Redescription of the Extinct Species *Callopistes bicuspidatus* Chani, 1976 (Squamata, Teiidae)

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Abstract.—We redescribe the holotype and only known material of the extinct teiid lizard *Callopistes bicuspidatus* Chani, 1976, from the late Miocene–early Pliocene of the Atlantic coast of Argentina. It would constitute a fossil record of the genus outside the present range of distribution restricted west of the Andes, but the characters used in the original description for the systematic assignation have had little attention and have been questioned in part. In this study, we confirm the generic assignment of these remains (as well as the validity of the species), based on characters different from those used in the original description. We also recognize many characters shared by *Callopistes* and the rest of the Tupinambinae teiids indicating the affinity of the genus to this subfamily. The paleoenvironmental conditions inferred from the accompanying vertebrate fauna for the late Miocene–early Pliocene of the fossil locality indicate that *C. bicuspidatus* exploited different environmental conditions than the extant species of the genus, especially regarding humidity and water availability.

Resumen.—En este trabajo redescribimos el holotipo y únicos restos conocidos del lagarto teido *Callopistes bicuspidatus* Chani, 1976, del Mioceno tardío–Plioceno temprano de la costa atlántica Argentina. Constituiría un registro fósil del género fuera de su actual rango de distribución, el cual se encuentra restringido al oeste de los Andes. Sin embargo, poca atención han recibido los caracteres utilizados para su asignación sistemática original, algunos de los cuales han sido cuestionados. En este estudio reconocemos distintos caracteres que confirman su asignación genérica y su validez específica. La mayoría de estos caracteres no fueron reconocidos en la descripción original. También reconocimos caracteres compartidos entre *Callopistes* y los restantes Tupinambinae indicando la afinidad del género con esta subfamilia. Las condiciones paleoambientales para el Mioceno tardío–Plioceno temprano de la costa Atlántica inferidas a partir de la fauna acompañante de vertebrados indican que *C. bicuspidatus* explotaba ambientes distintos a los de sus congéneres actuales, en particular en lo relacionado a la disponibilidad de agua y humedad.

The Teiidae are conspicuous members of the American lizard fauna widely distributed in South America (north of the 40th parallel south), with some genera reaching Central America and the Caribbean, and only one genus in the Nearctic region (Harvey et al., 2012). Although they have an abundant fossil record (Albino and Brizuela, 2014), their origin, thought to be in the Cretaceous–Paleogene (Giugliano et al., 2007), is elusive and still unknown. According to Venczel and Codrea (2016), teiids were first recovered in the Late Cretaceous (early Maastrichtian) of Europe, represented by an extinct clade (*Barbatteius* and *Meyasaurus*). The first crown teiids were from the early Paleogene of Argentina and Brazil, with *Lumbrerasaurus scagliai* Donadío, 1985, and an indeterminate Teiidae, respectively (Carvalho, 2001; Brizuela and Albino, 2016). No teiids have yet been recovered from the South American Oligocene. The family reappears in the Miocene with extant and extinct genera. Among Tupinambinae, the extant genus *Tupinambis* is recognized for the first time in the Miocene of Argentina and Colombia (Sullivan and Estes, 1997; Brizuela and Albino, 2004, 2008; Albino et al., 2006, 2013), whereas the extinct genus *Paradracaena* is recorded in the Miocene of Colombia, Peru, and possibly Brazil (Sullivan and Estes, 1997; Hsiou et al., 2009; Pujos et al., 2009). After the Miocene, *Tupinambis* is reported continuously throughout South America (Brizuela, 2010; Brizuela and Albino, 2012a,b; Albino and Brizuela, 2014). Apart from *Tupinambis* and *Paradracaena*, the other Tupinambinae genus recognized in the fossil record is the extant *Callopistes*, from the late Miocene–early Pliocene of the Atlantic coast of Argentina (Chani, 1976).

The extinct species *Callopistes bicuspidatus* was described and named by Chani (1976) who considered that the characters sustaining its taxonomic allocation in the genus *Callopistes* are 1) height/length ratio of the maxilla, 2) parietal length, and 3) weak heterodonty with unicuspid anterior teeth and bicuspid posterior teeth. According to Chani (1976), the absence of posterior tricuspid teeth makes this species distinct from the extant species of the genus (*C. maculatus* and *C. flavipunctatus*).

Callopistes bicuspidatus is known from only the Atlantic Coast of southern South America, outside the current distribution of the genus that is restricted to the west of the Andes from Ecuador to Chile (Harvey et al., 2012). This extinct species has been mentioned in several studies that have always noted the geographic discrepancy with the present-day distribution of the genus (e.g., Báez and Gasparini, 1977; Gasparini et al., 1986), but only Estes (1983:94) addressed the taxonomic conclusion of Chani (1976), considering it as "undoubtedly correct" but offering no additional information. Contrary to this opinion, Brizuela (2010) established that not all of the diagnostic characters given by Chani (1976) can be verified. Further complicating this issue is the lack of widely accepted osteological synapomorphies and autapomorphies regarding the genus. Therefore, a revision of this fossil is needed under the new knowledge produced since its original publication to enable a better supported systematic assignation. In this contribution, we redescribe the holotype of *Callopistes bicuspidatus*, and in doing so we analyze different characters or character states that would enable a better osteological description of the genus *Callopistes*.

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Recently, Harvey et al. (2012) performed an extensive study of external anatomical characters of Teiidae. This study resulted in a new phylogenetic arrangement significantly different from those based on osteology (e.g., Nydam et al., 2007). Consequently, Harvey et al. (2012) proposed a new taxonomy with four new genera (*Ameivula*, *Aurivela*, *Contomastix*, and *Medopheos*) and resurrected two more genera (*Holcosus* and *Salvator*). Harvey et al. (2012) taxonomically arranged these genera in three subfamilies: Callopistinae, Teiinae, and Tupinambinae. Similar results for Teiidae generic relations where obtained by Goicoechea et al. (2016) using nucleotide sequences, and resurrecting the Teiinae genus *Pholidoscelis* and erecting *Glaucomastix*. Unfortunately, the data sets of these studies (Harvey et al., 2012; Goicoechea et al., 2016) were not comprised mainly of osteological characters, the only relevant data sets for the evaluation of paleontological specimens. Therefore, because most of the characters and character states analyzed by Harvey et al. (2012) (and even more those of Goicoechea et al., 2016) cannot be used to evaluate fossils, we follow here the phylogeny and taxonomy proposed by Nydam et al. (2007), although recognizing the genera status among Teiinae proposed by Reeder et al. (2002). We recognize two subfamilies of crown Teiidae: the Teiinae (*Ameiva*, *Aspidoscelis*, *Cnemidophorus*, *Dicrodon*, *Kentropyx*, and *Teius*) and Tupinambinae (*Callopistes*, *Crocodilurus*, *Dracaena*, *Lumbrerasaurus*, *Paradracaena*, and *Tupinambis*).

The fossil specimen consists of an incomplete partially articulated skull and mandibles recovered by Dr. José Fernando Bonaparte from the sea-cliffs at the Farola Monte Hermoso locality (Coronel Rosales County, 37 km west of Monte Hermoso), Buenos Aires province, Argentina (Fig. 1). The fossils were collected from Sandbank #3 of Bonaparte (1960) (limolita arenosa of the "Hermosense típico"), near the base of the cliff (Chani, 1976). Farola Monte Hermoso has been prospected since the 19th century and has become an important fossil locality, being assigned as type locality for the Monte Hermoso Formation and the Montehermosan SALMA (South American Land Mammal Age) (Zavala, 1993; Tomassini et al., 2013). According to Zavala (1993), this formation was deposited in a fluvial environment with a high suspension load, characterized by muddy, sinuous rivers. Vertebrate fauna such as fish, amphibians, squamates, turtles, and mammals were preserved in this environment (see updated list in Tomassini et al., 2013). The biostratigraphy and age of this formation are currently debated. Until recently, two biozones were recognized in these cliffs: the inferior *Trigodon gaudryi* Biozone (stratigraphic basis of the Montehermosan Stage/Age, late Miocene–early Pliocene) and the *Neocavia depressidens* Biozone (stratigraphic basis of the early Chapadmalalian Stage/Age, late Miocene–early Pliocene) (Cione et al., 2007; Deschamps et al., 2012). Tomassini et al. (2013) conducted studies on the faunal association of Farola Monte Hermoso, and they only recognized one biozone, the *Eumysops laeviplicatus* Biozone, restricting its age to the early Pliocene; however, this conclusion has been methodologically questioned (e.g., Nicoli, 2015). We therefore follow the more traditional position of Cione et al. (2007) until this issue is resolved.

The fossil material studied here was compared directly with osteological material of extant representatives of the Teiidae family (Appendix 1). Images of the fossils were obtained using a digital camera or scanning electron microscope at the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia"
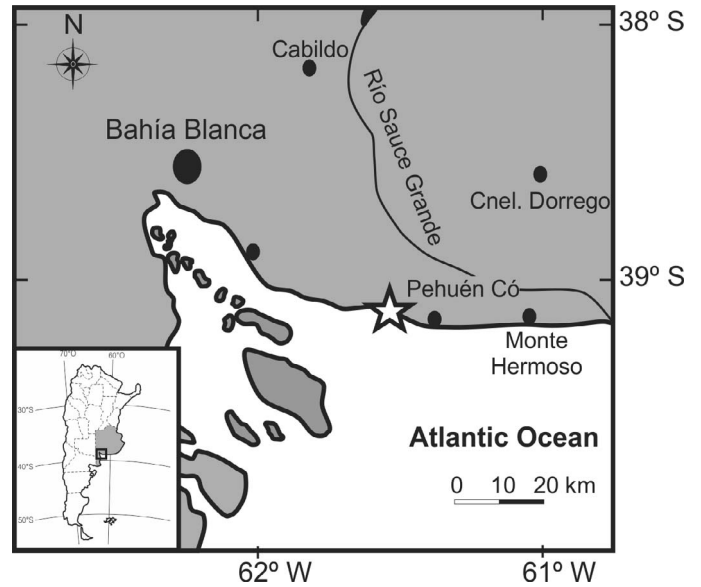

FIG. 1.   Location map of the Farola Monte Hermoso locality (38°58′S, 61°41′W), Argentina. Buenos Aires province in gray; star, Farola Monte Hermoso.

(MACN). Throughout the descriptions, roman numerals are used to denote absolute tooth positions, whereas letters are used for relative tooth positions.

Institutional Abbreviations.—QCAZR, Museo de Zoología de la Pontificia Universidad Católica del Ecuador sección Reptiles, Quito, Ecuador; FML, Fundación Miguel Lillo, Colección Herpetológica, Universidad Nacional de Tucumán, San Miguel de Tucumán, Argentina; MACN, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Ciudad Autónoma de Buenos Aires, Argentina; MNHNC, Museo Nacional de Historia Natural, Santiago, Chile; MZUSP, Museu de Zoologia, Universidade de São Paulo, São Paulo, Brazil; NMNH, National Museum of Natural History, Washington, DC; PVL, Colección Paleontología Vertebrados, Fundación Miguel Lillo, Universidad Nacional de Tucumán, San Miguel de Tucumán, Argentina; UMMZ, University of Michigan Museum of Zoology, Ann Arbor, Michigan; UNC, Universidad Nacional de Córdoba, Córdoba, Argentina; UNMdP, Colección Herpetológica, Universidad Nacional de Mar del Plata, Mar del Plata, Argentina; UNMdP-O, Colección Herpetológica–Sección Osteología, Universidad Nacional de Mar del Plata, Mar del Plata, Argentina; UNNE, Universidad Nacional del Nordeste, Resistencia y Corrientes, Argentina.

SYSTEMATIC PALEONTOLOGY

Squamata Oppel, 1811
Scleroglossa Estes, de Queiroz, and Gauthier, 1988
Autarchoglossa Wagler, 1830
Scincomorpha Camp, 1923
Lacertoidea Camp, 1923
Teioidea Estes, de Queiroz, and Gauthier, 1988
Teiidae Gray, 1827
Tupinambinae Bonaparte, 1831
Callopistes Gravenhorst, 1838

Type Species.—*Callopistes maculatus* Gravenhorst, 1838
Amended Osteological Diagnosis.—*Callopistes* differs from other teiids in possessing the following unique combination of features: a marked wedge between rami of the premaxillary process of the
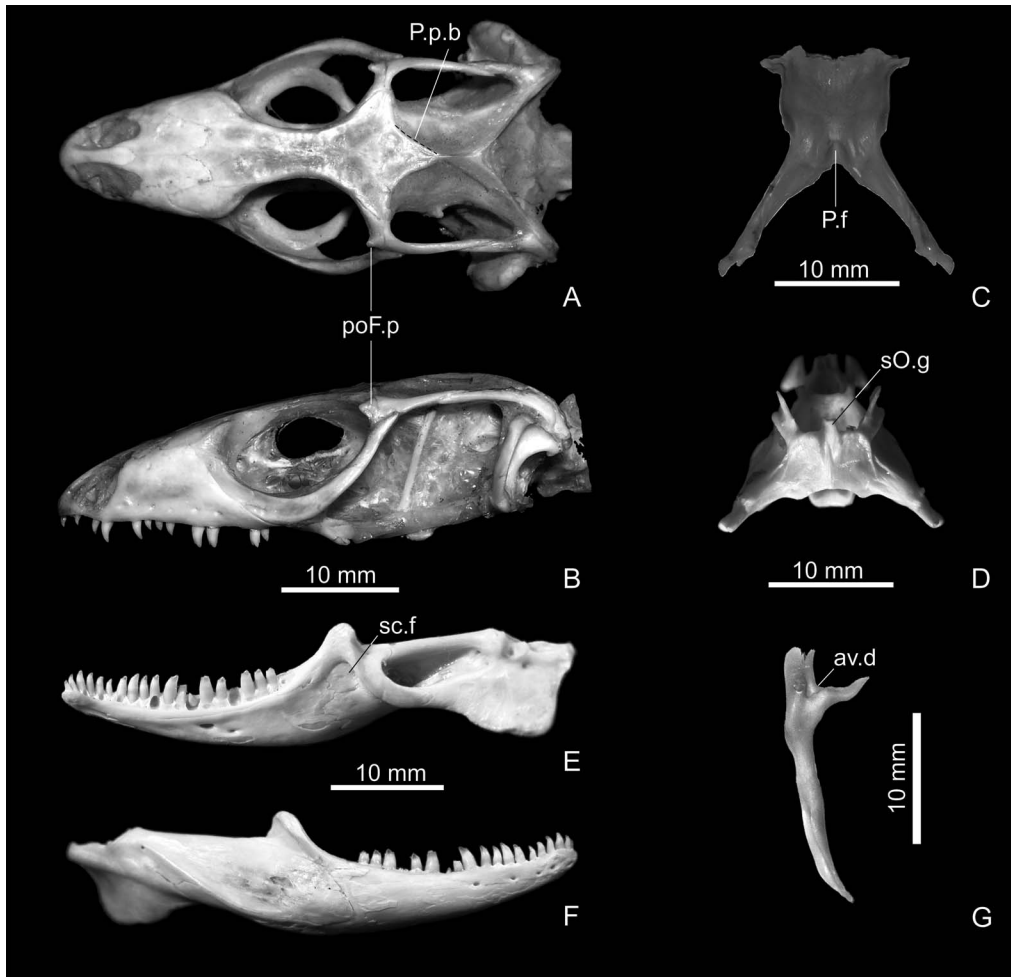
FIG. 2.   Skull of *Callopistes maculatus*. Skull MNHNC 4112 in dorsal (A) and lateral (B) views; parietal and supratemporals MNHNC 4113 in ventral view (C); braincase MNHNC 4113 in dorsal view (D); right hemimandible (MNHNC 4113) in medial (E) and lateral (F) views; pterygoid in ventral view (G). Abbreviations: av.d, anteroventral depression of the pterygoid; P.f, parietal fossa; poF.p, postfrontal protuberance; P.p.b, parietal plateau border; sc.f, subcoronoid fenestra (the bone exposed is the surangular); sO.g, supraoccipital groove.

maxilla; an evident anterior projected protuberance of the postfrontal (Fig. 2A, B); and an anteriorly displaced parietal fossa of the parietal (Fig. 2C). In this genus the posterior buttress of the maxilla is a low, wide, and poorly defined vertical crest, with a low, rounded dorsal protuberance; the parietal plateau has marked, straight borders (unlike the curved borders of *Tupinambis*) (Fig. 2A); the fronto-parietal roof is flat; the quadrate lacks the anteroposterior expansion observed in other Tupinambinae (Fig. 2B); the supraoccipital crest is replaced distally by a deep groove (Fig. 2D); the pterygoid presents an anteroventral depression (Fig. 2G); the dentary, in lateral view, presents a straight dorsal outline (Fig. 2F); the dentary posterior processes delimit, in lateral view, an important concavity that accommodate mainly the surangular and less so the angular (Fig. 2F); the splenial posterior border is vertical in medial view with an irregular suture, and with a small, anteriorly directed wedge at mid height (Fig. 2E); the splenial delimits the subcoronoid fenestra (Fig. 2E); the articular crest is very prominent; the medial expansion of the retroarticular process is a robust crest; and the contact between clavicles are dorsal to the interclavicular process of the interclavicle. Among Tupinambinae, the posterior projections of the premaxillary palatal shelf are shared only with *Dracaena*; whereas pterygoid teeth are present only in *Callopistes* and *Paradracaena*. Unlike the other Tupinambinae, the crest on the

crista transversalis is weak in *Callopistes*, and the hypapophysis of the third cervical vertebra is anteriorly orientated.

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Callopistes bicuspidatus Chani, 1976
Figures 3–5

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Type Material.—PVL 4618, incomplete partially articulated skull and mandibles. The remains include articulated left lacrimal, maxilla, prefrontal, jugal, and palatine (PVL 4618-1); isolated parietal (PVL 4618-2); articulated left postorbital and postfrontal (PVL 4618-3); isolated right dentary (PVL 4618-4); incomplete left hemimandible including angular, articular, dentary, splenial, and surangular (PVL 4618-5). The maxilla and dentaries each preserve nearly complete dental series.

Geographic Provenance.—Farola Monte Hermoso (38°58′S, 61°41′W), southeastern Buenos Aires province, Argentina.

Stratigraphic Provenance.—Sandbank #3 of the Monte Hermoso Formation (Bonaparte, 1960). This bank has been correlated to the *Trigodon gaudryi* Biozone that corresponds to the bioestratigraphic base of the Montehermosan Piso/Age (Cione and Tonni, 2005), dated to the late Miocene–early Pliocene (Cione et al., 2007).

Amended Osteological Diagnosis.—*Callopistes bicuspidatus* is characterized by an anterior extension of Meckel's canal below the symphysis and a short anterolateral process of the coronoid compared to the anterior extension of the angular/surangular. It
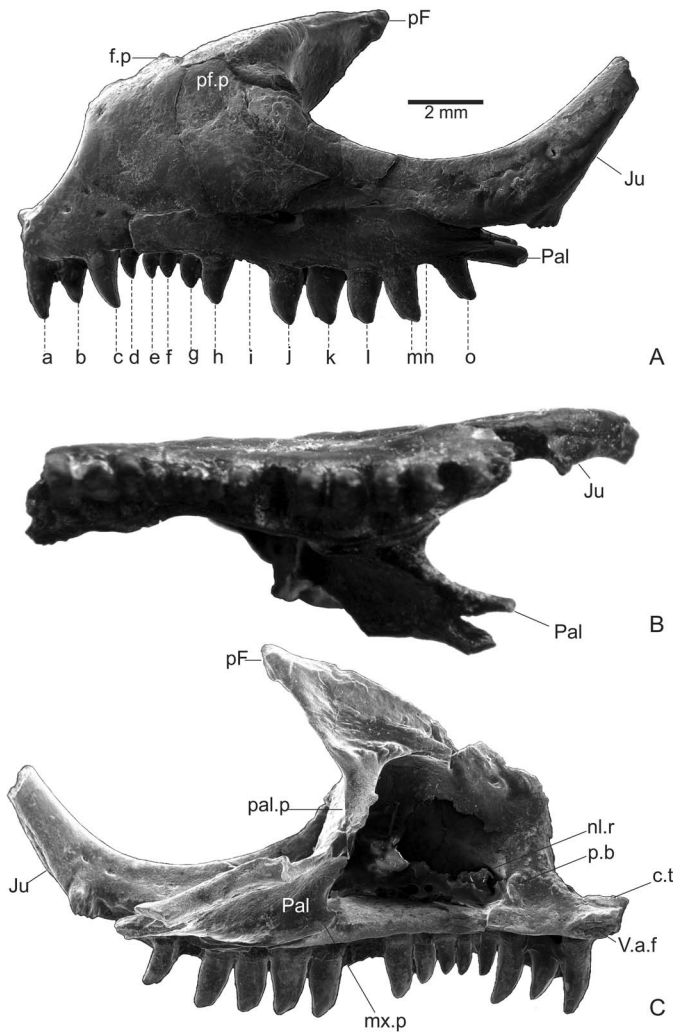
FIG. 3. Skull of *Callopistes bicuspidatus* Chani (1976) from the late Miocene–early Pliocene of Argentina. PVL 4618-1 in lateral (A), ventral (B), and medial (C) views. Abbreviations: c.t, crista transversalis; Ju, jugal; f.p, frontal process; p.b; posterior buttress; pF, prefrontal; pf.p, prefrontal process; Pal, palatine; pal.p, palatine process; mx.p, maxillary process of the palatine; nl.r, nasolacrimal ridge; V.a.f, vomer articulation facet.

differs from both extant species of the genus (*C. maculatus* and *C. flavipunctatus*) in having only bicuspid (no tricuspid) posterior teeth on the dentary and maxilla. It further differs from *C. maculatus* in possessing a much reduced posteromedial process of the postfrontal and the absence of postfrontal-jugal contact.

Redescription.—Fragment PVL 4618-1 (Fig. 3A–C) corresponds to the anterior left side of the skull and conserves the maxilla, prefrontal, lacrimal, jugal, and palatine bones. The maxilla is the largest bone of the set. Labially, the maxilla is smooth, without ornamentation, and is pierced by six labial foramina. The facial process presents an anteroposterior development of the dorsal end. Only the wide base of the frontal process is preserved. The prefrontal process is located posterior to the preserved portion of the frontal process (Fig. 3A). The anterior border of the facial process constitutes the posterior border of the fenestra exonarina whose lateral outline is slightly concave and vertical. The lingual and labial rami of the premaxillary process do not preserve their anterior terminal ends. There is a deep, vertical gutter between rami (medially displaced) that can be interpreted as the notch

seen in *C. maculatus* (MNHNC 4113). Part of a dorsoventrally extended articulation facet for the vomer is visible medially, upon the lingual ramus of the premaxillary process. Dorsally on the lingual ramus it is possible to observe the crista transversalis and its crest, both of which are poorly preserved. The depression that housed the vomeronasal organ is visible posterior to the crista transversalis as a shallow depression located posterior to the fenestra exonarina. Posterior to the vomeronasal depression is the posterior buttress (Brizuela and Albino, 2016). The posterior buttress is a vertical crest, dorsally simple but with a slight constriction immediately above the supradental shelf. The nasolacrimal ridge (=semilunar crest) is well defined and ends above the posterior buttress, posterior to which it delimits the deep nasolacrimal fossa of the facial process. The supradental shelf is fractured posteriorly to the posterior buttress. Anteriorly, the supradental shelf has a weak dorsoventral development delimiting the fenestra for the vomeronasal organ. Its maximum dorsoventral development is anterior to the articulation facet for the palatine, where it delimits labially the lateral posterior end of the coana. The dental series is lying between the parapet and the supradental ridge. It is anteriorly incomplete preserving 15 tooth positions with 13 complete teeth. Teeth (i) and (n) are missing. Tooth implantation is subpleurodont, where tooth positions are flanked by slim, mesial and distal interdental septa of distinct bone tissue, with cementum further binding teeth to the maxilla. A moderate sulcus dentalis is present between the bases of the teeth and the supradental ridge. The first preserved tooth (a) is unicuspid, high and mesiodistally compressed at the base. Apically, it is incomplete, but its conic form and slight posterior curvature are evident. The following tooth (b) presumably broke off and was later glued in the dental position in an erroneous orientation, where its mesial face is facing lingually. In other aspects it is similar to tooth (a) and (c). Teeth (d) to (f) are small and unicuspid. Apically, they are labiolingually compressed and less curved than the previously described teeth. Teeth (g) and (h) are similar in shape but larger than the previous teeth, although not as large as the anterior-most teeth. A small protuberance is insinuated on the mesial face of the tooth (h), posterior to which a mesiodistally orientated crest is developed. Teeth (j) to (o) are the largest of the series. These teeth are weakly bicuspid, their bases are similar to that of the first conserved tooth. The cusps in these teeth are separated by short, superficial intercuspidal grooves (i.e., vertical indentation between cusps). The distal, dominant cusp is conic, labiolingually compressed, and slightly curved distally. The mesial accessory cusp is much smaller, and it presents diverse degrees of differentiation among teeth. These cusps are compressed with little apical development (i.e., the mesial cusp does not alter significantly the lateral outline of the teeth). Resorption zones are present lingual to tooth positions (a), (c), (e), (g), (j), and (l). These pits are marked, subcircular, and deep.

The prefrontal is nearly complete and slightly displaced leaving exposed part of the articulation facet for the prefrontal process of the maxilla. The supraorbital process is well-developed, and has a large, robust oval crest on its orbital border. The prefrontal is excavated posterior to this crest. The palatine process is developed, it is inferred that in life this process greatly delimited the orbitonasal fenestra, excluding the frontal from the fenestra. The articulation with the palatine is through a large and concave suture. Laterally, the lacrimal and palatine processes delimit the medial border of the lacrimal foramen.
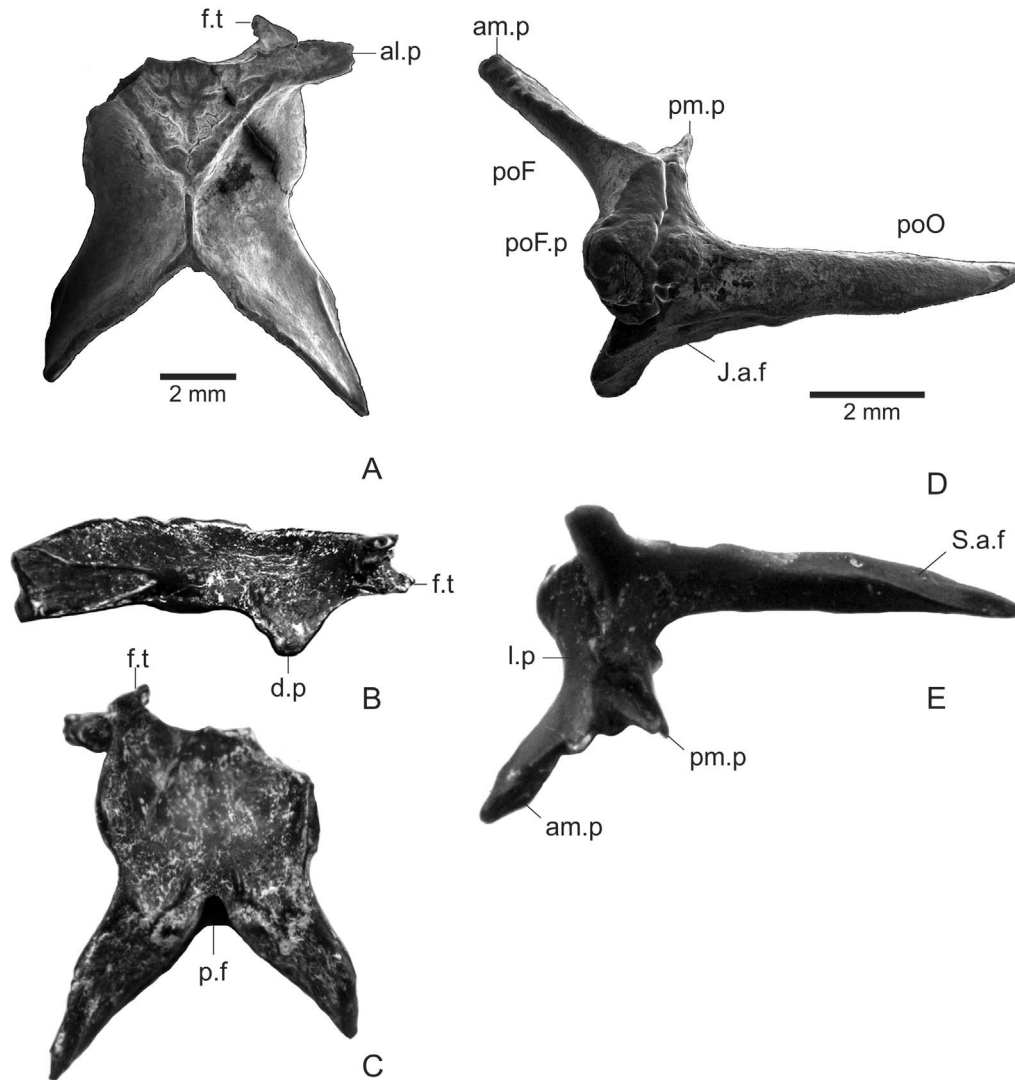
FIG. 4. Skull elements of *Callopistes bicuspidatus* Chani (1976) from the late Miocene–early Pliocene of Argentina. Frontal (PVL 4618-2) in dorsal (A), lateral (B), and ventral (C) views; postorbital and postfrontal (PVL 4618-3) in lateral (D) and medial (E) views. Abbreviations: al.p, anterolateral process; am.p, anteromedial process; d.p, descendant process; S.a.f, squamosal articulation facet; f.t, frontal tab; J.a.f, jugal articulation facet; l.p, lateral process; p.f, parietal fossa; poF, postfrontal; poF.p, postfrontal protuberance; pm.p, posteromedial process, poO, postorbital.

The lacrimal is a flat bone, that in lateral view it is of constant width, with a slight increase dorsally. The orbital border of this bone is more robust than the maxillary border. The suture with the prefrontal is straight, obliquely disposed, whereas the suture with the jugal is a short wedge, passing posterior to the jugal.

The jugal presents a boomerang shape, and the distal end of the temporal process is missing. The maxillary process is robust and somewhat concave laterally. Four suborbital and two maxillary nerve foramina are conserved. Ventrally, the articulation facet for the ectopterygoid is exposed, robust, and rugose.

The palatine does not conserve the vomerine process nor the distal end of the pterygoid process (Fig. 3B, C). The maxillary process is anteroposteriorly developed. The palatine sulcus (sensu Montero et al., 2004) is deep. There are three foramina of the palatine plexus seen dorsally on the anteroposterior groove. Laterally, the maxillary process constitutes the medial border of the infraorbital foramen. Dorsally, the palatine articulates with the prefrontal.

The parietal (PVL 4618-2) (Fig. 4A–C) is isolated and almost completely preserved and is missing its left anterolateral process, the left descending process, and the distal ends of the supratemporal process. The right anterolateral process is well developed and transversely orientated, constituting the antero-medial border of the supratemporal fenestra. In ventral view (Fig. 4C), medially to the base of the anterolateral process, is the lateral border of the right frontal tab. In dorsal view (Fig. 4A) the mandibular adductor musculature greatly advances on the dorsal surface of the parietal. The left and right adductors ultimately come in contact at the posterior-mid section of the parietal. Therefore, the parietal plateau (i.e., part of the parietal table not covered by musculature) is triangular, with the frontoparietal suture as the triangle's base and the apex posteriorly directed on the parietal midline. The lateral borders of the parietal plateau are well defined by two marked, robust, and irregular ridges. These ridges meet medially and continue posteriorly as a thin sagittal crest. The dorsal surface of the parietal plateau is irregular, with grooves and rugosities.
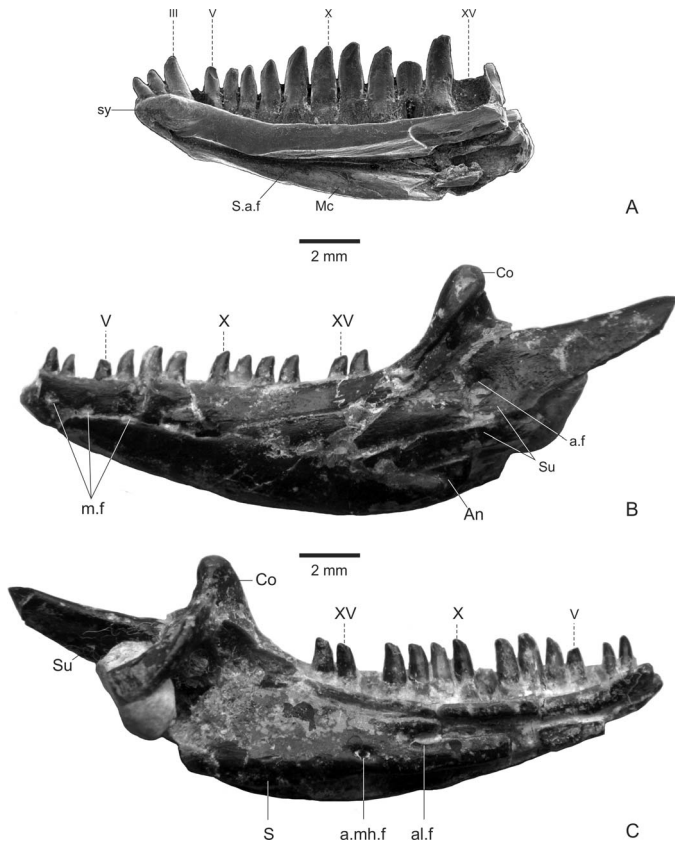
Fig. 5. Hemimandible elements of *Callopistes bicuspidatus* Chani (1976) from the late Miocene–early Pliocene of Argentina. Right dentary (PVL 4618-5) in medial view (A); left hemimandible (PVL 4618-5) in lateral (B) and medial (C) views. Abbreviations: a.f, anterior surangular foramen; al.f, alveolar foramen; a.mh.f, anterior mylohyoid foramen; An, angular; Co, coronoid; Mc, Meckel's canal; m.f, mental foramina; S.a.f, splenial articulation facet; S, splenial; Su, surangular; sy, symphysis.

Ventrally, the parietal fossa is anteriorly displaced and posteriorly opened (Fig. 4C). In lateral view (Fig. 4B) the (right) descendant process is triangular and large. On the supratemporal process there are clearly defined articulation facets for the supratemporals.

The left postfrontal and postorbital are articulated (PVL 4618-3) (Fig. 4D, E). Both bones are firmly united, although not fused, as they are clearly differentiated from each other by an evident suture. The postfrontal presents a large anteromedial process and a small posteromedial process. Dorsally on the posteromedial process, a transverse crest delimits the articulation facet for the frontal (anterior) and parietal (posterior) (Fig. 4E). The lateral process is cylindrical, and it extends ventrally excluding most of the postfrontal from the orbit. Ventrally, the lateral process widens, forming a large, robust and irregular protuberance that projects into the orbit (anterodorsal tuberosity of Venczel and Codrea, 2016). The postorbital is a bone restricted mostly to the temporal area. The jugal process of the postorbital reaches the orbit as a thin wedge, inserted below the postfrontal and above the jugal. The main development of the postorbital is on its anterior end, where it forms continuity with the anterior protuberance of the postfrontal. The articulation facet for the jugal is ventrolaterally orientated and separated from the articulation facet for the squamosal, that is ventromedially orientated (Fig. 4E).

Fragment PVL 4618-4 corresponds to the anterior part of a right dentary (Fig. 5A). This is a robust bone, labially smooth with five mental foramina, the last of which is located between teeth XII and XIII. Labially, the posterior end of the dentary is fractured and somewhat displaced. Between the parapet and subdental ridge is an almost complete dental series, delimited by a narrow sulcus dentalis. Ventral to these structures, at the anterior end, there is a simple symphysis followed by a well-developed suprameckelian lip that extends along the entirety of the conserved fragment. Immediately posterior to the symphysis, the suprameckelian lip is slightly convex, but posteriorly it is flat and progressively loses dorsoventral development. Meckel's canal is wide and opened to the symphysis, ending slightly under it. The dorsal articulation facet for the splenial develops to the VIII tooth position on the suprameckelian lip; the anterior aperture of Meckel's canal is anterior to this point. Below tooth position XIV, the inferior alveolar canal is exposed on Meckel's canal roof. The dental characteristics of this dentary are similar to those described for the maxilla. The first 15 functional tooth positions are preserved, all with teeth, except for tooth IV and XV. Teeth are in close contact with each other, and the anterior teeth (I–VIII) are low, whereas the posterior teeth are taller (IX–XV). The first three teeth are unicuspid and form a gradient of increasing height. Their bases are cylindrical, high, and slightly mesiodistally compressed. Apically, they end in a high cone, labiolingually compressed, with a weak distal curvature. There is also a subtle anteroposterior orientated ridge on the mesial face that is more evident on teeth III to VII. Tooth VII is similar to tooth II. From tooth VIII onward, the apical lateral outlines present a straight and oblique mesial border. This border corresponds to the previously mentioned ridge that is now preceded by a subtle protuberance. A shallow intercuspidal groove is observed posterior to this protuberance. As observed in the maxilla, the main cusp is the distal cusp, whereas the mesial cusps present different degrees of differentiation, but they are clearly bicuspid. Posterior to the last complete tooth position (XV) is the mesial wall of another tooth (XVI). Six resorption zones are present lingually to tooth positions II, IV, VII, IX, XI, and XIII. They are subcircular, the most posterior are deeper, probably because of a more advanced state.

The left hemimandible (PVL 4618-5) is composed of robust bones (Fig. 5B, C), but it is incompletely preserved, fragmented, and reconstructed. All bones are more or less preserved except for the articular. The dentary is almost complete, missing the anterolabial end. Its labial surface is smooth and bears a minimum of three mental foramina. A longitudinal crevice runs through the line of mental foramina; therefore, more foramina could have been present. The dorsal outline of the dentary is straight, whereas posteriorly the posterodorsal and posteroventral processes delimit a deep wedge. This wedge receives almost exclusively the surangular, whereas the angular is restricted to the ventral area. The dental series is demarcated by a narrow sulcus dentalis. Posterior to the symphysis, the suprameckelian lip is slightly convex, but thereafter it is flat and subsequently loses height. Meckel's canal is covered by the splenial. Meckel's canal is wide, medially opened, not restricted anteriorly, and extends anteriorly shortly below the symphysis. The anterior aperture of Meckel's canal extends to tooth position IV. Implantation characteristics are as those previously described. The dental series is complete, with 16 functional tooth positions, all with teeth except for positions I, IV, IX, and XIV. The six anterior teeth form a gradient of increasing height, but thereafter tooth height is constant. Teeth II and III are unicuspid,

straight, and small; their bases are oval in section because of mesiodistal compression. Tooth V is apically broken. Tooth VI is similar in shape to teeth II and III, but larger and with the apical end slightly curved distally. Teeth VII and VIII are similar to tooth VI, but somewhat larger and distally broken. Teeth X to XVI are high and slightly bicuspid like those described for the maxilla and right dentary. The splenial is triangular, flat, and extends to tooth position IV. Its anterior end is fractured and displaced, whereas the posterior end is not completely conserved. The alveolar foramen is larger and anteriorly located with respect to the smaller anterior mylohyoid foramen, and these foramina are located close to teeth XII and XV, respectively. The coronoid is completely conserved. Its lateral processes are short, and the anterolateral process does not surpass the last tooth position anteriorly, whereas the posterolateral process is much reduced and rests on the surangular. Although the posteromedial process does not conserve its distal end, it is clearly the largest of the ventral processes of the coronoid. This is a long, robust process that is posteriorly curved. Its anterior face is crossed by an evident, robust vertical crest. The anteromedial process is fractured, somewhat displaced, and poorly preserved. It is short and does not extend beyond the last tooth position; therefore, the ventral border of this process and that of the suprameckelian lip are continuous. The subcoronoid fenestra is delimited by the medial processes. Within the fenestra is a displaced bone fragment that would correspond to the coronoid facet of surangular (glue hinders its correct observation). The dorsal process of the coronoid is well developed; high; and characterized by an oblique, lateral crest. The surangular is cracked and incomplete, not conserving the posteromedial end. The surangular presents a lateral depression below the coronoid where the anterior surangular foramen is located. The anterior-most end of the surangular occupies almost exclusively the posterior wedge of the dentary. Lingually, the dorsal border of the mandibular fossa is cylindrical, robust, and somewhat larger anteriorly. Only the anterior-most end of the angular is preserved, and it is partially covered by the posteroventral process of the dentary.

Taxonomic Comments.—The studied specimen presents three characters shared by Borioteiioidea (Polyglyphanodontia) and Teiidae: abundant cement deposits at the base of the teeth (PVL 4618-1, 4618-4, and 4618-5); deep, subcircular resorption zones (i.e., replacement pits) (PVL 4618-1 and 4618-4); and a hypertrophied splenial with an important anterior development (PVL 4618-4/5) (Nydam et al., 2007).

Various character states allow the inclusion of the specimen among Teiidae. Contrary to the opinion of Chani (1976), the parietal (PVL 4618-2) is wider than long (length, 6.44 mm; width, ~10.44 mm) as in the Teioidea (=Gymnophthalmoidea of Goicoechea et al., 2016), whereas in the Borioteiioidea the relation is the opposite (Denton and O'Neill, 1995; Nydam and Cifelli, 2002; Nydam et al., 2007). Furthermore, the lack of a parietal foramen, the presence of descending process, the adductor musculature occupying more than two thirds of the parietal length, and an opened parietal fossa are characters present in Teiidae and not Borioteiioidea (Denton and O'Neill, 1995; Nydam and Cifelli, 2002; Nydam et al., 2007). The presence of a crista transversalis, and not a robust anterior buttress, is another character supporting affinities of the fossil with Teiidae (Brizuela and Albino, 2016). Furthermore, in the left hemimandible (PVL 4618-5), the anterior process of the coronoid overlaps the posterodorsal process of the dentary, an inverse disposition of what is observed in the Borioteiioidea

(Nydam et al., 2007). According to our observations, the fossil material also has the following features in common with Teiidae: two dorsal processes on the maxillary facial process (frontal and prefrontal processes, anterior and posterior, respectively); more than five labial foramina; posterior buttress behind the fenestra exonarina; supradental shelf not medially extended (as in Gymnophthalmidae); prefrontal with two evident crests; reduced parietal table by the advance of the adductor musculature; suprameckelian lip tapered posteriorly; abundant cementum at tooth bases; and deep resorption zones for replacement teeth.

Several characters of both the skull and jaw allow the assignation to Tupinambinae. The fossil shares with Tupinambinae a sigmoid ventral margin of the maxilla, a concave lateral face on the jugal, and the supratemporal fenestra delimited anteromedially by the parietal (Sullivan and Estes, 1997; Nydam et al., 2007; Brizuela, pers. obs.). Comparing to Teiinae, the dentary of the fossil and those of Tupinambinae share an anteriorly unrestricted Meckel's canal. Camolez and Zaher (2010) observed that within the splenial the anterior inferior alveolar foramen is posterior to the anterior mylohyoid foramen in Teiinae, whereas this relation is inverse in Tupinambinae and the studied fossil specimen. Also, the following trends are observed in Tupinambinae as well as in the fossil: presence of a dorsal crest on the crista transversalis, posterior buttress weakly developed, adductor musculature widely expanded upon the parietal, and posterodorsal and posteroventral processes of the dentary delimiting a large wedge outline.

Chani (1976) used the relationship between the length and the height of the maxilla to differentiate between Teiidae genera. According to our data, however, this character is considered invalid to discern members of this family, because this relationship remains constant (Fig. 6).

An aspect that we find promising for the osteological recognition of *Callopistes* among teiids is the morphology of the posterior end of the splenial. We observed that in the majority of teiids the splenial forms an oblique, concave to convex, wedge. *Aspidoscelis calidepis* is an exception because the wedge is horizontal. In *Callopistes* the posterior limit of the splenial is vertical (straight with an irregular suture) with a small, anteriorly directed wedge at mid height. Nevertheless, this useful character cannot be used to determine the fossil specimen because this part of the splenial is broken and covered with glue.

Among Tupinambinae, the parietal plateau of PVL 4618-2 more closely resembles that of *Callopistes*, *Paradracaena*, and *Tupinambis*, bearing a very thin sagittal crest posterior to the parietal plateau. This crest is much wider in *Dracaena* and *Crocodilurus*. The sharp straight borders of the parietal plateau further manifests the affinities of the specimen with *Callopistes*, whereas they are blunt and concave in *Tupinambis* and *Paradracaena*. Other features of the fossil specimen that are present in *Callopistes* are the greater development of the dorsal end of the posterior buttress that is almost absent in the other Tupinambinae; the surangular almost excluding the angular from the posterior wedge of the dentary (when the surangular is more represented in the dentary posterior wedge of the other Tupinambinae); and the straight dorsal outline of the dentary, also shared with the Teiinae. In addition, the fossil and *Callopistes* have a marked anterior protuberance of the postfrontal that projects into the orbit.

As stated, Estes (1983) considered the identification of the specimen by Chani (1976) as correct, although he did not mark
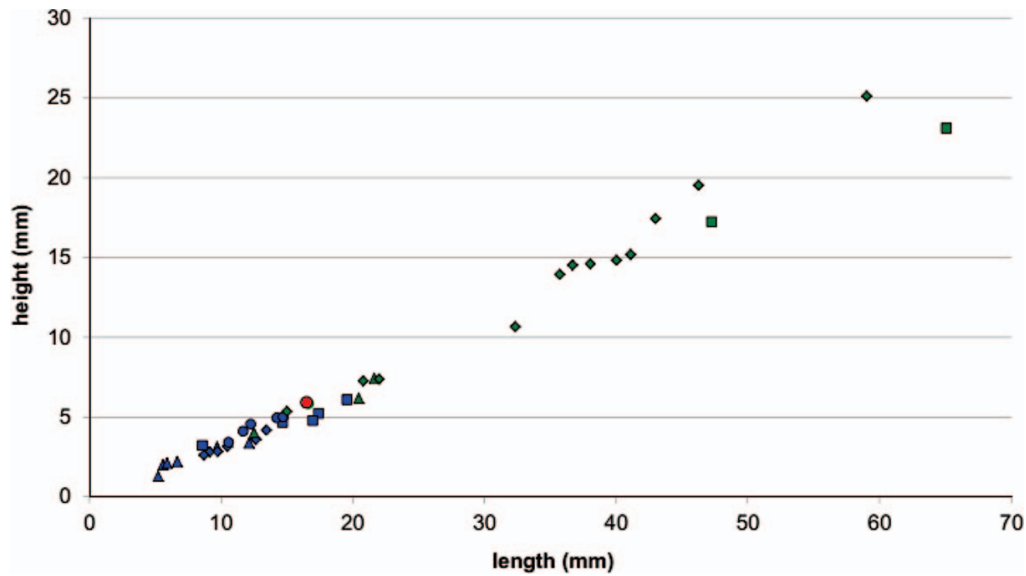
FIG. 6. Maxillae length vs. height relation of different Teiidae genera. In blue, Teiinae (square, *Ameiva*; triangle, *Cnemidophorus*; diamond, *Aspidoscelis*; circle, *Teius*; dash, *Kentropyx*); in green, Tupinambinae (triangle, *Crocodilurus*; circle, *Callopistes*; diamond, *Tupinambis*; square, *Dracaena*); and red circle, *Callopistes bicsupidatus*.

any other comment in this sense. Estes (1983), following Presch (1974a), considered the following as cranial diagnostic characters of *Callopistes*: the absence of the dorsal process of the squamosal, little contribution of the ectopterygoid to the suborbital fenestra (mentioned as inferior orbital foramen), and the presence of a marked sagittal crest on the parietal. Only the last character can be evaluated on the fossil material here studied. As mentioned, the sagittal crest is common to all Tupinambinae. The remaining characters listed by Estes (1983) are present in most Tupinambinae; therefore, they cannot be considered autapomorphies of the genus *Callopistes*. According to the phylogenetic analysis of Teiidae of Nydam et al. (2007), *Callopistes* retains the plesiomorphic condition of the tooth implantation similar to that present among the "cnemidophorine" Teiinae. Among Tupinambinae teiids, the subpleurodont implantation, with tooth positions delimited by interdental septa and not masked by cementum, is a condition present only in *Callopistes*. This genus also exhibits weak heterodonty that, according to Presch (1974b), varies among both extant species. In *C. flavipunctatus*, posterior teeth are bicuspid and tricuspid in both maxillae and dentaries, and they are only bicuspid in *C. maculatus* (Presch, 1974b). The last comment is modified here as both bicuspid and tricuspid teeth have since been confirmed in the posterior dentition of maxillae and dentaries of *C. maculatus* available in the compared material. In these tricuspid teeth, the central cusp is dominant, whereas the mesial accessory cusps are small, although the mesial is slightly larger than the distal. Among Tupinambinae, ontogenetic changes in dentition have been documented only in *Tupinambis* (Presch, 1974b; Dessem, 1985; Brizuela and Albino, 2010). Ontogenetic changes for *Callopistes* are unknown. Therefore, the fossil differs from both *C. maculatus* and *C. flavipunctatus*, because all of the posterior teeth are bicuspid (i.e., no tricuspid teeth are present). The specimen further differs from *C. maculatus* in the short anterolateral process of the coronoid that does not extend beyond the anterior projection of the surangular and angular.

In conclusion, we have recognized several diagnostic characters for *Callopistes*, some of which can be seen in the fossil material. Therefore, we consider *C. bicsupidatus* as a valid

species, but diagnosed on different characters than those originally proposed during its erection (Chani, 1976).

DISCUSSION

Systematic Considerations.—Based on their phylogenetic study, Harvey et al. (2012) erected the new subfamily Callopistinae to accommodate *Callopistes* as its only genus. In this hypothesis, Callopistinae is sister to all other teiids (Harvey et al., 2012) and these osteological characters diagnose it: the presence of a flat frontoparietal roof, the lack of parietal foramen, and the lack of subcoronoid fenestra (=surangular fenestra). Nevertheless, the last two states could not be verified as diagnostic. The absence of parietal foramen is common to all teiids and the subcoronoid fenestra is present in the specimens of *C. maculatus* used for comparison (Appendix 1). Furthermore, this last feature is common in teiids except for *Dracaena*, because of the ventral development of the coronoid between its medial processes. The most common morphology of the subcoronoid fenestra is that of the coronoid facet of surangular that is medially exposed under the coronoid and ventrally limited by the articular. This condition changes in *Crocodilurus amazonicus* and most *Tupinambis* species (*T. duseni*, *T. quadrilineatus*, and *T. rufescens*) where the splenial borders the subcoronoid fenestra anteriorly and the articular posteriorly. The case in *Callopistes* is different, because the splenial greatly borders the subcoronoid fenestra (Fig. 2E). Therefore, only the flat fronto-parietal roof of *Callopistes* would be an autapomorphy of Callopistinae. This state is also shared with *Aspidoscelis exsul* (*Ameiva exsul* in Harvey et al., 2012).

Because we were able to find more similarities between *Callopistes* and the rest of the Tupinambinae than with the Teiinae (e.g., relative positions of the splenial foramina, adductor musculature delimiting a parietal plateau), we support a point of view consistent with osteological based phylogenies (e.g., Denton and O'Neill, 1995; Sullivan and Estes, 1997; Nydam et al., 2007). The recognition of this genus as Tupinambinae is consistent with recent molecular study of Tucker et al. (2016). Also, several osteological characters observed on extant *Callopistes*, and not preserved in *C.*

bicuspidatus, are of taxonomic interest. Some of them have previously been recognized (e.g., flat frontoparietal roof, Presch, 1974a), whereas others are easily observed (Fig. 2) (quadrate not expanded anteroposteriorly, supraoccipital distally grooved, premaxillary palatal shelf posterior extensions, pterygoid ventral depression) or have been discussed above (splenial characteristics, subcoronoid fenestra). They could be synapomorphies of the genus.

Other outstanding characters involve the articular crest and the morphology of the medial expansion of the retroarticular process. The articular bone (or articular-prearticular complex) presents anterior and retroarticular processes, which are united by the articular crest (=prearticular crest of Estes et al., 1988). This crest is very well developed in *Callopistes* (Fig. 2E, F), more than in the other Tupinambinae. Also the medial expansion of the retroarticular process is more robust and less defined in *Callopistes* than in most teiids, which have a thin, straight crest (it is vertical in *Crocodilurus amazonicus* and ventrally curved in *Cnemidophorus ocellifer* and *Ameiva ameiva*).

Paleoenvironmental and Paleobiogeographical Considerations.—As mentioned, the systematic allocation of the specimen PVL 4618 from Farola Monte Hermoso to the genus *Callopistes* suggests an important discrepancy between the past and present distribution of this genus. The current distribution of the both species of *Callopistes* is restricted to the west of the Andes, whereas the fossil species *C. bicuspidatus* was recognized in the Atlantic Coast of Argentina.

Chani (1976) proposed that *Callopistes* would have had originated during the Miocene. Nonetheless, molecular data indicate this genus would have diverged from all other Tupinambinae during the Paleocene (Giugliano et al., 2007). These same data indicate that the two extant species diverged during the Oligocene. The sister position of *Callopistes* to the rest of Tupinambinae and the recognition of this subfamily in the Eocene (Donadío, 1985; Carvalho, 2001; Brizuela and Albino, 2016) favor the hypothesis of an early origin of the genus as suggested by Giugliano et al. (2007). Thus, *Callopistes* would have had an extended and unknown evolutionary history in South America where *C. bicuspidatus* could have been a representative of the ancestral populations of the genus distributed east of the Andes. The major uplift of the mountain system during the Eocene (Incaic phase, late Eocene, Ortiz-Jaureguizar and Cladera, 2006) would have been caused the divergence of the species and its persistence until the Miocene–Pliocene. The present distribution of the genus is therefore relictual, whereas the estimated time of dispersion of both extant species coincides with important tectonic events that further elevated the Andes mountain system (Pehuenche Middle Miocene, Ortiz-Jaureguizar and Cladera, 2006).

Callopistes is presently distributed from southern Ecuador through Peru and in north central Chile (Harvey et al., 2012) in a range of harsh conditions of temperature and water availability. This region corresponds to the Desert Biogeographical Province (Andean-Patagonic Domain) that extends through the Pacific coast of South America between parallels 5°S and 30°S (Cabrera and Willink, 1980). It is a latitudinally extended area characterized by warm and very dry climate because of the effects of the Humbolt's current of the Pacific Ocean. Precipitation does not exceed 110 mm/yr, and it is not regularly distributed, with greater precipitation in the north and south than the center (Arica and Iquique, Chile) where precipitation is close to zero (Cabrera and Willink, 1980). In this extended geographic region, *C. flavipunctatus* and *C. maculatus* present an allopatric

distribution, with *C. flavipunctatus* distributed to the north (south Ecuador and Peru) and *C. maculatus* to the south (Chile from 24°S to 37°S; Vidal and Díaz-Páez, 2006). In the north, *C. flavipunctatus* is found on the both sides of the Western Andean Mountain Range (Crespo and Koch, 2015) within the Equatorial Dry Forest ecoregion, whereas further south its distribution reaches the Pacific Desert (Venegas, 2005). In the highland region of Peru (Piura, Lambayeque, Cajamarca, and La Libertad departments) and in the Equatorial Dry Forest, the mean temperature is ~15.47°C, whereas in the coastal areas the mean temperature reaches 28.8°C (Fierro-Zapata and Pérez-Díaz, 2007). *Callopistes maculatus* extends south to the VII Region of Chile (Vidal and Díaz-Páez, 2006). In this region (e.g., Parque Nacional Bosque Fray Jorge) temperature varies from ~25°C in summer to ~21°C in winter (Kelt et al., 2004). In these environments, *C. maculatus* presents a seasonal behavior, being more active in spring and summer, and presenting a preferred body temperature of approximately 39°C (Cortes et al., 1992). Therefore, according to the present distribution of both species of *Callopistes*, this genus is restricted to annual mean temperatures >15°C and extremely arid environments (<110 mm/yr). These conditions clearly contrast with the proposed hypothesis of the paleoenvironment for the Montehermosan in Farola de Monte Hermoso.

At present, the region of Farola Monte Hermoso is known as Dry Pampa (Prieto, 2000). It is characterized by a warm climate, with mean annual temperatures between 13 and 17°C, and with mean precipitation varying between 500 and 800 mm/yr (Cabrera and Willink, 1980; Prieto, 2000); however, the paleoenvironmental reconstructions suggest different conditions in the past. Because the lack of paleobotanical evidence, these reconstructions are built only on the abundant and diverse vertebrate content of the formation as mentioned previously. Based mainly on mammals, most reconstructions generally agree the paleoenvironment was similar to that of the Chaco region (Tonni, 1974; Chani, 1976; Gonzaga, 1996) that is characterized by seasonal rains that vary from 500 mm/yr in the west to 1,200 mm/yr in the east, and with mean annual temperatures between 20 and 23°C (Cabrera and Willink, 1980). In contrast, other authors consider the Montehermosan to have had a wetter grasslands setting (Pascual, 1984; Pascual et al., 1996).

The paleoherpetofauna of Farola Monte Hermoso in addition to *Callopistes* preserved amphibians (*Rhinella* cf. *R. Schneideri*, *Ceratophrys ameghinorum*, and *Lepidobatrachus australis*), a testudinid (?*Chelonoides australis*), and other squamates (Gasparini and Báez, 1975; Gasparini et al., 1986; de la Fuente, 1997; Fernicola, 2001; Albino et al., 2009; Tomassini et al., 2011, Nicoli, 2015). Among the squamates, snakes are represented by an indeterminate Boinae (Albino, 1992; Albino and Carlini, 2008), an indeterminate Colubridae (Albino, 1989), and a Viperidae aff. *Bothrops* (Albino and Montalvo, 2006), whereas lizards include only the Teiidae *Tupinambis* (Albino et al. 2009). The Boinae are currently absent from this region and are confined to the north of 34°S (Giraudo and Scrocchi, 2002), where temperatures are higher than 13–17°C (Cabrera and Willink, 1980). The presence of these snakes suggests a warmer climate during the Montehermosan than at present, in agreement with the Chaco paleoenvironmental interpretation (Albino, 1992). In the same sense, the amphibians, and possibly the giant turtle ?*Chelonoides australis*, also support higher temperatures (Gasparini et al., 1986; Tomassini et al., 2011; Zacarias et al., 2014; Nicoli, 2015). Humidity inferences are less delimited, but lower distributional

limits of *Lepidobatrachus* (350 mm/yr) and *Tupinambis* (200 mm/yr) suggest that rainfall regime during the Montehermosan could have had lower limits close to these values. Likewise, the precipitation parameters inferred from the mammalian Montehermosan fauna suggest a minimum precipitation of 500 mm/yr (Pascual and Odreman Rivas, 1971; Chani, 1976). Therefore, we interpret that the climatic requirements of *C. bicuspidatus* would have been different from that of the extant species, especially regarding humidity and water availability.

According to our revision, *Callopistes bicuspidatus* is a valid species, although supported on different characters than those originally proposed by Chani (1976). The Tupinambinae genus *Callopistes* therefore includes three species: the extant *C. flavipunctatus* and *C. maculatus* and the extinct *C. bicuspidatus*. The genus would have originated in the Paleocene, whereas the two extant species differentiated during the Oligocene. *Callopistes bicuspidatus* probably originated before the Incaic phase of the Andean orogeny (Eocene). The evolutionary history at both sides of the Andes might explain the different ecological and environmental conditions exploited by the extinct species with respect to the extant species. It exploited more humid conditions than the living species of the genus.

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APPENDIX 1

Reference Material

Ameiva ameiva, UNMdP 796, UNMdP 1235, UNNE 1374, UNNE 1365, UNMdP-O 27, UMMZ 149442, UMMZ 176270, NMNH 257529, NMNH 257530, NMNH 292414, NMNH 292419, NMNH 290898; *Ameiva bifrontata*, UMMZ 149443, UMMZ 149444, UMMZ 150782, UMMZ 149449; "*Ameiva*" *exsul*, UMMZ 149448, UMMZ 200865; "*Cnemidophorus*" *lacertoides*, UNMdP-O 80; *Cnemidophorus lemniscatus*, UMMZ 189452; *Cnemidophorus longicauda*, UNMdP-O 51, UNMdP-O 52, UNMdP-O 81; *Cnemidophorus ocelifer*, UMMZ 149522; *Cnemidophorus serranus*, UNC C371, UNMdP-O 82; *Cnemidophorus tergolaevigatus*, UNMdP-O 83; *Kentropyx viridistriga*, UNNE 4647, UNNE 1062; *Kentropyx calcarata*, NMNH 292412, MZUSP 81580, MZUSP 82978; *Aspidoscelis cadilipes*, UMMZ 149550, UMMZ 149457, UMMZ 149459, UMMZ 149460; *Aspidoscelis communis*, UMMZ 149574; *Aspidoscelis cozumela*, UMMZ 149464; *Aspidoscelis deppii*, UMMZ 149551, UMMZ 149552; *Aspidoscelis exsanguis*, UMMZ 138822, UMMZ 149569; *Aspidoscelis gularis*, UMMZ 149553; *Aspidoscelis sexlineata*, NMNH 313460, UMMZ 149576; *Teius teyou*, UNMdP-O 15, UNMdP-O 16, UNMdP-O 22, UNMdP-O 23, UNC C365, UNNE 1398, UNNE 8715; *Teius oculatus*, UNC C360, UNC C368, UNC C369, UNMdP-O 53, UNNE 4464, UNNE 4462; *Teius suquiensis*, UNC C366; UNC C367; UNMdP-O 84, UNMdP-O 85; *Callopistes maculatus*, MNHNC 4112, MNHNC 4113; *Dicrodon guttulatum*, QCAZR 2139; *Tupinambis duseni*, MZUSP 92131; *Tupinambis merianae*, UNMdP-O 1 to 14, UNMdP-O 17 to 20, UNMdP-O 24 to 26; UNMdP-O 28, UNMdP-O 32, UNMdP-O 33, UNMdP-O 35, UMMZ 190109; *Tupinambis quadrilineatus*, MZUSP 84921, MZUSP 84928; *Tupinambis rufescens*, UNMdP-O 36, FML 7545, FML 7547, FML 1336, FML 2560, MZUSP 93082, MZUSP 93083, MZUSP 93084, NMNH 342486; *Tupinambis teguixin*, NMNH 220279, MZUSP 92087, MZUSP 92149; *Crocodilurus amazonicus*, MZUSP 8526, MZUSP 12624, MZUSP 92074; *Dracaena guianensis*, MZUSP 40082, NMNH 220278; *Dracaena paraguayensis*, MZUSP 62849.