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CLADISTIC ANALYSIS OF TEIIDAE (SQUAMATA) BASED ON MYOLOGICAL CHARACTERS

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The cranial musculature of twelve (12) species of all genera of Teiidae was compared and analyzed for taxonomic significance. Using 70 myological cranial characters a cladistic analysis of the taxa mentioned was performed. Parsimony analysis were conducted with the program PeeWee. To root the trees, *Sphenodon*, one lacertid, six gymnophthalmids, and two scincids, were added to the matrix. Only one tree was obtained with a fit = 295.0 and length = 195. There is a split between teiids and gymnophthalmids, but no between Teiini and Tupinambini. Podarcis is part of a clade with scincids. The scincids are a monophyletic group. These clade is the sister group of gymnophthalmids, except *Echinosaura* and *Pantodactylus* which are related to teiids. Teiids are monophiletics (except for *Pantodactylus*).

Key words: Teiidae, Cranial myology, Phylogeny.

INTRODUCTION

The phenetic and phylogenetic relationships among the Teiidae groups have been revised by Vanzolini and Valencia (1965), Gorman (1970), Presch (1974, 1983), Rieppel (1980), and Krause (1996), based on diverse lines of evidence: chromosomes, osteology, myology, etc. In most analyses the existence of two monophyletic groups, Teiini and Tupinambini, is sustained, although the relationships within these groups remain unresolved (Krause, 1996). At present, relationships of the family Teiidae with other lizard families are not completely defined either (Estes et al., 1988; but see Caldwell, 1999).

The cranial myology of Teiidae has been studied only in scattered genera such as *Ameiva* (Poglayen-Neuwall, 1954), *Cnemidophorus* (Lakjer, 1926), and *Tupinambis* (Lakjer, 1926; Poglayen-Neuwall, 1954; Gomes, 1974). There are more general analyses by MacLean (1974), regarding only the hyoid musculature, and Rieppel (1980), referring exclusively to jaw musculature.

Using cladistic methodology, in this study we investigate: 1) if there is a pattern of cranial myology exclusive to the family Teiidae, and 2) if the teiid taxon groupings obtained from cranial myology characters are congruent with recognized hypotheses (Rieppel, 1980; Estes et al., 1988; Krause, 1996).

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MATERIAL AND METHODS

Sixty-one alcohol preserved specimens representing 12 species of all genera of Teiidae were used (see *Appendix I*). Voucher specimens are housed in the collection of the Instituto de Herpetología, Fundación Miguel Lillo, Tucumán, Argentina. Head musculature was dissected to determine origins and insertions. Bones and cartilages of some specimens were stained with alizarin red S and Alcian blue 8GX, respectively, as described by Wassersug (1976). Outline drawings were made using a camera lucida.

Muscles were classified as proposed by Lakjer (1926), Haas (1973), and Oelrich (1956).

For the cladistic analysis, a matrix for 70 myological characters (Table 1) was analyzed with the program PeeWee (Goloboff, 1993). PeeWee find most parsimonious trees under predefined weights. 300 ratchet iterations (factor default 20%) (Nixon, see Horovitz, 1999) saving one tree by iteration were performed. Additional trees were search with TBR (tree bisection-reconnection branch swapping).

Rooting the cladogram at the outgroup established polarity for all characters on the cladogram (Nixon and Carpenter, 1993). To root our tree, data of

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TABLE 1. Data Matrix Used in Cladistic Analysis

	0		1		2		3		4		5		6	
	01234	56789	101234	56789	201234	56789	301234	56789	401234	56789	501234	56789	601234	56789
Sphenodon	02021	-1-01	12-11	0-300	1-1-1	100-0	51020	-120A	20-10	--20-	-----	-----	-1-0-	-----
Podarcis sicula	021-1	-1--0	11-10	1-200	01021	01110	20110	-0111	01010	--102	11210	00--0	01100	---0-
Chalcides chalcides	121-1	-1--0	01-10	1-200	00021	00110	10000	-0111	21011	10-12	01010	00--0	10101	---0-
Mabuya frenata	011-1	-1--0	01-10	1-001	00011	00100	00000	-0001	11101	10-10	01021	11000	01111	---00
Proctoporus guentheri	02010	0---0	10-10	1-000	011-1	01100	20100	-0101	01111	10-01	01220	11--0	1100-	-----
Proctoporus pachyurus	02010	0---0	10-10	1-001	01021	01100	20100	-0101	01111	12-01	00220	11--0	11100	-101-
Calyptommatus leiolepis	00011	-1-10	11-10	10-00	01000	--110	40001	10111	01110	--002	01211	10--0	11104	-110-
Vanzosaura rubricauda	00011	-1-10	11-10	10-00	00001	01110	20101	-0011	01110	--001	02211	00--0	11002	--10-
Echinosaura horrida	00010	0---0	01-10	1-000	01021	001A0	D2100	10011	11110	--001	01210	100-0	11001	-1100
Pantodactylus schreibersi	10000	1---0	01-10	1-011	01021	00110	22000	00101	11110	--001	01220	211-0	11-02	-1011
Dracaena paraguayensis	02001	-02-0	1-00-	10-00	01021	01120	22100	-0111	21110	--001	01200	11100	11003	-1121
Tupinambis rufescens	020A0	2---0	11-10	1-00A	011-1	01110	22100	10111	01A1A	01-01	02210	1101A	11A00	-10A0
Cnemidophorus longicaudus	000A0	2---0	1A-10	1-00A	0C1-1	0111A	2E100	001A1	01110	--00A	022C0	C1A10	A1102	-101A
Cnemidophorus ocellifer	00001	-01-0	1-A10	1-A0A	011-1	0111A	2E100	00111	A1110	--001	0C2C0	B1A10	11100	-101A
Dicrodon guttulatum	00001	-01-0	1-110	1-001	011-1	01111	2-101	00111	01010	--000	02210	21-10	1100-	-10--
Kentropix lagartija	00001	-01-0	1-010	1-100	011-1	01110	22100	00111	01110	--001	01210	200-0	11100	-1010
Crocodilurus lacertinus	0B001	-00-0	11-10	11-00	01021	01110	22100	-01-1	01110	--00C	01200	00--1	11000	-110-
Callopistes maculatus	02001	-1-10	11-10	10-00	01021	01110	22100	-0101	01110	--001	01220	30--1	01001	-012-
Ameiva ameiva	0-011	----0	1-110	1-000	01021	01110	2-100	10111	11000	--001	01110	11011	-1001	0-100
Teius oculatus	0-011	-00-0	1-010	1-100	01021	01100	22100	10111	11000	--002	02210	1101-	-1002	1-000
T. teyou	0-011	-00-0	1-010	1-100	01021	01100	22100	10111	01010	--001	02210	11011	-1002	1-000
T. suquiensis	0-011	-00-0	1-010	1-100	01021	01100	22100	10111	01010	--001	02210	11011	-1002	1-000

Note. A) States 0 and 1; B) states 0 and 2; C) states 1 and 2; D) states 2 and 3; E) states 1, 2, and 3.

Sphenodon from the literature (Haas, 1973; Lakjer, 1926) were added to the matrix and also data of one lacertid, six gymnophthalmids, and two scincids as outgroups. Only unambiguous changes are considered as synapomorphies for groups (see Table 2). Since many of the multistate characters could be arranged in a logical series, we scored them as additives (cc+: 1, 3, 5, 7, 11, 17, 21, 23, 28, 31, 33, 37, 40, 46, 49, 51 – 53, and 55).

Nodes support was estimated by Bremmer relative support value (Goloboff, see Horovitz, 1999). Parsimony jackknifing was performed using the programs Jak.run and Fq.run. Jak.run can be executed from PeeWee, and this program randomly generate matrixes eliminating 36% of the characters. It is possible to select the command for tree-searching and also the cut-off value (default: 50%).

RESULTS

1.1. Characters description

1.1.1. *Adductors mandibulae*

1.1.1.1. *Adductor mandibulae externus*

An aponeurosis covers partially the *adductors mandibulae*. It extends ventrally from the border of the jugal, squamosal, and anterior border of the quadrate. It is wide at its origin and narrow at its insertion. The ligament joining the quadrate to the maxillary bones constitutes the ventral border of the aponeurosis. The ligament inserts on the external surface of posterior end of the lower jaw (Fig. 1).

Variations:

Character 0: *Adductor* aponeurosis: (0) not pigmented; (1) pigmented.

Character 1: *Adductor* aponeurosis size: (0) scarcely noticeable; (1) narrow; (2) wide.

The m. *levator anguli oris* (= *adductor mandibulae externus* 1[a] of Lakjer, 1926) is a very thin but wide of approximately rectangular shape. It covers the middle third of the underlying m. *adductor externus*. The anterior and dorsal fibers lie parallel to the ventral border of jugal. The ligament joining the quadrate and the posterior angle of the maxilla constitutes the ventral margin of the muscle. This muscle inserts on the *mundplatt* by means of a thin aponeurosis (Fig. 1).

Variations:

Character 2: *Levator anguli oris*: (0) present; (1) absent.

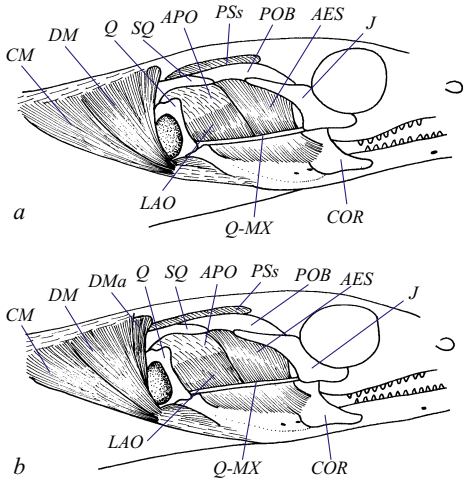

Fig. 1. Lateral view of muscles showing the mm. *levator anguli oris* (character 2 – 8) and *depressor mandibulae* (character 44 – 48). *a*) *Depressor mandibulae* unique; *b*) *depressor mandibulae* divided. **Abbreviations:** *AES*, m. *adductor mandibulae externus superficialis*; *APO*, aponeurosis of the adductors; *CM*, m. *cervicomandibularis*; *DM*, m. *depressor mandibulae*; *DMa*, m. *depressor mandibulae* anterior; *DMp*, m. *depressor mandibulae* posterior; *J*, jugal; *LAO*, m. *levator anguli oris*; *PSs*, m. *pseudotemporalis superficialis*; *Q*, quadrate; *Q-MX*, quadrate-maxillary ligament; *SQ*, squamosal.

Character 3: *Levator anguli oris* shape: (0) wide triangular; (1) narrow triangular; (2) narrow rectangular.

Character 4: *Levator anguli oris* origin: (0) includes postorbital and jugal; (1) does not include postorbital and jugal.

Character 5: *Levator anguli oris* origin including postorbital and jugal: (0) postorbital and jugal; (1) jugal, postorbital, and squamosal; (2) jugal, postorbital, squamosal, and quadrate.

Character 6: *Levator anguli oris* origin not including postorbital: (0) includes quadrate; (1) does not include quadrate.

Character 7: *Levator anguli oris* origin not including postorbital but including quadrate: (0) includes jugal, squamosal, and quadrate; (1) includes squamosal and quadrate; (2) includes just quadrate.

Character 8: *Levator anguli oris* origin not including jugal: (0) includes just postorbital; (1) includes both postorbital and squamosal.

The m. *retractor anguli oris* is approximately triangular. Its origin is formed by a tendon, but the posterior fibers originate directly from the near by quadratojugal and jugal, and from the posteroventral sur-

TABLE 2. Synapomorphies of the Main Nodes of the Cladogram, with the Relationships between Teiidae and Gymnophthalmidae

Node	Synapomorphies
Node 22	Tendenous system (character 10): very developed → developed
	Adductor mandibulae externus profundus origin including quadrate extends over (character 21): quadrate-prootic → quadrate
	Pseudotemporalis profundus expansion (character 32): very expanded → scarcely expanded
	Depressor mandibulae superficialis (character 44): undivided → divided
	Depressor mandibulae profundus (character 48): absent → present
	Genioglossus contact (character 52): with contact along all the mid-ventral line → without contact with the contralateral muscle
Node 23	*Levator anguli oris* (character 2): present → absent
Node 24	*Levator anguli oris* origin (character 4): does not include postorbital-jugal → includes postorbital-jugal
	Adductor mandibulae externus superficialis origin including postorbital (character 11): extends on postorbital-squamosal-quadrate → extends on jugal-postorbital-squamosal-quadrate
	Pseudotemporalis superficialis origin not including postorbital extends over (character 28): parietal-prootic crista alaris → parietal
	Levator pterygoidei length (character 38): short → long
	Depressor mandibulae superficialis (character 44): undivided → divided
	Mandibulohyoideus I shape (character 53): trapezoidal → rectangular
	Mandibulohyoideus II (character 56): absent → present
Node 25	*Adductor mandibulae externus medialis* insertion extends over (character 19): just bodenaponeurosis → both coronoid-bodenaponeurosis
Node 26	Adductor aponeurosis size (character 1): wide → narrow
	Pterygomandibularis shape (character 34): bulky → flattened
	Mandibulohyoideus I origin (character 54): mid region of the dentary → posterior region of the dentary
Node 27	*Adductor mandibulae externus profundus* insertion including manipular fossa, extends over (character 23): mandibular fossa-coronoid-bodenaponeurosis → just mandibular fossa
Node 28	*Pseudotemporalis profundus* insertion extends over (character 31): mandibular fossa-coronoid → mandibular fossa
Node 29	*Levator anguli oris* origin (character 4): does not include postorbital-jugal → includes postorbital-jugal
	Levator anguli oris origin including postorbital-jugal (character 5): jugal-postorbital-squamosal → jugal-postorbital-squamosal-quadrate
	Hyoglossus origin (character 51): ceratobranchial I → ceratobranchial I-epibranchial I
Node 30	*Mandibulohyoideus* II (character 56): present → absent
Node 32	Sexual dimorphism in the *pterygomandibularis* (character 35): present → absent
	Mandibulohyoideus I insertion (character 55): ceratobranchial I → ceratobranchial I-epibranchial I
Node 33	*Adductor mandibulae externus profundus* insertion extends over (character 22): including mandibular fossa → bodenaponeurosis
	Sternohyoideus aponeurosis (character 67): no pigmented → pigmented
	Sternohyoideus insertion (character 68): ceratobranchial I-basihyal → ceratobranchial I
Node 35	*Adductor mandibulae externus medialis* origin including parietal, extends over (character 17): parietal-prootic → parietal-prootic-quadrate
	Pseudotemporalis superficialis origin not including postorbital, extends over (character 28): parietal-prootic crista alaris → parietal

TABLE 2 (continued)

Node	Synapomorphies
	Hyoglossus origin (character 51): ceratobranchial I → ceratobranchial I-epibranchial I
	Sternohyoideus aponeurosis (character 67): no pigmented → pigmented
Node 36	*Levator anguli oris* shape (character 3): wide triangular → narrow triangular
	Intermandibularis anterior profundus aponeurosis (character 42): present → absent
Node 37	*Levator anguli oris* not including postorbital but including quadrate (character 7): includes squamosal-quadrate → includes jugal-squamosal-quadrate
	Mandibulohyoideus III (character 59): absent → present
Node 38	*Mandibulohyoideus* II insertion (character 58): basihyal-entoglossal process → basihyal
Node 39	*Levator anguli oris* shape (character 3): narrow triangular → wide triangular
	Mandibulohyoideus II (character 56): absent → present
Node 40	*Pseudotemporalis profundus* insertion extends over (character 31): mandibular fossa-coronoid → mandibular fossa-coronoid-bodenaponeurosis
Node 41	*Levator anguli oris* shape (character 3): narrow rectangular → narrow triangular
	Retractor anguli oris (character 9): present → absent
	Adductor mandibulae externus superficialis origin including postorbital (character 11): postorbital-squamosal → postorbital-squamosal-quadrate
	Adductor mandibulae externus superficialis insertion including coronoid, extends on (character 14): coronoid-bodenaponeurosis-articular-angular → coronoid-bodenaponeurosis-articular
	Adductor mandibulae externus medialis origin including parietal, extends over (character 17): parietal-squamosal → parietal-prootic, or parietal-prootic-quadrate, or parietal-prootic-quadrate-squamosal-postorbital
	Adductor mandibulae externus profundus origin includes (character 20): parietal-prootic → quadrate
	Adductor mandibulae externus profundus insertion extends over (character 22): bodenaponeurosis → including mandibular fossa
	Adductor mandibulae posterior origin (character 25): without tendon → with tendon
	Pseudotemporalis superficialis origin extends over (character 27): parietal-postorbital → not including postorbital
	Pseudotemporalis profundus origin extends over (character 30): epipterygoid-parietal-membranous wall of the braincase → epipterygoid-crista alaris-parietal
	Pseudotemporalis profundus expansion (character 32): scarcely expanded → very expanded
	Pterygomandibularis origin (character 33): divided in 4 slips without tendon → divided in 2 slips with tendon
	Pterygomandibularis atypicus (character 36): present → absent
	Levator pterygoidei length (character 38): long → short
	Protractor pterygoidei origin (character 40): prootic → basisphenoid-prootic
	Retractor pterygoidei (character 41): present → absent
	Intermandibularis anterior profundus shape (character 43): rectangular → irregular
	Depressor mandibulae superficialis origin extends over (character 47): parietal-squamosal-posterior arcade-*ligamentum nuchae* → parietal-*spinalis capitis*

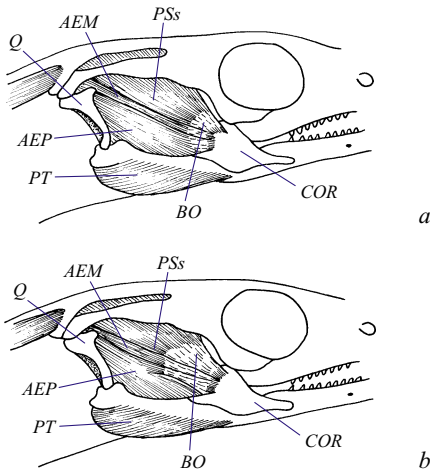

Fig. 2. Tendinous system (character 10). *a*) Tendinous system developed; *b*) tendinous system very developed. **Abbreviations:** *AEM*, m. *adductor mandibulae externus medialis*; *AEP*, m. *adductor mandibulae externus profundus*; *BO*, bodenaponeurosis; *COR*, coronoid; *PSs*, m. *pseudotemporalis superficialis*; *PT*, m. *pterygomandibularis*; *Q*, quadrate.

face of the temporal fossa. It inserts along the fold connecting the lateral and the medial rectal plate.

Variations:

Character 9: *Retractor anguli oris*: (0) absent; (1) present.

The tendinous system in general is well developed. It divides the *adductor externus* mass in muscles well differentiated: m. *adductor mandibulae externus superficialis*, m. *adductor mandibulae externus medialis*, m. *adductor mandibulae externus profundus*, and m. *adductor mandibulae* posterior (Fig. 2).

Variations:

Character 10: Tendinous system: (0) developed; (1) very developed.

The m. *adductor mandibulae externus superficialis* is bulky and irregular. It completely covers the independent m. *adductor mandibulae externus medialis* (Fig. 1).

Variations:

Character 11: *Adductor mandibulae externus superficialis* origin including postorbital: (0) extends on jugal, postorbital, squamosal, and quadrate; (1) extends on postorbital, squamosal, and quadrate; (2) extends on postorbital and squamosal.

Character 12: *Adductor mandibulae externus superficialis* origin not including postorbital: (0) extends on jugal, squamosal, and quadrate; (1) extends on squamosal and quadrate.

Character 13: *Adductor mandibulae externus superficialis* insertion: (0) does not include coronoid; (1) includes coronoid.

Character 14: *Adductor mandibulae externus superficialis* insertion including coronoid: (0) extends on coronoid, bodenaponeurosis, and articular; (1) extends on coronoid, bodenaponeurosis, articular, and angular.

The m. *adductor mandibulae externus medialis* is bulky and wide at the origin, and narrow at the insertion. It is located external to the m. *pseudotemporalis superficialis* and partially covers the anterior end of the m. *adductor mandibulae externus profundus* (Fig. 2).

The bodenaponeurosis is a conjunctive lamina that serves as the insertion of several mm. *adductor* of the lower jaw. It transmits the forces to the dorsal margins of the coronoid and postcoronoid portion of the lower jaw (Gorniak et al., 1982).

Variations:

Character 15: *Adductor mandibulae externus medialis*: (0) divided; (1) undivided.

Character 16: *Adductor mandibulae externus medialis* origin not including parietal extends over: (0) prootic; (1) prootic and squamosal.

Character 17: *Adductor mandibulae externus medialis* origin including parietal extends over: (0) parietal and prootic; (1) parietal, prootic, and quadrate; (2) parietal, prootic, quadrate, squamosal, and postorbital; (3) parietal and squamosal.

Character 18: Position of the temporal artery: (0) temporal artery located over *pseudotemporalis superficialis*; (1) temporal artery located over *adductor mandibulae externus medialis*.

Character 19: *Adductor mandibulae externus medialis* insertion extends over: (0) just bodenaponeurosis; (1) both coronoid and bodenaponeurosis.

The m. *adductor mandibulae externus profundus* is think and approximately triangular. It covers completely the m. *adductor mandibulae* posterior, and covers partially the m. *pseudotemporalis profundus* (Fig. 2).

Variations:

Character 20: *Adductor mandibulae externus profundus* origin includes: (0) quadrate; (1) parietal and prootic.

Character 21: *Adductor mandibulae externus profundus* origin including quadrate extends over: (0) quadrate; (1) quadrate and prootic; (2) quadrate, prootic, and parietal.

Character 22: *Adductor mandibulae externus profundus* insertion: (0) including mandibular fossa; (1) bodenaponeurosis.

Character 23: *Adductor mandibulae externus profundus* insertion including mandibular fossa, extends over: (0) just mandibular fossa; (1) mandibular fossa and coronoid; (2) mandibular fossa, coronoid, and bodenaponeurosis.

The m. *adductor mandibulae* posterior is relatively small, triangular-shaped, and partially covers the m. *protractor pterygoidei*. This adductor originates on the medial margin of the proximal end of the quadrate.

Variations:

Character 24: *Adductor mandibulae* posterior: (0) absent; (1) present.

Character 25: *Adductor mandibulae* posterior origin: (0) with tendon; (1) without tendon.

Character 26: *Adductor mandibulae* posterior insertion extends over: (0) just the mandibular fossa; (1) both the mandibular fossa and Meckel's canal.

1.1.1.2. *Adductor mandibulae internus*

The m. *pseudotemporalis superficialis* is thin, wide, and fan-shaped (being wide at its origin, and narrow at the point of insertion). It partially covers the m. *pseudotemporalis profundus*. The middle portion of the *pseudotemporalis superficialis* is pierced by the maxillary branch of the trigeminus nerve (Fig. 3).

Variations:

Character 27: *Pseudotemporalis superficialis* origin extends over: (0) parietal and postorbital; (1) not including postorbital (Fig. 3).

Character 28: *Pseudotemporalis superficialis* origin not including postorbital, extends over: (0) parietal; (1) parietal and prootic crista alaris; (2) parietal, crista alaris, and squamosal (Fig. 3).

Character 29: *Pseudotemporalis superficialis* insertion extends over: (0) bodenaponeurosis; (1) both coronoid and bodenaponeurosis.

The m. *pseudotemporalis profundus* is thin and very wide, approximately quadrangular. It encloses the epipterygoid anterior, external and posteriorly. It is larger than the m. *pseudotemporalis superficialis*, and covers completely the mm. *levator* and *protractor pterygoidei*. The posterior border of insertion is bordered by the mandibular branch of the trigeminus nerve (Fig. 3).

Variations:

Character 30: *Pseudotemporalis profundus* origin extends over: (0) epipterygoid; (1) epipterygoid and crista alaris; (2) epipterygoid, crista alaris, and parietal; (3) epipterygoid, crista alaris, parietal, and frontal; (4) crista alaris and parietal; (5) epipterygoid, parietal, and membranous wall of the braincase (Fig. 4).

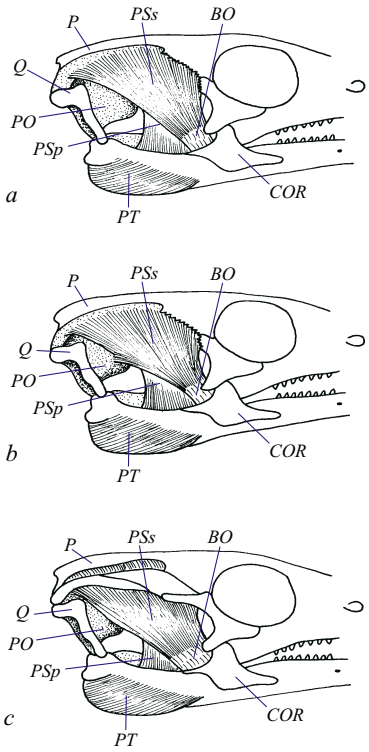

Fig. 3. Origin of the m. *pseudotemporalis superficialis* (characters 27 and 28). *a*) Origin on the parietal; *b*) on the parietal and crista alaris; *c*) on the parietal, prootic, and squamosal. In (*a*) and (*b*) the zigomatic arch are removed. **Abbreviations:** *BO*, bodenaponeurosis; *COR*, coronoid; *P*, parietal; *PO*, prootic; *PSp*, m. *pseudotemporalis profundus*; *PSs*, m. *pseudotemporalis superficialis*; *PT*, m. *pterygomandibularis*; *Q*, quadrate; *SQ*, squamosal.

Character 31: *Pseudotemporalis profundus* insertion extends over: (0) mandibular fossa; (1) mandibular fossa and coronoid; (2) mandibular fossa, coronoid, and bodenaponeurosis.

Character 32: *Pseudotemporalis profundus* expansion: (0) scarcely expanded; (1) very expanded (Fig. 4).

The m. *pterygomandibularis* is pear-shaped. It lies ventral to the pterygoid. It originates on the ventral external surface of the anterior end of the ectopterygoid by means of a prominent, strong, and wide tendon. The latter extends over the ventral surface of approximately one third of the length of the muscle and has the shape of an aponeurosis. The medial fi-

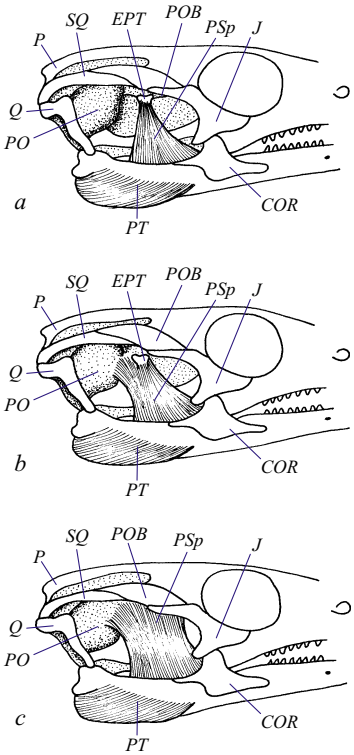

Fig. 4. Origin (character 30) and expansion (character 32) of the m. *pseudotemporalis profundus*. *a*) Origin on the epipterygoid; *b*) on the epipterygoid and crista alaris; *c*) on the epipterygoid, crista alaris, and parietal. **Abbreviations:** *COR*, coronoid; *EPT*, epipterygoid; *J*, jugal; *P*, parietal; *PFR*, prefrontal; *PO*, prootic; *PSp*, m. *pseudotemporalis profundus*; *PT*, m. *pterygomandibularis*; *Q*, quadrate; *SQ*, squamosal.

bers of the muscle originate on the ventromedial surface of the pterygoid, at the level of the basipterygoid process of the basisphenoid, and they attach to the quadrate process of the pterygoid. The m. *pterygomandibularis* inserts on the ventromedial surface of the retroarticular process of the jaw (Figs. 2 – 9).

The mm. *adductor mandibulae internus* group has a high degree of constancy in all saurians. As a whole, the external shape and position of origin and insertion make this set of muscles the most characteristic of the adductor series (Haas, 1960). The size of the head produced by m. *pterygomandibularis* may be important in determining the outcome of assessment and aggressive interactions among males (Anderson and Vitt, 1990).

Variations:

Character 33: *Pterygomandibularis* origin: (0) divided in two slips with tendon; (1) divided in two slips without tendon; (2) divided in four slips without tendon.

Character 34: *Pterygomandibularis* shape: (0) bulky; (1) flattened.

Character 35: Sexual dimorphism in the *pterygomandibularis* (muscle more developed in males): (0) absent; (1) present.

The m. *pterygomandibularis atypicus* arises from the dorsal surface of the palatine and ventral parts of the interorbital septum, an origin ventral to the eye and well anterior to that of the m. *pterygomandibularis typicus*. The m. *pterygomandibularis atypicus* has a restricted insertion on the medial surface of the mandible, ventral to the coronoid bone.

Variations:

Character 36: *Pterygomandibularis atypicus*: (0) absent; (1) present.

1.1.2. *Constrictor internus*

1.1.2.1. *Constrictor internus dorsalis*

The m. *levator pterygoidei* is flat and slender, narrow at its origin. It lies medial and parallel to the epipterygoid, in front of the crista alaris of the prootic and covers partially the m. *protractor pterygoidei*. The m. *levator pterygoidei* originates by means of aponeurosis, on the ventral external surface of the parietal, near of the parietal-epipterygoid joint. The muscle inserts on the medial border of the dorsal surface of the mid region of the pterygoid, slightly posterior to the pterygoid-ectopterygoid joint.

Variations:

Character 37: *Levator pterygoidei* shape: (0) triangular; (1) trapezoidal; (2) rectangular.

Character 38: *Levator pterygoidei* length: (0) long; (1) short (Fig. 5).

The m. *protractor pterygoidei* is flat, short, and approximately rectangular. It contacts with the m. *pterygomandibularis*. It lies ventromedial to the m. *levator pterygoidei*.

Variations:

Character 39: *Protractor pterygoidei*: (0) absent; (1) present.

Character 40: *Protractor pterygoidei* origin: (0) basisphenoid; (1) basisphenoid and prootic; (2) prootic.

The m. *retractor pterygoidei* (= *levator bulbi*, after Haas, 1973) is well developed in *Sphenodon*; it is divided in a complicated dorsal and ventral portion.

Variations:

Character 41: *Retractor pterygoidei*: (0) present; (1) absent.

1.1.2.2. *Constrictor internus ventralis*

In all the specimens analyzed, the m. *intermandibularis anterior* only presents its deep layer. The m. *intermandibularis anterior profundus* is flat and very thin. It is continuous with the m. *intermandibularis* posterior, and partially covers the m. *genioglossus* and the mm. *mandibulohyoideus* I and II. The m. *intermandibularis anterior profundus* originates on the ventromedial surface of the middle third of the dentary at the level of the posterior mental foramen. The fibers interdigitate with those of the m. *mandibulohyoideus* I. This muscle joins to the m. *intermandibularis anterior profundus* of the opposite side at the mid-ventral line.

Variations:

Character 42: *Intermandibularis anterior profundus* aponeurosis: (0) absent; (1) present.

Character 43: *Intermandibularis anterior profundus* shape: (0) irregular; (1) rectangular.

The m. *intermandibularis* posterior is flat, thin, and approximately rectangular. It partially covers the ventral exposure of the m. *pterygomandibularis*, the mm. *mandibulohyoideus* I and II, and the m. *omohyoideus*. It originates on the external surface of the retroarticular process. This muscle joins to the m. *intermandibularis* posterior of the opposite side at the mid-ventral line. No variations are found in the analyzed groups.

1.1.3. Constrictor of the neck and throat

The m. *depressor mandibulae* could be single or divided in a superficial and a deep layer. When it is divided, it could present an anterior and a posterior part.

The anterior part of m. *depressor mandibulae superficialis* is fusiform, wide at the origin, and shapes the posterior limit of the tympanum. It inserts on the external surface of the retroarticular process, medial to the insertion of the m. *depressor mandibulae superficialis* posterior, by means of a noticeable tendon which arises from the medial portion of the m. *depressor mandibulae superficialis* anterior.

The posterior part of m. *depressor mandibulae superficialis* is flat and approximately rectangular; it is wide at its origin and gradually tapers at its insertion. It covers partially the lateral cervical region and extends over the mm. *sternocleidomastoideus*, *trapezius*, and the posterior external portion of the *pterygomandibularis*. The posterior part of m. *depressor mandibulae superficialis* originates on the m. *spinalis capitis* by means of a fascia. This muscle inserts on the dorsolateral surface of the retroarticular process, behind and ventrally to the tympanum and externally to the insertion of the m. *depressor mandibulae superficialis* anterior.

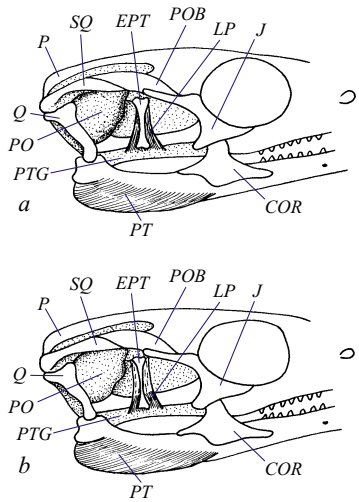

Fig. 5. M. *levator pterygoidei* length (character 38). *a*) Long; *b*) short. **Abbreviations:** *COR*, coronoid; *EPT*, epipterygoid; *J*, jugal; *LP*, m. *levator pterygoidei*; *P*, parietal; *PFR*, prefrontal; *PO*, prootic; *PT*, m. *pterygomandibularis*; *PTG*, pterygoid; *Q*, quadrate; *SQ*, squamosal.

The single m. *depressor mandibulae* presents an incipient division at its insertion. This muscle is flat and fan-shaped; it is wide at the origin, and gradually tapers at the point of insertion. It partially covers the lateral cervical region, and extends over the mm. *sternocleidomastoideus*, *trapezius*, and the posterior and external portion of the *pterygomandibularis*. The undivided m. *depressor mandibulae* originates on the m. *spinalis capitis* by means of a fascia. The anterior fibers extends on the dorsal surface of the posterior process of the parietal. This group of fibers inserts on the dorsal surface of the retroarticular process by means of a noticeable tendon that comes from the middle portion of the muscle. The posterior fibers cross over the anterior ones, and they insert directly on the external surface of the retroarticular process.

The m. *depressor mandibulae profundus* is present only in Mabuya frenata. It is thin and approximately rectangular, and it shapes the posterior border of the tympanum, partially covering it. The m. *depressor mandibulae profundus* originates on the posterior end of the posterior process of the parietal. It inserts on the retroarticular process, medial to the insertion of the insertion of the m. *depressor mandibulae superficialis* anterior and posterior.

Fischer and Tanner (1970) report an undivided m. *depressor mandibulae* in all teiids except *Tupinambis*, but is present also in *Ameiva undulata parva* and *Cnemidophorus tigris*. *Eumeces gilberti* has a m. *depressor mandibulae* with two distinct bundles (Nash and Tanner, 1970). We found the same characteristic in *Chalcides chalcides* and *Mabuya frenata*. *Sauromalus*, *Ctenosaura*, and *Dipsosaurus* have this muscle divided in three bundles (Avery and Tanner, 1964). In Scincidae this muscle is quite complex (Haas, 1973).

Variations:

Character 44: *Depressor mandibulae superficialis*: (0) undivided; (1) divided (Fig. 1).

Character 45: *Depressor mandibulae superficialis* anterior origin extends over: (0) parietal; (1) parietal and m. *spinalis capitis* (Fig. 1).

Character 46: *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 (Fig. 1).

Character 47: *Depressor mandibulae superficialis* origin extends over: (0) parietal and *spinalis capitis*; (1) parietal, *spinalis capitis*, and squamosal; (2) parietal, squamosal, posterior arcade, and *ligamentum nuchae* (Fig. 1).

Character 48: *Depressor mandibulae profundus*: (0) absent; (1) present.

The m. *cervicomandibularis* is narrow and approximately rectangular in shape. It originates on the dorsal fascia on the mm. *spinalis capitis*. The m. *cervicomandibularis* partially covers the m. *pterygomandibularis*, and it inserts on a common fascia with the m. *intermandibularis* posterior (Fig. 1).

Variations:

Character 49: *Cervicomandibularis* shape: (0) narrow and covers partially the *pterygomandibularis*; (1) wide and covers partially the *pterygomandibularis*; (2) wide and covers completely the *pterygomandibularis*.

Character 50: *Cervicomandibularis* insertion: (0) undivided; (1) divided.

1.1.4. Tongue muscles

The m. *hyoglossus* is flat, thin, and roughly rectangular. It is slightly expanded at its origin and insertion. It lies medial to the m. *pterygomandibularis*, and covers the m. *branchiohyoideus*. The m. *hyoglossus* originates on the anterior surface of the middle third of the ceratobranchial I; the origin could also extends over the adjacent epibranchial. The muscle inserts on the posterior end of the fascia of the tongue.

Variations:

Character 51: *Hyoglossus* origin: (0) ceratobranchial I and basihyal; (1) ceratobranchial I; (2) ceratobranchial I and epibranchial I.

The m. *genioglossus* is elongated and approximately rectangular; it is narrow at its origin and thick at its insertion. The m. *genioglossus* originates on the ventromedial surface of the anterior end of the dentary. It inserts on the ventral surface of the posterior end of the lingual fascia, contacting with the insertion of the m. *hyoglossus* figs. 6 and 7).

Variations:

Character 52: *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.

1.1.5. Hyoid muscles

The m. *mandibulohyoideus* I is wide, flat, and thin, and it gradually tapers toward the insertion. It lies external to the m. *mandibulohyoideus* II and medial to the m. *pterygomandibularis*. The m. *mandibulohyoideus* I covers completely the m. *hyoglossus* and partially the m. *genioglossus*. The muscle originates on the ventromedial surface of the dentary, interdigitating with the fibers of the origin of the deep layer of the m. *intermandibularis anterior*.

Variations:

Character 53: *Mandibulohyoideus* I shape: (0) triangular; (1) trapezoidal; (2) rectangular (Fig. 6).

Character 54: *Mandibulohyoideus* I origin: (0) mid region of the dentary; (1) posterior region of the dentary.

Character 55: *Mandibulohyoideus* I insertion: (0) ceratobranchial I and basihyal; (1) ceratobranchial I; (2) ceratobranchial I and epibranchial I; (3) ceratobranchial I, basihyal, epibranchial I, and entoglossal process.

The m. *mandibulohyoideus* II is flat, elongated, and approximately fusiform. The contralateral muscle runs parallel to it, and they contact with each other at the mid-ventral line. They become separated at the level of the basihyal. The m. *mandibulohyoideus* II partially covers the mm. *genioglossus* and *hyoglossus*. It originates on the posterior surface of the mandibular symphysis by means of a long and narrow aponeurosis that is common to the muscles at either side. The m. *mandibulohyoideus* II inserts on the ventroanterior surface of the proximal end of the ceratobranchial I.

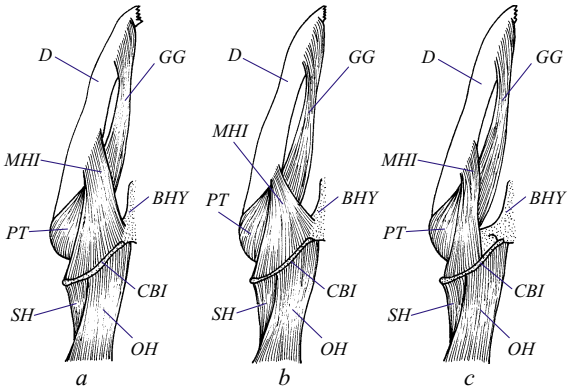

Fig. 6. M. *mandibulohyoideus* I shape (character 53). *a*) Trapezoidal; *b*) triangular; *c*) rectangular. **Abbreviations:** *BHY*, basihyal; *CBI*, ceratobranchial I; *D*, dentary; *GG*, m. *genioglossus*; *MHI*, m. *mandibulohyoideus* I; *OH*, m. *omohyoideus*; *PT*, m. *pterygomandibularis*; *SH*, m. *sternohyoideus*.

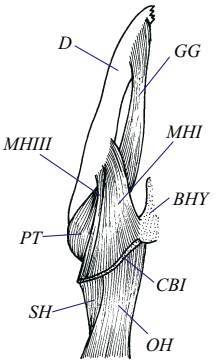

Fig. 7. M. *mandibulohyoideus* III (character 59). **Abbreviations:** *BHY*, basihyal; *CBI*, ceratobranchial I; *D*, dentary; *GG*, m. *genioglossus*; *MHI*, m. *mandibulohyoideus* I; *MHIII*, m. *mandibulohyoideus* III; *OH*, m. *omohyoideus*; *PT*, m. *pterygomandibularis*; *SH*, m. *sternohyoideus*.

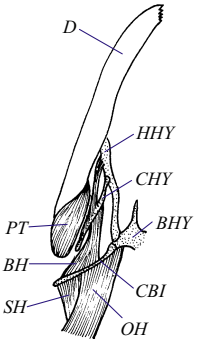

Fig. 8. M. *ceratohyoideus* (character 61). **Abbreviations:** BH, m. *branchiohyoideus*; *BHY*, basihyal; *CBI*, ceratobranchial I; *CH*, m. *ceratohyoideus*; *CHY*, ceratohyal; *D*, dentary; *HHY*, hypohyal; *OH*, m. *omohyoideus*; *PT*, m. *pterygomandibularis*; *SH*, m. *sternohyoideus*.

Variations:

Character 56: *Mandibulohyoideus* II: (0) absent; (1) present.

Character 57: Division of the *mandibulohyoideus* II: (0) divided; (1) undivided.

Character 58: *Mandibulohyoideus* II insertion: (0) basihyal and entoglossal process; (1) basihyal

The m. *mandibulohyoideus* III is narrow, short, and flat. It lies parallel to the external border of the m. *hyoglossus*, and ventromedial to the m. *pterygomandibularis*. The m. *mandibulohyoideus* III originates on the ventromedial surface of the posterior end of the dentary, dorsally to the origin of the m. *mandibulohyoideus* I. It inserts on the anterior surface of the distal end of the ceratobranchial I.

Variations:

Character 59: *Mandibulohyoideus* III: (0) absent; (1) present (Fig. 7).

The m. *branchiohyoideus* is thin, elongated, and roughly triangular; it tapers toward the insertion. The external fibers are attached to the ventral surface of the anterior half of the ceratohyal. The m. *branchiohyoideus* lies medial to the m. *pterygomandibularis* and parallel and ventral to the ceratohyal. It inserts on the ventral surface of the ceratohyal-hypohyal joint (Figs. 8 and 9).

Variations:

Character 60: *Branchiohyoideus* origin: (0) ceratobranchial I; (1) ceratobranchial I and epibranchial I.

The m. *ceratohyoideus* is small, approximately rectangular, and very thin. It originates on the distal end of the ceratobranchial I, close to the origin of the m. *branchiohyoideus*. The m. *ceratohyoideus* inserts on the anterior end of the hypohyal.

Variations:

Character 61: *Ceratohyoideus*: (0) absent; (1) present (Figs. 8 and 9).

The m. *geniohipohyoideus* is narrow, approximately rectangular, and very thin. It lies medial to the m. *pterygomandibularis*. The m. *geniohipohyoideus* originates on the medial surface of the dentary, posterior to the insertion of the m. *mandibulohyoideus* I. It inserts on the distal end of the ceratohyal.

Variations:

Character 62: *Geniohipohyoideus*: (0) absent; (1) present.

A particular muscle was observed only in *Mabuya frenata*. This muscle, here named X, is rectangular, wide at the origin, flat, and thin. It partially covers the m. *mandibulohyoideus* I, m. *mandibulohyoideus* II, m. *hyoglossus*, and m. *omohyoideus*. It originates on the external surface of the mid third of the mandible. Its medial fibers insert on the ventral surface of the basihyal, and its external fibers insert by means of a fascia, on the ventral muscles of the neck. It contacts with the contralateral muscle at the insertion.

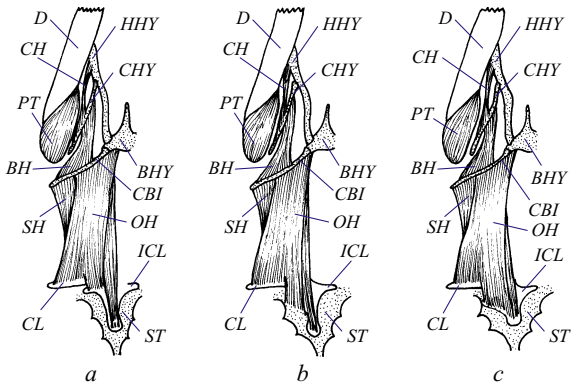

Fig. 9. Origin of the m. *omohyoideus* (character 64). *a*) Origin on the clavicular bar and interclavicle; *b*) on the clavicular bar and sternum; *c*) on the clavicular bar, sternum, and interclavicle. **Abbreviations:** *BH*, m. *branchiohyoideus*; *BHY*, basihyal; *CBI*, ceratobranchial I; *CH*, m. *ceratohyoideus*; *CHY*, ceratohyal; *CL*, clavicle; *D*, dentary; *HHY*, hypohyal; *ICL*, interclavicle; *OH*, m. *omohyoideus*; *PT*, m. *pterygomandibularis*; *SH*, m. *sternohyoideus*; *ST*, sternum.

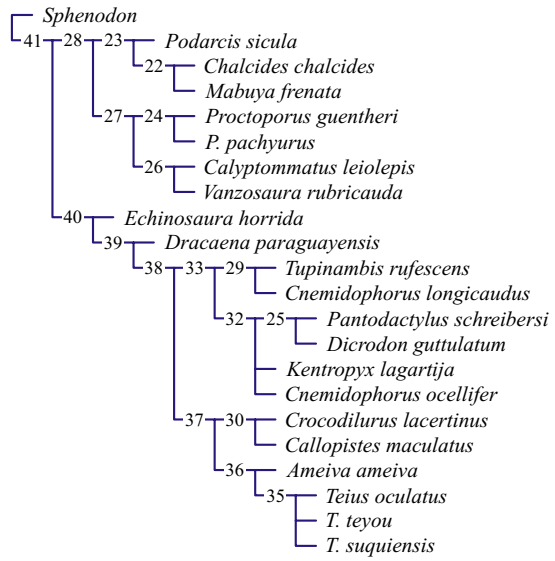

Fig. 10. The single most parsimonious tree of the relationships of Teiidae, obtained using PeeWee program. Based on data of Table 1 (Data Matrix).

Variations:

Character 63: Muscle X: (0) absent; (1) present.

The m. *omohyoideus* is wide, flat and irregular, and it extends further at the origin. It covers the ventrolateral cervical region. This muscle lies ventral to the m. *sternohyoideus* and the m. *sternothyroideus* and partially covers them (Figs. 6 – 8).

Variations:

Character 64: *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 (Fig. 9).

Character 65: *Omohyoideus* insertion not including basihyal: (0) ceratobranchial I; (1) ceratobranchial I and ceratobranchial II.

Character 66: *Omohyoideus* insertion including basihyal: (0) ceratobranchial I, ceratobranchial II, and basihyal; (1) ceratobranchial I and basihyal.

The m. *sternohyoideus* is flat, thin, and roughly triangular. It is narrow at the origin and it expands at the point of the insertion. In the taxa examined, this muscle partially covers the pectoralis and originates on the ventromedial surface of the interclavicle, ventral to the m. *pectoralis*, by means of a wide and thin aponeurosis, that is shared with the contralateral muscle (Figs. 6 – 9).

Variations:

Character 67: *Sternohyoideus* aponeurosis: (0) pigmented; (1) no pigmented.

Character 68: *Sternohyoideus* insertion: (0) ceratobranchial I and basihyal; (1) ceratobranchial I; (2) ceratobranchial I, epibranchial I, and basihyal.

The m. *sternothyroideus* is formed by a narrow band of fibers that diverge from the body of the m. *sternohyoideus*. It lies parallel and external to the trachea and to the ceratobranchial II. The m. *sternothyroideus* inserts on the external surface of the anterior end of the ceratobranchial II.

Variations:

Character 69: *Sternothyroideus*: (0) absent; (1) present.

1.2. Cladistic analysis

The cladistic analysis yielded a single tree (Fig. 10) with fit of 294.0 and length of 195. *Echinosaura* is the sister taxon of teiids (node 40; Fig. 10); this clade is supported by the insertion of the m. *pseudotemporalis profundus* on the mandibular fossa, coronoid, and bodenaponeurosis (31.2). Rieppel (1980) considers that this muscle has an anterior additional head at the origin, but we can not differentiate it. Thus, in node 40, the insertion of this muscle is wider than in node 28.

The monophyly of teiids (node 39, Fig. 10) is supported by two synapomorphies: m. *levator anguli*

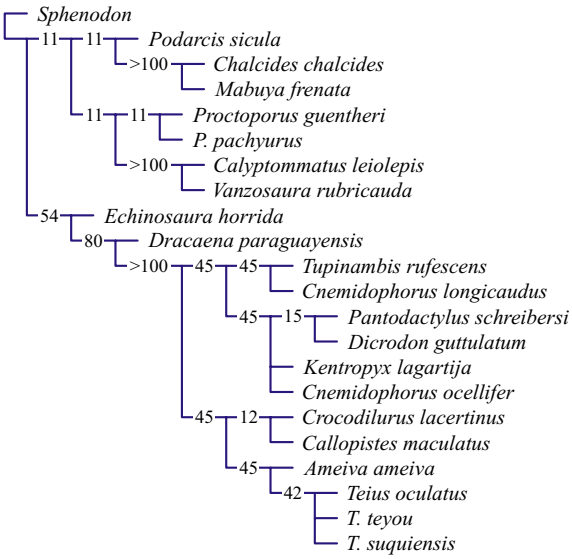

Fig. 11. Tree that shows Bremmer support values.

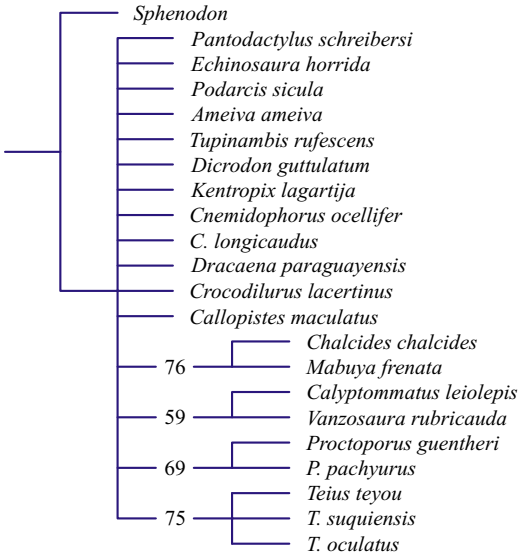

Fig. 12. Tree that shows Jackknifing values.

oris wide and triangular (3.0), and m. *mandibulohyoideus* II present (56.1). The m. *levator anguli oris* is narrow and rectangular in the outgroup; narrow and triangular in node 41, and it reverts to narrow and triangular in node 36. The variation of m. *mandibulohyoideus* II has a similar distribution. The muscle is absent in node 41, it is present in node 39; it reverts to absent in node 30; and it presents a convergence in node 24. *Pantodactylus* is included within the teiids clade. It shares with Dicrodon the insertion of the m. *adductor mandibulae externus medialis* on the coronoid and bodenaponeurosis. In most of the specimens analyzed, the insertion of this muscle is on the bodenaponeurosis, and the insertion on the coronoid and bodenaponeurosis is acquired independently by five other taxa.

Podarcis is the sister taxon of scincids that were analyzed and both are the sister group of gymnophthalmids analyzed (except for *Echinosaura* and *Pantodactylus*).

Node 27 (Fig. 10) (gymnophthalmids except *Echinosaura* and *Pantodactylus*) is supported by one synapomorphy (23.0). The monophyly of *Podarcis* + scincids (node 23, Fig. 10) is supported by one synapomorphy (2.1). The clade of gymnophthalmids + (*Podarcis* + scincids) (node 28, Fig. 10) is supported by one synapomorphy (31.0).

The support values for the clades are high with both, jackknifing and bremmer, only for (*Chalcides* + *Mabuya*) and (Caliptomatus + Vanzosaura). Teiids clade has a very high support with bremmer (Fig. 11), but has no support with jackknifing (Fig. 12).

DISCUSSION

In our analysis, teiids are monophyletic but not the gymnophthalmids (see the position of *Echinosaura* and *Pantodactylus*). In general, those results are congruent with the analysis of many authors with respect to the monophyly of teiids (MacLean, 1974; Rieppel, 1980; Presch, 1983; Krause, 1996). Gymnophthalmids are considered monophyletic by those authors (but see Hoyos, 1998). In our results, most gymnophthalmids are not the sister group of teiids, but they are of lacertid + scincids analyzed (however these nodes have very low support, see Fig. 11). This phylogenetic conclusion is surprising, even considering the recent cladistic analysis of Caldwell (1999).

Haas (1973) considered the muscle *levator anguli oris* present in all lizards. However the clade 23 (*Podarcis* + scincids) is sustained by the absence of the m. *levator anguli oris*. Rieppel (1980) observed this muscle when he analyzes the trigeminal musculature of some scincids. We have not found this muscle in either *Mabuya* or *Chalcides*, indicating that this character is variable within the family and should be analyzed in more specimens.

Within node 39 there are no differences between Teiini and Tupinambini. Rieppel (1980) states that Teiini and Tupinambini share a number of features:

a) extension of the m. *adductor mandibulae* posterior into Meckel's canal of the lower jaw. We found that in teiids but also in gymnophthalmids and lacertids. However, our results indicate that this condition has been acquired independently by all these taxa. b) Expansion of the origin of the m. *pseudotemporalis superficialis* all along the medial margin of the upper temporal fossa. In general, our results are congruent with his, except that it is not clear if Rieppel (1980) considers this expansion restricted to the anterior part of the medial margin of the upper temporal fossa as we have done. If this correspondence exists, then we are in complete agreement with his statement. c) Development of a supplementary anterior head of the m. *pseudotemporalis profundus*. We were unable to recognize this character state in our sample.

We were unable to find a distinction between Teiini and Tupinambini. Our results are not coincident with the intergeneric relationships currently accepted. For example, in our results, *Ameiva* is more related to Teius than *Cnemidophorus*, opposed to what was proposed by Vanzolini and Valencia (1965). The species of Teius conform a monophyletic group. We see that the congruence within the minor levels of our cladogram are rather exceptional, for example, *Callopistes* + *Crocodilurus*, congruent with Rieppel's hypothesis (1980).

It has not always been possible to relate the differences between myological patterns and functional aspects. The feeding mechanisms proposed by MacLean (1974) for Teiinae and Gymnophthalminae, which he correlates with variations in the cranial osteology, do not require a differentiation in the cranial myology. In the inertial feeding mechanism of the Teiinae, "...the frontal-parietal joint serves to raise the snout segment relative to the occipital segment..." Iordansky (1970) attributes the movement of the muzzle unit (snout segment) to the action of the m. *pseudotemporalis profundus*. It would be expected appreciable differences between gymnophthalmids and teiids in this muscle if "...morphology and ecology clearly indicate that Teiinae and Gymnophthalminae are natural groups..." (MacLean, 1974). This is not the case: any of the three characters related to the m. *pseudotemporalis profundus* discriminate clearly between the two groups. There are several nodes sustained by apomorphies related to the mm. pseudotemporalis (22, 24, 28, 35, 40, and 41), but these nodes include scincids, gymnophthalmids as well as teiids.

We have been unable to recognize groups that demonstrate variations in the morphology of the floor of the mouth which could be related to food manipulation, obtaintion of food, or sensory functions, as did Tanner and Avery (1982). Most of our characters of the throat musculature, show minimal, but recognizable, variations; but not even major variations, as the presence or absence of some muscles (e.g., mm. *mandibulohyoideus* II and III), could be correlated with functional patterns such as those considered by Tanner and Avery (1982).

We conclude that cranial myology characters are congruent with other sources of data only at the level of more inclusive groups, and this is what we previously considered as a "general anatomical pattern" defined by their correspondent synapomorphies (Abdala and Moro, 1996; Moro and Abdala, 1998). Therefore, we can postulate the existence of a general teiid pattern (node 39), shared also by *Pantodactylus*. We also distinguish a gymnophthalmid pattern (node 27) with some incongruences (*Echinosaura* and *Pantodactylus*).

That results are in congruence with the findings of many other authors: i.e., Fisher and Tanner (1970) state "...at the family level, however, myology appears to be a sufficiently stable character to be of phylogenetic use..." Iordansky (1970) considers that "...the jaw muscles are built after the <u>same plan</u> in the representatives of Lacertidae, Varanidae, Scincidae, Anguidae, and Zonuridae. The differences of the jaw muscles of these lizards are comparatively insignificant" (author's underlining). Haas (1973) also states that the throat muscles of *Tupinambis* display a "scincoid pattern" (also see Tanner, 1952; Robison and Tanner, 1962; Avery and Tanner, 1964).

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APPENDIX I.
MATERIAL ANALYZED

Teiidae

Argentina:

– *Ameiva ameiva*: FML 03637 (2 ♀♀) — Aguas Blancas, Dto. Orán, Salta; FML 03249 (1 ♂ and 1 ♀) — Campo Grande, Finca Los Colorados, 100 km EN of J. V. González, Dto. Anta, Salta.

– *Cnemidophorus ocellifer*: FML 03389 (two specimens) — Finca Pozo Largo, 8 km 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 S of J. V. González and 12 km to the E of Finca San javier, Dto. Anta, Salta; FML 03409 (four specimens) — Finca Pozo Largo, 8 km S of J. V. González and 12 km to the E of Finca San javier, Dto. Anta, Salta.

– *Cnemidophorus longicaudus*: FML 00078 (2 ♂♂) — Valle de Santa María, Catamarca; FML 02761 (1 ♂) — Lucio V. Mansilla, Dto. Tulumba, Córdoba.
– *Kentropix lagartija*: FML 01186 — Río Loro, Dto. Burruyacu, Tucumán.
– *Teius oculatus*: FML 03625 (1 ♀) — Way to Cuadro Nacional by Ferrocarril to Mendoza, San Rafael, Dto. San Rafael, Mendoza; FML 03629 (1 ♂ and 1 ♀) — Río Cuarto, Dto. Río Cuarto, Córdoba; FML 03630 (2 ♀♀) — Río Cuarto, Dto. Río Cuarto, Córdoba; FML 03632 (1 ♂) — Achiras, Dto. Río Cuarto, Córdoba; FML 03633 (1 ♀) — Alpa Corral, Dto. Río Cuarto, Córdoba.
– *Teius suquiensis*: FML 03626 (1 ♀) — Mina Clavero, Dto. San Alberto, Córdoba; FML 03627 (1 ♂) — Mina Clavero, Dto. San Alberto, Córdaoba; FML 03628 (1 ♀) — left margin of the Río Xanaes (ex Río Segundo), in the cross with Rute National 36, Despeñaderos, Dto. Santa María, Córdoba; FML 03631 (1 ♀) — San Roque, Dto. Punilla, Córdoba.
– *Teius teyou*: FML 00290 (2 ♀♀) — Hickmann, Dto. San Martín, Salta; FML 03634 (1 ♀) — Medio Naranjo, Dto. Cruz del Eje, Córdoba; FML 03435 (1 ♂) — Guanaco Muerto, Dto. Cruz del Eje, Córdoba; FML 03636 (1 ♂ and 1 ♀) — Sierra San Marcos, Dto. Cruz del Eje, Córdoba.
– *Tupinambis rufescens*: PT 0084 (1 ♀) — J. V. González, Salta Forestal, cross with Rute 41, Dto. Anta, Salta; PT 0085 (1 ♂) — J. V. González, Salta Forestal, cross with Rute 41, Dto. Anta, Salta; PT 0597 — 44 km E of J. V. González, Laguna Verde, Dto. Anta, Salta; PT 0889 — 41 km E of J. V. González, Laguna Verde, Dto. Anta, Salta; FML 06412 (1 ♀) — 8 km E and 8 km S of J. V. González, El Guayacán, Dto. Anta, Salta; FML 06413 (1 ♂) — 8 km E and 8 km S of J. V. González, El Guayacán, Dto. Anta, Salta; FML 06423 (1 ♂) — 8 km E and 8 km S of J. V. González, El Guayacán, Dto. Anta, Salta; FML 06425 (1 ♀) — 8 km S and 40 km E of J. V. González, Puesto Amoate, Dto. Anta, Salta; FML 07428 (1 ♀): 41 km E of J. V. González, Salta Forestal, Dto. Anta, Salta; FML 07429 (1 ♂) — 8 km S and 40 km E of J. V. González, Puesto Amoate, Dto. Anta, Salta; FML 07431 (1 ♂) — 8 km E and 8 km S of J. V. González, El Guayacán, Dto. Anta, Salta; FML 07432 (1 ♂) -8 km S and 40 km E of J. V. González, Puesto Amoate, Dto. Anta, Salta; FML 07433 (1 ♂) — 8 km E and 8 km S of J. V. González, El Guayacán, Dto. Anta, Salta; FML 07434 (1 ♂) — 8 km E and 8 km S of J. V. González, El Guayacán, Dto. Anta, Salta.

Brazil:
– *Crocodilurus lacertinus*: MZUSP 12622 — Oriximiná, Pará; MZUSP 16307 — Oriximiná, Pará.
– *Dracaena paraguayensis*: MZUSP 52369 — Fazenda Acarizal, Río Paraguai, Mato Grosso.

Chile:
– *Callopistes maculatus*: MZUSP 58107 — Freirina a El Morado, Atacama.

Ecuador:
– *Echinosaura horrida*: MZUSP 54452 — Pichincha, Centro Científico Río Palenque (Lago Creek); MZUSP 54454 — Pichincha, Centro Científico Río Palenque (Lago Creek).

Peru:
– *Dicrodon guttulatum*: FML 02017 — Talara.

Gymnophthalmidae

Argentina:
– *Pantodactylus schreibersi*: FML without number (2 ♀♀) — orillas del Río Grande, Potrero de las Tablas, Tucumán.

Brazil:
– *Calyptommatus leiolepis*: MZUSP 71339 — Ibiraba, Bahia; MZUSP 71367 — Ibiraba, Bahia.
– *Vanzosaura rubricauda* (= *Gymnophthalmus multiscutatus*): MZUSP 71683 — Vacaria, Bahia; MZUSP 71703 — Vacaria, Bahia.

Peru:
– *Proctoporus guentheri*: FML 02010 — Río Crespón, Yama Zera.
– *Proctoporus pachyurus*: FML 01970 — La Florida, near Tacna (3000 m ***above sea level???***).

Scincidae

Argentina:
– *Mabuya frenata*: FML 00277 — Aguaray, Orán, Salta; FML 01713 — Misión Tacaaglé, Formosa.

Italia:
– *Chalcides chalcides chalcides*: FML 03712 — orilla izquierda del arroyo Torrente Farma, Comuna de Monticiano, Prov. Siena, Toscana.

Lacertidae

Italia:
– *Podarcis sicula*: FML 03714 — Matera, Comuna y Prov. de Matera, Basilicata.

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