



<https://doi.org/10.33256/hj29.1.2336>

A new species of *Contomastix* (Squamata, Teiidae) supported by total evidence, with remarks on diagnostic characters defining the genus

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Formerly *Cnemidophorus* was thought to be the most speciose genus of Teiidae. This genus comprised four morphological groups that were later defined as four different genera, *Ameivula*, *Aurivela*, *Cnemidophorus* and *Contomastix*. The last appears as paraphyletic in a recent phylogenetic reconstruction based on morphology, but monophyletic in a reconstruction using molecular characters. Six species are allocated to *Contomastix*. One of them, *C. lacertoides*, having an extensive and disjunct geographic distribution in Argentina, Uruguay and Brazil. Preliminary analyses revealed morphological differences among its populations, suggesting that it is actually a complex of species. Here, we describe a new species corresponding to the Argentinian populations hitherto regarded as *C. lacertoides*, by integrating morphological and molecular evidence. Furthermore, we demonstrate that the presence of notched proximal margin of the tongue is a character that defines the genus *Contomastix*.

Key words: *C. lacertoides* species group, lizards, Reptilia, South America, systematics

INTRODUCTION

The family Teiidae is distributed throughout the New World, from the northern United States to Argentina, in a wide variety of habitats ranging from extremely arid deserts to tropical rainforests (Pough et al., 2004; Vitt & Caldwell, 2014). One of the most speciose genera of this family was formerly known as *Cnemidophorus* Wagler. Cei (1993) proposed three species groups for the Argentinian taxa of *Cnemidophorus* on the basis of pholidosis and anatomical characters; (a) the *C. longicaudus* (sic) species group for lizards exhibiting a unique preauricular flap, a markedly bilobate posterior margin of the tongue, and granular supraorbital semicircles, (b) the *C. lacertoides* species group for those with a notched posterior margin of the tongue, lacking granular supraorbital semicircles and a preauricular flap, and (c) the *C. lemniscatus* species group for taxa exhibiting a markedly bilobate posterior margin of the tongue and granular supraorbital semicircles, without a preauricular flap. This last group was later split by Cabrera (2004). Thus, the *C. lemniscatus* species group exclusively included all of the species in which males bear preanal spurs, whereas the *C. ocellifer* species group included all the species in which males lack preanal spurs.

Reeder et al. (2002) inferred a phylogeny of the family Teiidae analysing diverse lines of evidence (data derived from mitochondrial ribosomal RNA genes, allozymes, and morphological characters). These authors demonstrated that *Cnemidophorus* was polyphyletic and assigned all the species of this genus from North America to the resurrected genus *Aspidoscelis* Fitzinger. However, this new systematic arrangement did not completely solve the polyphyly of *Cnemidophorus*, as the clades of three of the four morphological species groups mentioned above (*longicauda*, *lacertoides* and *lemniscatus*) were more closely related to clades of other genera of the family than among themselves. The phylogenetic position of the *C. ocellifer* species group could not be accurately determined in their study due to inadequate data.

While the polyphyly of *Cnemidophorus* remained unresolved, their diversity was noticeably increased with the description of many new species [e.g., Colli et al., 2003 (*Cnemidophorus mumbuca*); Cabrera, 2004 (*Cnemidophorus tergoaevigatus*); Colli et al., 2009 (*Cnemidophorus jalapensis*); Cabrera & Carreira, 2009 (*Cnemidophorus charrua*); Ugueto et al., 2009 (*Cnemidophorus senectus* and *Cnemidophorus flavissimus*); Ugueto & Harvey, 2010 (*Cnemidophorus leucopsammus* and *Cnemidophorus rostralis*); Arias et al., 2011a (*Cnemidophorus confusionibus* and

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Cnemidophorus venetacaudus); Arias et al., 2011b (*Cnemidophorus nigrigula* and *Cnemidophorus cyanurus*); Cabrera, 2012 (*Cnemidophorus abalosi*); Silva & Ávila-Pires, 2013 (*Cnemidophorus pyrrhogularis*)]. In general, these descriptions of new species were based only on morphology, coloration and/or meristic variables. Furthermore, some new species were described from just one or few localities, and/or their characteristics were compared to a limited number of species of congeners, some of which belonged to a different morphological group from the new lineage.

Harvey et al. (2012) conducted a phylogenetic analysis of the family Teiidae based on morphological characters and resolved the polyphyly of *Cnemidophorus*, assigning each previously known species group described by Cei (1993) and Cabrera (2004) to a different genus: (a) the name *Cnemidophorus* remains for the species of the *C. lemniscatus* species group; (b) the species of the *C. ocellifer* species group now correspond to the new genus *Ameivula*; (c) the new genus *Aurivela* includes the two apomorphic species of the *C. longicauda* species group formerly known as *Cnemidophorus longicauda* and *Cnemidophorus tergoaevigatus*, and (d) the new genus *Contomastix* comprises the species of the *C. lacertoides* species group.

The arrangement of Harvey et al. (2012) has been supported by two recent phylogenetic studies using several molecular markers, 48 mitochondrial and nuclear loci in Goicoechea et al. (2016), and 316 nuclear loci in Tucker et al. (2016). However, Goicoechea et al. (2016) split the genera *Ameivula* and *Ameiva*, resurrecting the genera *Glaucomastix* to include the species of the *Ameivula littoralis* species group, and *Pholidoscelis* for all the West Indies *Ameiva*.

The genus *Contomastix* includes the species *Contomastix lacertoides* (Duméril & Bibron), *Contomastix leachei* (Peracca), *Contomastix serrana* (Cei & Martori), *Contomastix vacariensis* (Feltrim & Lema) and *Contomastix charrua* (Cabrera & Carreira). Harvey et al. (2012) added *Cnemidophorus vittatus* Boulenger to the group, indicating that this species, together with *C. lacertoides* and *C. leachei*, lack a lingual sheath and have a straight posterior margin of the tongue rather than a heart-shaped one. However, they did not include tongue morphology in their phylogenetic reconstruction, arguing that this character is unreliable and difficult to assess. In their study, *Contomastix* was not recovered as monophyletic, with *C. lacertoides* placed outside the clade containing *C. serrana* and *C. vittata*. Based on their results, Harvey et al. (2012) considered that there is “no single unique character that distinguishes *Contomastix* from all other teiids” and suggested that additional research is needed to determine if the distinctive characters of *C. lacertoides* exclude it from the genus *Contomastix*. However, in a more recent phylogenetic analysis, Tucker et al. (2016) recovered a clade that includes *C. vacariensis*, *C. serrana*, and *C. lacertoides*.

Contomastix lacertoides is a small long-tailed striped terrestrial lizard. This species is distributed in a large region encompassing southern Brazil (the coast of the state of Santa Catarina and the southern half of the state

of Rio Grande do Sul), almost all of Uruguay, and two small disjunct areas in Argentina: the south end of the Sierras de Córdoba system, in Córdoba province, and the Sierras de Ventania system, in Buenos Aires province (Cei, 1993; Lema, 1994; Vrcibradic et al., 2004; Carreira et al., 2005). The type locality for the species is Montevideo, Uruguay (Duméril & Bibron, 1839). Our preliminary revisions indicated that there are morphological differences among the populations of *C. lacertoides* from southern and eastern of Uruguay in relation to the other populations of the species, suggesting that *C. lacertoides* is actually a complex of species (Cabrera & Carreira, 2009; Cabrera, 2015).

One of the basic tasks in systematic research is to reach a more stable taxonomy and accurate species delimitation. Therefore, the use of multiple lines of evidence in order to provide stronger support for proposals of nomenclatural action is advisable. In this paper we describe a new species corresponding to the Argentinian populations hitherto regarded as *C. lacertoides*, by integrating morphological and molecular evidence. We also aim to determine if there are any morphological characters that define the genus *Contomastix*.

METHODS

Morphological analyses

We examined 40 specimens (23 males, 13 females, and 4 juveniles) of *C. lacertoides* sensu stricto from 23 localities in Uruguay, 15 specimens (7 males, 5 females, and 3 juveniles), and 23 specimens (12 males, 6 females, and 5 juveniles) of *C. lacertoides* sensu lato from one locality in the Sierras de Córdoba, Argentina and 4 localities in the Sierras de Ventania, Argentina, respectively. These samples comprised all the available Uruguayan specimens of this lizard known to us, and most of the Argentinian ones lodged in the national museums of both countries. This lizard is harder to find in the wild nowadays than before. We also examined other species of the genus: *C. charrua* (3 males, 6 females, one locality), *C. leachei* (2 males, 2 localities), *C. serrana* (5 males, 5 females, and 4 juveniles, 10 localities) and *C. vacariensis* (4 males, 3 females, 4 localities) (Fig. 1). Since we had no access to specimens of *C. vittata*, morphological data were obtained from the original description (Boulenger, 1902, one specimen) and from the studies of Vance (1978, the same specimen, re-evaluated) and Harvey et al. (2012, $n = 9$, all from Bolivia). Additional data for *C. leachei* and *C. vacariensis* were taken from Cei & Scrocchi (1991) and Feltrim & Lema (2000), respectively. The tongue morphology in *Contomastix* spp. was compared to that of *Ameiva ameiva*, *Ameivula abalosi*, and *Aurivela longicauda*. The specimens examined and the institutions in which they are housed are detailed in Appendix 1.

A standard morphological protocol for lizard taxonomy study was made following the definitions of Peters (1964), Smith (1995), Markežich et al. (1997), and Cabrera (2012). Measurements were taken to the nearest 0.1 mm with digital callipers under a dissecting stereomicroscope. The minimum size at which these

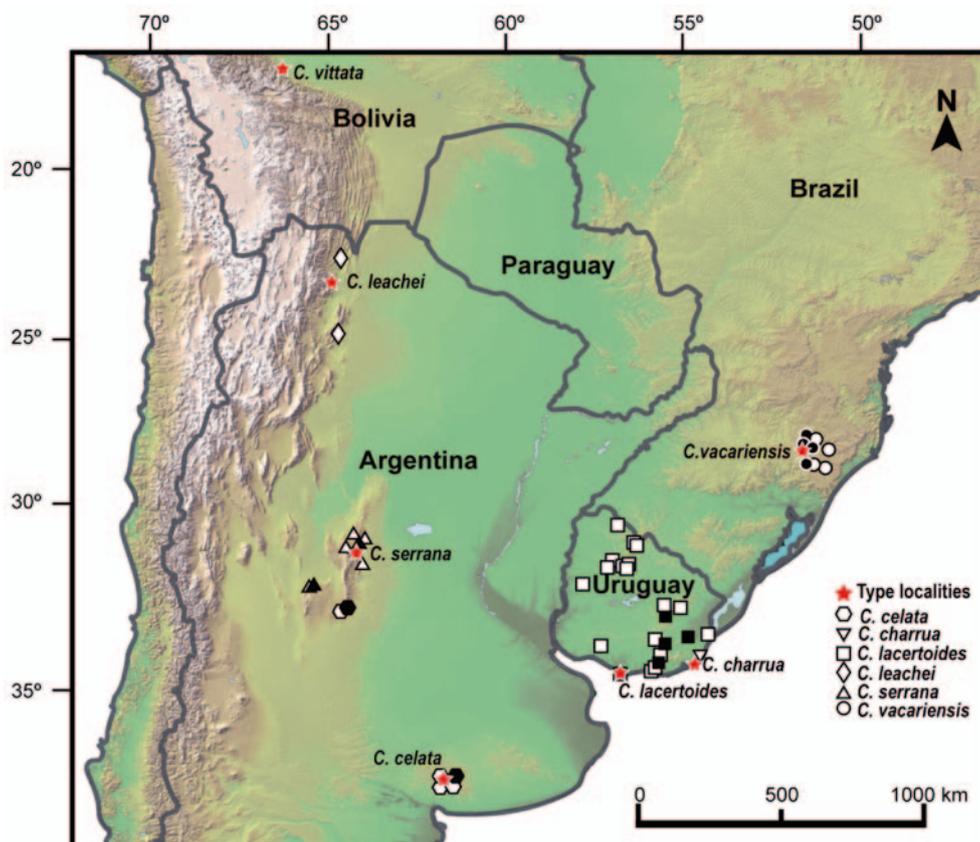


Figure 1. Geographic distribution of the specimens examined. Open symbols identify lizards whose morphology was analysed; black symbols, those used in molecular analyses. Each reference may represent more than one lizard in cases of close localities. The samples widely cover the range of all the species except for *C. vittata*. Base map by courtesy NASA/JPL Caltech.

species reach sexual maturity is unknown; however, specimens with snout-vent length (SVL) less than 45 mm were not considered for morphometric and meristic analyses in order to exclude allometric bias. Sex was determined by gonad inspection through a short incision on the left side of the belly in intact specimens without everted hemipenis. Coloration data were obtained from live specimens, field notes, literature, and photographs.

Morphometric characters included are: snout-vent length (SVL), along the midventral line from the tip of snout to the posterior edge of the preanal flap; head length (HL), from the tip of snout to the posterior margin of the ear, along the medial axis of the head; head depth (HD), measured vertically at the level of contact between frontal and frontoparietal scales; snout length (SL), from the tip of snout to the anterior limit of the frontal scale; axilla to groin distance (AG), from the posterior margin of the forelimb insertion to the anterior margin of the hindlimb insertion, on the left side of the body.

Meristic characters recorded were: dorsal scales around the body but excluding enlarged ventrals (DS), counted at mid axilla to groin distance; scales at midbody between the medialmost light stripes (SPV); dorsal scales along the body (DAS), counted on midline from behind the occipitals to the first transverse row of tail scales; transverse rows of ventral scales along midventral line (TVS), from behind the granular scales posterior to the gular fold to the anterior margin of the hindlimbs; longitudinal rows of ventral scales (LVS), at mid axilla to groin distance; supralabial scales (SLB), counted on left

side from behind rostral to the last scale bordering the upper edge of the mouth; infralabial scales (ILB), counted on left side from behind mental to the angle of mouth (rictus ori); chin shields in contact on midline (CH); supraocular scales (SOC), counted on left side; parietal plates (PAP), counted as: interparietal + frontoparietals + parietals, but excluding the postparietals (= occipitals); gular folds (GF), including gular and pregular folds, if present; total number of femoral pores (FP); lamellar scales under the fourth finger of the left hand including the one below the claw (FFS); lamellar scales under the fourth toe of the left foot including the one below the claw (FTS).

Categorical characters included are: presence or absence of spots on infralabial scales (SIL); presence or absence of vertebral light stripe (VLS); condition (continuous, broken, or spotted) of the dorsolateral light stripe (the stripe running from the superciliaries along the body onto the tail) (DLS); condition (continuous, broken, or spotted) of the lateral light stripe (the stripe running from the suborbital region to the hindlimb) (LLS); presence or absence of dark pigment in any portion of ventral scales (VM); morphology (notched or bilobate) of the proximal margin of the tongue (PMT). This set of characters has proved to be reliable and robust in works dealing with cnemidophorine lizards at species group-level. Harvey et al. (2012) proposed a large set of character definitions for the phylogenetic analysis of the family Teiidae. We found most of them inapplicable to the present work, either because they are invariant

within the genus *Contomastix* (83 characters) or within *C. lacertoides* sensu lato (13 characters) or inapplicable to the genus (5 characters).

Comparisons were made among the geographical groups of *C. lacertoides* (Sierras de Córdoba, Sierras de Ventania and Uruguay) and among the different lineages within the genus *Contomastix*. All statistical analyses were performed using the InfoStat software v. 2015p (Di Rienzo et al., 2015) at a $p \leq 0.05$ significance level.

DNA extraction, PCR amplification and sequencing

Sample tissues (liver and/or muscle) were collected from four specimens of *C. lacertoides* sensu stricto from four localities in Uruguay and from three specimens of each of the two disjunct areas of distribution in Argentina (Fig. 1). We also obtained samples from two specimens of *C. serrana*, one from *Aurivela longicauda*, one from *Teius teyou* and one from *Salvator merianae*. Total genomic DNA was extracted from alcohol-preserved tissues, using a saline extraction method (Bruford et al., 1992). Fragments of the 16S, ND4, c-mos, and NTF3 genes were amplified using the primers and conditions specified in Appendix 2. The PCR products were sequenced in an automated DNA sequencer (ABI PRISM 3730x1 DNA) by Macrogen Korea Inc.

Phylogenetic analyses

Phylogenetic analyses were performed at the nucleotide level based on a matrix that included new sequences obtained in this study, and available sequences from GenBank of species with at least two of the genes analysed from almost all genera of the subfamily Teiinae. Taking into account that the phylogenetic hypothesis of Harvey et al. (2012), based on morphological characters, differs substantially from the hypotheses based on DNA (Reeder et al., 2002, Giugliano et al., 2013, Tucker et al., 2016), we used the genus *Salvator* as outgroup. Species, specimens, and GenBank accession numbers are listed in Appendix 3.

We performed multiple-sequence alignments for each gene using MAFFT software version 7 (Katoh & Standley, 2013). Phylogenetic relationships for the combined matrix of mitochondrial and nuclear DNA were analysed using Maximum Parsimony (MP), Maximum Likelihood (ML), and Bayesian inference (BI). MP analysis was made with PAUP 4.0.B10 (Swofford, 2003), with equal weighting for all characters and gaps treated as missing data. The Wagner algorithm was used for the heuristic search of the phylogenetic reconstructions with the TBR branch swapping algorithm. Then, the minimum length trees were summarised in a majority-rule consensus tree. The node support was evaluated by 1000 bootstrap replicates.

The best-fitting model of sequence evolution was selected using JModeltest2 (Darrriba et al., 2012), under the Akaike information criterion (AIC) for ML and the Bayesian information criterion (BIC) for BI (Appendix 2). ML trees were constructed using the online version of PhyML 3.0 (<http://www.atgcmontpellier.fr/phyml/>; Guindon et al., 2010). The selected model was GTR+G, and it was used for the analyses; 1000 bootstrap

replicates were performed. Bayesian analyses were performed using MrBayes 3.1.2 (Ronquist & Huelsenbeck, 2003), conducting two independent Markov chain Monte Carlo simulations (with four chains each) for 2 million generations, sampling every 1000 generations, and discarding the first 25% of the samples as burn-in. The convergence to stable values and Effective Sample Size (ESS) were checked with Tracer v1.5 (Rambaut & Drummond, 2007). The two runs converged on very similar posterior estimates with an average standard deviation of split frequencies of 0.01.

The Kimura 2 parameter genetic distances (K2P) were calculated for the 16S gene using Mega 7.0 software (Kumar et al., 2016). The nuclear genes were not used to calculate genetic distances due to their low level of variability.

RESULTS

Morphological analyses

There were no significant differences (Wilcoxon test) in any morphometric character between the Argentinian populations of *C. lacertoides*, so they were pooled as one. Between the Uruguayan and Argentinian populations, five morphological characters differed significantly (Kruskal-Wallis tests): DS, ($H=15.52$, $p<0.001$), SPV, ($H=28.14$, $p<0.001$), DAS ($H=39.96$, $p<0.001$), FFS ($H=8.78$, $p<0.01$), and FTS ($H=12.84$, $p<0.001$) (Fig. 2). These data indicate that Uruguayan lizards have smaller and more numerous dorsal scales than the Argentinian ones and more lamellae under the fourth finger and fourth toe (Table 1).

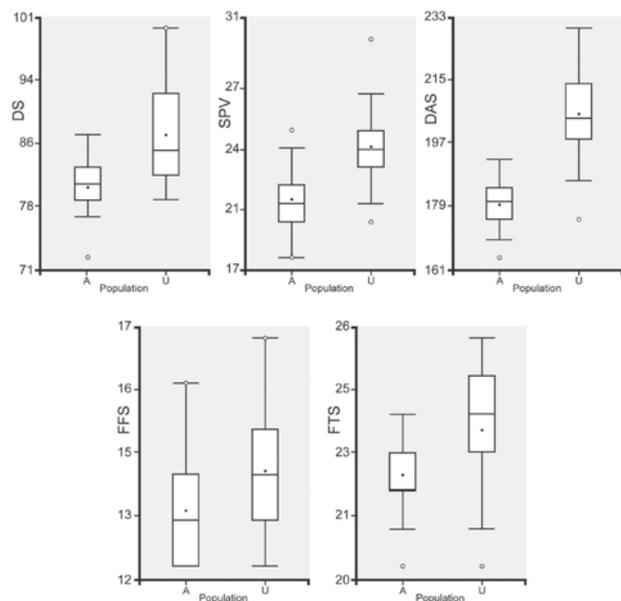


Figure 2. Box-plots illustrating meristic differences between the Argentinian (A) and Uruguayan (U) samples of *Contomastix lacertoides* sensu lato. DAS, dorsal scales along the body; DS, dorsal scales across midbody; FFS, lamellae under the fourth finger; FTS, lamellae under the fourth toe; SPV, scales at midbody between the medialmost light stripes.

Phylogenetic analyses

The database used includes a total of 2486 base-pairs.

Table 1. Character variation in all the species of *Contomastix*. Measurements expressed in mm. Values indicate Mean \pm SD, except for *C. vittata* (Mean \pm SE), and range in parentheses. Data for *C. vittata* extracted from Boulenger (1902), Vance (1978), and Harvey et al. (2012); tongue morphology of *C. leachei* according Cei & Scrocchi (1991).

	<i>Contomastix celata</i> new sp.	<i>C. charrua</i>	<i>C. lacertoides</i>	<i>C. leachei</i>	<i>C. serrana</i>	<i>C. vacariensis</i>	<i>C. vittata</i>
<i>n</i> (sex)	20 (M), 9 (F)	3 (M), 6 (F)	23 (M), 13 (F)	2 (M)	5 (M), 5 (F)	4 (M), 3 (F)	9
SVL (Max.)	70.3	75.2	74.0	66.8	61.4	72.1	76
HL	14.2 \pm 1.3 (11.4-16.3)	15.6 \pm 0.4 (13.7-16.9)	14.8 \pm 1.2 (12.4-17.3)	15.4 \pm 2.9 (12.5-18.2)	13.2 \pm 0.2 (12.2-14.4)	15.9 \pm 0.4 (14.5-17.6)	12
HD	6.5 \pm 0.6 (5.4-7.5)	7.5 \pm 0.3 (6.6-8.6)	6.7 \pm 0.6 (5.6-8.0)	6.3 \pm 0.9 (5.4-7.2)	5.8 \pm 0.2 (5.1-6.4)	7.0 \pm 0.3 (6.2-8.0)	?
SL	5.0 \pm 0.5 (4.2-6.1)	5.2 \pm 0.1 (4.5-5.7)	5.0 \pm 0.4 (4.0-5.9)	5.3 \pm 1.0 (4.3-6.3)	4.5 \pm 0.1 (4.3-4.9)	5.5 \pm 0.2 (4.9-6.3)	?
AG	29.6 \pm 3.8 (22.5-35.5)	33.4 \pm 1.5 (27.6-39.2)	30.3 \pm 3.2 (21.6-37.5)	27.9 \pm 3.2 (24.7-31.1)	28.5 \pm 1.1 (23.6-34.1)	32.5 \pm 0.8 (29.9-36.3)	?
DS	80.8 \pm 3.8 (72-87)	90.2 \pm 2.2 (81-98)	86.8 \pm 6.0 (79-100)	87.0 \pm 2.0 (85-89)	69.7 \pm 1.3 (63-75)	95.7 \pm 1.2 (89-98)	64
SPV	21.1 \pm 1.6 (18-25)	41.3 \pm 11.5 (12-94)	24.1 \pm 1.9 (20-30)	26.0 \pm 0.0 (26)	20.0 \pm 0.6 (16-22)	25.0 \pm 0.9 (22-29)	?
DAS	179.0 \pm 6.9 (164-193)	203.7 \pm 1.5 (201-206) M, 216.8 \pm 3.1 (208-229) F	204.7 \pm 13.6 (175-230)	182.0 \pm 4.0 (178-186)	166.0 \pm 3.7 (146-177)	218.9 \pm 2.8 (212-233)	?
TVS	31.9 \pm 1.2 (30-34)	33.4 \pm 0.3 (32-35)	32.1 \pm 1.0 (31-35)	33.0 \pm 0.0 (33)	31.5 \pm 0.3 (30-33)	32.4 \pm 0.7 (31-36)	32 \pm 1 (30-33)
LVS	9.9 \pm 0.4 (8-10)	10.0 \pm 0.0 (10)	10.0 \pm 0.2 (9-10)	10.0 \pm 0.0 (10)	8.3 \pm 0.2 (8-9)	9.1 \pm 0.4 (8-10)	10
SLB	6.8 \pm 0.8 (6-8)	7.1 \pm 0.2 (6-8)	6.9 \pm 0.5 (6-8)	7.5 \pm 0.5 (7-8)	6.0 \pm 0.0 (6)	6.7 \pm 0.2 (6-7)	6-7
ILB	5.6 \pm 0.6 (5-7)	5.9 \pm 0.3 (5-7)	5.7 \pm 0.6 (5-7)	6.0 \pm 0.0 (6)	5.2 \pm 0.1 (5-6)	5.6 \pm 0.2 (5-6)	5-7
CH	2.0 \pm 0.5 (0-4)	1.8 \pm 0.2 (0-2)	1.8 \pm 0.6 (0-2)	2.0 \pm 0.0 (2)	2.0 \pm 0.0 (2)	1.4 \pm 0.4 (0-2)	0-2
SOC	3.7 \pm 0.5 (3-4)	3.1 \pm 0.1 (3-4)	3.4 \pm 0.5 (3-4)	3.5 \pm 0.5 (3-4)	3.2 \pm 0.1 (3-4)	3.1 \pm 0.1 (3-4)	2-4
PAP	5.0 \pm 0.0 (5)	5.0 \pm 0.0 (5)	5.0 \pm 0.0 (5)	5.0 \pm 0.0 (5)	5.0 \pm 0.0 (5)	5.0 \pm 0.0 (5)	5
GF	2.0 \pm 0.0 (2)	1.8 \pm 0.2 (1-2)	2.0 \pm 0.3 (1-3)	2.0 \pm 0.0 (2)	2.0 \pm 0.0 (2)	2.0 \pm 0.0 (2)	?
FP	19.9 \pm 1.6 (16-23)	20.2 \pm 0.3 (19-22)	19.6 \pm 1.3 (16-22)	23.5 \pm 1.5 (22-25)	19.7 \pm 0.3 (18-21)	19.9 \pm 0.5 (18-22)	19-25
FFS	13.1 \pm 1.2 (12-16)	14.0 \pm 0.2 (13-15)	14.1 \pm 1.2 (12-17)	15.5 \pm 1.5 (14-17)	14.5 \pm 0.2 (14-16)	15.0 \pm 0.4 (14-16)	14 \pm 1 (13-15)
FTS	22.2 \pm 1.2 (20-24)	22.6 \pm 0.6 (20-25)	23.6 \pm 1.5 (20-26)	27.5 \pm 0.5 (27-28)	25.3 \pm 0.5 (23-28)	23.7 \pm 0.7 (21-27)	25 \pm 1 (24-28)
SIL	Present	Present	Present	Present	Present	Present	Present
VLS	Absent	Absent	Absent	Absent	Absent	Absent	Absent
DLS	Broken/ continuous	Continuous (if present)	Mostly continu- ous	Continuous	Continuous	Spots/dashes	Continuous
LLS	Mostly broken	Continuous (if present)	Broken/ continu- ous	Continuous	Continuous	Spots/dashes	Continuous
VM	Present	Present	Present	Present	Mostly present	Present	Present
PMT	Notched	Notched	Notched	Notched	Notched	Unknown	Notched

The phylogenetic trees obtained with MP, ML and BI yielded highly similar estimates of phylogenetic relationships among the taxa; in general, the nodes received less support in the MP analyses (Fig. 3). The specimens of *C. lacertoides* from the two regions in Argentina group together with high support values (1.00/97/100 with BI, ML, and MP, respectively). The Argentinian group is the sister clade of that formed by the specimens of *C. lacertoides* from Uruguay and both group together in a cluster with the clade of *C.*

vacariensis. *Contomastix serrana* appears to be basal for the genus. The genus *Contomastix* is recovered as monophyletic with a high support values (1.00/100/100) and with none of its specimens grouping with any other teiid genus. *Cnemidophorus* and *Ameivula* are also recovered as monophyletic (0.99/100/84 and 0.98/59/-, respectively).

Regarding the phylogenetic relationships among the genera, three clades can be observed: i) *Contomastix* grouping together with *Aurivela* (0.99/62/--); ii)

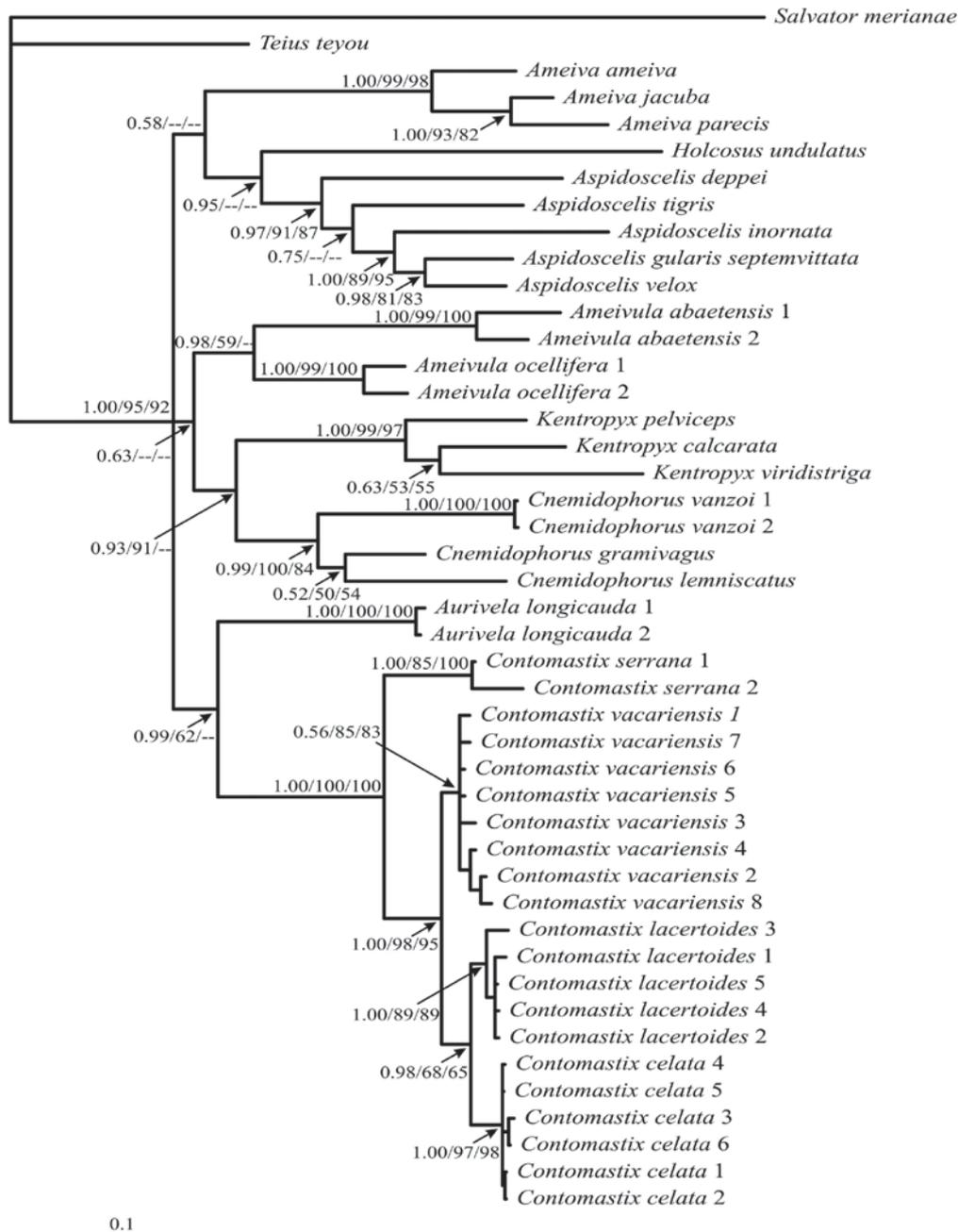


Figure 3. Bayesian phylogram of the 50% majority-rule consensus tree of the subfamily Teiinae based on the 16S, ND4, c-mos and NTF3 data sets. The node supports are: Bayesian posterior probabilities/bootstrap support after 1000 replicates in ML analysis/bootstrap support after 1000 replicates in MP analysis.

Cnemidophorus as the sister taxon of *Kentropyx* (0.93/91/-) and both grouping together with *Ameivula*, although without support (0.63/--/--); iii) *Aspidoscelis* as the sister taxon of *Holcosus* (0.95/--/--) and both grouping together with *Ameiva* with low support (0.58/--/--). *Teius* is recovered basal to these three clades.

The mean K2P genetic distances within clades of *Contomastix* were 0.4%/0.5% for genes 16S and ND4, respectively. Among clades of *Contomastix* the genetic distances were 3.3%/7.7% for genes 16S and ND4, respectively. Such distances range from 1.6%/4% (Uruguayan *C. lacertoides* - Argentinian *C. lacertoides*) to 6.7% /11.8% (*C. serrana* - Argentinian *C. lacertoides*). In

general, the genetic distance within each clade was one order of magnitude lower than the distance between them in *Contomastix*. The genetic distances among species within the genera of the subfamily Teiinae were on average 7.9%/16.1% and range, for the gene 16S, from 6.9% for species of *Ameiva* to 9.5% for species of *Kentropyx*. The genetic distances for the gene ND4 range from 15.1% for species of *Kentropyx* to 17.5% for species of *Ameivula*.

Based on the morphological differences among Argentinian and Uruguayan populations, and on the results of the phylogenetic analyses and genetic distances, the Argentinian populations are recognised as a new species and described here.

Contomastix celata new species (Figs 4–7, Table 1)

Holotype. MZUC-C 672, adult male, from Villa La Arcadia (38°06'50.42" S, 61°46'22.4" W, 423 m a.s.l.), Partido de Coronel Suárez, Buenos Aires Province, Argentina. 15 September 2012. Collected by D. Di Pietro. The acronym MZUC corresponds to Museo de Zoología, Universidad Nacional de Córdoba, Argentina.

Paratypes. MACN 32867 (adult male) and MLP.S 1049/1050 (adult female and male, respectively) from Sierra de Ventania, Ernesto Tornquist Provincial Park, Partido de Tornquist, Buenos Aires Province, Argentina. 16 March 1985. Collected by J. Cranwell, G. Gnida and J. Soroka. MLP.S 1166 (adult female) from Achiras, Río Cuarto Department, Córdoba Province, Argentina. 19 November 1991. Collected by R. Martori and L. Aun. MZUC-C 563 (adult male) from Achiras, Río Cuarto Department, Córdoba Province, Argentina. 4 November 1990. Collected by L. Avila and A. Pettinichi. MZUC-C 567 (adult female) from Achiras, Río Cuarto Department, Córdoba Province, Argentina. 29 December 1990. Collected by L. Avila. MZUC-C 676 (juvenile) from Piedra del Aguila (33°09'33.7"S, 64°59'10.6"W, 828 m a.s.l.), Achiras, Río Cuarto Department, Córdoba Province, Argentina. 11 March 2013. Collected by M. R. Cabrera and R. Torres.

Diagnosis. A small-to-medium sized lizard (70.3 mm maximum SVL), recognisable by the following combination of characters in both sexes: 72–87 granular dorsal scales across midbody; 164–193 dorsal scales along midline; 18–25 scales at midbody between the medialmost light stripes; 10, rarely 8, longitudinal rows of quadrangular ventral scales; 16–23 femoral pores in total; 12–16 subdigital lamellae under fourth finger; 20–24 lamellae under fourth toe; 3–4 supraoculars on each side. *Contomastix celata* can be distinguished phenotypically from *C. leachei* (character states in parenthesis) by having fewer lamellar scales under fourth toe (20–24 vs. 27–30), lateral light stripe broken (continuous), and dorsal ground colour brown (greenish). It is distinguishable from *C. serrana* (character states in parenthesis) in having fewer lamellar scales under fourth toe (20–24 vs. 23–28), more dorsal scales across (72–87 vs. 63–75) and along the body (164–193 vs. 146–177), 10, rarely fewer, longitudinal rows of ventral scales versus generally 8 in *C. serrana*, and dorsolateral and/or lateral light stripes usually broken (both invariably continuous). *Contomastix celata* is distinguishable from the probably extinct *C. charrua* in having a smaller body (SVL up to 70.3 mm vs. 75.2 mm), fewer dorsal scales across midbody (72–87 vs. 81–98) and along the body (164–193 vs. 201–229), and in always having a striped pattern, whereas *C. charrua* is completely unstriped or has two thin light stripes on each side of the body, with feeble to no expression of black bars between them. It is distinguishable from *C. vacariensis* in having fewer dorsal scales across midbody (72–87 vs. 89–98) and along the body (164–193 vs. 212–233), and a different pattern of the light stripes, which in *C. vacariensis* is formed by dots or spots. *Contomastix celata*

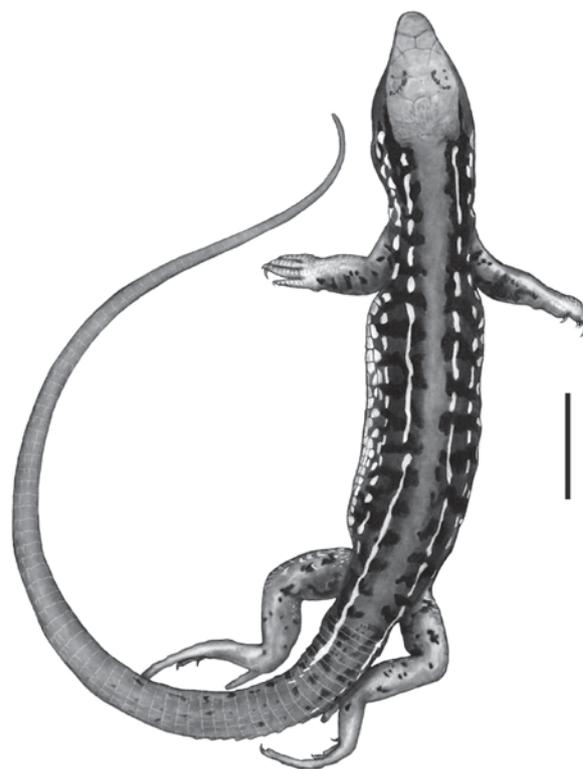


Figure 4. *Contomastix celata* new sp. Body aspect and pattern of the holotype (MZUC-C 672) in dorsal view. Scale bar = 1 cm.

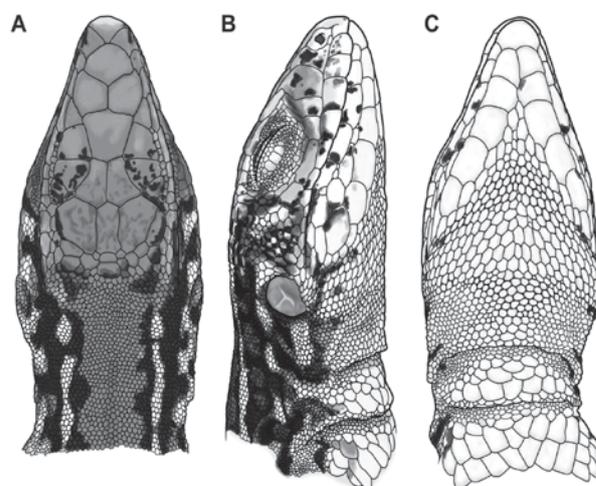


Figure 5. *Contomastix celata* new sp. Head of the holotype in dorsal (A), lateral (B), and ventral (C) view.

is distinguishable from *C. vittata* in having a smaller body (SVL up to 70.3 mm vs. 76 mm), more dorsal scales across midbody (72–87 vs. 64), and fewer lamellar scales under the fourth toe (20–24 vs. 24–28), and frequently broken light lateral stripes (continuous in *C. vittata*). *Contomastix celata* most closely resembles *C. lacertoides* in size, body habitus, colour and pattern. It is distinguishable from the latter in having fewer dorsal scales across midbody (72–87 vs. 79–100) and along the body (164–193 vs. 175–230), fewer scales at midbody between the medialmost light stripes (18–25 vs. 20–30), and (statistically) fewer subdigital lamellae on both fourth finger and fourth toe.



Figure 6. Coloration in life of *Contomastix celata* (MZUC-C 677) from Achiras, Córdoba, Argentina.

Description of holotype. MZUC-C 672, adult male, snout-vent length 62.9 mm, head length 15.4 mm, tail complete. Head triangle-shaped in dorsal aspect, with sides slightly concave. Canthus rostralis blunt but evident, snout length 5.7 mm, 1.5 times longer than eye length. Rostral convex, visible from above and below, partially incised on both sides in front of the anterior nasal scale. Nasals large, paired, with the nostril situated almost entirely in each anterior nasal scale; middorsal contact between anterior nasals prevented by the posterior angle of the rostral. Each anterior nasal contacts rostral, frontonasal, posterior nasals, and supralabial 1 scales. One posterior nasal on each side, slightly convex and smaller than the anterior nasal, contacts anterior nasal, frontonasal, prefrontal, loreal, and supralabials 1–2. Loreal large, concave, single, contacting postnasal, prefrontal, supraocular 1, first superciliary, preocular, and supralabial 3. Frontonasal rhomboidal, wider than long. Two large prefrontals, in broad contact with each other in the midline, each also contacting frontonasal, posterior nasal, loreal, frontal, and supraocular 1. Frontal single, flat, large, subhexagonal with straight borders, narrow behind; its two anteriormost sides contacting prefrontals,

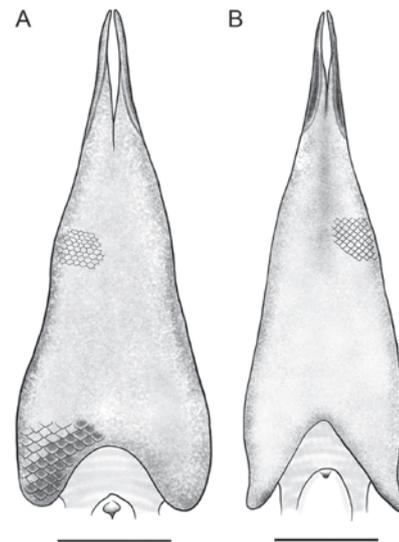


Figure 7. Dorsal view of the tongue and glottis of *Contomastix celata* (MZUC-C 671), detailing juxtaposed papillae anteriorly and imbricate papillae to behind, and its notched proximal end (A); Tongue and glottis of *Ameivula abalosi* (LECOH 00579), with subimbricate papillae covering the whole surface (here partly highlighted) and bilobate proximal end (B), a condition shared with the species of the genus *Aurivela*. Scale bars = 2.5 mm.

its lateral sides contacting supraoculars 1 and 2, and its two posterior sides contacting the anterior side of frontoparietals. Two frontoparietal plates, subpentagonal with external border concave, in broad contact with each other along midline, its lateral sides contacting supraoculars 2, 3 and a small postorbital scale, and its posteriormost sides contacting parietal and interparietal plates. Two broad parietals, rugose, subpentagonal separated by a rugose interparietal on the midline, subpentagonal, two times longer than wide, with lateral sides long and parallel; its anterior and posterior sides, straight and short. The right parietal limited externally by a large, ovate, convex scale. Occipitals polygonal to oval scales, wider than long, behind parietal and interparietal plates, followed by much smaller granular scales on the neck. Supraoculars convex, four on each side, the first contacting loreal, prefrontal, frontal, supraocular 2, and first superciliary scales. Supraoculars 2 to 4 separated from superciliaries by a single row of small granules. Superciliaries 5/5 in a row, the first two longer than the others. Eyelids finely granular, lower eyelid with a group of 3/4 quadrangular scales in its centre, surrounded by granular scales. Suboculars 4/4, large, all contacting supralabials, the first higher than long, in broad contact with loreal and touching the first superciliary. First three suboculars markedly keeled near their upper borders. Supralabials 6/7, with rounded free border, notched at the margin where each scale contacts its neighbours. Temple and cheek with swollen granular to polygonal scales. Ear opening oval nearly round, slightly higher than wide, surrounded by tiny granular scales.

Mental subtriangular, wider than long, followed in the midline by the first pair of chin shields. Postmental

absent. Infralabials 6/6. All, except the first one, longer than high; first infralabial contacting mental and first chin shield, the second contacting first and second chin shields, the third contacting second and third chin shields. The other infralabials separated from the chin shields by a row of sublabials in a single or double row. Five pairs of large, subquadrangular chin shields, the first two pairs in broad contact in the midline. A field of oval scales between chin shields, replaced in the gular region by larger and flatter polygonal scales in the plane between the ears, followed by nine or ten rows of rounded, smaller scales and by a field of large imbricate mesoptychial plates prior to the gular fold. Well defined gular fold, lined by granules. Scales on nape and sides of the neck granular.

Dorsal and flank scales granular, convex, 83 across midbody and 193 in the middorsal line from the nape to the base of tail. At ventral, a field of large polygonal imbricate scales, roughly arrayed in three rows, on upper chest between the insertion of humeri. Posterior to this field a series of ventral plates, smooth, mostly rectangular, wider than long, the external ones in each row having curved lateral sides. Seven scales in the row between axillae, 10 midventrally and 8 in the last transverse row, near groin. One or two scales smaller than ventrals at the extreme of some rows; 31 transverse rows of ventrals on the midventral line. Four large preanal plates, polygonal, preceded and flanked by smaller flat scales. A field of granules posterior to vent. Anal spurs absent.

On forelimbs, suprabrachial and postbrachial scales large, imbricate, in longitudinal rows to elbow, those of the anteriormost row larger and wider than long. Prebrachials rounded, sub-imbricate. Axillary and infrabrachial scales granular, very small. Infra-antibrachial and post-antibrachial scales granular, small, juxtaposed. Two rows of large preantibrachials, imbricate, wider than long, gradually increasing in width towards the hand. Hand pentadactyl, with long, sharp claws. Subdigital lamellae smooth, 14 under left fourth finger, those under first finger followed by a row of three prominent scales proximal to wrist. Palm granular. Two prominent scales forming an outer metacarpal tubercle. Dorsum of manus with rows of imbricate plates wider than long, arrayed along the axis of each digit as supradigital lamellae. A row of granular scales between supradigital and subdigital lamellae, continued on digits 3–5, interrupted on digit 2, and absent on first finger. Suprafemoral and postfemoral scales granular, juxtaposed. Prefemoral and infrafemoral scales large, imbricate, organized in rows, reaching the knee. Eighteen femoral pores in total. Supratibial, pretibial, and post-tibial scales granular and juxtaposed. Infratibial scales large and imbricate, arrayed in three rows. Pes pentadactyl, thin digits with sharp claws shorter than those in hands. Subdigital lamellae smooth, 21 under left fourth toe. Sole granular. Foot dorsum with imbricate supradigital lamellae in rows over each digit.

Scales on tail dorsum quadrangular, longer than wide, keeled, becoming progressively mucronate from tail base to the tip; keels on scales forming continuous carinae. Ventral and lateral tail scales longer than wide, imbricate, becoming progressively keeled distally, but less markedly

than in dorsals. Twenty-seven scales around tail on its fifth complete postcloacal whorl.

Coloration and pattern. Dorsal head scales shiny, light brown. Dorsal neck surface and central field along the body dorsum light brown, clearing gradually to greyish light brown on tail. No vertebral stripe. A thin white dorsolateral stripe, unevenly interrupted, along each side of the body, starting on the neck behind superciliaries and continuing to the tail, where it fades out. A lateral white string of dashes and spots along each side of body, starting below and behind the eye, touching upper border of the ear and running along flank, parallel to the dorsolateral stripe. The lateral white markings extend on to the thigh anterodorsally and posterodorsally and continue on the lateral side of the body up to the tail. It becomes indiscernible on the tail because it is located at the limit of the greyish brown dorsum and the white venter of tail. A white ventrolateral string of dots starts below the tympanum and runs along flank almost parallel to the lateral white string of markings. Both lateral and ventrolateral traces are generally broader than the dorsolateral stripe. Colour of flanks between dorsolateral stripe and lateral strings, brown, with a series of bold black bars, some of them bifurcated as inverted “Vs” or “Ys”. A series of bold black indentations above the white dorsolateral stripe, fading on tail. Dorsum of arms and legs brown, with irregular black marks and occasional lighter blotches. Supradigital lamellae of hand and foot ivory. Dorsum and upper sides of tail light greyish brown, with feeble dark marks. Sides of head brown, lighter than dorsum. Supra- and infralabials white, with black marks on the margins of most scales. Ventral surfaces of head, neck, body, limbs and tail pearly white, with black marks on the two or three external rows of ventral scales.

Variation. The white dorsolateral stripe is continuous in some individuals, while in others it is fragmented as long dashes all along its extension (Fig. 6). In the former the lateral white trace (i.e., the second in dorsum-to-venter order) is neither continuous nor a string of dots but a stripe with few sparse breaks. The ventrolateral white trace is never continuous. There is no difference between male and female adult colour patterns. Juveniles of both sexes have the lateral and ventrolateral light stripes yellowish instead of white, and the field between them is darker than in adults. No appreciable changes in pattern or colour in preservative (70% ethanol).

Geographic distribution. *Contomastix celata* is endemic to Argentina and is associated to rocky grassland habitats in two mountain systems: the south of Sierras de Córdoba in the centre of the country, and Sierras de Ventania in Buenos Aires province (Fig. 1). Both mountain systems are separated by 560 km of vast plains (Pampas landscape). These lowlands seem unsuitable for the species, according to its saxicolous habits and the lack of reliable records of its presence there. The nearest population of the sister species *C. lacertoides* (in San José Department, Uruguay) is approximately 600 km distant from the *C. celata* populations in the Sierra de Ventania

system. The basal species, *C. serrana*, is geographically the closest to *C. celata*, but they are not sympatric.

Etymology. The specific epithet is an adjective derived from the Latin word *celatus* (*celata* in feminine form), meaning hidden or concealed, in reference to the phenotypical similarity to *Contomastix lacertoides*, under whose name these populations have been hitherto masquerading.

Cytogenetics. The karyotype of the population of *C. celata* in Sierras de Córdoba is $2n = 52$ with 26 macrochromosomes (12 pairs telocentric, 1 pair submetacentric) and 26 microchromosomes (*Delia Aiassa*, pers. comm.). It is different from the karyotype of *C. lacertoides* from Uruguay described by Cole et al. (1979), which is $2n = 50$ with 26 macrochromosomes (12 pairs telocentric or essentially so, and one pair of submetacentric) and 24 microchromosomes. The karyotype of the populations of *C. celata* from Sierras de Ventania remains unknown.

Phylogenetic relationships of the new species. In the morphological analysis, meristic characters easily distinguish *C. celata* from *C. lacertoides* sensu stricto and from the other species of the *Contomastix* genus. However, *C. celata* and *C. lacertoides* show greater similarity between them, suggesting that these two lineages are sister species, which is evidenced in the phylogenetic reconstruction (Fig. 3). The tree shows two well supported clades, one including the sequences of specimens from Argentina (now *C. celata*) and another comprising the sequences of individuals from Uruguay (*C. lacertoides* sensu stricto).

Conservation status. In the more recent evaluation of conservation status for the Argentinian species of lizards and amphisbaenids (Abdala et al., 2012) the populations of *C. lacertoides* in Argentina (now *C. celata*) were listed as Vulnerable, based mainly on anthropogenic effects on the areas where this species distributes in the country. Now, having recognised those populations as a new species with a restrictive range, the status of *C. celata* should be carefully analysed in the next re-evaluation.

DISCUSSION

Harvey et al. (2012) transferred the content of the *C. lacertoides* species group as well as *Cnemidophorus vittatus* to a new genus, *Contomastix*. However, they did not identify any unique characters to distinguish *Contomastix* from all other teiid lizards. They did not consider tongue morphology in their phylogenetic reconstruction, although this character defines the *C. lacertoides* species group, according to Ceï (1993:371). We examined the lingual morphology in *C. celata* (Fig. 7) and compared it to the tongues of *C. charrua*, *C. lacertoides* sensu stricto and *C. serrana* (Cabrera & Carreira, unpubl. data), *C. leachei* (fide Ceï & Scrocchi, 1991), and *C. vittata* (fide Harvey et al., 2012). We confirm that at least six of the seven species of the genus *Contomastix* present a

notched proximal margin of the tongue and lack of lingual sheath around its base. As for *C. vacariensis*, there is no published information about its tongue morphology, and specimens for dissection were unavailable to us. Regarding *C. vittata* there is some disagreement among different authors. This species was originally described by Boulenger (1902) as *Cnemidophorus vittatus*, although he did not mention the tongue morphology in his description. Later, Vance (1978) redescribed the holotype and indicated that it shows a lingual sheath between the tongue and the larynx, and therefore he transferred it to the genus *Ameiva*. Harvey et al. (2012) confirmed that *Contomastix vittata* has the same tongue morphology as *C. lacertoides* and *C. leachei*, as originally stated by Ceï & Scrocchi (1991), i.e., lingual sheath absent and notched proximal margin of the tongue instead of bilobate as it is seen in *Ameivula*, *Aurivela* and *Cnemidophorus* (Fig. 7). We verified that the tongues of both *Ameivula* and *Aurivela* have the proximal end bilobate, and scale-like papillae subimbricate. The papillae on the tongue of *C. celata* are juxtaposed anteriorly but progressively imbricate towards posterior. *Ameiva ameiva* (MZUC-C 470, not pictured) markedly differs from these two types by bearing clearly imbricate papillae all along the dorsal surface of its elongate tongue, and by the presence of lingual sheath. Based on this information, we consider the presence of a notched proximal margin of the tongue a synapomorphy of the genus *Contomastix*, which distinguishes it from all the other teiid genera.

In our phylogenetic analysis *Contomastix* appears as monophyletic, in agreement with the results of Tucker et al. (2016). However, we recovered the clade of *C. lacertoides* - *C. celata* as the sister taxa of *C. vacariensis*, with *C. serrana* in a basal position in the genus. Tucker et al. (2016) recovered *C. serrana* as the sister taxon of *C. lacertoides* (although considering the provenance of its specimen this would correspond to *C. celata*) and *C. vacariensis* as the basal species for the genus. New phylogenetic analyses including all the lineages of the genus will help to understand their relationships. Feltrim & Lema (2000) indicated that *C. vacariensis* is morphologically similar to *C. lacertoides*, which is in accordance with our phylogenetic reconstruction. This does not agree with Harvey et al. (2012) findings, who recovered *Contomastix* as paraphyletic, placing *C. lacertoides* outside the clade containing *C. serrana* and *C. vittata*. They mention having analysed two more species of *Contomastix* (*C. leachei* and *C. charrua*), but they did not include them in their phylogenetic analysis. Harvey et al. (2012) indicated that *C. lacertoides* differs considerably from its congeners in scutellation, hemipenis morphology and coloration. This discrepancy could have originated because they grouped as *C. lacertoides* specimens that correspond, according to their provenance, to *C. lacertoides* sensu stricto (Uruguay: Maldonado Department, Sierra de Animas), to *C. lacertoides* sensu lato (Brazil: Rio Grande do Sul State, Osório), and to the new species described here as *C. celata* (Argentina: Córdoba Province, Achiras).

The relationship between *Contomastix* and *Aurivela* was not recovered in previous molecular reconstructions

(Reeder et al., 2002; Giugliano et al., 2013; Goicoechea et al., 2016) in which *Aurivela* appears as the sister taxon of *Aspidoscelis*. This could be due to the fact that only one specimen of *C. lacertoides* was included in those analyses. Tucker et al. (2016) in their study included *C. lacertoides*, *C. serrana* and *C. vacariensis*; *Aurivela* appears basal to a clade including *Contomastix*, *Ameivula* and *Glaucomastix*. Phylogenetic reconstructions grouping cis-Andean South American distribution clades imply a more coherent biogeographic hypothesis than those grouping these clades with a Central and North American-distribution clade, *Aspidoscelis*.

The conservation status of the species of *Contomastix* is important because their distributions are relatively restricted, most being localized endemics and rare. According to the criteria used by the International Union for Conservation of Nature (IUCN, 2018), four of its species are categorised: *C. charrua* (EX = Extinct), *C. vittata* (CR = Critically Endangered), *C. vacariensis* (DD = Data Deficient) and *C. serrana* (LC = Least Concern). Categorisations for *C. lacertoides* and *C. leachei* remain unpublished.

ACKNOWLEDGEMENTS

Work was supported by Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET, Argentina; grant PIP 6312) and by Secretaría de Ciencia y Tecnología, Universidad Nacional de Córdoba, (SeCyT-UNC, Argentina; Project 05/I460). Collecting permits provided by Dirección de Recursos Naturales, Secretaría de Ambiente, Gobierno de la Provincia de Córdoba, and Organismo Provincial para el Desarrollo Sostenible, Buenos Aires. We are grateful to D. Aiassa, C. Cabrera, R. Cardoso Vieira, I. Lombardo, M. I. Medina, R. Torres, L. Verrastro and J. Zanotelli for participating in field works, collect of lizards, laboratory assistance, and/or providing of photographs, specimens and biological data. We also thank J. Faivovich, G. Carrizo and S. Nenda (MACN and MACN exCENAI), J. Williams (MLP.S), N. Pelegrin (LECOH), A. Brigada and B. Espeche (CH-UNSL), and M. Borges Martins (UFRGS) for the loan of specimens, and J. Mariano and two anonymous reviewers for comments that improved the manuscript. Manuel Sosa made all the drawings.

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APPENDIX 1

Specimens examined are referred to by their catalogue number except otherwise indicated. Acronyms: CH-UNSL, Colección Herpetológica de la Universidad Nacional de San Luis, Argentina; LECO, Laboratorio de Ecología y Conservación de la Herpetofauna, Instituto de Diversidad y Ecología Animal (IDEA-UNC), Córdoba, Argentina; MACN and MACN (exCENAI), Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina; MLP.S, Museo de La Plata, La Plata, Argentina; MNHN, Museo Nacional de Historia Natural, Montevideo, Uruguay; MZUC-C, Museo de Zoología, Universidad Nacional de Córdoba, Argentina; PQDN, Proyecto Quebradas del Norte, Facultad de Ciencias, Universidad de la República, Uruguay; SC, Field collection of Santiago Carreira; UFRGS, Laboratório de Herpetologia, Instituto de Biociências, Universidade Federal do Rio Grande do Sul, Brazil; ZVC-R, Colección Zoológica de Vertebrados, Facultad de Ciencias, Universidad de la República, Uruguay.

Ameiva ameiva

ARGENTINA. El Chaco Province: Comandante Fernández Department: Presidencia Roque Sáenz Peña, MZUC-C 470.

Ameivula abalosi

ARGENTINA. Córdoba Province: Tulumba Department: About 10 km W from Lucio V. Mansilla, LECO 00579.

Aurivela longicauda

ARGENTINA. San Juan Province: Caucete Department: Médanos Grandes, MZUC-C 446.

Contomastix celata new sp.

ARGENTINA. Buenos Aires Province: Partido de Coronel Suárez: Villa La Arcadia, MZUC-C 671, 672 (holotype), 673; Partido de Tornquist: Abra de la Ventana, MACN 20862. Sierra de Ventania, MACN 32199, 32883, 32997, MACN (exCENAI) 336, 339, MLP.S 967. Sierra de Ventania, Ernesto Tornquist Provincial Park, MACN 32864, 32867 (paratype), 32868, 32874/76, 32878, MLP.S 1049 (paratype), 1050 (paratype), 1051, 1564/65. Sierra de Ventania, Villa Ventana, MLP.S 1052/54. Córdoba Province: Río Cuarto Department: Achiras, MZUC-C 559/62, 563 (paratype), 564/66, 567 (paratype), 568, 676 (paratype), 677/78, MLP.S 1165, 1166 (paratype).

Contomastix charrua

URUGUAY. Rocha Department: Cabo Polonio, MNHN

03423 (holotype), 03422 and 03424 (paratypes); ZVC-R 1856 and 1865 (paratypes), 2505/06, 2519/20.

Contomastix lacertoides

URUGUAY. Artigas Department: Nacientes del Arroyo Pintado, ZVC-R 4835/36. Lavalleja Department: Asperanzas de Polanco, ZVC-R 5042/43; Environs of Lascano, SC-406; Predio Papazián, near Mariscalá, MNHN 9744, SC-413; Route 8, Km 131 Establecimiento "El Penitente", ZVC-R 5350. Maldonado Department: Cerro de Animas, MLP.S 965; Route 60, ZVC-R 5304; Sierra de Animas, ZVC-R 3891, 4358/59. Montevideo Department: Cerro de Montevideo, ZVC-R 1265/66. Paysandú Department: Route 90, Establecimiento "El Refugio", ZVC-R 4889; Route 26, Km 147, between Arroyo Laureles and Arroyo Perdido, ZVC-R 5361. Rivera Department: Gajo Arroyo Lunarejo, ZVC-R 5119; Puntas del Arroyo Lunarejo, ZVC-R 4518/19. Rocha Department: Castillos, MACN 1126/28; San Miguel National Park, ZVC-R 1810. San José Department: Sierra de Mahoma, ZVC-R 5566. Tacuarembó Department: Road to Valle Edén, ZVC-R 5306; Pozo Hondo, ZVC-R 5139, 5413; Pozo Hondo, Route 26, Km 200, ZVC-R 5233; Valle Edén, ZVC-R 4504. Treinta y Tres Department: Cuenca del Arroyo Avería, 20 km E Valentines, PQDN 370; Quebrada de los Cuervos, ZVC-R 1348, 1351, 1353, 1355, 1382, 4569/70, 4578, 4751; Santa Clara de Olimar, ZVC-R 1263.

Contomastix leachei

ARGENTINA. Salta Province: Orán Department: Río Pescado and Serranía Las Pavas, southwestern end of Baritú National Park, MACN 32299. Rosario de la Frontera Department: Rosario de la Frontera, MLP.S 1064.

Contomastix serrana

ARGENTINA. Córdoba Province: Colón Department: Cabana, MACN 12509; MLP.S 1055. Punilla Department: Road to Pampa de Olaen, MZUC-C 243; Carlos Paz, MZUC-C 572/73; Carlos Paz, Estancia Vieja, MLP.S 1164; Cosquín, MACN 36176; Los Chorrillos, MZUC-C 571, 574, MLP.S 1163; Tanti, MZUC-C 569/70; Valle Hermoso, CH-UNSL 0558. Santa María Department: Alta Gracia, MLP.S 1066, 1305. San Luis Province: Ayacucho Department: Río Nogolí, CH-UNSL 0457.

Contomastix vacariensis

BRAZIL. Rio Grande do Sul State: Bom Jesus, UFRGS 4564, 4780, 4783; Jaquirana, UFRGS 5273; Vacaria, UFRGS 4723/24. Santa Catarina State: Capão Alto, UFRGS 4843.

APPENDIX 2

Locus, primer sequence, source, aligned fragment length (FL), and models of sequence evolution selected for the four loci used in this study.

Locus	Primer sequence	Source	FL	Selected model
16S	F: CGCCTGTTTATCAAAAACAT R: CCGGCTGAACTCAGATCACGTA	Gifford et al. (2004)	548	GTR+I+G
ND4	F: TGACTACCAAAAGCTCATGTAGAAGC R: TACTTTTACTTGGATTGCACCA	Forstner et al. (1995)	889	HKY+G
NTF3	F: ATGTCATCTTGTTTTATGTGATATT R: ACRAGTTTTRTGTYYTCTGAAGTC	Townsend et al. (2008)	653	HKY+I+G
c-mos	F: GCGGTAAGCAGGTGAAGAAA R: TGAGCATCCAAGTCTCCAATC R*: AGRGTGATRWCAAANGARTARATGTC	Saint et al. (1998)	396	HKY+G

* Used only for *Teius teyou*

APPENDIX 3

List of species, identification codes of specimens analysed and GenBank accession numbers for the four loci used in this study.

Species	Specimen voucher	16S	ND4	c-mos	NTF3
<i>Ameiva ameiva</i>		AY359493	AF151206	KC109625	---
<i>Ameiva jacuba</i>	CHUNB 47996	JQ762444	---	KC109626	---
<i>Ameiva parecis</i>	CHUNB 11655	JQ762442	---	KC109632	---
<i>Ameivula abaetensis</i> 1	MZUSP 104240	KF957470	KF957534	---	KF957566
<i>Ameivula abaetensis</i> 2	MZUSP 104250	KF957485	KF957549	---	KF957581
<i>Ameivula ocellifera</i> 1		AF420759	AF420914	AF420862	---
<i>Ameivula ocellifera</i> 2		AY217992	AF151205	AY217890	---
<i>Aspidoscelis deppei</i>		AY046473	KF555555	---	---
<i>Aspidoscelis gularis septemvittata</i>		AY046485	AF026179	---	---
<i>Aspidoscelis inornata</i>		AY046478	AF026174	---	---
<i>Aspidoscelis tigris</i>		AY046494	AF026172	AF039481	EU390903
<i>Aspidoscelis velox</i>		KC621326	KC621494	EU116675	EU108017
<i>Aurivela longicauda</i> 1	CH-UNSL 0561	KY020123	MF039743	MF039730	KY020108
<i>Aurivela longicauda</i> 2		AY046481	---	KC109630	---
<i>Cnemidophorus gramivagus</i>		AY046474	---	KC109627	---
<i>Cnemidophorus lemniscatus</i>		AY046480	AF026171	KC109629	---
<i>Cnemidophorus vanzoi</i> 1	Co140	DQ168986	DQ168990	---	---
<i>Cnemidophorus vanzoi</i> 2	Co141	DQ168987	DQ168991	---	---
<i>Contomastix celata</i> 1	MZUC-C 671	KY020117	MF039738	MF039724	KY020102
<i>Contomastix celata</i> 2	MZUC-C 672	KY020118	MF039739	MF039725	KY020103
<i>Contomastix celata</i> 3	MZUC-C 673	KY020119	---	MF039726	KY020104
<i>Contomastix celata</i> 4	MZUC-C 676	KY020120	MF039740	MF039727	KY020105
<i>Contomastix celata</i> 5	MZUC-C 677	KY020121	MF039741	MF039728	KY020106
<i>Contomastix celata</i> 6	MZUC-C 678	KY020122	MF039742	MF039729	KY020107
<i>Contomastix lacertoides</i> 1	AMNH R-115938	AY046479	---	---	---
<i>Contomastix lacertoides</i> 2	PQDN 370	KY020113	MF039734	MF039720	KY020098
<i>Contomastix lacertoides</i> 3	SC 406	KY020114	MF039735	MF039721	KY020099
<i>Contomastix lacertoides</i> 4	SC 413	KY020115	MF039736	MF039722	KY020100
<i>Contomastix lacertoides</i> 5	MNHN 9744	KY020116	MF039737	MF039723	KY020101
<i>Contomastix serrana</i> 1	CH-UNSL 0457	KY020111	MF039732	MF039718	KY020096
<i>Contomastix serrana</i> 2	CH-UNSL 0558	KY020112	MF039733	MF039719	KY020097
<i>Contomastix vacariensis</i> 1	UFRGST 124	KY933592	---	---	---
<i>Contomastix vacariensis</i> 2	UFRGST 130	KY933593	---	---	---
<i>Contomastix vacariensis</i> 3	UFRGST 132	KY933594	---	---	---
<i>Contomastix vacariensis</i> 4	UFRGST 134	KY933595	---	---	---
<i>Contomastix vacariensis</i> 5	UFRGST 144	KY933596	---	---	---
<i>Contomastix vacariensis</i> 6	UFRGST 156	KY933597	---	---	---
<i>Contomastix vacariensis</i> 7	UFRGST 158	KY933598	---	---	---
<i>Contomastix vacariensis</i> 8	UFRGST 191	KY933599	---	---	---
<i>Holcosus undulatus</i>		HM012699	---	JN090144	---
<i>Kentropyx calcarata</i>		AF420760	AF420913	AF420864	---
<i>Kentropyx pelviceps</i>		AY046501	---	KC109633	---
<i>Kentropyx viridistriga</i>		EU345182	AF151207	---	---
<i>Teius teyou</i>	CH-UNSL 0478	KY020110	MF039731	MF039717	KY020095
<i>Salvator merianae</i>	M303	KY020109	KF034085	MF039716	KY020094