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Cladistic Analysis of Iguania and a Fossil Lizard from the Late Pliocene of Northwestern Argentina

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ABSTRACT.—A fragmentary fossil lizard from Uquía Formation (Late Pliocene), Jujuy Province, Argentina, is described. The material consists of disarticulated cranial bones from the snout and jaw that were part of a microvertebrate fossil assemblage generated by accumulation of predatory birds pellets. The phylogenetic analysis of 396 morphological characters indicates a sister-group relationship between the new taxon and a clade formed by the families Liolaemidae, Leiocephalidae, and Tropiduridae. Its uncertain position and substantial morphological differences justify its placement in a new genus. We present a detailed osteological description of the material, and compare the morphological features with other Iguanoidea. In the context of this new analysis of Iguania, we included *Pristiguana brasiliensis*, the oldest known iguanian from South America. The results of this analysis support the monophyletic status of Iguanoidea and other groups within Iguania that are named and diagnosed.

RESUMEN.—Describimos restos fragmentarios de un lagarto fósil procedente de la Formación Uquía (Plioceno Tardío) en la Provincia de Jujuy, Argentina. El material consiste de huesos craneales desarticulados del hocico y la mandíbula que fueron recuperados de un ensamble fósil de microvertebrados, el cual es una acumulación de egagrópilas generado por la actividad trófica de aves depredadoras. El análisis filogenético de 396 caracteres morfológicos indica que el nuevo taxón es el grupo hermano de un clado formado por las familias Liolaemidae, Leiocephalidae y Tropiduridae. La posición dudosa de este fósil y las substanciales diferencias morfológicas justifican clasificarlo como un género nuevo. Incluimos una descripción morfológica detallada del material fósil y comparamos su anatomía con otros miembros de Iguanoidea. En el contexto de este nuevo análisis de Iguania, incluimos a *Pristiguana brasiliensis*, el cual hasta hoy es el iguanio más viejo que se conoce de América del Sur. Los resultados de este análisis filogenético apoyan el estatus monofilético de Iguanoidea y de otros grupos dentro de Iguania, los cuales se definen y diagnostican.

The suborder Iguania is a diverse group of lizards with nearly 1,300 named extant species (Vitt and Caldwell, 2008; Uetz, 2010), and traditionally it includes the families Agamidae, Chamaleontidae, and Iguanidae (McDowell and Bogert, 1954; Romer, 1956). The name Iguanidae in taxonomy is used both in a broad and narrow sense; for this reason a review of Iguania's taxonomic history is warranted. Cuvier (1817) recognized *Iguaniens* divided into *Stellions* and *Agames*, with the latter including both most agamids and iguanids of later authors. Cuvier (1829) recognized *Iguaniens* divided into *Agamiens* and *Iguaniens propres*. Although this classification scheme incorporated other extinct groups, such as metriorhynchids, pterodactyls, dinosaurs, and mosasaurs, these two main components represent current members of Iguania. Duméril and Bibron (1854) removed from the iguanians or *Eunotes* those extinct groups and kept two sections at the subfamily level: one of them with the teeth fixed on top of the superior edge of the jaws or *Acrodontes* (*Agamiens*); and the other with the teeth attached on the inner edge of a maxillary trough or *Pleurodontes* (*Iguaniens propres*), although these names can be traced back earlier for several different taxa (e.g., Wagler, 1830). Subsequently, these two subfamilies were elevated to suborder level, and these names were Latinized from French into Acrodonta and Pleurodonta (Cope, 1864). Cope used these names for entirely different taxa than the one used by Duméril and Bibron; the composition of these groups changed: chameleons and *Sphenodon* were added to Acrodonta; and Pleurodonta included Iguania (Anolidae and Iguanidae), Diploglossa (Anguidae, Gerrhonotidae, and Helodermatidae), Thecaglossa (Varanidae), Leptoglossa (Teiidae, Lacertidae, Chalcididae, and Eublepharidae), and Typhlopidae (Anelytropidae,

Acontiidae, and Aniellidae). Boulenger (1884, 1885a,b, 1887) placed the extant members of Iguania in two groups: chameleons in the suborder Rhytroglossa; and Agamidae and Iguanidae together with the remaining lacertilian groups in Lacertilia Vera. Some variations to this classification include the formation of Ascalabota with three sections: Gekkota, Iguania, and Rhytroglossa (Camp, 1923; Romer, 1933). Subsequently, the Infraorder Iguania was established as the three families noted above (McDowell and Bogert, 1954; Romer, 1956), and this classification scheme has been continued (e.g., Gauthier, 1984; Estes et al., 1988; Vorobyeva and Chugunova, 1991; Metzger and Herrel, 2005).

It has been problematic to find adequate synapomorphic morphological characters that support the monophyly (holophyly sensu Ashlock, 1971) of Iguanidae s.l. (Smith, 2009); because of this, it has been considered a metataxon (Gauthier, 1984; Estes et al., 1988). Etheridge and de Queiroz (1988) apply Iguanidae as a morphotypic concept to describe the historical basis of the taxon and identified eight major clades within this group: morunasaur, anolids, tropidurines, crotaphytines, sceloporines, iguanines, basiliscines, and oplurines. This suprageneric arrangement corroborated to some extent the so-called Old Tree that R. Etheridge drew about 1962 for E. Williams (Etheridge and de Queiroz, 1988). Frost and Etheridge (1989), using morphological data, were not able to corroborate the monophyletic status of "Iguanidae" and proposed, rather than maintain, the unsupported groups, Agamidae and "Iguanidae," to recognize as families, sedis mutabilis, the largest historical groups that were found in their strict consensus tree of Iguania (Chamaeleonidae including Agaminae, Chamaeleoninae, Leiolepidinae; Corytophanidae, Crotaphytidae, Hoplocercidae, Iguanidae, Opluridae, Phrynosomatidae, Polychrotidae, and Tropiduridae that included Leiocephalinae, Liolaeminae, and Tropidurinae). With this action, the groupings of Etheridge and de Queiroz (1988) were formalized into families. Based on results from molecular data, Macey et al.

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(1997) recommended that these groups should be kept as subfamilies within Iguanidae s.l.; these results were corroborated in subsequent molecular analyses (Saint et al., 1998; Schulte et al., 1998; Harris et al., 2001; Schulte and Cartwright, 2009). Frost et al. (2001a) reformulated Iguania with the resurrection of the subordinated taxa Acrodonta and Pleurodonta and split the former family Tropiduridae into three families: Leiocephalidae, Liolaemidae, and Tropiduridae. Schulte et al. (2003) concurred that Iguanidae encompasses the eight groupings of Etheridge and de Queiroz (1988) and that this group corresponded with Pleurodonta of Frost et al. (2001a) but suggested leaving the families of Frost and Etheridge (1989) as subfamilies. Using morphological characters, Smith (2009) recovered a monophyletic Iguanidae s.l., which was composed of two major clades: Clade A—Polychrotinae, Corytophaninae, Iguaninae, Hoplocercinae, and Crotaphytinae; Clade B—Oplurinae, Tropidurinae, and Phrynosomatinae.

The resurrection of Pleurodonta (Frost et al., 2001a) and its application to Iguanidae s.l. is not consistent with the original group proposed by Cope (1864). Henceforth, we will use the name Iguanoidea (Stannius, 1856; does not = Pleurodonta of Cope, 1864); this name was applied to a tribe within Pachyglossa and is equivalent to the traditional Iguanidae. This name needs to be distinguished from the similar name Iguanoides (Oppel, 1811) ranked as a family and used for a group more closely approximating the modern Iguania. Similarly, Hay (1930) used the name Iguanoidae (ranked as a superfamily) for a group equivalent to Iguania of Camp (1923). On the other hand, Chamaeleonoidea (Vidal and Hedges, 2009), which has been used for the clade formed by Agamidae and Chamaeleontidae is redundant with Acrodonta. The latter term should be used, despite the fact that the acrodonty is not unique for this group. On the contrary, this is a main variant of pleurodonty in lizards (Estes et al., 1988; Alifanov, 1996) and has been developed independently in other lepidosaurs (e.g., acrodont sphenodonts and amphisbaenians; Gauthier et al., 1988; Fraser and Benton, 1989; Montero and Gans, 2008; Jones et al., 2009) from pleurodont ancestors (Augé, 1997). Iguanoidea encompasses all the 11 extant families recognized by Frost et al. (2001a; viz. Corytophanidae, Crotaphytidae, Hoplocercidae, Iguanidae, Leiocephalidae, Leiosauridae, Liolaemidae, Opluridae, Phrynosomatidae, Polychrotidae, and Tropiduridae; although the monophyly of Polychrotidae has been questioned, in this paper we use Polychrotidae as the clade formed by *Polychrus*, *Anolis*, and the leiosaur polychrotids). This classification scheme seems to well represent the established groupings within the clade in question, and many of these clades have been corroborated with molecular and morphological data (de Queiroz, 1987; McGuire, 1996; Reeder and Wiens, 1996; Harvey and Gutberlet, 2000; Frost et al., 2001a,b; Schulte et al., 2003; Vieira et al., 2005; Conrad et al., 2007; Conrad and Norell, 2007; Conrad, 2008; Torres-Carvajal and de Queiroz, 2009), although some of them are not strongly supported (Schulte and Cartwright, 2009). Today there is still not agreement on the higher-level taxonomy of these groupings, and both familial (e.g., Conrad, 2008; Pincheira-Donoso et al., 2008) and subfamilial (e.g., Hedges and Vidal, 2009; Schulte and Cartwright, 2009; Smith, 2009; Vidal and Hedges, 2009) ranks are being applied widely to the same taxa.

The iguanian fossil record in South America is fragmentary (Báez and Gasparini, 1979; Albino, 2008); the oldest record is *Pristiguana brasiliensis* from the Late Cretaceous of Brazil (Estes and Price, 1973; Estes, 1983). A fossil from the early Late Cretaceous (Cenomanian-Turonian) found in Rio Negro, Argentina, was attributed tentatively to Iguanidae s.l. (Iguanoidea) based on the hourglass shape of the frontal bone and the dermal sculpturing composed of tubercles (Apesteguía et al., 2005), but this character combination is not exclusive to

this group. On the contrary, it is widespread in many fossil and extant squamates (Conrad, 2008). Other South American fossil iguanoids include several species of *Erichosaurus* from the Miocene of Argentina (viz. *Erichosaurus diminutus*, *Erichosaurus bombimaxilla*, *Erichosaurus debilis*, Ameghino, 1899; nomen dubium sensu Estes, 1983; Albino, 1996), *Pristidactylus* sp. from the Miocene of Argentina (Albino, 2008), *Leiosaurus bellii* from the Pleistocene of Argentina (Duméril and Bibron, 1837; van Devender, 1977; *Leiosaurus marellii* (Rusconi, 1937) from the Middle Pleistocene of Argentina was reassigned to *Amphisbaena marellii* by Torres and Montero, 1998a, b), *Iguana* sp. from the Late Pleistocene of Ecuador (Hoffsteter, 1970; Báez and Gasparini, 1977), *Liolaemus* sp. from the Miocene and the Late Quaternary of Argentina (Albino, 1998, 2005, 2008), and an array of undetermined iguanians from the Late Paleocene of Brazil, Early Paleocene of Bolivia, Miocene of Argentina, and Middle Miocene of Colombia (Estes, 1961, 1983; Gasparini et al., 1986; Albino, 2008 and references therein).

Currently only three families of Iguanoidea occur in the southern part of South America: Polychrotidae, Liolaemidae, and Tropiduridae (Peters et al., 1986; Avila-Pires, 1995). Polychrotidae and Liolaemidae are large units within Iguania and include the species-rich genera *Anolis* and *Liolaemus* with more than 300 and 200 species, respectively (Frost et al., 2001a; Poe, 2004; Losos, 2009; Nori et al., 2010; Üetz, 2010). In South America, these lizards exploit a diversity of habitats and diets, and some of them occur in localities above 4,000 m and tepid latitudes in Tierra del Fuego (Ceí, 1986, 1993; Díaz Gómez and Lobo, 2006; Nori et al., 2010).

The discovery of a fossil iguanoid in Argentina offers new information about the morphological diversity of this group. The fossil material consists of the tooth-bearing marginal bones. These bones exhibit the common tricuspid tooth crown morphology of iguanians in the maxilla and the dentary (Edmund, 1969; Etheridge and de Queiroz, 1988) and the pleurodont implantation. It is not possible to assign the new fossil material described here to any of the extant families, and it is not a nested member of any currently named genera. This and the unique combination of character states present in this fossil lead us to allocate it to a new genus and species.

MATERIALS AND METHODS

Fossil material was collected by two of the authors (PO and DGL) in San Roque, near Humahuaca town, Jujuy province, northwestern Argentina (Fig. 1). The material was deposited in the Colección de Paleontología de Vertebrados Lillo, Tucumán, Argentina (PVL).

The remains come from a midden of pellets generated by the trophic activities of predatory birds. This assemblage includes several micromammal species (marsupials and rodents), as well as remains of small birds, lizards, and frogs. The material was obtained through dry and wet sieving with a mesh of 0.1 mm following the methodology of McKenna et al. (1994).

Institutional Abbreviations.—Abbreviations used follow Leviton et al. (1985) and the following unlisted collections: DGM, Divisão de Geologia e Mineralogia (Rio de Janeiro, Brazil); FBC, Collection of Felix B. Cruz (Bariloche, Argentina); GS, Collection of Gustavo Srocchi (Tucumán, Argentina); MAN, Collection of Mark Norell, American Museum of Natural History; MCN, Museo de Ciencias Naturales, Universidad Nacional de Salta (Salta, Argentina); MZFC, Museo de Zoología Alfonso L. Herrera (Ciudad de México, Mexico); PVL, Colección de Paleontología de Vertebrados Lillo (Tucumán, Argentina); REE, Collection of Richard Etheridge, San Diego State University (San Diego, CA); RT, Collection of Richard Thomas, University of Puerto Rico (San Juan, Puerto Rico); UCA, University College London, Anatomy, Susan Evans collection (London).

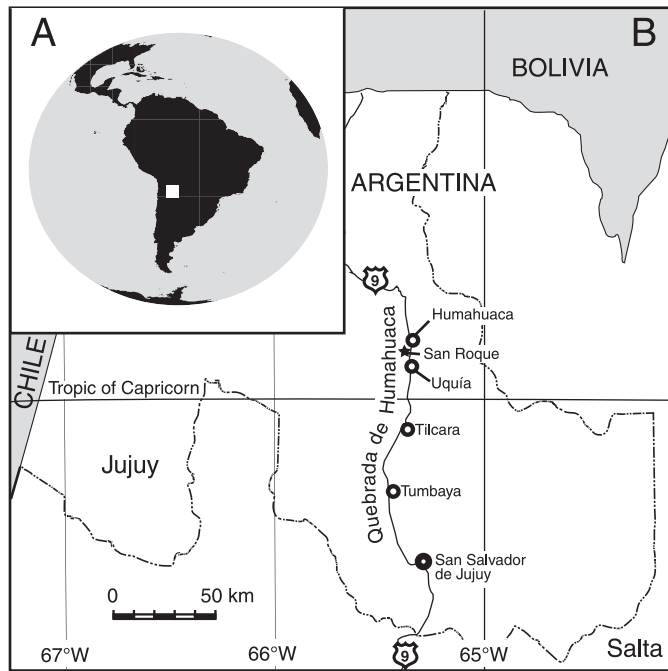


FIG. 1. (A) Location of Jujuy Province in South America, white square on map. (B) Black star indicates the position of San Roque (*Uquiasaurus* type locality) in the Quebrada de Humahuaca.

Phylogenetic Data Set.—We used a total of 396 characters (complete data set available from the authors), 1–364 (Conrad, 2008); 365 (character 19 in Etheridge and de Queiroz, 1988); 366–390, all the nonredundant characters from Frost and Etheridge (1989) not included in Conrad (i.e., 3–4, 12, 15, 19, 23, 31, 38, 42–45, 50–51, 53, 55–57, 59–60, 62, 64–67), and six new characters: 391. Premaxilla, number of premaxillary tooth loci, the tooth count indicates the character state, this is possible because the computer program TNT allows morphological characters with up to 32 states when using alphanumerical codes (Goloboff et al., 2008a). 392. Premaxilla, ascending nasal process: (0) short, approximately twice the length of the premaxillary teeth; (1) long, more than twice the length of the premaxillary teeth. 393. Maxilla, number of maxillary tooth loci: (0) between 10 and 20; (1) between 21 and 30. These intervals were intended to cover variation among iguanoids (Table 1). We use such large intervals because the maxillary tooth count is variable, even within congeneric species. For instance, *Iguana delicatissima* and *Iguana iguana* present about 20 and 27 teeth loci, respectively (see figures in Conrad and Norell, 2010). Some Squamata present one maxillary tooth (e.g., viperids), while others present more than 30 (e.g., *Uroplatus* gecko). 394. Maxilla, a wide posterior offset is placed labial to the tooth row: (0) absent; (1) present. 395. Maxilla, palatine flange process with well-developed triangular projection: (0) absent; (1) present. This character differs from character 32 in Conrad (2008) in that we explicitly refer to the triangular shape, which is independent of the presence of this flange. 396. Dentary, number of tooth loci in the dentary: (0) between 10 and 20; (1) between 21 and 30. The argument expressed in character 393 applies here, for instance, *I. delicatissima* and *I. iguana* present about 21–23 and 28 teeth loci, respectively (see figures in Conrad and Norell, 2010).

For the Uquía fossil, we were able to score 54 characters (13%), and for *P. brasiliensis* 35 (8.8%). The latter was scored using published descriptions (Estes and Price, 1973; Estes, 1983). For comparative purposes, 85 species from 20 collections were reviewed directly or indirectly from published descriptions and high-resolution X-ray computed tomography

available on “The Digital Morphology Library” (<http://digimorph.org/>) (Table 1, Appendix 1). We excluded most of the fossils outside Iguanomorpha because they are not relevant for the relationships within the ingroup. We kept Kuehneosauridae, *Ardeosaurus brevipes*, *Bavarisaurus macrodactylus*, *Eichstaettisaurus schroederi*, *Scandensia ciervensis*, AMNH gekkonomorph, *Parviraptor estesi*, *Parviraptor* cf. *estesi*, *Gobekko cretaceus*, *Baiguis parvus*, *Globaura venusta*, *Myrmecodaptria microphagosa*, *Eoxanta lacertifrons*, *Tepexisaurus tepexii*, and *Parmeosaurus scutatus*. The tree was rooted with the lepidosauriomorph *Marmoretta oxoniensis* from the Middle Jurassic of Scotland (Evans, 1991; Waldman and Evans, 1994).

Character Weighting.—The analysis was performed in TNT (Goloboff et al., 2008a) under implied weighting (Goloboff, 1993). Implied weights provide a better implementation of parsimony (Goloboff, 1993, 1995), and it has been shown that it produces more stable results to character and taxon addition (Goloboff, 1997; Ramírez, 2003; Goloboff et al., 2008b). A *k*-value of 20 was used for implied weights because it guarantees that highly homoplastic characters do not exceed 15 times the weight of the nonhomoplastic character (Goloboff et al., 2008b). To check the stability of results using several weighting functions (Ramírez, 2003; Miranda, 2009), we performed an exploration of integer *k*-values between 10 and 30. For each *k*-value, we performed a search for the most parsimonious trees by means of 100 independent replications of a Wagner tree and TBR, followed by 100 rounds of ratchet (Nixon, 1999) and drift (Goloboff, 1999). The consensus of the resulting trees was compared with the preferred results under *k* = 20, counting the number of common nodes and the SPR distance among trees.

Search for the Most Parsimonious Trees.—The command *xmult* was executed until 50 independent hits of the most parsimonious trees were found. Each run of *xmult* consists of five independent Wagner trees with TBR, followed by more aggressive searches using sectorial searches, 100 ratchet and tree drift rounds, and finally subjecting the obtained tree to tree fusing (Goloboff, 1999).

Measures of Tree Support.—Symmetrical resampling was calculated as support measure of clades (Goloboff et al., 2003); this provides a better idea of clade support (when weighting is used) than other resampling alternatives such as jackknife or bootstrap. One thousand replicates were performed, each one using 20 Wagner trees collapsed with TBR (Goloboff and Farris, 2001), with 20 rounds of ratchet and keeping all 20 trees. The support of the groups was calculated with the raw frequency of the group and scaled with the frequency of the most frequent contradictory group (GC, Goloboff et al., 2003); frequencies were plotted on the consensus of most parsimonious trees. Bremer support was estimated using 20,000 trees up to 0.04 extra costs.

SYSTEMATIC PALEONTOLOGY

Squamata Oppel, 1811

Iguanomorpha Sukhanov, 1961

Iguania, Cope, 1864

Iguanoidea, Stannius, 1856 incertae sedis

† *Uquiasaurus* new genus

Type species *Uquiasaurus heptanodonta*

Figures 2–4

Included species †*Uquiasaurus heptanodonta* new species

Etymology.—Lizard from Uquía after the bearing geologic formation, and *heptanodonta* meaning seven teeth, in reference to the number of premaxillary teeth.

Holotype.—Premaxilla (PVL 6388, Figs. 2A–B, 4).

Paratypes.—Maxilla (PVL 6395), three right dentaries (PVL 6387, PVL 6391, PVL 6394), three left dentaries (PVL 6389, PVL 6392, PVL 6393) (Figs. 2C–E, 3A–G).

TABLE 1. Distribution of additional morphological characters within Iguanoidea. a = K. de Queiroz (unpubl. data); b = The Deep Sealy Project, Digimorph CT scan; c = Private collection of C. Bell, d = F. Lobo (unpubl. data).

Family	Species (N)	Premaxillary teeth range	Maxillary teeth range	Dentary teeth range	Wide maxillary posterior offset	Palatine flange well developed	Nasal overlap the premaxilla	Ascending nasal process	Source
Corytophanidae	<i>Basiliscus vittatus</i> (7)	7-10	—	—	—	—	—	—	a
	<i>B. plumifrons</i> (6)	7-10	—	—	—	—	—	—	a
	<i>B. basiliscus</i> (7)	9-10	23	22-28	no	no	no	long	a; b; Frost and Etheridge, 1989; FMNH 165622, KU 93452
Crotaphytidae	<i>Corytophanes cristatus</i> (5)	7-9	24	—	no	yes	no	long	a; b; FMNH 69227
	<i>C. hernandezi</i> (1)	9	—	—	—	—	—	—	a
	<i>Laemactis serratus</i> (2)	7-8	—	—	—	—	—	—	a
	<i>Crotaphytus antiquus</i> (4)	5-6	15-19	21-24	—	—	—	—	McGuire, 1996
	<i>C. binctores</i> (24)	5-7	15-21	18-28	—	—	—	—	McGuire, 1996
	<i>C. collaris</i> (50)	5-8	14-22	16-26	no	yes	yes	long	b; McGuire, 1996; FMNH 48667
	<i>C. dickersonae</i> (16)	6-9	16-25	19-31	no	yes	—	long	McGuire, 1996; REE 2777
	<i>C. grismeri</i> (5)	6-8	16-21	19-26	—	—	—	long	McGuire, 1996; MZFC 6651
	<i>C. insularis</i> (5)	6	15-20	22-28	—	—	—	—	McGuire, 1996
	<i>C. nebris</i> (17)	5-7	15-23	19-30	—	—	—	—	McGuire, 1996
	<i>C. reticulatus</i> (25)	5-7	14-21	17-25	—	—	—	—	McGuire, 1996; REE 2912
	<i>C. vestigium</i> (28)	6-7	15-22	19-28	—	yes	—	—	McGuire, 1996; REE 2826
	<i>Gambelia copei</i> (9)	7	19-23	23-29	—	—	—	—	McGuire, 1996; REE 2912
	<i>G. silus</i> (31)	5-7	14-20	19-25	—	—	—	long	McGuire, 1996; CAS 22713
	<i>G. wislizenii</i> (53)	6-8	15-24	18-31	yes	yes	no	long	a; b; McGuire, 1996; REE 2918, YPM 14380
Hoplocercidae	<i>Enyaliodes laticeps</i> (2)	7-12	—	—	—	—	—	—	a
	<i>E. oslaughnessyi</i> (1)	7-8	—	—	—	—	—	—	a
	<i>E. praestibilis</i> (1)	10	—	—	—	—	—	—	a
Iguanidae	<i>Morunasaurus amularis</i> (2)	9-12	19-20	25	yes	no	no	long	a; Estes et al., 1988; REE 1956
	<i>Hoplocercus spinosus</i> (4)	6	—	18	—	—	—	—	a; Etheridge and de Queiroz, 1988; REE 359
	<i>Amblyrhynchus cristatus</i> (2)	7	—	18	—	—	—	short	de Queiroz, 1987; MVZ 67721, REE 1396
	<i>Brachylophus fasciatus</i> (1)	6	21	19	no	no	no	long	b; FMNH 210158
	<i>Brachylophus vitiensis</i> (1)	9	20	22	no	no	no	long	de Queiroz, 1987; MCZ 160254
Leiocephalidae	<i>Conolophus</i> (2)	7	—	—	—	—	—	long	de Queiroz, 1987; MVZ 77314, REE 439
	<i>Ctenosaura pectinata</i> (2)	11	22-25	32	no	no	no	long	b; c; Oelrich, 1956
	<i>Cyclura cornuta</i>	9	—	—	—	—	—	long	de Queiroz, 1987; REE 383
	<i>Iguana delicatissima</i> (2)	7-8	20	21-23	no	no	no	long	de Queiroz, 1987; Conrad and Norell, 2010; MCZ 16157, MCZ 60823
	<i>I. iguana</i> (3)	7	27	28	no	no	no	long	de Queiroz, 1987; Evans, 2003; Conrad and Norell, 2010; AMNH R 74736, REE 453
Leiosauridae	<i>I. sp.</i> (1)	7	24-26	21	no	no	no	long	Evans, 2009; UCA uncatalogued
	<i>Dipsosaurus dorsalis</i> (1)	6	18	22-23	yes	no	yes	long	b; de Queiroz, 1987; YPM 14376
	<i>Sauromalus obesus</i>	4	—	23	—	—	—	long	de Queiroz, 1987; REE 467
	<i>Leiocephalus carinatus</i>	—	—	25	—	—	—	—	Frost and Etheridge, 1989; Conrad and Norell, 2007; UMMZ 149104
	<i>Leiosaurus paronae</i> (1)	4	19	18	no	—	yes	long	MACN 4386
Opluridae	<i>Pristidactylus torquatus</i> (2)	7	16	18	yes	no	no	long	b; FMNH 206964
	<i>Chalarodon madagascariensis</i> (3)	6	21	26	yes	yes	yes	long	a; Blanc, 1965
	<i>Oplurus cyclurus</i> (3)	6	16	18	yes	yes	yes	long	a; b; YPM 12861
	<i>O. cuvieri</i> (3)	5-6	—	—	—	—	—	—	a
	<i>O. quadrimaculatus</i> (2)	6	—	—	—	—	—	—	a

TABLE 1. Continued.

Family	Species (N)	Prenaxillary teeth range	Maxillary teeth range	Dentary teeth range	Wide maxillary posterior offset	Palatine flange well developed	Nasal overlap the premaxilla	Ascending nasal process	Source
Phrynosomatidae	<i>Phrynosoma hernandesi</i> (3)	7	20	21	no	yes	no	long	TNHC 11839
	<i>Uta stansburiana</i> (1)	7	20	26	yes	yes	no	long	b; FMNH 213914
	<i>Anolis carolinensis</i> (1)	9	21	25	no	no	no	long	b; FMNH 242298
	<i>Diplolaemus bibroni</i> (3)	6	12-4	17	no	yes	yes	long	Conrad et al., 2007; MACN 35850, REE 2506
Tropiduridae	<i>Polychrus marmoratus</i> (1)	9	17	24	no	yes	no	long	b; FMNH 42501
	<i>P. guttorosus</i> (1)	9	17	—	no	no	—	—	Conrad et al., 2007; AMNH R 32675
	<i>Stenocercus guentheri</i> (1)	6	18	20-21	yes	yes	no	short	Torres-Carvajal, 2003; KU 147412
	<i>S. apurimacensis</i> (1)	—	—	23	—	—	—	—	Frost, 1992; KU 134284
	<i>Tropidurus bogerti</i> (1)	—	—	20	—	—	—	—	Frost, 1992; USNM 300598
	<i>T. melanopleurus</i> (1)	6	—	22	—	—	no	long	Frost, 1992; KU 136367
	<i>T. plica</i> (1)	5	21	19-22	yes	yes	no	long	b; Frost, 1992; FMNH 81451, MAN 76
	<i>T. umbra</i> (1)	—	19	—	—	—	—	—	Frost, 1992; KU 146659
Liolaemidae	<i>T. stolzmanni</i> (1)	—	—	21	—	—	—	long	Frost, 1992; KU 134747
	<i>Uranoscodon superciliosus</i>	—	—	22	—	—	—	—	Frost, 1992; REE 16600
	<i>Ctenoblepharys adpersa</i> (5)	6	17-20	20	yes	yes	yes	short	Etheridge, 1995; Lobo and Quinteros, 2005; LACM 49147
	<i>Liolaemus archefornis</i> (1)	6	18	23	yes	yes	yes	short	FML 21346
	<i>L. bellii</i> (1)	6	17	19	yes	yes	yes	short	b; MVZ 125659
Phrynosomatidae	<i>L. darwini</i> (1)	6	17	22	yes	yes	yes	short	FML 01995
	<i>L. boulengeri</i> (1)	6	16	20	yes	yes	yes	short	FML 00291
	<i>L. cei</i> (2)	—	16-17	—	yes	yes	yes	short	d; MCN 908, MCN 909
	<i>L. dorbignyi</i> (1)	6	16	25	yes	yes	yes	short	FML 1855-3
	<i>L. fitzingeri</i> (1)	6	15	21	yes	yes	yes	short	FML 17147
	<i>L. huacatuasicus</i> (1)	6	17	22	yes	yes	yes	short	FML 22320
	<i>L. kriegi</i> (1)	6	16	23	yes	yes	yes	short	FML 17762
	<i>L. kollegh</i> (4)	6	15-16	22	yes	yes	yes	short	FML 20391, FML 20392, FML 20393
	<i>L. laurenti</i> (4)	—	17-8	—	yes	yes	yes	short	d; MCN 318, MCN 319, MCN 321, MCN 326
	<i>L. lincomaculatus</i> (1)	6	11	16	yes	yes	yes	short	FML 02129-3
	<i>L. multicolor</i> (1)	6	15	22	yes	yes	yes	short	FML 3347-4
	<i>L. orientalis</i> (1)	6	15	22	yes	yes	yes	short	FML 00928-1
	<i>L. ornatus</i> (1)	6	16	22	yes	yes	yes	short	FML 63489-2
	<i>L. pictus</i> (1)	6	17	21	yes	yes	yes	short	FML 01781
	<i>L. petrophilus</i> (1)	6	18	23	yes	yes	yes	short	FML 13081
	<i>L. ramirezae</i> (4)	6	15-18	20-23	yes	yes	yes	short	FML 03333/1-4
	<i>L. wiegmanni</i> (1)	6	18	20	yes	yes	yes	short	FML 01321
	<i>Phymaturus spectabilis</i> (2)	6	15-16	—	yes	yes	yes	short	GS 3173, GS 3176
	<i>P. excelsus</i> (7)	5-6	14-18	—	yes	yes	—	short	Lobo and Quinteros, 2005; MCN 1582, FML 22058, FML 22059, FML 22060, FML 22061, FML 22062, FML 22063
	<i>P. mallimacci</i> (4)	—	16-17	—	yes	yes	—	short	Lobo and Quinteros, 2005; MCN 920, REE 2002, REE 2035
	<i>P. cf. palluma</i> (8)	—	15-18	—	yes	yes	—	short	Lobo and Quinteros, 2005; REE 2036, REE 2037, REE 2312, REE 2313, REE 2315; MVZ 9290, MVZ 292904, MVZ 92908
	<i>P. payunae</i> (4)	—	15-17	—	yes	yes	—	short	Lobo and Quinteros, 2005; REE 2330, REE 2331. REE 2332, REE 2339, REE 2360
	<i>P. punae</i> (2)	5	15-17	—	—	—	—	—	FBC 392, FBC 394

TABLE 1. Continued.

Family	Species (N)	Premaxillary teeth range	Maxillary teeth range	Dentary teeth range	Wide maxillary posterior offset	Palatine flange well developed	Nasal overlap the premaxilla	Ascending nasal process	Source
	<i>P. roigorum</i> (5)	—	16–17	—	yes	yes	—	short	d; REE 2323, REE 2324, REE 2325, REE 2327
	<i>P. somuncurensis</i> (5)	—	16–18	—	yes	yes	—	short	Lobo and Quinteros, 2005
	<i>P. spurcus</i> (3)	6	15–17	20–23	yes	yes	—	short	FML 21493, FML 21494, FML 21495
	<i>P. tenebrosus</i> (6)	6	14–18	22–23	yes	yes	—	short	FML 22073, FML 22074, FML 22075, FML 22077, FML 22078
	<i>P. vociferator</i> (4)	—	15–16	—	yes	yes	—	short	Lobo and Quinteros, 2005
	<i>P. zapalensis</i> (2)	—	16	—	yes	yes	—	short	Lobo and Quinteros, 2005
Incertae Sedis	† <i>Uquiasaurus heptanodonta</i>	7	17–18	20–21	yes	yes	yes	short	PVL 6387, PVL 6388, PVL 6389, PVL 6391, PVL 6392, PVL 6393, PVL 6394, PVL 6395
	† <i>Pristiguana brasiliensis</i>	—	—	~21–22	—	—	—	—	Estes and Price, 1973; DGM 552

Type Locality and Stratigraphy.—San Roque (23°14'32.9"S, 65°21'55.5"W; 2,940 m elevation), at 4.4 km south-southwest of Humahuaca town, Humahuaca Department, Jujuy Province, Argentina (Fig. 1). Late Pliocene, middle unit of Uquía Formation composed of reddish clays or muds interbedded with reddish fine sand. Known only from the type locality and stratigraphic provenance.

Diagnosis.—A small lizard with seven premaxillary, 17–18 maxillary, and between 18 and 21 heterodont teeth. Premaxilla overlapped laterally by the nasal bones. The maxilla presents a wide offset on the labial side of the posterior teeth.

Geology and Material.—The Uquía Formation crops out in the Quebrada de Humahuaca, Jujuy province, Argentina. This unit is found in the context of the Eastern Cordillera, a mountainous system that is limited by the Argentinean puna or Altiplano on the east. This formation is mainly composed of siltstones, claystones, and sandstones interbedded with tuff and conglomerate beds, and it is related to fluvial environments. The age of the Uquía Formation was established in previous works as Middle Pliocene to Early Pleistocene (Marshall et al., 1982; Prado et al., 1998, 2000; Cione and Tonni, 1999). Biochronologically, the Uquía Formation has been divided in three units (Castellanos, 1950). The lower unit has been assigned to late Chapadmalalan SALMA (South American Land Mammal Age), the middle unit to Marplatán SALMA, and the upper unit to Ensenadan SALMA (Reguero et al., 2007). The Uquía Formation bears a very important record of fossil vertebrates, not only for the abundant specimens and taxa recovered but also because it documents the first stages of the Great American Biotic Interchange (GABI) in South America (Reguero et al., 2007). However, this record is mainly restricted to medium and large mammals, with scarce evidence of microvertebrates. Recent field trips to the locality of San Roque allowed the discovery of a noteworthy fossil assemblage of microvertebrates. The study of these fossils contributed to the recognition of the first amphibians and reptiles recorded from this unit.

Description.—The individual bones were disarticulated but closely clustered on the sediment; the elements could be provisionally associated based on size, overall morphology, preservation, and provenance. Six of the dentaries can be attributed to the same species (Fig. 3).

The premaxilla (Figs. 2A–B, 4) are unpaired. This element is well preserved and almost complete. The ascending nasal process (Fig. 2A, asnp) is short (twice the length of the premaxillary teeth) and presents its widest point in the base, from where its margins start to converge posteriorly into a rounded point. In dorsal view and posterior to the widest point, the ascending nasal process presents shelves in the margins to receive the nasal bones (Fig. 2A, n-pmx). This indicates that the nasal bones overlapped the premaxilla, a character that has been proposed for Liolaemidae (Frost and Etheridge, 1989) but also present in other iguanoids (Table 1). In posterior view, the premaxilla present a well-defined septonasal crest (Fig. 2B, snc). The palatal shelf is broken, but the shape of the bone suggests that it was present. The premaxilla preserves three teeth, but it bears seven tooth loci (Fig. 2B, 1–7). The three preserved teeth do not show any sign of replacement or resorption foramina. Two of the teeth are complete, and one is broken. All of them are closely spaced but are not ctenodont. The teeth are pleurodont, isodont, and cylindrical with blunt crowns. There is no rostrum anterior to the premaxillary teeth, and this bone had a sutural contact with the maxilla. A portion of the premaxilla that corresponds with the external naris vestibule is located in a very anterior position.

A left maxilla (Figs. 2C–E, 4) is also fairly complete. This bone does not show any sign of dermal sculpturing. The nasal process of the maxilla is located anterior to the midpoint of the

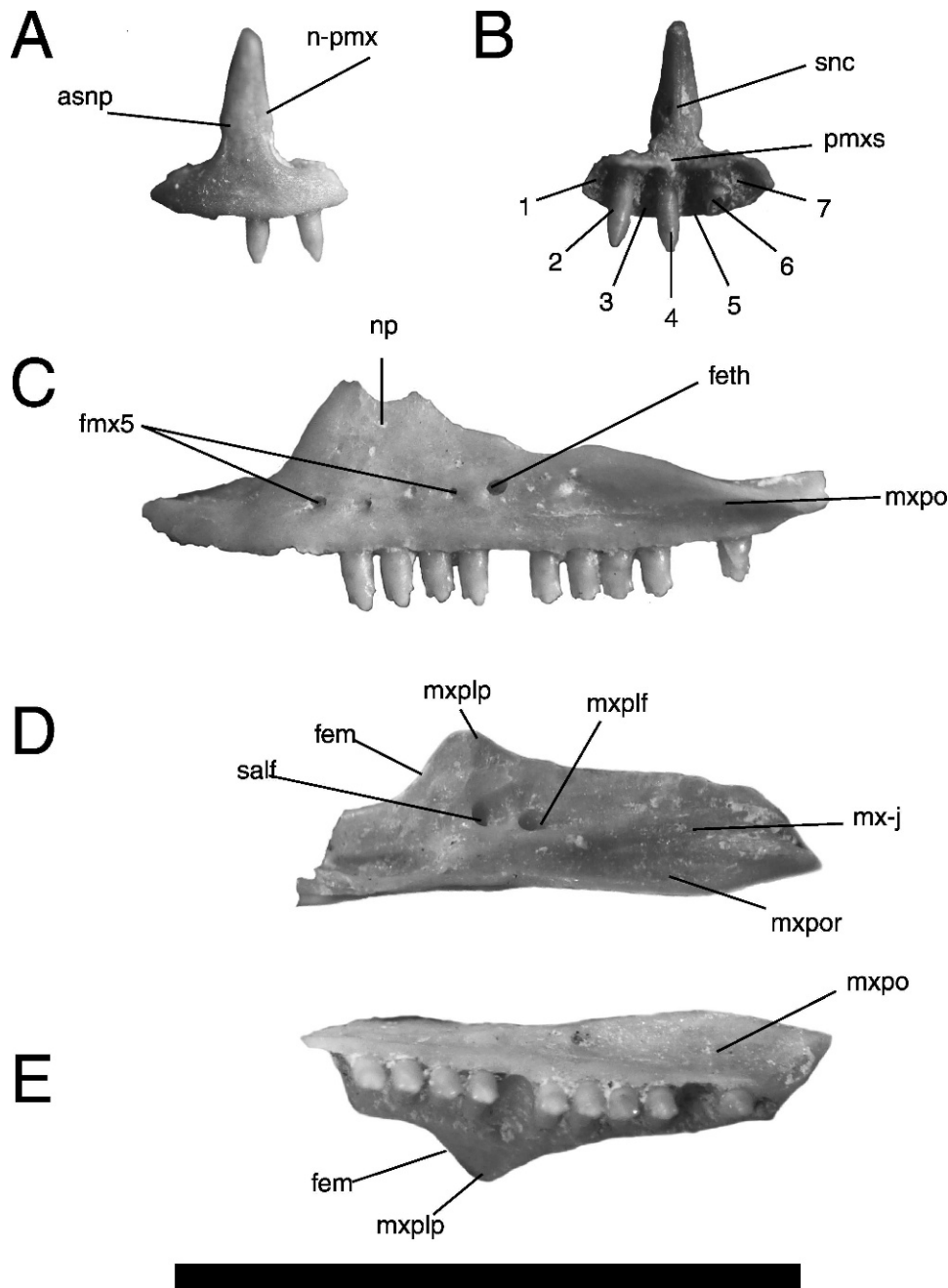


FIG. 2. Skull bones of *Uquiasaurus heptanodonta*. Premaxilla (PVL 6388) in anterior (A) and posterior (B) views. Lateral (C), dorsal (D), and ventral (E) views of the maxilla (PVL 6395). Abbreviations: asnp, ascending nasal process; fem, fenestra exchoanalis margin; feth, foramen for the cutaneous branch of the lateral ethmoidal nerve; fmx5, small foramina for cutaneous branches of the maxillary division of the cranial nerve V; np, nasal process; lf, lacrimal duct (foramen); mx-j, sutural area for the jugal; mxplf, maxilopalatine foramen; mxplp, palatine process of the maxilla; mxpo, maxilla posterior offset; mxpor, maxilla posterior offset roof; n-pmx, shelve of premaxilla for the overlap of the nasal. Scale bar equals 5 mm. Note that the anterior premaxillary process of the maxilla (C) is missing from the dorsal (D) and ventral (E) views.

maxilla (Fig. 2C, np). The anterior margin of the external nares starts ascending gradually but soon becomes steep as in Opluridae, Tropiduridae, Liolaemidae, and Leiocephalidae (Conrad, 2008). Along its inferior border, the maxilla is pierced by four small foramina for cutaneous branches of the maxillary division of the cranial nerve V and caudally by a larger one that opens posteriorly that was probably for the foramen for the cutaneous branch of the lateral ethmoidal nerve (Oelrich, 1956; Fig. 2C, fmx5 and feth), previously identified as an enlarged maxillary nutritive foramina in Tropiduridae (Frost, 1992). Although the prefrontal is not present, it is evident that the maxilla only overlapped this element anteriorly. The antero-medial process of the maxilla (maxillary lappets) indicates that

they did not separate the vomer from the premaxilla and did not contact its fellow as in chamaeleontiform iguanians (Parker, 1881). The palatal shelf of the maxilla indicates that it did not contact the vomer; thus, the dermal palate presented the paleochoanate condition (Lakjer, 1926; Rieppel et al., 2008). A palatine process is well developed and flares out medially (Fig. 2D–E, mxplp). Its anterior flange participated in the fenestra exchoanalis (Fig. 2D–E, fem). Lateral to this palatine process, the superior alveolar foramen is visible, which opens dorsoposteriorly (Fig. 2D, salf). Posterior to this foramen, there is a maxilopalatine foramen (Fig. 2D, mxplf), and presumably of equal diameter to the lacrimal duct, a similar condition is present in *Tropidurus*, *Uracentron*, and *Strobilurus* (Frost, 1992),

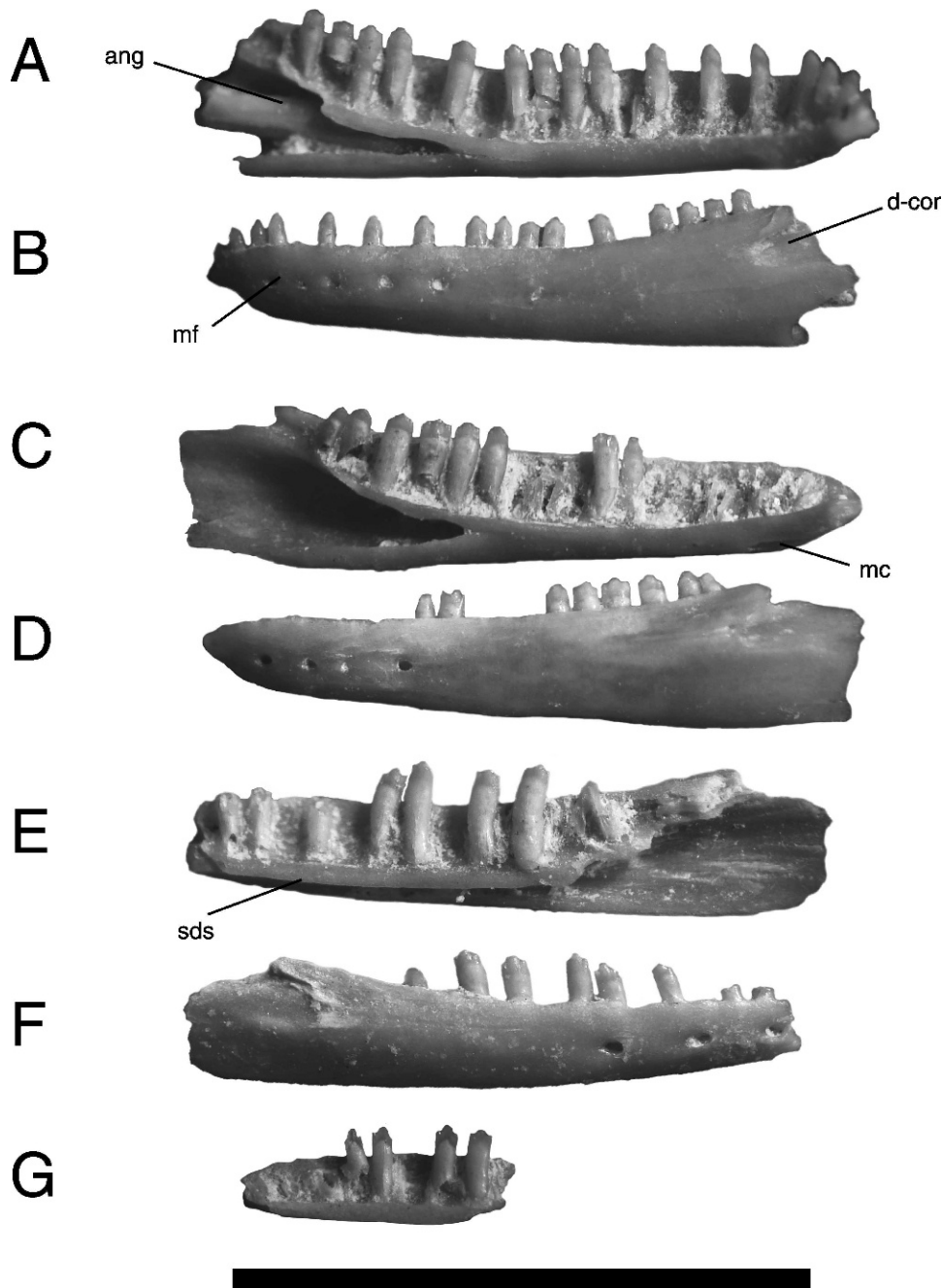


FIG. 3. Labial and lingual views of jaws of *Uquiasaurus heptanodonta*. (A–B) PVL 6389; (C–D) PVL 6393; (E–F) PVL 6391; (G) PVL 6387. Abbreviations: ang, angular; d-cor, sutural area for coronoid; mc, Meckel canal anterior aperture; mf, mental foramen. Scale bar = 5 mm.

Liolaemus, and *Phymaturus* (Etheridge, 1995). The jugal articulation suture is dorsal to the maxilla (Fig. 2D, mx-j) and indicates that this bone formed only the anterior portion of the orbit. The tooth row extended beyond the first quarter of the eye socket. The maxilla preserves nine teeth, but we estimate that it bears between 17 and 18 tooth loci. None of the anterior teeth are preserved, but these could be unicuspidated like in many iguanoid groups (e.g., *Anolis*, *Brachylophus*, *Ctenosaura*, *Gambelia*, *Liolaemus*, *Tropidurus*, *Polychrus*, *Stenocercus*, *Uta*). The preserved maxillary teeth are posterior to the fifth or fourth. These teeth are pleurodont with almost parallel, straight margins with no waist and three well-differentiated crowns as in some *liolaemids* (Etheridge, 1995, 2000; Lobo, 2001; Lobo and Abdala, 2001). The interdental space in the maxilla is larger than in the premaxilla. The medial crown is more elevated in the teeth of the midpoint of the maxilla compared to the ones in

the posterior portion, but all teeth are similar in diameter. The replacement in these teeth was lingual as indicated by the nutritive foramina. Maxillary teeth are carinated in the lingual margin. There is a wide posterior offset on the labial side of the posterior teeth that shifts the tooth row medially (Fig. 2E, mxpe).

The dentary (Figs. 2A–G, 3) is a tubular and straight bone with the Meckelian canal entirely fused and no indication of a suture that has an opening anteriorly. A fused Meckelian canal is also present in the *Liolaemus chiliensis* group (Etheridge and de Queiroz, 1988; Etheridge, 1995; Lobo, 2001; Lobo and Abdala, 2001) and the *Phymaturus patagonicus* group (Etheridge and de Queiroz, 1988; Etheridge, 1995; Lobo and Quinteros, 2005) but is absent in some *Liolaemus*, *Phymaturus*, and *Ctenoblepharys adspersa* (Etheridge, 1995). The anterior portion of the dentary is low and duplicates its size posteriorly.

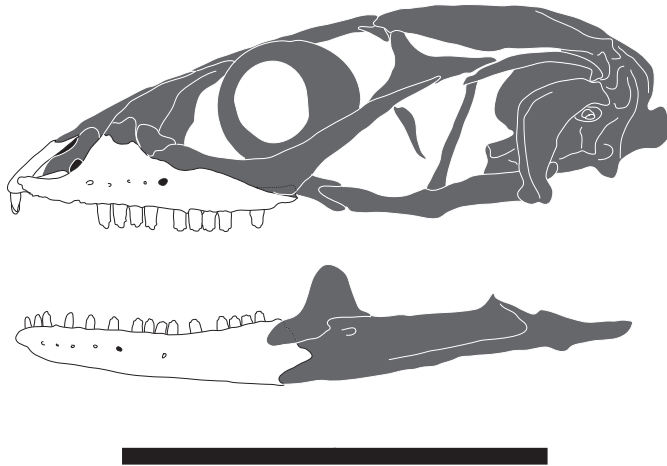


FIG. 4. Position of fossil material of *Uquiasaurus* using a *Liolaemid* lizard as template. The unpreserved parts were inferred from the high-resolution X-ray computed tomography of *Liolaemus bellii* (MVZ 125659). Scale bar = 1 cm.

According to the inferred sutures for the postdentary bones, especially the coronoid (Fig. 3B, 4), the dentary could have extended briefly beyond the tip of the coronoid eminence or finish just below it but not as much as in *Liolaemus* in which it extends beyond this process (Etheridge and de Queiroz, 1988; Etheridge, 1995). We infer that the dentary participated in the dorsal border of the inferior alveolar foramen. The dentaries present a variable number of teeth loci (18, 21). One dentary preserves almost all of the teeth (Fig. 3A–B) showing heterodont dentition, the first eight present simple crowns, and the rest of them are tricuspid. The interdental space is similar to that present in the maxillary teeth.

Associated Material.—A right dentary (PVL 6390, Fig. 5) with 19 teeth. This bone is 1.5 times larger than the rest of the material. The Meckelian canal in this specimen is open, but this could be an artifact of preservation. It presents 19 teeth, and their morphology is heterogeneous, with simple crowned anterior teeth and the rest of them tricuspidated, a condition that is present in many pleuronodon iguanians. In this dentary, the surangular process could have extended beyond the coronoid eminence, as in *Liolaemus*. We speculate that this jaw belongs to a lizard of the genus *Liolaemus* based in the inferred posterior extension of the dentary (Etheridge, 1995).

New Information on the Phylogeny of Iguanomorpha.—We found 50 hits of the most parsimonious trees (MPT) with searches using 50 independent executions of xmult. Three MPT were found with a score of 65.85166 (see strict consensus, Figs. 6–7). The search results, relative to our preferred results with $k = 20$, were stable across several k -values. Results were equal to $k = 20$ for 18–19 and differ in less than five nodes and three SPR movements from $k = 10$ –23. Hence, the results were very stable to the variations of k -values. Across these different values, the position of *Pristiguana* and *Uquiasaurus*, as well as the position and monophyly of Priscagamidae, Iguanoidea, and Gobiguaniidae, were supported. The group support values for most clades are low. Low support values are common in complex matrices (e.g., Lopardo, 2005) and are obtained when the same characters that support a group also contradict it (Goloboff et al., 2003). In some cases for GC-measure, some groups appear contradicted by the resampled data. It is known that GC have this behavior in some cases (see Goloboff et al., 2003), and the presence of missing data in the matrix may contribute to these results.

The current analysis was able to find a well-resolved Iguania. The optimization of characters in our tree differs from the diagnosis of the groups presented by Conrad (2008). We listed



FIG. 5. (A–B) Mandibular ramus of specimen PVL 6390 in (A) labial and (B) lingual views. Scale bar = 5 mm.

these characters in the Appendix 2 and provide a diagnosis for those groups not recovered previously.

The lack of quadratojugal 54 (1) unites the Late Triassic glires lizards (Stein et al., 2008) from the family Kuehneosauridae with Squamata. A frontal bone with concave sides 57 (2) is a synapomorphy for Iguanomorpha and *Hoyalacerta sanzi* is the most basal iguanomorph member of this clade. *Pristiguana brasiliensis* is the sister taxon of *Huehucuetzpalli mixtecus* based on two synapomorphies from the coronoid, abutting contact with the dentary 194 (1) and the presence of an anterodorsal buttress 199 (1).

The basic split between the Chamaeleontiformes and Iguanoidea was also corroborated. Each one of these clades presents their own Late Cretaceous family from the Gobi Desert. According to our analysis, *Isodontosaurus gracilis* is not a chamaeleontiform; therefore, in our analysis, the formula Priscagamidae + Acrodonta (Conrad, 2008) becomes equivalent to Chamaeleontiformes. This group was defined before as Chamaeleonoidea (Alifanov, 1996) but differs in that it does not include Hoplocercidae.

The fossil clade Priscagamidae (Alifanov, 1989; synonymous with Priscagaminae, Borsuk-Bialynicka and Moody, 1984) is clearly associated with the extant acrodonts (agamids and chameleons) but appears as a separated family from “Agamidae,” corroborating that the agamid features are plesiomorphic (Alifanov, 1989). Agamidae was recovered as paraphyletic (see a similar problem in Frost and Etheridge, 1989).

Iguanoidea is supported by six characters: 78 (0) posterior margin of the parietal fossa open; 140 (1) reduced entocarotid fossa; 181 (1) Meckelian canal partially closed; 239 (1) dorsal margin of atlas posteroventrally inclined; 370 (0) angular contacting the splenial on the lingual side; and 372 (0) first cervical ribs on the fourth vertebra. Smith (2009) presented six additional characters to diagnose this clade, including premaxillary process of maxilla with two foramina, a strong process projects anteriorly from the ventral margin of the planum antorbitale, commissura vomeronasalis present and complete, vestibulum nasi elongate and about as long as nasal capsule or longer, vestibulum nasi S-shaped in a horizontal plane, scapulocoracoid with scapular fenestra. The Clade A obtained by Smith (2009) was not recovered, but Clade B is congruent with our results.

Gobiguania, Polychrotidae, and Hoplocercidae share three characters: 143 (1) posterolateral ventral flanges of sphenoid overlying the basioccipital; 261 (1) clavicles strongly curved or angled; and 395 (0) palatine triangular flange absent.

Gobiguania was defined as all taxa closer to *Anchaurosaurus gilmorei* than to *I. iguana*, *Crotaphytus collaris*, or *Agama agama* and was diagnosed by three unambiguous synapomorphies (Conrad and Norell, 2007). The phylogenetic position of *I. gracilis*, *Polrussia mongoliensis*, and *Igua minuta* has been uncertain (Borsuk-Bialynicka and Alifanov, 1991; Gao and Norell, 2000). *Polrussia* has been suggested to be closer to

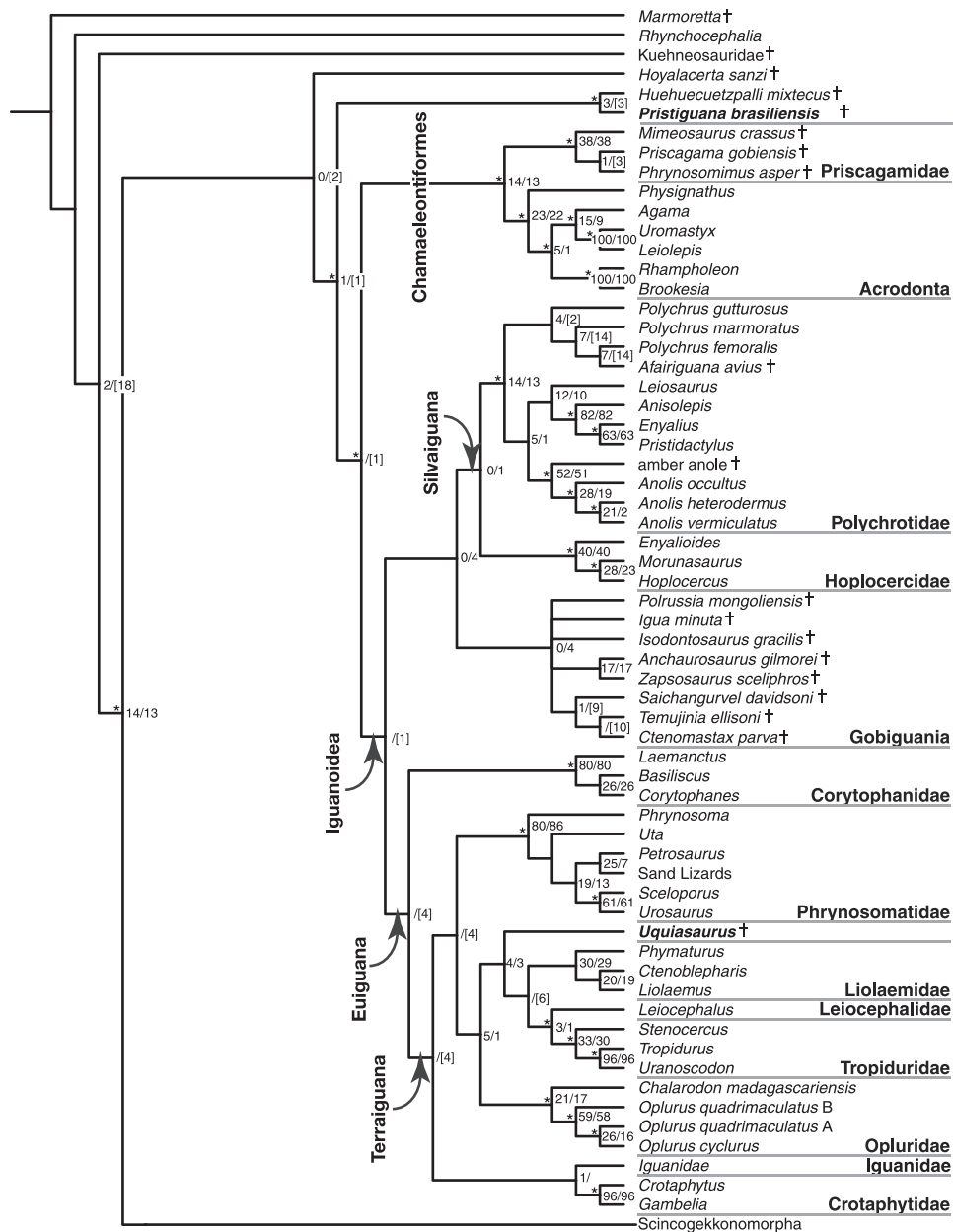


FIG. 6. Relationships within Iguanomorpha based on morphology. Strict consensus tree of the three most parsimonious trees (cost under $k = 20$, 65.85166). Numbers in front of nodes correspond to group frequencies/GC (difference in frequencies for groups supported-contradicted). Brackets indicate negative values. An asterisk (*) in front of the node indicates that Bremer support values are higher than 0.02.

Opluridae (Borsuk-Bialynicka and Alifanov, 1991), and *Igua* has been differentiated from *Ctenomastax* by the tricuspid dentition (Gao and Norell, 2000). In previous revisions, both *Polrussia* and *Igua* have been recognized as similar in general appearance to the gobiguanians and allied to *Chalarodon* (Conrad and Norell, 2007) or placed in an unresolved position within Iguanomorpha (Conrad, 2008). We found a clade that includes Gobiguania (viz., *Saichangurvel*, *Ctenomax*, *Temujinia*, *Anchaurosaurus*, and *Zapsosaurus*; Conrad and Norell, 2007), along with *Polrussia*, *Igua*, and *Isodontosaurus* (Figs. 6, 7). Since Gobiguania was proposed as a stem-based name, the definition applies to the clade found. Gobiguania is supported by two synapomorphies: 9 (0) prefrontal without sculpturing; and 71 (1) presence of frontoparietal fontanelle. Gobiguania is the sister group of a clade formed by Polychrotidae and Hoplocercidae and shares with them three characters: 143 (1) ventral flanges of sphenoid overlaying the basiooccipital; 261 (1) clavicle

strongly curved or angulated; and 395 (0) palatine flange process without triangular projection.

Polychrotidae and Hoplocercidae form a clade here named Silvaiguana, meaning forest iguana and alluding to their general preference for those woodland areas. Silvaiguana is diagnosed by four characters: 26 (0) presence of strong palatal processes of the maxilla; 60 (1) frontal with dorsoventral inflation; 90 (1) tubercle in the suture between the postfrontal and postorbital; and 138 (1) prootic with reduction of crista prootica.

The remaining families within Iguanoidea (viz., Corytophanidae, Phrynosomatidae, Liolaemidae, Leiocephalidae, Tropiduridae, Opluridae, Iguanidae, and Crotaphytidae) form a clade here named Euiiguana. This is a poorly supported clade and is united by two characters: 181 (2) Meckelian canal closed and fused; and 393 (1) between 21 and 30 maxillary tooth loci.

This clade's basal branches are Corytophanidae and a clade here named Terraiguana, meaning ground iguana and alluding

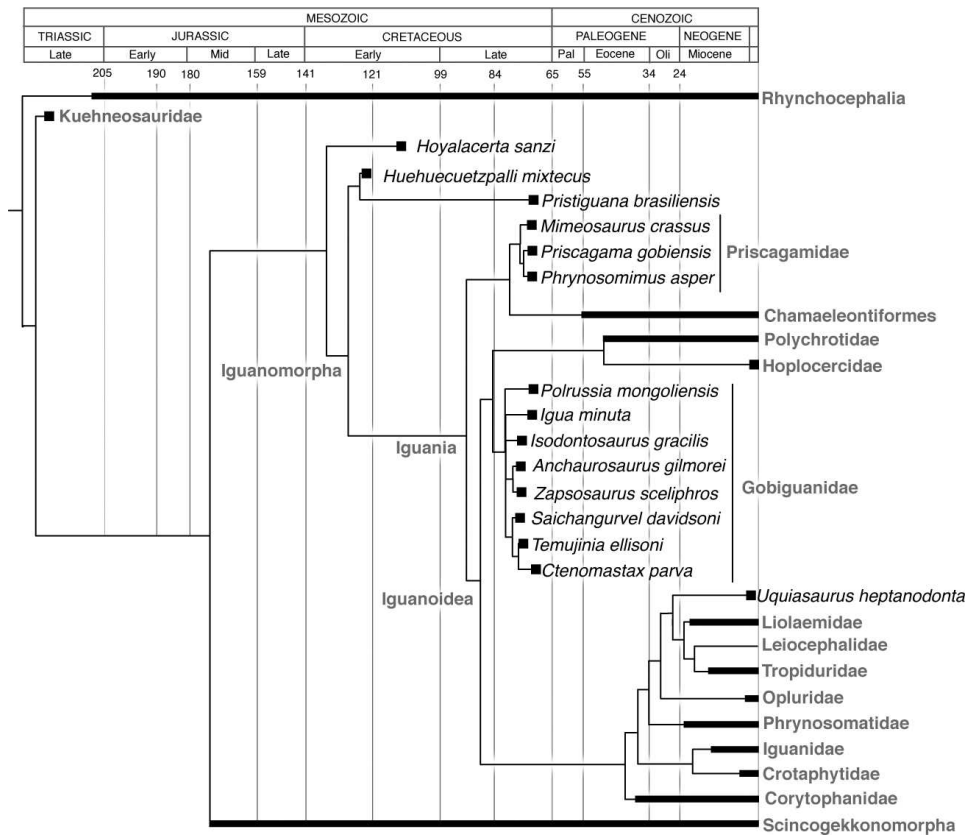


FIG. 7. Temporally calibrated cladogram showing the consensus tree obtained. Scleroglossan representatives were collapsed into Scincogekkonomorpha. Fossil taxa printed in black lettering. Figure modified from Conrad (2008).

to the general saxicolous and land dwelling preferences of the majority of its members (Phrynosomatidae, Liolaemidae, Leiocephalidae, Tropiduridae, Opliridae, Iguanidae, and Crotophytidae): Terraiguana is diagnosed by four characters: 52 (1) jugal mostly dorsal to the maxilla; 105 (1) ectopterygoid oriented anterolaterally (at more than 30 degrees from perpendicular to sagittal for the skull); 273 (1) sternum fontanelle present; and 394 (1) maxilla with wide posterior offset labial to the tooth row.

Terraiguana is divided in two groups. One of them is formed by Iguanidae and Crotophytidae and is diagnosed by three characters: 21 (0) nasals presenting an extensive internasal contact; 90 (1) absence of a tubercle in the suture between the postfrontal and postorbital; and 263 (1) presence of a second emargination in the coracoid. The other group is formed by Phrynosomatidae, Opluridae, Tropiduridae, Liolaemidae, and Leiocephalidae and is diagnosed by five unambiguous synapomorphies: 26 (0) nasal process of the maxilla located at or anterior to midpoint of the maxilla; 176 (1) posterior mylohyoid foramen located posterior to the coronoid apex; 183 (1) dentary contributing to the dorsal border of the anterior inferior alveolar foramen; 257 (1) anterior presacral ribs expanded and flattened; and 376 (0) at least one subocular scale conspicuously enlarged. The latter clade contains an unnamed clade formed by Opluridae, Tropiduridae, Liolaemidae, and Leiocephalidae (Conrad, 2008). The support for this clade is low and is diagnosed by 1 (0) anteorbital snout less than 30% of the total length and 18 (1) premaxilla overlapped by the nasals. *Uquiasaurus* falls within this group, allied to Liolaemidae, Leiocephalidae, and Tropiduridae (the tropidurines, Etheridge and de Queiroz, 1988). This clade is diagnosed by character 392 (0), which is a short ascending nasal process of the premaxilla, approximately twice the length of the premaxillary teeth. This is congruent with the results of Smith (2009) where this clade was diagnosed by three characters, large fenestra septi nasi,

fenestra superior nasi perforating tectum nasi, and gular fold incomplete medially or absent. *Uquiasaurus* differs from the remaining tropidurines by the character 183 (1), which is the participation of the dentary in the dorsal border of the inferior alveolar foramen.

Osteological Comparison of *Uquiasaurus* with Tropidurines.—Although the phylogenetic analysis was unable to allocate *Uquiasaurus* to any of these extant families, we discuss some morphological features in an attempt to suggest the affinities of *Uquiasaurus* with extant tropidurines. Liolaemidae and Tropiduridae are the most morphologically similar families to *Uquiasaurus* and present similar distribution ranges in the southern part of South America. Prior to the analysis, we dismissed any possible association with polychrotids (the other family distributed in the southern part of South America) because these present a very long ascending nasal process, they lack a palatine flange process with well-developed triangular projection and the wide maxillary posterior offset (Fig. 8A).

The shape of the posterior margin of the ascending nasal process in *Uquiasaurus* and liolaemids is sharp pointed and differs from that in the tropidurids *Tropidurus* (= *Plica*) *plica* that present a wider process and *Stenocercus guentheri* where the posterior end is blunt. Additionally, *Uquiasaurus* shares with *Liolaemus* and *Ctenoblepharys* the ascending nasal process overlapped by the nasals (Fig. 2A; Frost and Etheridge, 1989), which is absent in some *Phymaturus* and in Tropiduridae (e.g., *Tropidurus plica*, Fig. 8D).

In general the osteology of *Uquiasaurus* is very similar to the members of the family Liolaemidae although none of the morphological characters that define Liolaemidae (Etheridge and de Queiroz, 1988; Etheridge, 1995; this work) can be observed in this fossil. Liolaemidae contains three genera: *Liolaemus*, *Ctenoblepharys*, and *Phymaturus* (Frost and Etheridge, 1989; Etheridge, 1995; Pincheira-Donoso et al., 2008), and each of these genera are well supported by morphological

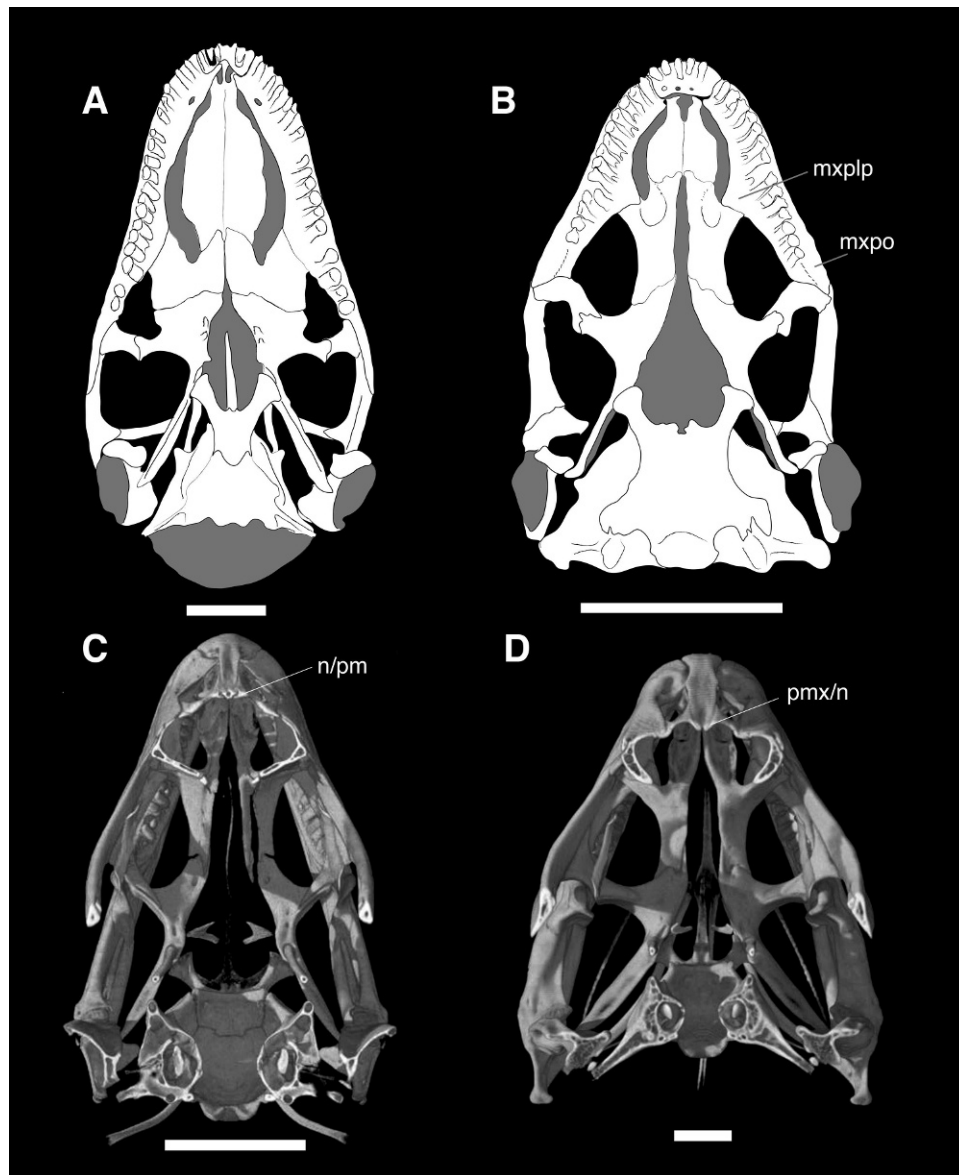


FIG. 8. Ventral view of some Iguanoidea. (A) *Anolis cuvieri* (Richard Thomas, personal collection) and (B) *Liolaemus darwini* (FML 01995). Dorsal view of (C) *Liolaemus bellii* (MVZ 125659), and (D) *Tropidurus plica* (FMNH 81451). Abbreviations: n, nasal; mxplp, palatine process of the maxilla; mxpo, maxilla posterior offset; pmx/n, premaxilla. Scale bar = 5 mm.

synapomorphies (Etheridge, 1995; Lobo, 2001; Avila et al., 2004; Lobo and Quinteros, 2005; Abdala, 2007). Based on molecular and morphological analysis, the relationships are (*Ctenoblepharys* (*Phymaturus*, *Liolaemus*)) (Schulte et al., 2003; Espinoza et al., 2004; Lobo and Quinteros, 2005) although in the current analysis *Phymaturus* was found basal to *Liolaemus* and *Ctenoblepharys*.

Etheridge and de Queiroz (1988) and Etheridge (1995) differentiated *Ctenoblepharys* from *Liolaemus* and *Phymaturus* by means of nine morphological characters and additionally used five more to differentiate *Ctenoblepharys* from *Liolaemus* and six to differentiate it from *Phymaturus*. We could only evaluate three of these characters. First, lacrimal foramen size was small in *Uquiasaurus* as in *Liolaemus* and *Phymaturus*. Second, a short dentary is present also in *Ctenoblepharys*. This character is relative to the surangular length because if the dentary is short, the surangular is long. It is difficult to establish this character for *Uquiasaurus* because only a small portion of the surangular is preserved. Nonetheless, by the posterior extension of the dentary with respect to the inferred

coronoid, we can determine that the dentary in *Uquiasaurus* was not as long as in *Liolaemus*. Finally, considering tooth morphology, *Ctenoblepharys* and *Liolaemus* differentiate from *Phymaturus* in having tricuspid marginal teeth with tapered crowns and small secondary cusps rather than expanded crowns with large secondary cusps, which is a similar condition found in *Uquiasaurus* (Figs. 1, 2). *Uquiasaurus* presents similar tooth morphology to *Liolaemus* but differs from it in the number of premaxillary teeth; *Liolaemus*, typically has six premaxillary teeth set close together (R. Etheridge, pers. comm.; Table 1). Among liolaemids, the number of premaxillary teeth is constant; most of the time, there are only six, although in some species of *Phymaturus* (*excelsus* and *punae*), five teeth are present. *Uquiasaurus* with seven teeth presents the highest number for Liolaemidae and Tropiduridae. *Uquiasaurus* also lacks some expanded premaxillary teeth present in *Phymaturus*.

Another character present in *Ctenoblepharys* is the palatine bearing a wide maxillary process. Although the palatine is not

preserved in *Uquiasaurus*, this maxillary process is overlapped by a palatine process of the maxilla, which in *Uquiasaurus* does not suggest that was articulated with a wide process in the palatine.

Uquiasaurus and the subfossil material of *Liolaemus multi-maculatus* and *Liolaemus darwini* (Albino, 2005) present similar tooth row length, but *Uquiasaurus* presents a slightly higher number of tooth loci (20–23), higher number of mental foramina (6–4), a Meckelian canal fused along all his way, and transition between conical and pointed teeth to tricuspidal occurring in the 7–8 tooth loci. The dentary presents a strong subdental shelf (Fig. 3E, sds). The dorsal border presents a small posterodorsal coronoid process; this process could not have approached the dorsal process. On the labial side, there are some mental foramina (Fig. 3B, df) that could be between four and six across the different jaws. The coronoid is not preserved, but the sutural impression was left on the labial side of the dentary. From this impression, it can be inferred that the anterior end of the coronoid clasps the dentary and that its height exceeds the contour of the mandible. The shape of the dentary also indicates that the splenial was long and that it extends anteriorly up to the level of the dentary tooth number 15, as in *Ctenoblepharys* (Etheridge, 1995).

CONCLUSIONS

Iguania is a diverse clade with an incompletely known fossil record (Conrad and Norell, 2007; Smith, 2009), especially in South America (Estes, 1983; Albino, 1996). The results from our phylogenetic analysis provide new ideas about the evolution of Iguanidae. Fossil lizards from the Gobi Desert represent important Late Cretaceous components of both Chamaeleonidae and Iguanoidea. Phylogenies dealing with iguanians, especially iguanoids, suffer from conflicting results and are weakly supported, a problem that is recurrent with different data partitions (Avery and Tanner, 1971; Etheridge and de Queiroz, 1988; Frost and Etheridge, 1989; Macey et al., 1997; Schulte et al., 1998, 2003; Frost et al., 2001a; Conrad, 2008; Smith, 2009). This analysis provides a new hypothesis of the relationships within Iguanomorpha and identifies new clades within Iguanoidea. Although some of these are weakly supported, they are generally congruent with recently morphological analysis (e.g., Smith, 2009). Further research considering all available morphological evidence and molecular information is required to provide a solid ground to understand the relationships within Iguania.

With the description of *Uquiasaurus* we provided evidence of a morphologically distinct group of lizards allied to the tropidurines. *Uquiasaurus* existed in a relatively recent epoch and probably occurred in sympatry with members of the genus *Liolaemus*. Finally, with the comprehensive morphological revision of the fossil material, it is not possible to establish precisely the affinities of *Uquiasaurus*, and its basal position with respect to the tropidurid clade is possibly attributable to the fragmentary nature of this fossil. More material that could be assigned to this genus is required to better understand its phylogenetic position within Iguanoidea.

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- Iguana iguana* AMNH R 74736; REE 453; *Dipsosaurus dorsalis* YPM 14376; *Sauromalus obesus* REE 467.
- Leiocephalidae: *Leiocephalus carinatus* UMMZ 149104.
- Leiosauridae: *Leiosaurus paronae* MACN 4386; *Pristidactylus torquatus* FMNH 206964.
- Opluridae: *Oplurus cyclurus* YPM 12861.
- Phrynosomatidae: *Phrynosoma hernandesi* TNHC 11839; *Uta stansburiana* FMNH 213914.
- Polychrotidae: *Anolis carolinensis* FMNH 242298; *Diplolaemus bibroni* MACN 35850, REE 2506; *Polychrus marmoratus* FMNH 42501; *Polychrus guttorosus* AMNH R32675.
- Tropiduridae: *Stenocercus guentheri* KU 147412; *Stenocercus apurimacus* KU 134284; *Tropidurus bogerti* USNM 300598; *Tropidurus melanopleurus* KU 136367; *Tropidurus plica* FMNH 81451, MAN 76; *Tropidurus stolzmanni* KU 134747; *Tropidurus umbra* KU 146659; *Uranoscodon superciliosus* REE 16600.
- Liolaemidae: *Ctenoblepharys adspersa* LACM 49147; *Liolaemus bellii* MVZ 125659; *Liolaemus darwini* FML 01995; *Liolaemus boulengeri* FML 00291; *Liolaemus ceii* MCN 908, MCN 909; *Liolaemus dorbignyi* FML 1855-3; *Liolaemus fitzingeri* FML 17147; *Liolaemus huacahuasicus* FML 22320; *Liolaemus kriegi* FML 17762; *Liolaemus kolongh* FML 20391, FML 20392, FML 20393; *Liolaemus laurenti* MCN 318, MCN 319, MCN 321, MCN 326; *Liolaemus lineomaculatus* FML 02129-3; *Liolaemus multicolor* FML 3347-4; *Liolaemus orientalis* FML 00928-1; *Liolaemus ornatus*; FML 63489-2; *Liolaemus pictus* FML 01781; *Liolaemus petrophilus* FML 13081; *Liolaemus ramirezae* FML 03333/1-4; *Liolaemus wiegmanni* FML 01321; *Phymaturus spectabilis* GS 3173, GS 3176; *Phymaturus excelsus* FML 22058, FML 22059–22063, MCN 1582; *Phymaturus mallimacci* MCN 920, REE 2002, REE 2035; *Phymaturus cf. palluma* REE 2036, REE 2037, REE 2312–2313, REE 2315, MVZ 9290, MVZ 292904, MVZ 92908; *Phymaturus payunae* REE 2330, REE 2331–2332, REE 2339, REE 2360; *Phymaturus punae* FBC 392, FBC 394; *Phymaturus roigorum* REE 2323–2325, REE 2327; *Phymaturus spurcus* FML 21493–21495; *Phymaturus tenebrosus* FML 22073–22075, FML 22077–22078).
- Incertae sedis: *Uquiassaurus heptanodonta* PVL 6387–6389, PVL 6391–6395. *Pristiguana brasiliensis* DGM 552.

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APPENDIX 1

List of Specimens

Polychrotidae now includes only *Polychrus*, and *Anolis* was placed in the separate family Dactyloidae on the basis of a phylogenetic analysis published subsequent to the initial acceptance of this paper (Townsend et al., 2011).

Corytophanidae: *Basiliscus basiliscus* FMNH 165622, KU 93452; *Corytophanes cristatus* FMNH 69227.

Crotaphytidae: *Crotaphytus collaris* FMNH 48667; *Crotaphytus dickersonae* REE 2777; *Crotaphytus grisei* MZFC 6651; *Crotaphytus reticulatus* REE 2912; *Crotaphytus vestigium* REE 2826; *Gambelia copei* REE 2912; *Gambelia silus* CAS 22713; *Gambelia wislizenii* REE 2918, YPM 14380.

Hoplocercidae: *Morunasaurus annularis* REE 1956; *Hoplocercus spinosus* REE 359.

Iguanidae: *Amblyrhynchus cristatus* REE 1396, MVZ 67721; *Brachylophus fasciatus* FMNH 210158; *Brachylophus vitiensis* MCZ 160254; *Conolophus* sp. MVZ 77314, REE 439; *Cyclura cornuta* REE 383; *Iguana* sp. UCA uncataloged; *Iguana delicatissima* MCZ 16157, MCZ 60823;

APPENDIX 2

Updated diagnosis of previously defined groups, prefix FE89 (Frost and Etheridge, 1989) and C08 (Conrad, 2008), asterisk (*) denotes a character previously defined for that group.

Iguanomorpha: C08-57(2).

Iguania: C08-9(1), C08-10(1), C08-11(1), C08-26(1)*, C08-34(1), C08-53(1), C08-105 (0), C08-240(0), C08-281(1).

Chamaeleontiformes: C08-7(2), C08-27(1)*, C08-49(1), C08-91(1), C08-214(1), C08-215(1), FE89-4(1).

Priscagamidae: C08-8(1)*, C08-27(1), C08-49(1), C08-91(1), C08-214(1), C08-215(1), FE89-4(1).

Acrodonta: C08-44(1), C08-173(2), C08-180(1), C08-182(1)*, C08-188(1)*.