>Pseudotemporalis superficialis</i> origin not including postorbital, extends over (character 38): parietal and prootic crista alaris → parietal <i>Pseudotemporalis profundus</i> insertion, extends over (character 41): mandibular fossa → mandibular fossa and coronoid <i>Levator pterygoidei</i> shape (character 49): rectangular → triangular <i>Intermandibularis anterior profundus</i> shape (character 56): fan-shaped → rectangular <i>Genioglossus</i> shape (character 71): rectangular → triangular <i>Genioglossus</i> aponeurosis (character 72): absent → present <i>Mandibulohyoideus</i> I insertion (character 75): ceratobranchial I and epibranchial I → ceratobranchial I
Node 93	80	<i>Cervicomandibularis</i> shape (character 67): narrow and partially covers the <i>pterygomandibularis</i> → wide and completely covers the <i>pterygomandibularis</i>
Node 95	75	<i>Pseudotemporalis profundus</i> insertion extends over (character 41): mandibular fossa → mandibular fossa, coronoid and bodenaponeurosis <i>Levator pterygoidei</i> (character 48): well developed → reduced <i>Levator pterygoidei</i> shape (character 49): rectangular → triangular <i>Depressor mandibulae superficialis</i> (character 59): divided → undivided <i>Mandibulohyoideus</i> I shape (character 74): trapezoidal → irregular * <i>Pseudotemporalis superficialis</i> origin not including postorbital, extends over (character 38): parietal and prootic crista alaris → parietal
Node 96	49	<i>Adductor mandibulae externus medialis</i> (character 96): undivided → divided <i>Pterygomandibularis</i> aponeurosis (character 45): not pigmented → scarcely pigmented <i>Mandibulohyoideus</i> I origin (character 73): mid region of the dentary → posterior region of the dentary
Node 100	79	<i>Omohyoideus</i> origin (character 87): clavicular bar and interclavicle → clavicular bar
Node 106	80	<i>Intermandibularis anterior profundus</i> — <i>mandibulohyoideus</i> II relation (character 57): both muscles are not attached → both muscles are attached
Node 113	77	<i>Pterygomandibularis</i> aponeurosis (character 45): not pigmented → scarcely pigmented
Node 114	75	<i>Omohyoideus</i> origin (character 87): clavicular bar → clavicular bar and interclavicle

TABLE 2 (continued)

Node	Relative branch support, %	Synapomorphies
Node 115	76	<i>Levator anguli oris</i> origin not including postorbital but including quadrate (character 8): includes jugal, squamosal, and quadrate → includes squamosal and quadrate <i>Levator anguli oris</i> insertion (character 10): without aponeurosis → with aponeurosis <i>Adductor mandibulae externus medialis</i> origin including parietal, extends over (character 22): [parietal, prootic, and quadrate] [parietal, prootic, quadrate, squamosal, and postorbital] [parietal, prootic, and quadrate] → parietal and prootic <i>Intermandibularis anterior profundus</i> aponeurosis (character 55): absent → present
Node 116	75	<i>Adductor aponeurosis</i> extension (character 1): narrow → wide <i>Levator anguli oris</i> extension (character 4): narrow triangular → wide triangular <i>Cervicomandibularis</i> shape (character 67): wide and completely covers the <i>pterygomandibularis</i> → narrow and partially covers the <i>pterygomandibularis</i> <i>Genioglossus</i> contact (character 70): with contact only at the origin end → without contact with the contralateral muscle
Node 117	75	<i>Sternohyoideus</i> insertion (character 91): ceratobranchial I → ceratobranchial I and epibranchial I
Node 118	75	<i>Adductor mandibulae</i> posterior tendon (character 34): tendon length is the same of quadrate length → tendon length is the half of quadrate length
Node 119	58	<i>Intermandibularis anterior profundus</i> aponeurosis (character 55): fan-shaped → irregular <i>Mandibulohyoideus</i> I insertion (character 75): ceratobranchial I → ceratobranchial I and epibranchial I * <i>Protractor pterygoidei</i> origin (character 52): basisphenoid → basisphenoid and prootic
Node 120	58	<i>Depressor mandibulae superficialis</i> anterior origin not including supraoccipital, extends over (character 61): parietal and spinalis capitis → parietal * <i>Levator anguli oris</i> origin not including postorbital but including quadrate (character 8): includes squamosal and quadrate → includes jugal, squamosal, and quadrate * <i>Depressor mandibulae superficialis</i> (character 59): undivided → divided
Node 122	56	<i>Mandibulohyoideus</i> III (character 81) absent → present <i>Omohyoideus</i> origin (character 87): clavicular bar → clavicular bar and sternum * <i>Pseudotemporalis superficialis</i> origin not including postorbital, extends over (character 38): parietal and prootic <i>crista alaris</i> → parietal * <i>Intermandibularis anterior profundus</i> aponeurosis (character 55): present → absent * <i>Hyoglossus</i> origin (character 69): ceratobranchial I → ceratobranchial I and epibranchial I
Node 124	33	<i>Levator anguli oris</i> extension (character 4): wide triangular → narrow triangular Sexual dimorphism in the <i>pterygomandibularis</i> (character 46): absent → present
Node 125	33	Division of the <i>mandibulohyoideus</i> II (character 77): undivided → divided <i>Mandibulohyoideus</i> II insertion including entoglossal process (character 80): basihyal and entoglossal process → basihyal <i>Sternohyoideus</i> aponeurosis (character 90): not pigmented → pigmented
Node 126	33	<i>Levator pterygoidei</i> length (character 50): long → short <i>Mandibulohyoideus</i> III (character 81): present → absent
Node 127	33	<i>Adductor externus mandibulae medialis</i> origin not including parietal, extends over (character 21): prootic and squamosal → prootic
Node 128	33	<i>Adductor mandibulae</i> posterior insertion, extends over (character 35): just the mandibular fossa → both the mandibular fossa and Meckel's canal <i>Pseudotemporalis profundus</i> expansion (character 42): scarcely expanded → very expanded
Node 135	79	<i>Pterygomandibularis</i> origin (character 43): divided in two sips with tendon → not divided
Node 136	85	<i>Tendinous</i> system (character 12): present → absent <i>Adductor mandibulae externus</i> (character 14): partially divided → not divided <i>Depressor mandibulae superficialis</i> (character 59): undivided → divided <i>Cervicomandibularis</i> (character 66): present → absent <i>Genioglossus</i> shape (character 71): rectangular → triangular <i>Mandibulohyoideus</i> II (character 76): present → absent
Node 137	80	<i>Levator anguli oris</i> (character 3): present → absent <i>Adductor mandibulae externus</i> (character 14): completely divided → partially divided <i>Pseudotemporalis superficialis</i> (character 36): present → absent <i>Protractor pterygoidei</i> origin (character 52): basisphenoid and prootic → basisphenoid * <i>Intermandibularis anterior superficialis</i> (character 54): present → absent

TABLE 2 (continued)

Node	Relative branch support, %	Synapomorphies
Node 138	75	Temporal artery (character 23): temporal artery visible → temporal artery not visible
Node 142	58	<i>Adductor aponeurosis</i> extension (character 1): wide → narrow <i>Levator anguli oris</i> extension (character 4): wide triangular → narrow triangular <i>Cervicomandibularis</i> shape (character 67): wide and partially covers the <i>pterygomandibularis</i> → wide and completely covers the <i>pterygomandibularis</i> <i>Mandibulohyoideus</i> I shape (character 74): trapezoidal → triangular <i>Mandibulohyoideus</i> III (character 81): present → absent * <i>Pseudotemporalis profundus</i> origin, extends over (character 40): epipterygoid, <i>crista alaris</i> , and parietal → epipterygoid * <i>Depressor mandibulae superficialis</i> (character 59): divided → undivided
Node 143	58	<i>Intermandibularis anterior profundus</i> shape (character 56): irregular → fan-shaped *Temporal fossa aponeurosis (character 2): pigmented → not pigmented * <i>Intermandibularis anterior superficialis</i> (character 54): absent → present
Node 144	49	<i>Branchiohyoideus</i> aponeurosis (character 83): absent → present
Node 145	39	<i>Pseudotemporalis profundus</i> insertion, extends over (character 41): [mandibular fossa and coronoid] [mandibular fossa, coronoid, and bodenaponeurosis] → mandibular fossa <i>Depressor mandibulae superficialis</i> (character 59): undivided → divided <i>Genioglossus</i> contact (character 70): with contact along all the mid-ventral line → with contact only at the origin end <i>Ceratohyoideus</i> (character 84): present → absent <i>Omohyoideus</i> insertion including basihyal (character 89): ceratobranchial I and basihyal → ceratobranchial I, ceratobranchial II and basihyal
Node 146	46	<i>Tendinous</i> system present (character 13): very developed → developed
Node 147		<i>Levator anguli oris</i> extension (character 4): narrow rectangular → wide triangular <i>Levator anguli oris</i> origin not including jugal (character 9): includes just postorbital → includes both postorbital and squamosal <i>Retractor anguli oris</i> (character 11): present → absent <i>Adductor mandibulae externus superficialis</i> origin not including parietal, but including postorbital (character 16): extends on postorbital and squamosal → extends on postorbital, squamosal, and quadrate <i>Adductor mandibulae externus superficialis</i> insertion including coronoid (character 19): extends on coronoid, bodenaponeurosis, articular, and angular → extends on coronoid, bodenaponeurosis, and articular <i>Adductor mandibulae externus medialis</i> origin including parietal, extends over (character 22): parietal and squamosal → parietal, prootic, and quadrate <i>Adductor mandibulae externus profundus</i> origin includes (character 28): parietal and prootic → quadrate <i>Adductor mandibulae externus profundus</i> insertion (character 30): only on bodenaponeurosis → including mandibular fossa <i>Adductor mandibulae posterior</i> tendon (character 33): without tendon → with tendon <i>Pseudotemporalis superficialis</i> origin (character 37): includes parietal and postorbital → does not include postorbital <i>Pseudotemporalis profundus</i> origin extends over (character 40): epipterygoid, parietal, and membranous wall of the braincase → epipterygoid, <i>crista alaris</i> , and parietal <i>Pterygomandibularis</i> origin (character 43): divided in four slips without tendon → divided in two slips with tendon <i>Pterygomandibularis atypicus</i> (character 47): present → absent <i>Protractor pterygoidei</i> origin (character 52): prootic → [basisphenoid] [basisphenoid and prootic] <i>Retractor pterygoidei</i> (character 53): present → absent <i>Intermandibularis anterior profundus</i> shape (character 56): rectangular → irregular <i>Depressor mandibulae superficialis</i> origin including parietal (character 64): parietal, squamosal, posterior arcade, and ligamentum nuchae → parietal and <i>spinalis capitis</i>

* Only in some trees.

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APPENDIX I SPECIMENS EXAMINED

The acronyms used correspond to: FML, Fundación Miguel Lillo; MACN, Museo Argentino de Ciencias Naturales, Argentina; MNHN, Museum National d'Histoire Naturelle, Paris, France; MZUSP, Museu de Zoologia Universidade de São Paulo, Brazil; NMW, Naturhistorisches Museum, Wien, Austria; PT, Projec-

to Tupinambis, Tucumán, Argentina; SDSU, San Diego University, USA.

Gekkonidae

Argentina: *Phyllopezus pollicaris*: FML 02913 (one male and one female) — Fuerte Esperanza, Gral. Güemes, Chaco. *Homonota fasciata*: FML 02137 (undet. sex) — Villa Luján, Catamarca; FML 00915 (one male and one female) — Catamarca. **Brazil:** *Bogertia lutzae*: MZUSP 54747 (undet. sex) — Salvador, Brotas. *Briba brasiliana*: MZUSP 73851 (undet. sex) — Macuje, Ba. *Gymnodactylus geckoides*: MZUSP 48128 (undet. sex) — Exu, Pe. *Hemidactylus mabouia*: FML 02142 (one male) — Gravatá, Santa Catarina; FML 02421 (undet. sex) — No data. *Vanzoia klugei*: MZUSP 59130 (one female) — Cabeceiras, Fazenda Bravo. **Chile:** *Phyllodactylus gerrhopygus*: FML 01563 (one male and one female) — between Hornitos and Tocopilla. *Garthia gaudichaudii*: MZUSP 45329 (undet. sex) — N. Caldera, Atacama. **Surinam:** *Thecadactylus rapicauda*: MZUSP 11476 (undet. sex) — Langaman-kondra.

Teiidae

Argentina: *Ameiva ameiva*: FML 03637 (two females) — Aguas Blancas, Dto. Orán, Salta; FML 03249 (one male and one female) — Campo Grande, Finca Los Colorados, 100 km to the EN to J. V. González, Dto. Anta, Salta. *Cnemidophorus ocellifer*: FML 03389 (two specimens, undet. sex) — Finca Pozo Largo, 8 km to the S of J. V. González and 12 km to the E of Finca San Javier, Dto. Anta, Salta; FML 03396 — Finca Pozo Largo, 8 km to the S of J. V. González and 12 km to the E of Finca San Javier, Dto. Anta, Salta; FML 03409 (four specimens, undet. sex) — Finca Pozo Largo, 8 km to the S of J. V. González and 12 km to the E of Finca San Javier, Dto. Anta, Salta. *Cnemidophorus longicaudus*: FML 00078 (two males) — Valle de Santa María, Catamarca; FML 02761 (one male) — Lucio V. Mansilla, Dto. Tulumba, Córdoba. *Kentropix lagartija*: FML 01186 (undet. sex) — Río Loro, Dto. Burreyacu, Tucumán. *Teius oculatus*: FML 03625 (one female) — Way to Cuadro Nacional by Ferrocarril to Mendoza, San Rafael, Dto. San Rafael, Mendoza; FML 03629 (one male and one female) — Río Cuarto, Dto. Río Cuarto, Córdoba; FML 03630 (two females) — Río Cuarto, Dto. Río Cuarto, Córdoba; FML 03632 (one male) — Achiras, Dto. Río Cuarto, Córdoba; FML 03633 (one female) — Alpa Corral, Dto. Río Cuarto, Córdoba. *Teius suquiensis*: FML 03626 (one female) — Mina Clavero, Dto. San Alberto, Córdoba; FML 03627 (one male) — Mina Clavero, Dto. San Alberto, Córdoba; FML 03628 (one female) — left margin of the Río Xanaes (ex Río

Segundo), in the cross with Rute National 36, Despeñaderos, Dto. Santa María, Córdoba; FML 03631 (one female) — San Roque, Dto. Punilla, Córdoba. *Teius teyou*: FML 00290 (two females) — Hickmann, Dto. San Martín, Salta; FML 03634 (one female) — Medio Naranjo, Dto. Cruz del Eje, Córdoba; FML 03435 (one male) — Guanaco Muerto, Dto. Cruz del Eje, Córdoba; FML 03636 (one male and one female) — Sierra San Marcos, Dto. Cruz del Eje, Córdoba. *Tupinambis rufescens*: PT 0084 (one female) — J. V. González, Salta Forestal, cross with Rute 41, Dto. Anta, Salta; PT 0085 (one male) — J. V. González, Salta Forestal, cross with Rute 41, Dto. Anta, Salta; PT 0597 (undet. sex) — 44 km to the E of J. V. González, Laguna Verde, Dto. Anta, Salta; PT 0889 (undet. sex) — 41 km to the E of J. V. González, Laguna Verde, Dto. Anta, Salta; FML 06412 (one female) — 8 km to the E and 8 km to the S of J. V. González, El Guayacán, Dto. Anta, Salta; FML 06413 (one male) — 8 km to the E and 8 km to the S of J. V. González, El Guayacán, Dto. Anta, Salta; FML 06423 (one male) — 8 km to the E and 8 km to the S of J. V. González, El Guayacán, Dto. Anta, Salta; FML 06425 (one female) — 8 km to the S and 40 km to the E of J. V. González, Puesto Amoate, Dto. Anta, Salta; FML 07428 (one female): 41 km to the E of J. V. González, Salta Forestal, Dto. Anta, Salta; FML 07429 (one male) — 8 km to the S and 40 to the E of J. V. González, Puesto Amoate, Dto. Anta, Salta; FML 07431 (one male) — 8 km to the E and 8 km to the S of J. V. González, El Guayacán, Dto. Anta, Salta; FML 07432 (one male) — 8 km to the S and 40 km to the E of J. V. González, Puesto Amoate, Dto. Anta, Salta; FML 07433 (one male) — 8 km to the E and 8 km to the S of J. V. González, El Guayacán, Dto. Anta, Salta; FML 07434 (one male) — 8 km to the E and 8 km to the S of J. V. González, El Guayacán, Dto. Anta, Salta. **Brazil:** *Crocodilurus lacertinus*: MZUSP 12622 (undet. sex) — Oriximiná, Pará; MZUSP 16307 (undet. sex) — Oriximiná, Pará. *Dracaena paraguayensis*: MZUSP 52369 (undet. sex) — Fazenda Acarizal, Río Paraguai, Mato Grosso. **Chile:** *Callopiastes maculatus*: MZUSP 58107 (undet. sex) — Freirina a El Morado, Atacama. **Peru:** *Dicrodon guttulatum*: FML 02017 (undet. sex) — Talara.

Gymnophthalmidae

Argentina: *Pantodactylus schreibersi*: FML with-out number (two females) — near Río Grande, Potrero de las Tablas, Tucumán. **Brazil:** *Calyptommatus leirolepis*: MZUSP 71339 (undet. sex) — Ibiraba, Bahia; MZUSP 71367 (undet. sex) — Ibiraba, Bahia. *Vanzosaura rubricauda* (= *Gymnophthalmus multiscutatus*): FML 08786, 08787 and 08788 (undet. sex) — Vacaria,

Bahia. **Ecuador:** *Echinosaura horrida*: MZUSP 54452 (undet. sex) — Pichincha, Centro Científico Río Palenque (Lago Creek); MZUSP 54454 (undet. sex) — Pichincha, Centro Científico Río Palenque (Lago Creek). **Peru:** *Proctoporus guentheri*: FML 02010 (undet. sex) — Río Crespón, Yama Zera. *Proctoporus pachyurus*: FML 01970 (undet. sex) — La Florida, near Tacna (3000 m).

Anguidae

Argentina: *Ophiodes* sp.: FML 01239 (undet. sex) — Barrio Judicial, San Miguel de Tucumán, Dto. Capital, Tucumán.

Scincidae

Argentina: *Mabuya frenata*: FML 00277 (undet. sex) — Aguaray, Orán, Salta; FML 01713 (undet. sex) — Misión Tacaaglé, Formosa. **Italia:** *Chalcides chalcides*: FML 03712 (undet. sex) — stream Torrente Farma, Comuna de Monticiano, Prov. Siena, Toscana. **Zaire:** *Feylinia elegans grandisquamis*: FML 01013 (undet. sex) — Omaniundu, Terr. De Lodja, Sankuru.

Lacertidae

Italia: *Podarcis sicula*: FML 03714 (undet. sex) — Matera, Comuna y Prov. de Matera, Basilicata.

Liolaemidae

Argentina: *Phymaturus punae*: FML 02942 (two males and two females) — Quebrada del Leoncito, on the way to Laguna Brava, Alto Jagüe, Dto. Gral. Sarmiento, La Rioja. *Phymaturus palluma*: FML 00630 (one male and one female) — Quebrada Aguas Calientes (Ojo del Salado), Catamarca. *Liolaemus abaucan*: FML 01814 (two males and two females) — Palo Blanco (Gruta Virgen del Valle), Dto. Tinogasta, Catamarca. *L. alticolor*: FML 02238 (two males and two females) — Hombro de las Pegmatitas (on the way to Huaca Huasi), Dto. Tafí del Valle, Tucumán. *L. archeoforus*: FML 01030 (one female) — Puesto Lebrun, Lago Buenos Aires, Santa Cruz. *L. bitaeniatus*: FML 02290 (four specimens, undet. sex) — Dique La Angostura, Dto. Tafí del Valle, Tucumán. *L. capillitas*: FML 01914 (four specimens, undet. sex) — La Ciénaga (Campo El Potrerito), Medaños, Dto. Tinogasta, Catamarca. *L. cuyanus*: (tree males and four females) FML 02021 — Medaños, Dto. Tinogasta, Catamarca; FML 02971 — Baldecito, Dto. Gral. San Martín, La Rioja; FML 02986 — 110, 7 km to the S of Villa Unión, over Rute Prov. 26, Dto. Independencia, La Rioja. *L. dorbignyi*: FML 02902 (one male) — 10 km to the S of Estación Muñano, to the

Nevados del Acay from 22 km de San Antonio de los Cobres, Dto. La Poma, Salta; FML 01669 (one female) — Co. De la Virgen, Cachi Adentro, Dto. Cachi, Salta. *L. famatinae*: FML 01720 (one male and one female) — Cueva de Pérez, Dto. Famatina, La Rioja. *L. huacahuasicus*: (two males and two females) FML 01224 — Filos “Los Heladitos,” “La Banderita,” “Rosado,” “El Overo,” Dto. Andalgalá, Catamarca; FML 02303 — Laguna de Huaca Huasi (E of Co. Isabel and W of Co. El Negrito), Dto. Tafí del Valle, Tucumán. *L. kingii*: FML 01652 (undet. sex) — Laguna Madre e Hija (Bosque Petrificado), Santa Cruz. *L. multicolor*: (two males and two females) FML 01873 — Abra Pampa, Dto. Cochino, Jujuy; FML 03347 — Route Prov. N° 74, 34 km NW of San Antonio de los Cobres, on the way to Sey, Dto. La Poma, Salta. *L. nigriceps*: FML 01635 (one male and one female) — Talud N loma S, Co. Socompa, Dto. Los Andes, Salta. *L. ornatus*: FML 01860 (two males and one female) — Las Grutas, Gendarmería, 20 km from Paso de San Francisco, Dto. Tinogasta, Catamarca. *L. pseudoanomalous*: FML 02087 (one female) — Campo de Laguna Larga, Antinaco, Dto. Famatina, La Rioja; FML 00309 (undet. sex) — Agua de la Peña, Ischigualasto, Dto. Valle Fértil, San Juan. *L. quilmes*: FML 01665 (two males and two females) — 3 km E of Cachi and 1 km W of Cachi, Dto. Cachi, Salta. *L. robermertensi*: FML 01488 (undet. sex) — Mollecito, Dto. Andalgalá, Catamarca. *L. salinicola*: FML 01907 (one male) — Medaños, Dto. Tinogasta, Catamarca; FML 01620 (one male) — 4 km Río de la Punta (31 km from Tinogasta), Dto. Tinogasta, Catamarca; FML 02877 (one female) — Los Medaños, 5 km N of Saujil, Dto. Tinogasta, Catamarca. *L. scapularis*: FML 02865 (one male and two females) — Los Médanos, Cafayate, Dto. Cafayate, Salta. *L. wiegmanni*: FML 01856 (two males) — Estancia Los Pinos, Sierra de Medina, Dto. Burruyacu, Tucumán; FML 01325 (two females) — La Echarada, S of Agua de las Palomas, Dto. Andalgalá, Catamarca.

Tropiduridae

Argentina: *Stenocercus caducus*: FML 00260 (undet. sex) — Yuto, Jujuy; FML 00901 (undet. sex) — Angosto del Río Pescado, Finca Arazayal, Dto. Orán, Salta. *S. doellojuradoi*: FML 02887 (undet. sex) — Caspi Corral, Dto. Figueroa, Santiago del Estero; FML 02905 (undet. sex) — Estancia Monte Redondo, 30 km, Ruta Nac. 34, Dto. Capital, Santiago del Estero; PT 2676 (undet. sex) — Finca Pozo Largo, Dto. Anta, Salta; FML 02708 (undet. sex) — Los Colorados, Dto. Anta, Salta. *S. roseiventris*: FML 00867 (undet. sex) — Angosto del Río Pescado, (580 – 640 m), Dto. Orán, Salta.; FML 00838 (undet. sex) — No data; FML 00903

(undet. sex) — Angosto del Río Pescado, Finca Araza-
yal, Dto. Orán, Salta; FML 03644 (undet. sex) — Finca
Yakulika, Angosto del Río Pescado, Dto. Orán, Salta.
Tropidurus hispidus: FML 00293 (2 specimens, undet.
sex) — Huyamampa, Dto. La Banda, Santiago del Estero;
FML 00499 (undet. sex) — El Ojito, Dto. Pellegrini,
Santiago del Estero. *T. spinulosus*: FML 00129 (2 speci-
mens, undet. sex) — La Matanza, Hickmann, Salta;
FML 03559 (2 specimens, undet. sex) — Campo
Grande, Finca Los Colorados (100 km NE of Joaquín
V. González), Dto. Anta, Salta; FML 03031 (undet. sex)
— Campo Grande, Finca Los Colorados (100 km NE of
Joaquín V. González), Dto. Anta, Salta; FML 03190 (3
specimens, undet. sex) — Campo Grande, Finca Los
Colorados (100 km NE of Joaquín V. González), Dto.
Anta, Salta; PT 0022 (undet. sex) — 24 km N of Salta
Forestal, Dto. Anta, Salta; PT 1485 (undet. sex) —
Finca Pozo Largo, Dto. Anta, Salta. *T. etheridgei*: FML
03562 (2 specimens, undet. sex) — Campo Grande, Finca
Los Colorados (100 km NE of Joaquín V. González),
Dto. Anta, Salta; PT 1426 (undet. sex) — Finca Pozo
Largo, Dto. Anta, Salta; PT 1527 (undet. sex) — Finca
Pozo Largo, Dto. Anta, Salta; PT 1619 (undet. sex) —
Finca Pozo Largo, Dto. Anta, Salta; PT 0595 (undet.
sex) — Finca Don Benigno, Dto. Anta, Salta. *T. melano-
pleurus*: FML 00875 (undet. sex) — Quebrada de
Acambuco, Salta. *T. plica*: SDSU 2102 (undet. sex) —
No data. *T. torquatus*: FML 00835 (2 specimens, undet.
sex) — Corrientes, Dto. Capital, Corrientes. *Uranosco-
don superciliosa*: SDSU 2113 (undet. sex) — No data.
Brazil: *Tropidurus hygomi*: FML 08796, 08797 and
08800 (undet. sex) — Santo Amaro das Brotas, Sergi-
pes. *T. oreadicus*: FML 08771 (undet. sex) — Bagagem,
Rio Tocantins, Pará; FML 08777 (undet. sex) — Serra
da Mesa (Ponto 4), Goiás. **Chile**: *Microlophus stolz-
mannii*: SDSU 3206 (undet. sex) — No data. *M. there-
sioides*: FML 03674 (undet. sex) — Caldera, Chile.

Polychrotidae

Brazil: *Polychrus acutirostris*: MZUSP 48151 and
48156 (undet. sex) — Exu, Pernambuco; MZUSP
08605 and 08611 (undet. sex) — Pesqueira, Pernam-
buco. **Chile**: *Pristidactylus volcanensis*: MNHN no
number (two specimens, undet. sex) — El Volcán. **No
data of locality**: *Pristidactylus valeriae* (undet. sex):
No data. *P. torquatus*: NMW 18198 and 18199 (undet.
sex) — No data.

Leiosauridae

Leiosaurus paronae: MACN 4386 (undet. sex) —
No data of locality. *L. belli*: NMW 12976 (undet. sex)
— No data of locality.

APPENDIX II. MATRIX COMPARED: TAXA AND CHARACTERS CODES

	1	2	3	4	5	6	7	8	9										
<i>Sphenodon</i>	01234	56789	01234	56789	01234	56789	01234	56789	01234	56789	012								
<i>Bogertia</i>	02001	1---0	01112	12-13	1-401	0101-	1-11-	010-0	51030	--102	0A200	-2--0	01---	01---	0---	---			
<i>Briiba</i>	--01-	----	-00-0	----	----	----	----	-0---	00000	00000	01010	11101	0-0--	00--1	20001	10-0-	-0010	000-1	010
<i>Phyllodactylus</i>	--01-	----	-00-0	----	----	----	----	-0---	01000	00000	01010	11101	0-0--	00--0	20001	00-0-	-0010	000-1	010
<i>Hemidactylus</i>	--01-	----	-00-0	----	----	----	----	-0---	00000	00000	01010	11101	0-0--	00--1	20001	10-0-	-0010	000-1	010
<i>Homonota</i>	--01-	----	-00-0	----	----	----	----	-0---	00000	00000	01010	11101	0-0--	00--0	20001	00-0-	-0010	000-1	010
<i>Phylllopezus</i>	--01-	----	-00-0	----	----	----	----	-0---	10000	00000	01010	11100	--1-	00--0	20001	10-0-	-0110	000-1	010
<i>Gymnodactylus</i>	--01-	----	-00-0	----	----	----	----	-0---	00000	00000	01010	11101	0-0--	00--0	20001	10-0-	-0010	000-1	010
<i>Garthia</i>	--01-	----	-00-0	----	----	----	----	-0---	00000	00000	01010	111-1	0-0--	00--0	20001	00-0-	-1110	000-1	010
<i>Vanzoia</i>	--01-	----	-00-0	----	----	----	----	-0---	00000	00000	01011	01100	0-0--	00--0	20001	00-0-	-0010	000-1	010
<i>Thecadactylus</i>	--01-	----	-00-0	----	----	----	----	-0---	00000	00000	01010	111-1	0-0--	00--1	20001	00-0-	-0010	000-1	010
<i>Chalcides</i>	1201-	----	-0102	11-12	0-201	01000	01101	01110	10010	0-002	11210	00101	110--	11200	01002	00-0-	-0000	101--	-00
<i>Pr. guentheri</i>	02011	00---	10112	10-12	1-001	01001	1-101	11100	20110	0-002	01010	10101	110--	01101	21003	11-0-	-0001	00---	---
<i>Pr. pachyurus</i>	02001	00---	10112	10-12	1-001	01101	00101	11100	20110	0-002	01101	10101	112--	01100	21003	11-0-	-0001	000-1	01-
<i>Pantodontius</i>	10000	01---	10102	11-12	1-001	11101	02101	11100	20110	00002	01110	10100	-----	01101	21003	-110-	-0101	002-1	01-
<i>Calipodommatius</i>	00001	1---1	10112	11-12	10-01	01001	00001	-1110	40011	01012	11010	10100	-----	01201	21012	10-0-	-0101	104-1	100
<i>Echinosauro</i>	00001	00---	10102	11-12	1-001	01001	0B101	011A0	C2110	01000	11110	10100	-----	01101	21002	1000-	-0101	001-1	1B0
<i>Vanzoosaura</i>	00011	1---1	10112	11-12	10-01	01000	00101	11110	20111	0-000	11010	10100	-----	01102	21012	40-0-	-0101	002-1	1B0

APPENDIX II (continued).

	1		2		3		4		5		6		7		8		9		
	01234	56789	01234	56789	01234	56789	01234	56789	01234	56789	01234	56789	01234	56789	01234	56789	01234	56789	012
<i>Mabuya</i>	0101-	-----	-0102	11-12	1-001	01100	01101	01100	00010	0-000	01110	11101	110--	11001	01013	1100-	00001	111--	-00
<i>Podarcis</i>	0201-	-----	-0112	11-12	1-201	01001	02101	11110	20120	0-002	11010	00100	-----	01211	21002	00--0	-0001	100--	-00
<i>T. stejnegeri</i>	0-001	1-00-	10112	1-012	1-101	01001	02101	11100	22110	01002	11010	00100	-----	01102	21002	1100-	11-01	0021-	000
<i>T. taeniatus</i>	0-001	1-00-	10112	1-012	1-101	01001	02101	11100	22110	01002	11010	00100	-----	01102	21002	1100-	11-01	0021-	000
<i>Ameiva</i>	0-001	-----	10112	1-112	1-001	01001	02101	11110	2-110	01002	11110	01100	-----	01101	11002	1100-	11-01	0010-	100
<i>Tupinambis</i>	0200A	02----	10112	11-12	1-001	01A01	1-101	11110	22110	01002	11010	A010A	101--	01102	21002	1100-	1A101	A00-1	0A1
<i>Dicrodon</i>	00000	1-01-	10112	1-112	1-001	01101	1-101	11111	2-111	00002	11010	00100	-----	01002	21002	21--0	10101	00--2	0--
<i>Kentropyx</i>	00000	1-01-	10112	1-012	1-101	01101	1-101	11111	22110	00002	11010	10100	-----	01101	21002	2000-	-0101	100-1	01-
<i>C. ocellifer</i>	00000	1-01-	10112	1-A12	1-A01	01A01	1-101	1111A	2D110	00002	11A10	10100	-----	0110D	2100C	B1A0-	10101	100-1	01-
<i>C. longicaudus</i>	0000A	02----	10112	1A-12	1-001	01A0D	1-101	1111A	2D110	00002	A1010	10100	-----	01D02	2100C	D1A0-	10A01	102-1	01-
<i>Dracaena</i>	02000	1-02-	10112	1-00-	1-0-01	01001	02101	11120	22110	0-002	11210	10100	-----	01101	21001	1110-	00101	003-1	120
<i>Crocodyllurus</i>	0B000	1-00-	10112	11-12	11-01	01001	02101	11110	22110	0-002	-1010	10100	-----	01D01	21001	00--0	-1001	000-1	100
<i>Callisotus</i>	02000	01----	10112	11-12	10-01	01001	02101	11110	22110	0-002	10100	10100	-----	01101	21003	-0--0	-1001	001-0	120
<i>T. oreadicus</i>	02000	02----	00102	10-12	1-201	01001	02101	01100	20010	00002	01011	11101	111--	01101	21002	2110-	-1110	000-0	150
<i>T. hygomi</i>	02000	02----	00102	10-12	1-201	01A01	02101	01110	20001	00002	01011	11101	111--	01101	11002	D110-	-1010	000-0	AE1
<i>T. melanopleurus</i>	01001	02----	10102	10-12	1-001	01002	02100	01111	22010	00002	01110	11100	-----	01202	21001	01101	-1110	0011-	110
<i>T. hispidus</i>	01001	1-01-	10102	10-12	1-011	01001	02101	01110	00010	00000	01111	11100	-----	01202	21001	11101	-0010	0001-	111
<i>T. spinulosus</i>	11001	02----	10102	10-12	1-001	01001	02101	01110	00010	00000	01111	11110	-----	01201	01001	11101	-0010	0001-	021
<i>T. etheridgei</i>	01001	1-01-	10102	10-12	1-001	01001	02101	01110	00010	00000	01111	11100	-----	01201	21001	11101	-0010	0001-	141
<i>T. plica</i>	01001	1-01-	10102	11-12	11-01	01001	00101	01101	20010	00000	01110	11100	-----	01201	11001	11101	-0010	0042-	111
<i>T. torquatus</i>	01001	02----	10102	11-12	1-101	01001	02101	01100	10010	00002	01011	11100	-----	01201	11001	11101	-0010	000-0	110
<i>M. stolzmanni</i>	01001	1-00-	10102	10-12	1-301	01001	02100	01110	00010	00002	01010	01101	101--	01201	11003	21101	-1110	001-0	141
<i>M. theresioides</i>	01001	1-00-	10102	10-12	1-101	11001	02101	01110	00010	00002	01110	01101	100--	01201	11001	21101	-1110	000-0	111
<i>S. caducus</i>	01001	1-00-	10102	10-12	1-101	A1001	02101	01110	00010	00002	01010	11101	101--	01201	31001	11101	-0000	0001-	111
<i>S. doelljurae</i>	01001	1-0A-	10102	10-12	1-400	-1002	02101	01101	12010	00001	01010	11101	110--	01201	21001	11101	-0110	001-0	111
<i>S. roseiventris</i>	A1001	1-0A-	10102	10-12	1-101	01001	02101	0111A	00010	00002	01A1A	11100	-----	01201	01001	11101	-00A0	001-0	111
<i>Uranoscodon</i>	01001	1-00-	10102	10-12	1-001	01001	02100	01100	00011	00002	01110	01100	-----	01201	21001	21101	-0010	0041-	110
<i>Ph. punae</i>	02000	1-00-	10102	1-010	1-401	00102	02100	01100	11010	00000	01111	02101	101--	01000	00103	11101	-0110	0001-	141
<i>Ph. palluma</i>	02000	1-00-	10102	1-010	1-401	00102	02100	01100	11010	00000	01110	02101	101--	01000	00103	11101	-0110	0001-	141
<i>L. abaucan</i>	02000	1-01-	00102	10-12	1-001	01001	02100	01110	20010	20002	01110	11101	101--	01000	01001	21101	-0110	001-0	141
<i>L. alticolor</i>	02000	1-01-	00102	10-12	1-001	01001	02100	01110	20010	20002	01110	11001	101--	01000	01001	21101	-0110	001-0	141
<i>L. archeforus</i>	02000	1-01-	00102	10-12	1-001	01001	02100	01110	20010	10002	01110	11001	101--	01200	01001	21101	-0110	001-0	141
<i>L. biteniatus</i>	02000	1-01-	00102	10-12	1-001	01001	02100	01110	20010	10002	01110	11101	101--	01001	01001	21101	-0110	001-0	141
<i>L. capitatus</i>	02000	1-01-	00102	10-12	1-001	01001	02100	01110	20010	10002	01110	11001	101--	01001	01001	21101	-0110	001-0	141
<i>L. cayanus</i>	02000	1-01-	00102	10-12	1-001	01001	02100	01110	20010	A0002	01110	11101	101--	01001	01001	21101	-0110	000-0	141
<i>L. dorbigyi</i>	02000	1-01-	00102	10-12	1-001	01001	02100	01110	20010	20002	01110	11101	101--	01001	01001	21101	-0110	001-0	141
<i>L. huacahuasicus</i>	02000	1-01-	00102	10-12	1-001	01001	02100	01110	20010	10002	01110	11001	101--	01001	01001	21101	-0110	001-0	141
<i>L. fumatinae</i>	02000	1-01-	00102	10-12	1-001	01001	02100	01110	20010	20002	01110	11101	101--	01001	01001	21101	-0110	001-0	141
<i>L. kingi</i>	02000	1-01-	00102	10-12	1-001	01001	02100	01110	20010	10002	01110	11001	101--	01201	01001	21101	-0110	001-0	141
<i>L. multicolor</i>	02000	1-01-	00102	10-12	1-001	01001	02100	01110	20010	20002	01110	11001	101--	01001	01001	21101	-0110	001-0	141

APPENDIX II (continued).

	1		2		3		4		5		6		7		8		9		
	01234	56789	01234	56789	01234	56789	01234	56789	01234	56789	01234	56789	01234	56789	01234	56789	01234	56789	012
<i>L. nigriticeps</i>	02000	1-01-	00102	10-12	1-001	01001	02100	01110	20010	10002	01110	11101	101--	01001	01001	21101	-0110	001-0	141
<i>L. ornatus</i>	02000	1-01-	00102	10-12	1-001	01001	02100	01110	20010	20001	01110	11101	101--	01001	01001	21101	-0110	000-0	141
<i>L. pseudoanomalus</i>	02000	1-01-	00102	10-12	1-001	01001	02100	01110	20010	10002	01110	11101	101--	01001	01001	21101	-0110	001-0	141
<i>L. quilmes</i>	02000	1-01-	00102	10-12	1-001	01001	02100	01110	20010	20002	01110	11101	101--	01001	01001	21101	-0110	001-0	141
<i>L. robermertensi</i>	02000	1-01-	00102	10-12	1-001	01001	02100	01110	20010	00002	01110	11101	101--	01001	01001	21101	-0110	001-0	141
<i>L. salinicola</i>	02000	1-01-	00102	10-12	1-001	01001	02100	01110	20010	20002	01110	11101	101--	01001	01001	21101	-0110	000-0	141
<i>L. scapularis</i>	02000	1-01-	00102	10-12	1-001	01001	02100	01110	20010	20002	01110	11101	101--	01001	01001	21101	-0110	000-0	141
<i>L. wiegmanni</i>	02000	1-01-	00102	10-12	1-001	01001	02100	01110	20010	20002	01110	11101	101--	01001	01001	21101	-0110	001-0	141
<i>P. valeriae</i>	02100	02---	10102	10-12	1-001	01001	02101	01100	20010	0-002	01010	10101	111--	00--1	11002	1110-	-1110	000-0	120
<i>P. torquatus</i>	02100	02---	10102	10-12	1-301	01001	02101	01110	20010	0-002	01010	10101	111--	01101	21002	1110-	-1110	000-0	110
<i>P. volcanensis</i>	02100	1-0A-	10102	11112	1-B01	01A01	02101	011AA	20010	0-002	01010	10101	111--	01A0D	11002	2110-	-1110	000-0	140
<i>L. paronae</i>	01001	1--2	10102	11-12	0-101	01001	02101	01100	D2010	1-010	01010	10100	----	0--1	11010	D111-	-1010	000-0	140
<i>L. belli</i>	02100	1-0A-	00102	11-12	0-F01	0100D	02101	01100	D2010	1-010	01010	10100	----	01001	11010	D111-	-1110	000-2	1-0
<i>Feylinia</i>	00-1-	-----	-0101	0--10	1-01-	-1001	010--	-0----	61011	0-002	01010	10100	----	11101	21003	11101	-1--0	000-1	---
<i>Polychrus</i>	02100	1--1	00112	11-12	11-01	01100	02100	01100	20010	0-002	01011	10101	110--	01001	11001	11100	-1100	001-0	0-0
<i>Ophiodes</i>	11100	1-1--	10102	1-012	0-101	01001	020--	-1110	10010	1-002	01011	11101	121--	01201	11012	30---	-0110	002-1	-00

A = 0 and 1; B = 0 and 2; C = 2 and 3; D = 1 and 2; E = 1 and 4; F = 0 and 3.