Cool Geckos: Does Plesiomorphy Explain Morphological Similarities between Geckos from the Southern Cone?

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Abstract.—The South American genus *Homonota* comprises 10 species of Broad-Headed Geckos that reach the austral limit for the Gekkota. Historically, morphological data have supported the monophyly of a group including *Homonota* and the Chilean genus *Garthia*, with the latter possibly embedded within the former. In contrast, molecular evidence indicates these two genera to be in separate clades and that *Homonota* is more closely related to the Leaf-Toed Geckos of the genus *Phyllodactylus*. Here, we analyze 592 morphological characters in *Garthia*, *Homonota*, and additional phyllodactylid geckos to evaluate their morphological similarities. Our results indicate that *Homonota* and *Garthia* share a great majority of both external and internal characters and are nearly indistinguishable on morphological grounds. These results are interpreted in the light of a recently published multigene molecular phylogeny, and they suggest the symplesiomorphic retention of many morphological states linked to miniaturization and terrestriality in *Garthia* and *Homonota*, and concomitant differentiation of the American Leaf-Toed Geckos.

Resumen.—El género *Homonota* del sur de América del Sur comprende diez especies de gecos de cabeza ancha, alcanzando el límite austral para los Gekkota. Históricamente, los datos morfológicos han apoyado la monofilia de un grupo que incluye *Homonota* y el género chileno *Garthia*, con la posibilidad de que el género anterior estuviese contenido en el primero. Por otro lado, la evidencia molecular reciente indica que éstos dos géneros forman dos clados separados y que *Homonota* está más cercano a los gecos con dedos en forma de hoja del género *Phyllodactylus*. En este trabajo, analizamos 592 caracteres morfológicos en *Garthia*, *Homonota*, además de otros de la familia Phllodactylidae con el propósito de evaluar las similitudes morfológicas. Nuestros resultados indican que *Homonota* y *Garthia* comparten la mayoría de caracteres externos e internos, y que son casi indistinguibles morfológicamente. Estos resultados son interpretados utilizando una filogenia molecular reciente de varios genes, y sugieren que *Garthia* y *Homonota* retienen una gran cantidad de simplesiomorfias, las cuales están asociadas a sus hábitos terrestres y a procesos de miniaturización, como también a su diferenciación de los gecos americanos con dedos de hoja.

The family Phyllodactylidae (Leaf-Toed Geckos, Gamble et al., 2008, 2011a) includes the genera *Asaccus*, *Garthia*, *Homonota*, *Gymnodactylus*, *Haemodracon*, *Ptyodactylus*, *Tarentola*, *Thecadactylus*, *Phyllodactylus*, and *Phyllopezus* (the Brazilian genus *Bogertia* was recently synonymized with *Phyllopezus*, Gamble et al., 2012a). This family has a disjunct geographical distribution, ranging from North and South America, the Caribbean, North Africa, Mediterranean region, Arabian Peninsula, and the Middle East (Gamble et al., 2008; Pough et al., 2016). Time-calibrated molecular phylogenies place the origin of the Phyllodactylidae in the Mid- to Early Late Cretaceous and suggest the New World forms (exclusive of the subgenus *Neotarentola*) radiated in America after one or more trans-Atlantic dispersal events from Africa to South America between 53 and 87 Ma at the earliest (Gamble et al., 2011a). The South American endemic *Homonota* originated during the Miocene, with estimates ranging from the Langhian (~15 mya, Morando et al., 2014) to the Burdigalian or Aquitanian (~20 mya, Gamble et al., 2011a).

Fossil geckos are uncommon overall (Daza et al., 2014), and this also is true for phyllodactylid geckos. Phyllodactylid fossils are restricted to *Tarentola* elements from the Miocene of Morocco (Rage, 1976) and Pliocene–Pleistocene of Spain (Blain and Bailon, 2006). Subfossil material has been recovered for *Tarentola americana* (Upper Pleistocene, Bahamas [Etheridge, 1966]; Pleistocene, Cuba [Koopman and Ruibal, 1955]), *Tarentola* sp.

(Tenerife [Bolet, pers. comm.]), *Thecadactylus rapicauda* (Upper Pleistocene–Holocene, Barbuda, West Indies and Yucatan [this material was initially mentioned by Langebartel, 1953 and subsequently confirmed by Auffenberg, 1958; Etheridge, 1964; and Estes, 1983]), and *Homonota* sp. (Quaternary, Argentina [Albino, 2005]). Also, Middle Miocene *Phyllodactylus* fossils from Slovakia (Estes, 1969, 1983) are now attributed to the sphaerodactylid genus *Euleptes* (Čerňanský and Bauer, 2010; Daza et al., 2014).

Homonota Gray (1845) is endemic to Southern Cone of South America, with a distributional range covering Bolivia, Paraguay, Uruguay, central west Brazil, and Argentina (Fig. 1; Kluge, 1964; Vanzolini, 1968; Peters and Donoso-Barros, 1970; Cei, 1986, 1993). It includes 10 described species of crepuscular geckos, nocturnal geckos, or both (viz. *andicola*, *borellii*, *darwinii*, *fasciata*, *rupicola*, *underwoodi*, *taragui*, *uruguayensis*, *whitii*, and *williamsii*; Morando et al., 2014). *Homonota* geckos are largely terrestrial, being found in sandy environments, under leaf litter, rocks, or in pieces of wood (Kluge, 1964; Cei, 1986, 1993). Most species have restricted distributions, but two species—*H. fasciata* and *H. darwinii*—have colonized large areas, apparently at least partly due to their strong anthropophilic associations, accidental introductions, and their capability to exploit a wide diversity of habitats (Kluge, 1964; Gómez and Acosta, 1998a,b). *Homonota fasciata* (including its synonyms *H. horrida* and *H. pasteuri*; Abdala and Lavilla, 1993) is known as an outcrop specialist (Fredericksen et al., 2003), but it seems to have experienced population declines in some areas correlated with microhabitat loss due to accidental wildfires (Pelegrin and Bucher, 2009).
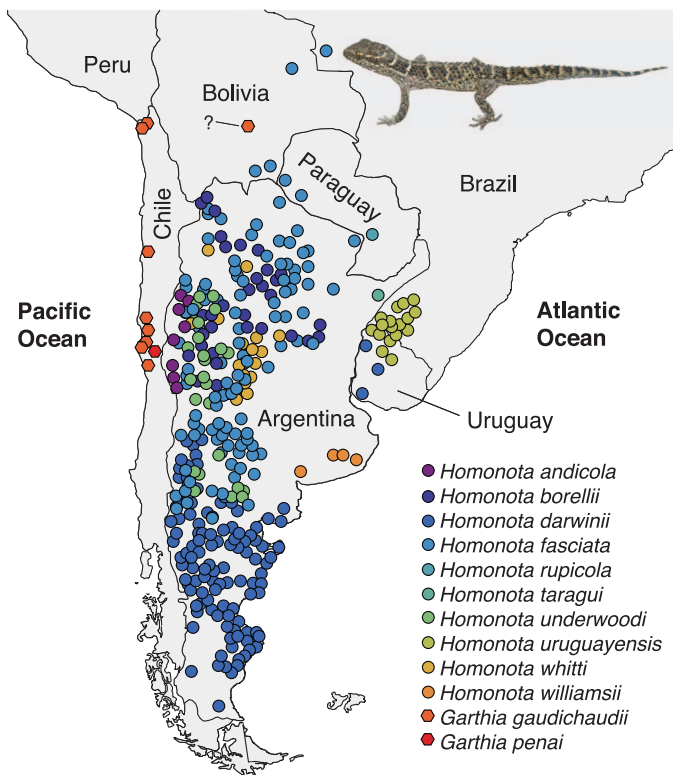
FIG. 1. Distributions *Garthia* and *Homonota*. Modified from Kluge (1964) and Morando et al. (2014) with the addition of *G. penai*, *H. rupicola*, and new localities from literature (Vanzolini and Donoso-Barros, 1966; Marquet et al., 1990; Martori and Aun, 1994; Lions et al., 1997; Acosta and Murúa, 1998; Guerreiro et al., 2005; Cacciali et al., 2007; Pelegrin and Bucher, 2009; Troncoso-Palacios, 2014) and data from the Instituto de Herpetología, Fundación Miguel Lillo, Argentina. Question mark indicates an unconfirmed record of *Garthia gaudichaudii* in Bolivia in Kluge (1964). Photo by D. Baldo, *Homonota fasciata* from Fuerte Esperanza, Departamento General Güemes, Provincia del Chaco, Argentina.

Homonota darwinii reaches the southernmost distribution for any gecko in the world (Abdala, 1998; Piantoni et al., 2006; Aguilar and Cruz, 2010), inhabiting the steppes of Patagonia to at least 54°S in Santa Cruz Province in Puerto Deseado, Argentina (Bauer, 2013; Vitt and Caldwell, 2014) and areas West of Rio Gallegos (Morando et al., 2014). These geckos have developed adaptations to cold temperatures such as protracted reproductive cycles, low reproductive output, long lifespan, late maturity, and enhanced parental care of fewer offspring (Piantoni et al., 2006; Ibargüengoytía and Casalins, 2007). Observations in captivity and in the wild indicate that this species opts for cooler retreat sites than *H. borellii* (Cruz et al., 2004), *H. fasciata* (Aun and Martori, 1994), and *H. underwoodi* (Werner et al., 1996). These adaptations seem to indicate physiological adaptations to cold temperatures, although under extreme cold conditions, *H. darwinii* selects diurnal retreats almost exclusively on the warmer western slopes of hills (Aguilar and Cruz, 2010; Weeks and Espinoza, 2013).

Diagnosing the genus *Homonota* has been problematic because its original description and the generic assignment of Southern Cone geckos has been a messy affair. Early taxonomists frequently focused so heavily on toepad characteristics of geckos that padless forms often were allocated to one of a few nonscansorial genera with little care for other putatively informative features (Russell and Bauer, 2002). In

this instance, species now assigned to *Homonota* (and the morphologically similar *Garthia*, see below) were variously placed in the genera *Gymnodactylus* Duméril & Bibron, 1836; *Saurodactylus* Fitzinger, 1843; and *Gonatodes* Boulenger, 1885 (see also Pincheira-Donoso, 2006; Uetz et al., 2016). Kluge (1964) reviewed the taxonomy of *Homonota*, synonymizing *Wallsaurus* Underwood, 1954, that had been established for *Gymnodactylus horridus*, but noting several external differences between *H. gaudichaudii* and other *Homonota*. In the following years, Donoso-Barros (1965a,b; see also Vanzolini and Donoso-Barros, 1966) described the genus *Garthia* with the Chilean endemic *G. gaudichaudii* as its type species. This taxonomic arrangement was followed in many subsequent publications (e.g., Donoso-Barros, 1966; Peters and Donoso-Barros, 1970; Abdala, 1996); nevertheless, *Garthia* has been treated as a synonym of *Homonota* by other authors (Kluge, 1991, 2001; Rösler, 1995, 2000; Pincheira-Donoso, 2006; Vidal et al., 2008). Recently, molecular phylogenies have confirmed the validity of *Garthia* and rejected the monophyly of a *Homonota* + *Garthia* clade (Gamble et al., 2008, 2011a; Morando et al., 2014).

Although there is strong support for Phyllodactylidae based on molecular data (Gamble et al., 2008), there are, so far, no morphological synapomorphies to diagnose this family or many of its constituent genera. The genus *Homonota* has previously primarily been differentiated from *Garthia* by the lack (*Homonota*) and presence (*Garthia*) of an ungual sheath for the retractile claws (Vanzolini and Donoso-Barros, 1966), although some other putatively diagnostic characters have been proposed (see below).

The main goal of this study was to examine in detail the internal and external morphology of phyllodactylid geckos and to generate more robust morphological diagnoses, especially of *Homonota* and *Garthia*. We evaluated the results of partitioned analyses of morphological and molecular data for all phyllodactylid genera and considered miniaturization and terrestriality as important factors shaping the morphology of these geckos.

MATERIALS AND METHODS

Anatomical Observations.—We reviewed the anatomy of 24 species of phyllodactylid geckos representing 10 genera by using material from specimens in 13 collections (Appendix 1, institutional abbreviations follow Leviton et al., 1985 and Sabaj Pérez, 2014). Observations were based on five different preparations: standard wet specimens, cleared and stained preparations, dry skeletons, X-rays, and CT scans (XRCT). Clearing and staining followed previously used protocols (Hanken and Wassersug, 1981; Bauer, 1986). We observed specimens with an MS6 dissecting microscope (Leica Microsystems, Wetzlar, Germany) photographed them with a Coolpix 995 (3.1 Megapixels, 3× Optical Zoom; Nikon Corp., Tokyo, Japan), and used Illustrator® CS3 13.0.2 (Adobe Systems, San Jose, California USA) to trace directly over the digital photographs; details of digital drawings were complemented with sketches made with a camera lucida. Three-dimensional models were generated using Avizo Lite 3D software (https://www.fei.com/software/amira-avizo/; FEI, Hillsboro, Oregon USA). XRCT data were obtained with an Xradia MicroCT scanner (Micro Photoincs, Inc., Allentown, Pennsylvania USA) at the University of Texas at Austin High-Resolution X-ray Computed Tomography Facility, Digimorph (http://digimorph.org). The morphological data set consists of 592 characters (401 cranium, 179 postcranium, and 11 from the

integument; project 2538 at http://www.morphobank.org) in 17 phyllodactylid species including all recognized extant genera and two outgroups (some species were used only for congeneric comparisons to determine interspecific variation). The characters examined are known to be variable among squamates and have been used in previous studies (Daza, 2008; Daza and Bauer, 2012). The morphological data set is a compiled list from 48 publications (Lakjer, 1927; McDowell and Bogert, 1954; Holder, 1960; Kluge, 1964, 1976, 1995; Vanzolini and Donoso-Barros, 1966; Meszoely, 1970; Rieppel, 1980a,b, 1984a; Gauthier, 1982, 1984; Borsuk-Białynicka, 1983; Estes, 1983; de Queiroz, 1987; Sumida and Murphy, 1987; Estes et al., 1988; Etheridge and de Queiroz, 1988; Gauthier et al., 1988; Grismer, 1988; Frost and Etheridge, 1989; Bauer, 1990a,b; Greer, 1990; Carroll and DeBraga, 1992; Kluge and Nussbaum, 1995; Abdala, 1996, 1998; McGuire, 1996; Bell, 1997; Norell and Gao, 1997; Evans and Barbadillo, 1998; Gao and Norell, 1998, 2000; Lee, 1998; Caldwell, 1999; Lee and Caldwell, 2000; Rieppel and Zaher, 2000; Tchernov et al., 2000; Kearney, 2003; Conrad, 2006, 2008; Conrad and Norell, 2006; Rieppel et al., 2008; Arnold, 2009; Daza, 2008; Daza and Bauer, 2012).

The species analyzed are interpreted as exemplars of their respective genera. For this reason, these characters ought to be considered general but not universal for each genus. Taxon sampling outside Phyllodactylidae is minimal considering the diversity of the Gekkota as a whole, and this might have some effect on the phylogenetic results. As our main focus was on the morphology of *Homonota* and *Garthia*; however, we think this limitation will not strongly affect our conclusions. Currently, there are no morphological synapomorphies for Phyllodactylidae. In addition, all previous morphological analyses including phyllodactylid geckos fail to recover a monophyletic group (Kluge and Nusbaum, 1995; Abdala and Moro, 1996; Abdala, 1998; Daza, 2008). We consider Phyllodactylidae as recovered from molecular data to be monophyletic (Gamble et al., 2008, 2011a) and evaluate the relationships within this group only.

Molecular Data.—We assembled a molecular genetic data set consisting of 5450 aligned base pairs (bp) of eight nuclear loci; the six protein-coding genes DMXL1 (970 bp), RAG1 (1071 bp), RAG2 (366 bp), C-MOS (375 bp), ACM4 (441 bp), and PDC (397 bp); and the two introns RBMX (600 bp) and ACA4 (1230 bp). Most of the data were previously published (Werneck et al., 2012; Morando et al., 2014; Gamble et al., 2015), but additional data were generated for some taxa using Sanger sequencing of polymerase chain reaction amplicons with primers from the literature (Gamble et al., 2008; Werneck et al., 2012; Morando et al., 2014). A complete list of sequences and taxa is included in Table S1 (Supplementary Data).

Phylogenetic Analyses.—The morphological data set was analyzed using maximum parsimony with the computer program TNT (Goloboff et al., 2001, 2008; Goloboff and Catalano, 2016). Twenty independent searches were completed using defaults of 'xmult' command plus 10 cycles of tree drifting (Goloboff, 1999).

The concatenated molecular genetic data were analyzed using maximum likelihood in the software RAxML-HPC BlackBox, version 8.2.9 (Stamatakis, 2014) implemented on the CIPRES (Cyberinfrastructure for Phylogenetic Research) Science Gateway (Miller et al., 2010). Nodal support was estimated using rapid bootstrapping, that was stopped automatically after 456 replicates, a restriction of the software. Optimal data partitioning and model selection were conducted with PARTITION-FINDER, version 1.1.0 (Lanfear et al., 2012), by using the greedy

search algorithm and Bayesian information criterion model selection.

RESULTS

Phylogenetic Relationships.—Results from the molecular (Fig. 2A) and the morphological (Fig. 2B) data sets produced discordant topologies. The molecular genetic data were consistent with recently published molecular phylogenies at well-supported nodes, including relationships among phyllodactylid genera (Gamble et al., 2008, 2011a, 2015) and among *Homonota* species (Morando et al., 2014). The analysis of the morphological data set produced 23 equally most parsimonious trees (MPTs). Seven trees showed a monophyletic Phyllodactylidae. *Garthia* was found to be sister to *Homonota* in 11 of the MPTs and nested with *Homonota* in 12 of the MPTs. We selected one of the MPTs as our preferred hypothesis (Fig. 2B, the most consistent with the molecular topology) and compared this MPT with the molecular tree by using TNT for topology compatibility (Goloboff, 2008), resulting in a low similarity score (0.37), and requiring 10 subtree pruning and regrafting moves to modify one tree into the other. To determine what nodes are the most stable between these two alternative hypotheses, we calculated a supertree (Goloboff et al., 2008; Fig. 2C). The supertree indicates three common nodes between the morphological and molecular data sets: Node 1, node 2, and node 3. Node 1 consists of Phyllodactylidae (Fig. 2), including a basal polytomy formed by Old World genera + *Tarentola* (secondarily colonizer of New World), *Thecadactylus* (New World, Caribbean, and northern South America), and the remaining New World genera. Node 2 is mainly southern South American clade (Fig. 2; with the exception of *Phyllodactylus* that extends into Central and southwestern North America and the Caribbean) consisting of *Homonota*, *Phyllodactylus*, *Gymnodactylus*, *Phyllopezus*, and *Garthia*. Node 3 consists of *Homonota* only (Fig. 2).

Diagnostic Features.—Due to the large discrepancies among the two data sets, we provide only defining features of clades recovered by both. Nodes are indicated in Figure 2C.

Node 1: Phyllodactylidae. Four unambiguous postcranial synapomorphies support the family Phyllodactylidae: (character 442, state 2, Fig. 3A), seven or more postxiphisternal inscriptional (ribs modal number), (character 478, state 0) distal two thirds of illium rod-like in profile, expanded posterolaterally, (character 481, state 1, Fig. 3B) metischial processes of ischium widely separated from one another, and (character 490, state 0, Fig. 3B) posterior border of ischial symphysis more or less straight.

Node 2. Southern South American clade: Three unambiguous, synapomorphies support this clade: (character 137, state 0) splenial overlaps the coronoid bone, (character 492, state 1) shallow intercondylar fossa, and (character 571, state 1) neural spine and chevrons of caudal vertebrae enlarged and subequal in size.

Node 3. Homonota: This genus was previously diagnosed by lack of an ungual sheath for the retractile claws (Vanzolini and Donoso-Barros, 1966), a variable feature among gekkotans; this character has been considered together with the presence of straight digits (Kluge, 1964) that also are present in *Garthia* as a diagnostic feature of geckos from the Southern Cone. Other traits previously used to diagnose *Homonota* include a combination of five characters (Kluge, 1964; Abdala, 1996, 1998): 1) the presence of a stapedial foramen, 2) three vertebrae in the pygial series, 3) the presence of a jagged tympanic edge with an
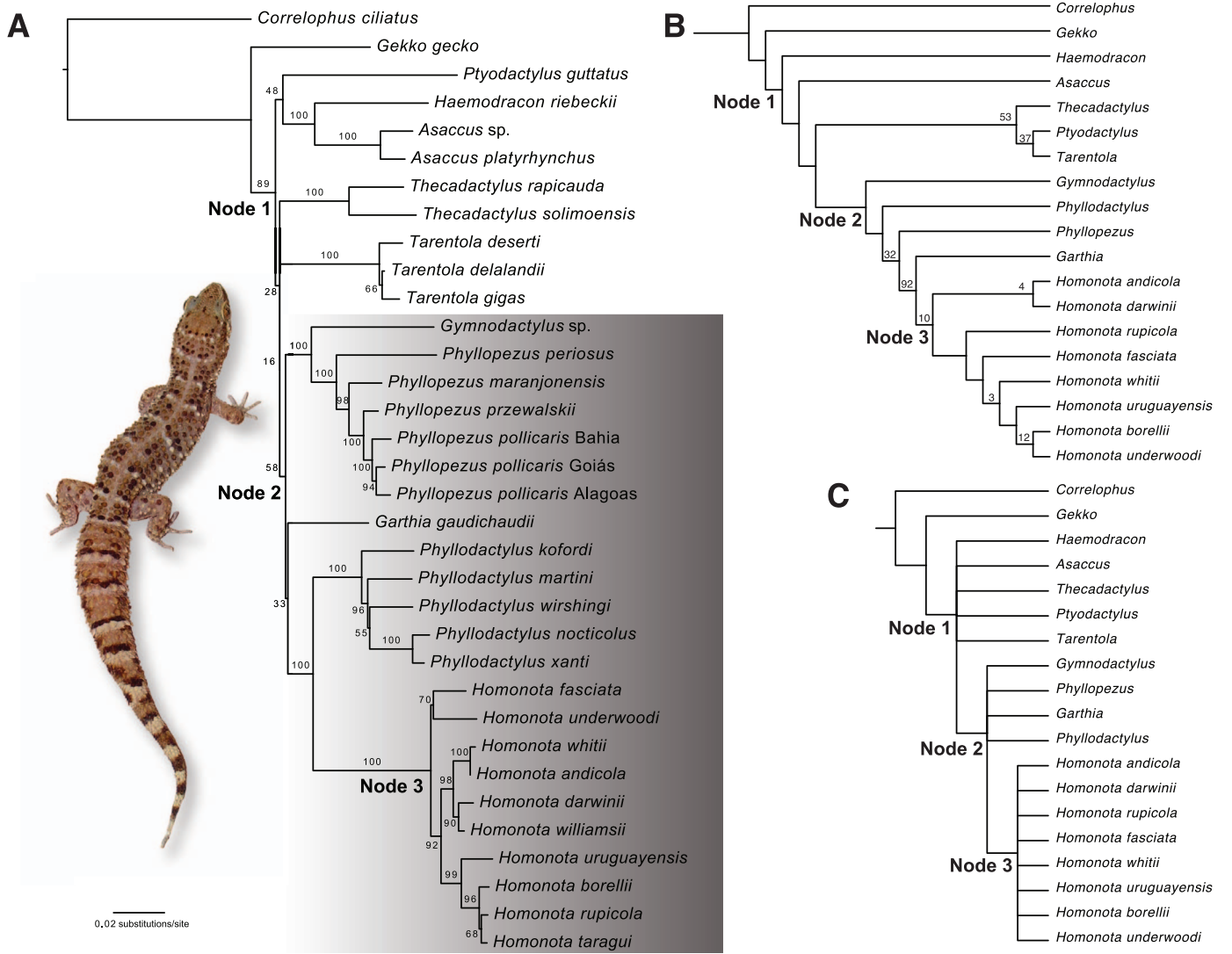
FIG. 2. Intergeneric relationships of Phyllodactylidae by using two data sets. (A) Results from partitioned maximum likelihood analysis of the concatenated molecular genetic data. Numbered nodes are referred to in text. (B) One of the MPTs obtained using morphological data. (C) A supertree obtained combining A and B, node numbers correspond to 1, Phyllodactylidae; 2, a mainly southern South America clade, with the exception of the more widespread genus *Phyllodactylus*; and 3, *Homonota*. Image of *Homonota fasciata*. Values on nodes represent bootstrap values.
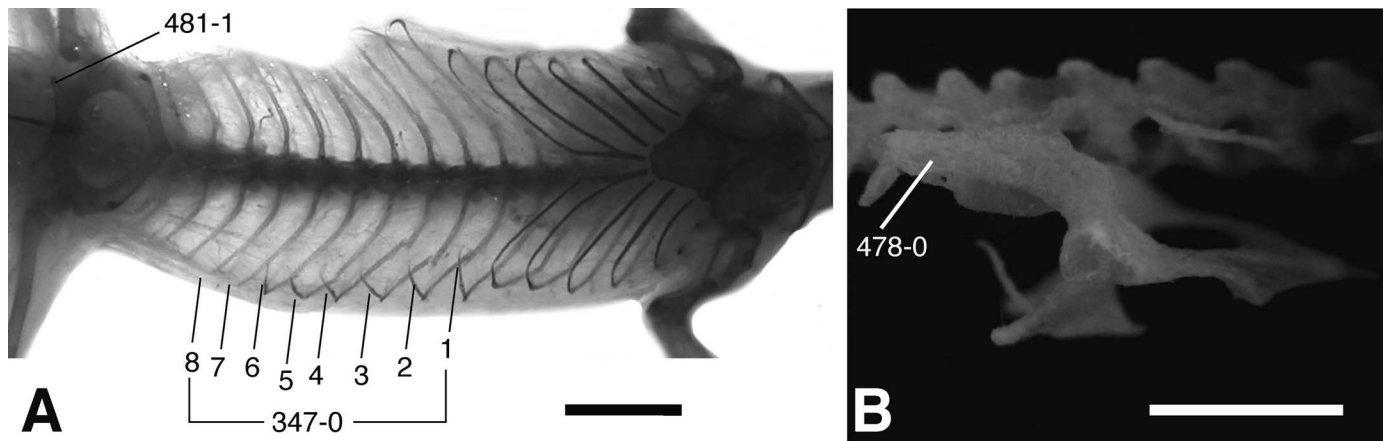

FIG. 3. (A) Ventral view of the trunk of *Phyllodactylus wirshingi* (CAS 175498). (B) Lateral view of the pelvis of *Phyllopezus pollicaris* (JFBM 15822).
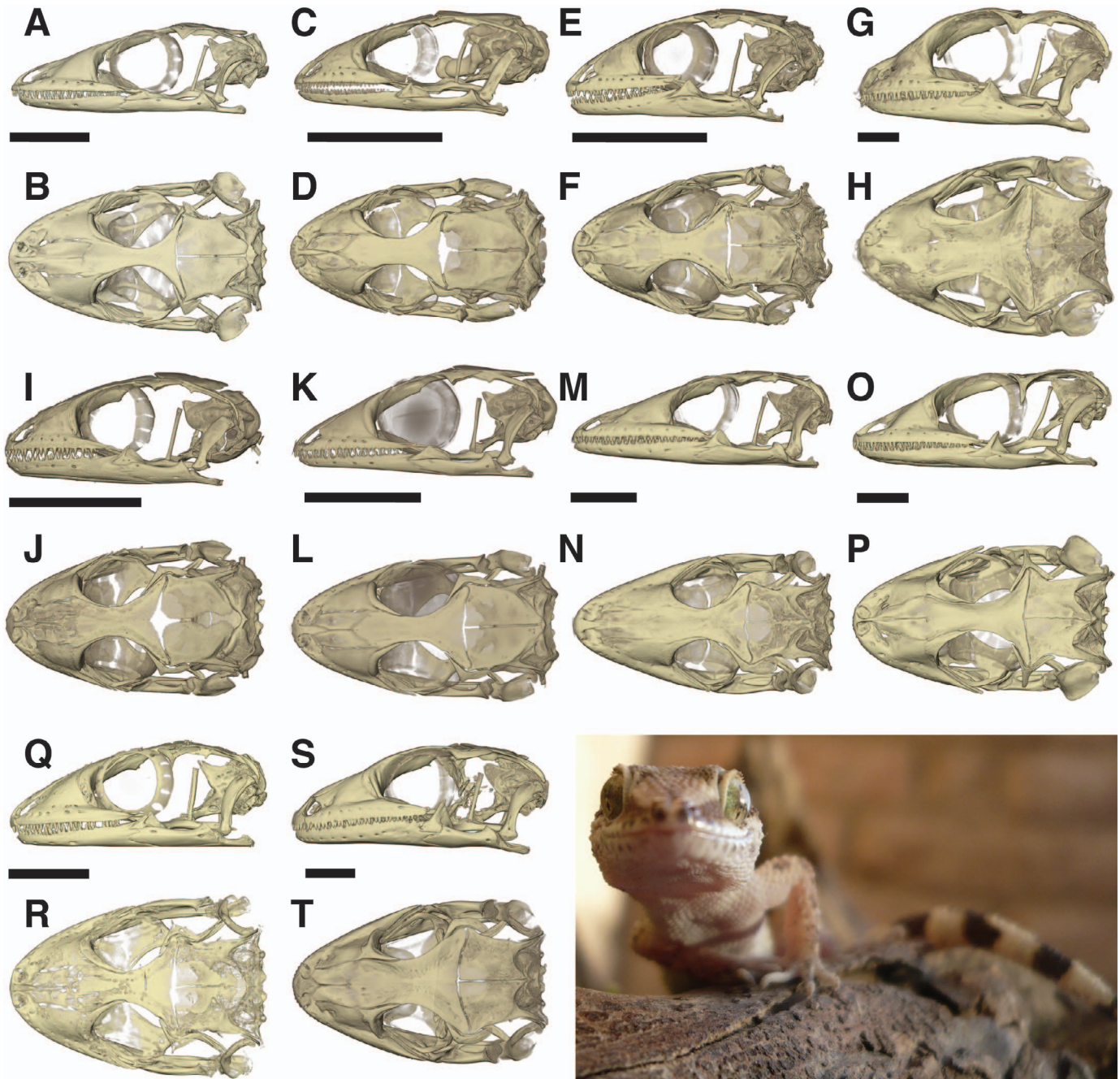
FIG. 4. Dorsal and lateral view of the skull of representatives from all phyllodactylid genera. (A–B) *Asaccus elisae* (CAS 218137). (C–D) *Garthia gaudichaudii* (UMMZ 111574). (E–F) *Gymnodactylus geckoides* (CAS 49397). (G–H) *Haemodracon riebeckii* (MCZ A-27255). (I–J) *Homonota fasciata* (CAS 84771). (K–L) *Phyllodactylus baurii* (CAS 09501). (M–N) *Phyllopezus lutzae* (MCZ R-46191). (O–P) *Ptyodactylus hasselquistii* (CAS 228536). (Q–R) *Tarentola mauritanica* (CAS 87112). (S–T) *Thecadactylus rapicauda* (CAS 95146). Scale bar = 5 mm. Photo inset: *Homonota fasciata* from Departamento Capital, Provincia de San Juan, Argentina. Photo taken in an urban dominated environment, courtesy of A. Laspiur.

angular slit, 4) straight digits, and 5) the absence of granular scales on the dorsum. In our analysis of *Homonota*, we found a new unambiguous synapomorphy: (character 339, state 2) splenial very reduced or fused to postdentary bones.

The morphological data set is congruent with previous findings about wide headedness in *Homonota*, especially in the muzzle region; the reduction of the size of the jugal (Figs. 4–5) has been observed in another South American gecko species, but from the family Sphaerodactylidae (*Chatogekko amazonicus*, Gamble et al., 2011b), and it might indicate some propensity toward the reduction of the jugal bones in small-bodied forms. In *Garthia*, this bone is not reduced and establishes contact with the prefrontal (Figs. 4–5). Jugal size is variable within *Homonota*; in *H. andicola*, *H. uruguayensis*, *H. borellii*, and *H. underwoodi*, this bone is of intermediate size (Fig. 5B, J, K, L), whereas it is very small or almost vestigial in *H. darwinii*, *H. fasciata*, and *H. whitii* (Fig. 5C, D, I).

Garthia: This genus was previously differentiated from *Homonota* based on the following combination of characters: 1) an enlarged rostral scale with arcuate posterior border
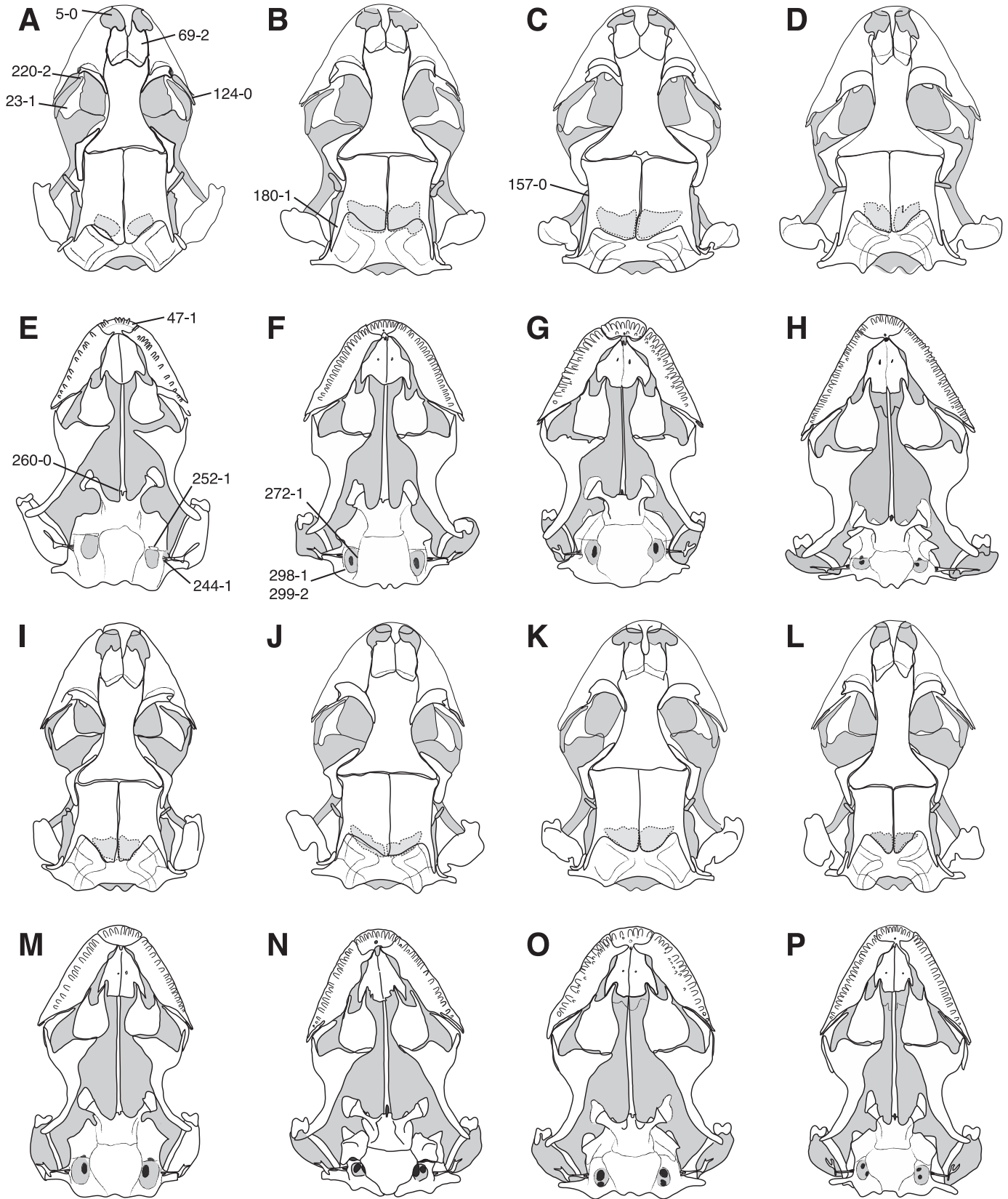
FIG. 5. Skull in dorsal and ventral view of *Garthia* and *Homonota* geckos. All drawings made at the same scale, skull length after specimen number. (A, E) *Garthia penai* (MZSP 60938; 11.7 mm). (B, F) *H. andicola* (FML uncatalogued; 11.4 mm). (C, G) *H. darwinii* (FML uncatalogued; 11.5 mm). (D, H) *H. fasciata* (FML 01495; 12.1 mm). (I, M) *H. whitii* (FML 03547; 11.1 mm). (J, N) *H. uruguayensis* (FML uncatalogued; 9.1 mm). (K, O) *H. borellii* (FML 00933; 9.95 mm). (L, P) *H. underwoodi* (FML uncatalogued; 11.8 mm). Numbers on the figure correspond to characters and character states described in the text.

FIG. 6. Morphological characters of *Garthia* and *Homonota*. (A, B) Labial and lingual view of the jaw of *Homonota darwinii* (FML uncatalogued, 13.61 mm); scheme of the anterior portion of the snout, showing the shape of rostral scale, nostril size, form o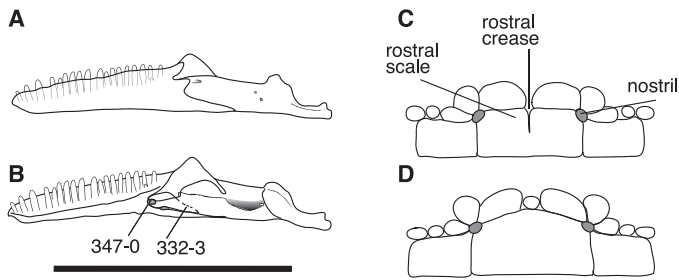f rostral crease, and associated scales in (C) *Homonota whitii* and (D) *Garthia gaudichaudii* (redrawn from Kluge, 1964). Scale bar = 10 mm. Numbers on the figure correspond to characters and character states described in the text.
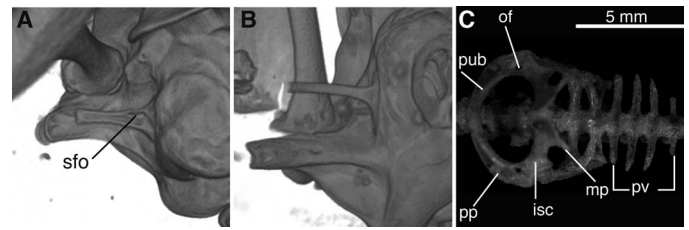

FIG. 7. Presence (A, *Garthia gaudichaudii*, UMMZ 111574) and absence (B, *Phyllodactylus baurii*, CAS 09501) of the stapedial foramen in phyllodactylids. (C) Pelvic girdle of *Homonota fasciata* (JFBM 15827) showing an ischium wider than pubis in ventral view and a posterior flange of ischium notably concave. Abbreviations: isc, ischium; mp, metischial processes; of, obturator foramen; pp, pectineal process; pub, pubis; pv, pygial vertebrae series.

(Vanzolini and Donoso-Barros, 1966); 2) nostril in contact with rostral, first labial, two small supranasals and granules of the snout (Vanzolini and Donoso-Barros, 1966); 3) lack of rostral crease on the rostral scale (Kluge, 1964); 4) fewer than 12 subdigital lamellae on the fourth finger (Kluge, 1964); and 5) all claws retractile into a sheath that is formed by one dorsal, roof-like scale and two ventrolateral scales (Vanzolini and Donoso-Barros, 1966).

Our analysis retrieved additional synapomorphies to diagnose *Garthia*: (character 12, state 0, Fig. 4) maxilla without dermal sculpturing; (character 69, state 2, Figs. 4, 5A) nasal bones narrow anteriorly and broad posteriorly; (character 124, state 0, Fig. 5A) jugal and squamosal aligned with one another in a parasagittal plane; (character 212, state 0, Fig. 4) ventrolateral process of pterygoid absent; (character 215, state 1) pterygoid small with a reduced facet for basipterygoid; (character 220, state 2, Fig. 5A) ectopterygoid very wide throughout most of its length; (character 252, state 1, Fig. 5E) foramen in the otooccipital-prootic suture; (character 349, state 1) coronoid overlaps the surangular posteriorly; (character 406, state 2) clavicular fenestra absent; (character 426, state 1) scapulocoracoid fenestra closed by epicoracoid bar; and (character 560, state 1) three pygial vertebrae. Other characters that differentiate *Garthia* from some, but not all, *Homonota* species are the size and shape of the jugal (extremely reduced in *H. darwinii* and *H. whitii*, Fig. 5), that in this genus is larger than in *Homonota* (Figs. 4–5), and the absence of a crease in the rostral scale (Kluge, 1964; Fig. 6D).

Symplesiomorphies of Garthia *and* Homonota.— The morphological results differ from previous morphological analyses (Abdala and Moro, 1996; Abdala, 1998) in which *Garthia* and *Homonota* were found to be distantly related. Our extensive morphological data set confirms the morphological similarity between these two genera that was used previously as an argument for their synonymy (e.g., Kluge, 1991, 2001; Rösler, 1995, 2000). Nonetheless, we found new morphological similarities between these two genera, as well as characters that serve to differentiate both genera (see above).

Homonota and *Garthia* share 12 common characters, here interpreted as symplesiomorphies (based on our acceptance of the molecular phylogeny): (character 6, state 0; Figs. 4–5) oval-shaped external narial vestibule; (character 24, state 1; Fig. 5) irregular-shaped suborbital fenestra (not oval, slit like or D shaped); (character 245, state 1; Figs. 5, 7) stapedial foramen

present; (character 260, state 0; Fig. 5) trabecula communis unfused; (character 273, state1; Fig. 5F) sphenooccipital tubercle of basioccipital without apophyses (Element "X," Gauthier et al., 2012); (character 298, state 1; Fig. 5F) oval-shaped occipital recess; (character 438, state 1) sternum and lateral arms of interclavicle separated by one third or less the length of the posterior process of the latter element; (character 468, state 1) metacarpals elongated, being twice the length of their corresponding phalanges; (character 479, state 0) ischium wider than pubis in ventral view; (character 490, state 1) posterior flange of ischium notably concave; and (character 509, state 1) metapodial elements I–IV approximately parallel to one another.

Morphological Comparisons of Homonota *Geckos and other Phyllodactylids*.— Phyllodactylid species exhibit a diversity of cranial sizes and shapes (Figs. 4, 8). The morphological analysis places *Asaccus* as sister to a clade formed by *Thecadactylus*, *Tarentola*, and *Ptyodactyus*, followed by all remaining phyllodactylid genera (Fig. 2B). These three genera are generally represented by large-sized geckos and together with *Asaccus*, possess parietal bones with a posterior medial projection that overlaps the supraoccipital (Fig. 3). *Thecadactylus* (Fig. 4) and *Tarentola* (Fig. 4) have an overall ovoid-shaped skull with stout frontal bones. *Asaccus* (Figs. 4, 8C) also has an ovoid skull, but its snout is very depressed and its frontal bone is slender; a slender frontal is also present in *Ptyodactylus* (Fig. 8B).

Ptyodactylus, *Tarentola*, *Thecadactylus*, *Phyllodactylus*, and *Phyllopezus* generally have skulls >20 mm in length, whereas in *Asaccus*, *Gymnodactylus*, *Homonota*, *Garthia*, and some miniaturized *Phyllodactylus* the skull length rarely surpasses 15 mm. In almost all the species with large skulls, the ratio between the muzzle unit and the parietal unit, as indicated by the position of the frontoparietal suture, is ~2:1. *Phyllopezus* and *Gymnodactylus* (Figs. 4, 8D, E) have comparable skull proportions to *Homonota* and *Garthia*, where the ratio between the skull units is roughly 1:1. These are proportions similar to those in the miniaturized sphaerodactyl gekkotans (Daza et al., 2008; Gamble et al., 2011b). *Homonota* also has one of the proportionally broadest snouts among gekkotans (Daza et al., 2009), with *H. darwinii*, *H. borellii*, *H. uruguayensis*, and *H. andicola* being the most extreme (Fig. 5); in this sense, they are similar to *Phyllopezus* (Fig. 4). The basicranium of *Homonota* is also wide (Figs. 4–5), producing changes in the position of the bones connecting different units of the skull. For example, the pterygoid is shifted laterally, making the lateral edge partially or, in dorsal view, completely visible (and sometimes also the bottom part of the epipterygoid, or the entire bone if the prootic crista alaris becomes exposed). The
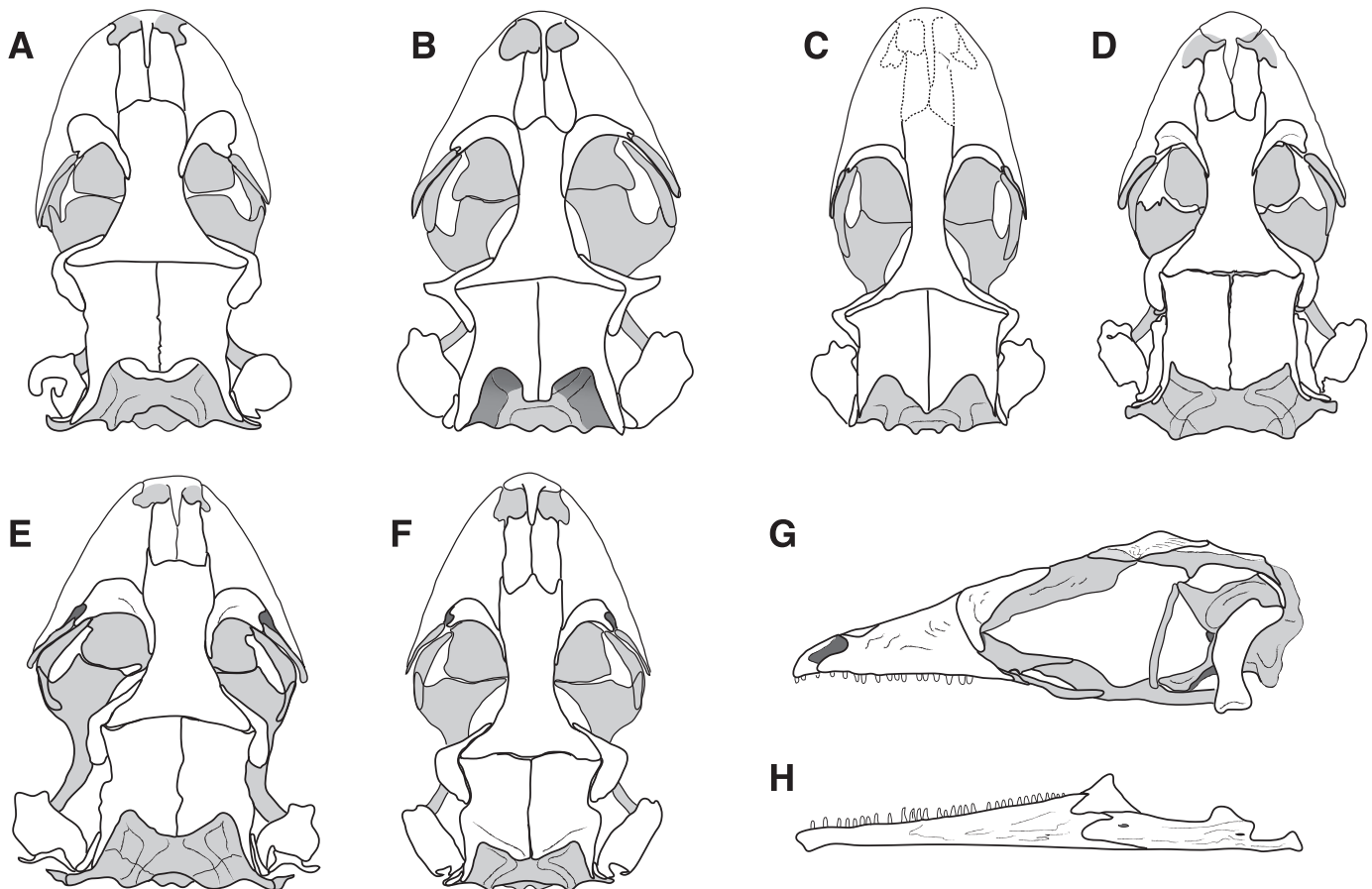
Fɪɢ. 8. Dorsal view of phyllodactylid geckos. Values next to the specimen number indicate total length, skull length after specimen number. (A) *Tarentola mauritanica* (AMNH 71591; 18.30 mm). (B) *Ptyodactylus hasselquistii* (FMNH 210095; 21.08 mm). (C) *Asaccus elisae* (BMNH uncataloged; 17.84 mm). (D) *Gymnodactylus geckoides* (CAS 49397). (E) *Phyllopezus pollicaris* (FML 02313; 18.14 mm). (F) *Phyllodactylus whirshingi* (CAS 175498; 17.55 mm). (G) *P. tuberculosus* (BMNH 1906.6.1.220, 24.76 mm). (H) Labial side of the jaw of *P. tuberculosus* (BMNH 1906.6.1.220; 25.21 mm). Dashed lines in (C) represent inferred sutures.

widening of the skull also affects the size of the suborbital fenestra. The prootic is exposed in dorsal view in *Homonota*, *Garthia*, and *Gymnodactylus*, but not in larger phyllodactylids, including *H. fasciata*, where the basicranium is completely roofed by the parietals (Fig. 5D).

Homonota and *Phyllodactylus* (Figs. 4, 8E–G) are very different morphologically; when these two genera were constrained to be monophyletic tree length with the morphological data set increased 21 steps and only four characters support this clade: (character 86, state 0) contact between the prefrontal and jugal absent, although in *P. wirshingi* this contact is variable and it is present in *P. tuberculosus* and *P. xanti*; (character 110, state 1) lacrimal foramen surrounded by maxilla and prefrontal, although in *P. tuberculosus* and *P. xanti* the jugal forms the posterior border of this foramen; (character 368, state 2) premaxillary tooth count 8–9; and (character 521, state 1) two plantar sesamoids.

Incongruence between Morphological and Molecular Hypotheses.— In recent analyses, *Homonota* and *Phyllodactylus* have been found as sister taxa (Gamble et al., 2011a; Morando et al., 2014; this study, Fig 2A). The position of *Garthia* within Phyllodactylidae is unstable, however; it was found nested within *Homonota* (external morphology, Kluge, 1964), or as sister to the gekkonid *Lygodactylus klugei* (i.e., *Vanzoia klugei*, skull morphology, Abdala, 1996), sister to or nested with *Homonota* (external and internal

morphology, this study), sister to *Phyllodactylus* + *Homonota* (five nuclear protein-coding genes, Gamble et al., 2010; two mitochondrial genes and seven nuclear protein-coding genes, Morando et al., 2014), sister to *Gymnodactylus* (Morando et al., 2014), or sister to *Gymnodactylus* + *Phylllopezus* by using morphological data only (this study). One of the MPTs from the morphological analyses places *Homonota* and *Garthia* as sister taxa, which is explained by the large number of symplesiomorphies (Table 1). Short, internal nodes and low support values at the base of the Phyllodactylidae (nodes 1 and 2, Fig. 2) suggest rapid cladogenesis early in phyllodactylid evolution that may make teasing apart phylogenetic relationships among some clades particularly troublesome.

Phyllodactylus geckos differ markedly from *Homonota* or *Garthia*. One factor that must be considered is that we used *P. wirshingi* in our analysis as surrogate for the entire genus; this species is restricted to the island of Puerto Rico (Weiss and Hedges, 2007) and is part of the *P. tuberculosus* group (Dixon and Huey, 1970). Because the composition of this group has not been corroborated by molecular data, the placement of *P. wirshingi* is tentative. We should bear in mind that *Phyllodactylus* has been previously considered to be a polyphyletic group consisting of several unrelated, or distantly related clades (Bauer et al., 1997) being artificially diagnosed by plesiomorphic digital characters (Russell, 1972), although currently the

TABLE 1. Number of morphological characters with a consistency index of 1 that support alternative positions of *Homonota*.

	Phyllodactylus + *Homonota*	*Garthia* + *Homonota*
Skull	8	24
Postcranium	5	10

monophyly of the New World *Phyllodactylus* no longer seems to be in question (Weiss and Hedges, 2007; Gamble et al., 2011a; Blair et al., 2015).

DISCUSSION

Data Set Incongruence.—Gamble et al. (2008) predicted that *Garthia*, *Gymnodactylus*, and *Phyllopezus lutzae* (previously *Bogertia lutzae*, Gamble et al., 2012a), taxa not represented in their analysis, would belong to the Phyllodactylidae. This hypothesis and the validity of *Garthia* as a genus separate from *Homonota* have been confirmed by recently published molecular analyses (Gamble et al., 2011, 2015; Morando et al., 2014). This new phylogenetic information indicates that *Garthia* is a cryptic lineage, largely morphologically indistinguishable from *Homonota* (although there are several diagnostic features, see above), and that the morphological information available in the past was insufficient to diagnose these two genera, despite the fact that their morphology had received considerable attention (Kluge, 1964, 1965; Vanzolini and Donoso-Barros, 1966; Abdala, 1990, 1993, 1994, 1995, 1996).

Incongruence between data sets has been explained as the outcome of one of the data sets simply being unreliable, and no method of phylogenetic reconstruction could be expected to recover the correct tree given the poor quality of the data (Swofford, 1991). Within squamate reptiles, one case that is commonly attributed to apparently misleading phylogenetic signal in the morphological data (Lee, 1998; Wiens et al., 2010; Gauthier et al., 2012; Losos et al., 2012) is the so-called fossorial group where many limb-reduced taxa are grouped together.

The analysis of large data set of anatomical characters facilitated understanding the relationship of *Garthia* and *Homonota*. There are morphological differences that serve to diagnose *Garthia* and *Homonota*, but these two genera also share a large list of morphological similarities that explain their previous synonymy (Rösler, 1995, 2000; Kluge, 2001; Pincheira-Donoso, 2006, Vidal et al., 2008). After examining the data, miniaturization and terrestriality in *Garthia* and *Homonota* seem to be two possible factors that may have contributed to their similar morphologies.

Miniaturization.—Considering the Phyllodactylidae, the body mass of the most australly distributed geckos, *Garthia* and *Homonota*, represent a counter example to Bergman's rule that states that body size increases in colder environments. The same opposite pattern is followed in other squamate groups that generally decrease in size with latitude and increase in size with temperature (Ashton and Feldmand, 2003; de Queiroz and Ashton, 2004). Body size reduction has some consequences for the morphology of the skeleton, especially the skull. Rieppel (1984b) observed that lizard skulls with lengths of ∼15 mm or less have the supraoccipital and the parietal at the same level, yielding closed posttemporal fossae. At this size the diameter of the otic capsule also is proportionally large.

Additional observations on miniaturized sphaerodactyl geckos include the development of a 1:1 ratio between the muzzle unit and the parietal unit (Daza et al., 2008; Gamble et al., 2011b). Both *Garthia* and *Homonota* exhibit the same ratio reported in miniaturized sphaerodactyl geckos. In both miniaturized sphaerodactyls and phyllodactylids, basicranium size is inversely proportional to the skull size as observed by Rieppel (1984b) in other lizards; as the skull become smaller, the proportional size of the braincase increases (here indicated by the size of the parietal unit). In addition, in both groups the muzzle becomes relatively shorter, but the bone configuration in *Garthia* and *Homonota* differs from the increased bone overlap typical of sphaerodactyl geckos (Daza et al., 2008); the snouts of *Homonota* and *Garthia* become shorter by a reduction in the proportional length of the nasals, maxillae, and jugals; therefore, there is no increased bone overlap. Future examination of miniaturized *Phyllodactylus* species such as *P. duellmani* and *P. papenfussi* (Dixon, 1960; Murphy et al., 2009) is required to corroborate whether they present a similar miniaturization pattern to the pattern observed in *Garthia* and *Homonota*.

Another morphological difference of *Garthia* and *Homonota*, relative to miniaturized sphaerodactylids, is that the paroccipital process and therefore the quadrate is not shifted anteriorly, having the quadrato-otooccipital joint in a posterolateral position as in large-headed geckos (Figs. 4I–J, 5). This might also be a factor contributing to a more laterally exposed pterygoid bone that is not present in miniaturized sphaerodactylids (Daza et al., 2008). These new observations reveal different patterns of skull morphology in miniaturization of gekkotans. In the case of the most austral genera in the world, *Garthia* and *Homonota* might have been affected by retention of many characters associated with terrestriality, instead of being an exceptional case of parallel evolution by regaining of all their shared characters.

Terrestriality.—Phyllodactylid geckos exhibit diverse morphologies that reflect adaptations to a wide range of habitats and substrates (Dixon and Huey, 1970; Cei, 1986, 1993; Marquet et al., 1990; Werner et al., 1996; Werneck et al., 2012). Adaptations to these diverse substrata include changes to both appendicular and skull morphology. Scansorial phyllodactylids, for example, have quite different limbs and digits compared to their terrestrial, padless relatives (Russell, 1979; Rothier et al., 2017). *Garthia* and *Homonota* also possess skulls similar to other extant terrestrial gekkotans that dwell in xeric environments (*Agamura*, *Bunopus*, *Pristurus*, *Ptenopus*, and *Teratoscincus*), where their snouts become short and high (Fig. 4; Daza et al., 2012). The terrestrial habitat preference of *Garthia* and *Homonota* may explain their strong resemblance to each other, including their similar appendicular morphology (e.g., long metacarpals, straight digits). Two evolutionary scenarios could produce the observed outcome. Similar morphologies could be a retention of the ancestral terrestrial condition, that is, symplesiomorphy, with genera such as *Phyllodactylus* and *Phyllopezus* independently moving into the derived, scansorial body form. Alternately, the similarities between *Garthia* and *Homonota* could represent convergence toward a terrestrial lifestyle and away from a scansorial ancestor as implied by Gamble et al. (2012b). Further work is needed to differentiate these alternative scenarios, but our results represent an important step in teasing apart the morphological similarities and differences that exist among diverse phyllodactylid genera.

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SUPPLEMENTARY DATA

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LITERATURE CITED

ABDALA, V. 1990. Descripción osteológíca de *Homonota horrida* (Sauria Gekkonidae). Acta Zoológica Lilloana 39:31–38.

ABDALA, V. 1993. Análisis fenético del género *Homonota* (Sauria: Gekkonidae). Acta Zoológica Lilloana 42:283–289.

ABDALA, V. 1994. Aportes a la osteología comparada en el genero *Homonota* (Sauria: Gekkonide). I. Cráneo. Acta Zoológica Lilloana 41:247–258.

ABDALA, V. 1995. Aportes a la osteología comparada en el género *Homonota*. II. Postcráneo. Acta Zoológica Lilloana 43:25–30.

ABDALA, V. 1996. Osteología craneal y relaciones de los geconinos sudamericanos (Reptilia: Gekkonidae). Revista Española de Herpetología 10:41–54.

ABDALA, V. 1998. Análisis cladístico del género *Homonota* (Gekkonidae). Revista Española de Herpetología 12:55–62.

ABDALA, V., AND E. E. LAVILLA. 1993. *Homonota fasciata* (Duméril y Bibron, 1836), nombre válido para *Homonota pasteuri* Wermuth, 1965 y *Homonota horrida* (Burmeister, 1861) (Sauria: Gekkonidae). Acta Zoológica Lilloana 42:279–282.

ABDALA, V., AND S. MORO. 1996. Cranial musculature of South American Gekkonidae. Journal of Morphology 229:59–70.

ACOSTA, J. C., AND F. MURÚA. 1998. Lista preliminar y estado de conservación de los reptiles del parque natural Ischigualasto, San Juan-Argentina. Multequina 7:49–59.

AGUILAR, R., AND F. B. CRUZ. 2010. Refuge use in a Patagonian nocturnal lizard, *Homonota darwini*: the role of temperature. Journal of Herpetology 44:236–241.

ALBINO, A. M. 2005. A Late Quaternary lizard assemblage from the southern Pampean region of Argentina. Journal of Vertebrate Paleontology 21:185–191.

ARNOLD, E. N. 2009. Relationships, evolution and biogeography of Semaphore geckos, *Pristurus* (Squamata, Sphaerodactylidae) based on morphology. Zootaxa 2060:1–21.

ASHTON, K. G., AND C. R. FELDMAND. 2003. Bergmann's rule in nonavian reptiles: turtles follow it, lizards and snakes reverse it. Evolution 57:1151–1163.

AUN, L., AND R. MARTORI. 1994. Biología de una población de *Homonota horrida*. Cuadernos de Herpetología 8:90–96.

AUFFENBERG, W. 1958. A small fossil herpetofauna from Barbuda, Leeward Islands, with the description of a new species of *Hyla*. Quarterly Journal of the Florida Academy of Sciences 21:248–253.

BAUER, A. M. 1986. Systematics, Biogeography and Evolutionary Morphology of the Carphodactylini (Reptilia: Gekkonidae). Unpubl. Ph.D. diss., University of California–Berkeley, USA.

BAUER, A. M. 1990a. Phylogenetic systematics and biogeography of the Carphodactylini (Reptilia: Gekkonidae). Bonner Zoologische Monographien 30:1–218.

BAUER, A. M. 1990b. Phylogeny and biogeography of the geckos of southern Africa and the islands of the western Indian Ocean: a preliminary analysis. Pp. 274–284 in G. Peters and R. Hutterer (eds.), Vertebrates in the Tropics: Zoologisches Forschungsmuseum Alexander Koenig, Germany.

BAUER, A. M. 2013. Geckos: The Animal Answer Guide. The Johns Hopkins University Press, USA.

BAUER, A. M., D. A. GOOD, AND W. R. BRANCH. 1997. The taxonomy of the Southern African leaf–toed geckos (Squamata: Gekkonidae) with a review of the Old World "*Phyllodactylus*" and the description of five new genera. Proceedings of the California Academy of Sciences 49:447–497.

BELL, G. L. 1997. A phylogenetic revision of North American and Adriatic Mosasauroidea. Pp. 293–332 in J. M. Callaway and E. L Nicholls (eds.), Ancient Marine Reptiles. Academic Press, USA.

BLAIN, H. A., AND S. BAILON. 2006. Catalogue of Spanish Plio-Pleistocene amphibians and squamate reptiles from the Museu de Geologia de Barcelona. Treballs del Museu de Geologia de Barcelona 14:61–80.

BLAIR, C., F. R. MÉNDEZ DE LA CRUZ, C. LAW, AND R. W. MURPHY. 2015. Molecular phylogenetics and species delimitation of leaf-toed geckos (Phyllodactylidae: *Phyllodactylus*) throughout the Mexican tropical dry forest. Molecular Phylogenetics and Evolution 84:254–265.

BORSUK-BIAŁYNICKA, M. 1983. The early phylogeny of Anguimorpha as implicated by craniological data. Acta Palaeontologica Polonica 28:5–105.

CACCIALI, P., I. ÁVILA, AND F. BAUER. 2007. A new species of *Homonota* (Squamata, Gekkonidae) from Paraguay, with a key to the genus. Phyllomedusa 6:137–146.

CALDWELL, M. W. 1999. Squamate phylogeny and the relationships of snakes and mosasauroids. Zoological Journal of the Linnean Society 125:115–147.

CARROLL, R. L., AND M. DEBRAGA. 1992. Aigialosaurs: Mid-Cretaceous varanoid lizards. Journal of Vertebrate Paleontology 12:66–86.

CEI, J. M. 1986. Reptiles del centro, centro-oeste y sur de la Argentina. Herpetofauna de las zonas áridas y semiáridas. Museo Regionale di Scienze Naturali Monografie (Torino) 4:1–527.

CEI, J. M. 1993. Reptiles del noroeste, nordeste y este de la Argentina. Herpetofauna de las selvas subtropicales, Puna y Pampas. Museo Regionale di Scienze Naturali Monografie (Torino) 14:1–949.

ČERŇANSKÝ, A., AND A. M. BAUER. 2010. *Euleptes gallica* Müller (Squamata: Gekkota: Sphaerodactylidae) from the Lower Miocene of North-West Bohemia, Czech Republic. Folia Zoologica 59:323–328.

CONRAD, J. L. 2006. An Eocene shinisaurid (Reptilia, Squamata) from Wyoming, U.S.A. Journal of Vertebrate Paleontology 26:113–126.

CONRAD, J. L. 2008. Phylogeny and systematics of Squamata (Reptilia) based on morphology. Bulletin of the American Museum of Natural History 310:1–182.

CONRAD, J. L., AND M. NORELL. 2006. High-resolution X-ray computed tomography of an Early Cretaceous gekkonomorph (Squamata) from Öösh (Övorkhangai; Mongolia). Historical Biology 18:405–431.

CRUZ, F. B., M. KOZYKARIASKI, M. G. PEROTTI, M. PUETA, AND L. MORENO. 2004. Variación diaria de la temperatura corporal en dos especies de lagartos nocturnos (Squamata, Gekkonidae, *Homonota*) con comentarios sobre el uso de refugios. Cuadernos de Herpetología 18:15–22.

DAZA, J. D. 2008. Cladistic Analysis of the Gekkota (Reptilia) by Means of Craniological Data. Unpubl. Ph.D. diss., University of Puerto Rico at Río Piedras, Puerto Rico.

DAZA, J. D., AND A. M. BAUER. 2012. A new amber-embedded sphaerodactyl gecko from Hispaniola, with comments on the morphological synapomorphies of the Sphaerodactylidae. Breviora 529:1–28.

DAZA, J. D., V. ABDALA, R. THOMAS, AND A. M. BAUER. 2008. Skull anatomy of the miniaturized gecko *Sphaerodactylus roosevelti* (Squamata: Gekkota). Journal of Morphology 239:1340–1364.

DAZA, J. D., A. HERRERA, R. THOMAS, AND H. J. CLAUDIO. 2009. Are you what you eat? A geometric morphometric analysis of gekkotan skull shape. Biological Journal of the Linnean Society 97:677–707.

DAZA, J. D., V. R. ALIFANOV, AND A. M. BAUER. 2012. A redescription and phylogenetic reinterpretation of the fossil lizard *Hoburogekko suchanovi*, 1989 (Squamata: Gekkota), from the Early Cretaceous of Mongolia. Journal of Vertebrate Paleontology 32:1303–1312.

DAZA, J. D., A. M. BAUER, AND E. D. SNIVELY. 2014. On the fossil record of the Gekkota. Anatomical Record 297:433–462.

DE QUEIROZ, K. 1987. Phylogenetic systematics of iguanine lizards. A comparative osteological study. University of California Publications in Zoology 118:1–203.

DE QUEIROZ, A., AND K. G. ASHTON. 2004. The phylogeny of a species-level tendency: species heritability and possible deep origins of Bergmann's rule in tetrapods. Evolution 58:1674–1684.

DIXON, J. R. 1960. Two new geckos, genus *Phyllodactylus* (Reptilia: Sauria), from Michoacan Mexico. Southwestern Naturalist 5:37–42.

DIXON, J. R., AND R. B. HUEY. 1970. Systematics of the lizards of the gekkonid genus *Phyllodactylus* of mainland South America. Natural History Museum of Los Angeles County Contributions in Science 192:1–78.

DONOSO-BARROS, R. 1965a. El género *Garthia* Donoso-Barros & Vanzolini y los geckos gimnolactilidos [sic] afines. Noticiario Mensual Museo Nacional de Historia Natural 103:5–8.

DONOSO-BARROS, R. 1965b. El género *Garthia* Donoso-Barros & Vanzolini y los geckos gimnodactílidos afines. Publicación Ocasional del Museo Nacional de Historia Natural (Santiago, Chile) 7:1–8.

DONOSO-BARROS, R. 1966. Reptiles de Chile. Ediciones de la Universidad de Chile, Chile.

ESTES, R. 1969. Die Fauna der miozänen Spaltenfüllung von Neudorf an der March (ČSSR) (Reptilia, Lacertilia). Akademie der Wissenschaften in Wien mathematisch-naturwissenschaftlichen Klasse 178:77–82.

ESTES, R. 1983. Sauria terrestria, Amphisbaenia. Gustav Fischer Verlag. Germany.

ESTES, R., K. DE QUEIROZ, AND J. GAUTHIER. 1988. Phylogenetic relationships within Squamata. Pp. 119–281 in R. Estes and G. Pregill (eds.), Phylogenetic Relationships of the Lizard Families, Essays Commemorating Charles L. Camp. Stanford University Press, USA.

ETHERIDGE, R. 1964. Late Pleistocene lizards from Barbuda, British West Indies. Bulletin of the Florida State Museum, Biological Sciences 9: 43–75.

ETHERIDGE, R. 1966. Pleistocene lizards from New Providence. Quarterly Journal of the Florida Academy of Sciences 28:349–358.

ETHERIDGE, R., AND K. DE QUEIROZ. 1988. A phylogeny of Iguanidae. Pp. 283–367 in R. Estes and G. Pregill (eds.), Phylogenetic Relationships of the Lizard Families, Essays Commemorating Charles L. Camp. Stanford University Press, USA.

EVANS, S. E., AND L. J. BARBADILLO. 1998. An unusual lizard (Reptilia: Squamata) from the Early Cretaceous of Las Hoyas, Spain. Zoological Journal of the Linnean Society 124:235–265.

FREDERICKSEN, N. J., T. S. FREDERICKSEN, B. FLORES, E. MCDONALD, AND D. RUMIZ. 2003. Importance of granitic rock outcrops to vertebrate species in a Bolivian tropical forest. Tropical Ecology 44:185–196.

FROST, D. R., AND R. ETHERIDGE. 1989. A phylogenetic analysis and taxonomy of iguanian lizards (Reptilia: Squamata). Miscellaneous Publication of the University of Kansas Museum of Natural History 81:1–65.

GAMBLE, T., A. M. BAUER, E. GREENBAUM, AND T. R. JACKMAN. 2008. Out of the blue: a novel, trans-Atlantic clade of geckos (Gekkota, Squamata). Zoologica Scripta 37:355–366.

GAMBLE, T., A. M. BAUER, G. R. COLLI, E. GREENBAUM, T. R. JACKMAN, L. J. VITT, AND A. M. SIMONS. 2011a. Coming to America: multiple origins of the New World geckos. Journal of Evolutionary Biology 24:231–244.

GAMBLE, T., J. D. DAZA, G. R. COLLI, L. J. VITT, AND A. M. BAUER. 2011b. A new genus of miniaturized and pug-nosed gecko from South America (Sphaerodactylidae: Gekkota). Zoological Journal of the Linnean Society 163:1244–1266.

GAMBLE, T., G. R. COLLI, M. T. RODRIGUES, F. P. WERNECK, AND A. M. SIMONS. 2012a. Phylogeny and cryptic diversity in geckos (*Phyllopezus*; Phyllodactylidae; Gekkota) from South America's open biomes. Molecular Phylogenetics and Evolution 62:943–953.

GAMBLE, T., E. GREENBAUM, T. R. JACKMAN, A. P. RUSSELL, AND A. M. BAUER. 2012b. Repeated origin and loss of adhesive toepads in geckos. PLoS ONE 7:e39429.

GAMBLE, T., E. GREENBAUM, T. R. JACKMAN, AND A. M. BAUER. 2015. Into the light: diurnality has evolved multiple times in geckos. Biological Journal of the Linnean Society 115:896–910.

GAO, K., AND M. A. NORELL. 1998. Taxonomic revision of *Carusia* (Reptilia: Squamata) from the Late Cretaceous of the Gobi Desert and phylogenetic relationships of the anguimorphan lizards. American Museum Novitates 3230:1–51.

GAO, K., AND M. A. NORELL. 2000. Taxonomic composition and systematics of late cretaceous lizard assemblages from Ukhaa Tolgod and adjacent localities Mongolian Gobi Desert. Bulletin of the American Museum of Natural History 249:4–52.

GAUTHIER, J. 1982. Fossil xenosaurid and anguid lizards from the early Eocene Wasatch Formation, southeast Wyoming, and a revision of the Anguioidea. Contributions to Geology, University of Wyoming 21:7–54.

GAUTHIER, J. 1984. A Cladistic Analysis of the Higher Systematic Categories of Diapsida. Unpubl. Ph.D. diss., University of California–Berkeley, USA.

GAUTHIER, J., R. ESTES, AND K. DE QUEIROZ. 1988. A phylogenetic analysis of Lepidosauromorpha. Pp. 15–98 in R. Estes and G. Pregill (eds.), Phylogenetic Relationships of the Lizard Families, Essays Commemorating Charles L. Camp. Stanford University Press, USA.

GAUTHIER, J. A., M. KEARNEY, J. A. MAISANO, O. RIEPPEL, AND A. D. B. BEHLKE. 2012. Assembling the squamate tree of life: perspectives from the phenotype and the fossil record. Bulletin of the Peabody Museum of Natural History 53:3–308.

GOLOBOFF, P. A. 1999. Analyzing large data sets in reasonable times: Solutions for composite optima. Cladistics 15:415–428.

GOLOBOFF, P. A. 2008. Calculating SPR distances between trees. Cladistics 24:591–597.

GOLOBOFF, P. A., AND S. A. CATALANO. 2016. TNT version 1.5, including a full implementation of phylogenetic morphometrics. Cladistics 32: 221–238.

GOLOBOFF, P. A., J. S. FARRIS, AND K. C. NIXON. 2001. T.N.T.: tree analysis using new technology. Program and documentation available from the authors at https://cladistics.org/tnt/. Archived by WebCite at http://www.webcitation.org/6krmFyBY9.

GOLOBOFF, P. A., J. S. FARRIS, AND K. C. NIXON. 2008 TNT, a free program for phylogenetic analysis. Cladistics 24:774–786.

GÓMEZ, P. F., AND J. C. ACOSTA. 1998a. Datos biológicos de *Homonota borelli* [sic] (Squamata, Gekkonidae) en la provincia de San Juan, Argentina. Boletin de la Sociedad de Biología de Concepción 69:123–129.

GÓMEZ, P. F., AND J. C. ACOSTA. 1998b. Introducción accidental de reptiles y anfibios en el Departamento de Caucete, San Juan, Argentina. Multequina 7:73–75.

GRAY, J. E. 1845. Catalogue of the Specimens of Lizards in the Collection of the British Museum. Trustees of the British Museum, England.

GREER, A. E. 1990. The Biology and Evolution of Australian lizards. Surrey Beatty & Sons Pty Limited, Australia.

GRISMER, L. L. 1988. Phylogeny, taxonomy, classification, and biogeography of eublepharid geckos. Pp. 369–469 in R. Estes and G. Pregill (eds.), Phylogenetic Relationships of the Lizard Families, Essays Commemorating Charles L. Camp. Stanford University Press, USA.

GUERREIRO, A., J. C. BALDONI, AND A. M. BRIGADA. 2005. Herpetofauna de Sierra de las Quijadas (San Luis, Argentina). Gayana 69:6–9.

HANKEN, J., AND R. WASSERSUG. 1981. The visible skeleton. A new double-stain technique reveals the native "hard" tissues. Functional Photography 16:22–26.

HOLDER, L. A. 1960. The comparative morphology of the axial skeleton in the Australian Gekkonidae. Journal of the Linnean Society of London (Zoology) 44:300–335.

IBARGÜENGOYTÍA, N. R., AND L. M. CASALINS. 2007. Reproductive biology of the southernmost gecko: *Homonota darwini* [sic]: convergent life-history patterns among Southern hemisphere reptiles living in harsh environments. Journal of Herpetology 41:72–80.

KEARNEY, M. 2003. Systematics of the Amphisbaenia (Lepidosauria: Squamata) based in morphological evidence from recent and fossil forms. Herpetological Monographs 17:1–74.

KLUGE, A. G. 1964. A revision of the South American gekkonid lizard genus *Homonota* Gray. American Museum Novitates 2193:1–41.

KLUGE, A. G. 1965. Noteworthy records of the gekkonid lizard genus *Homonota* Gray from Argentina. Bulletin Southern California Academy of Sciences 64:127–131.

KLUGE, A. G. 1976. Phylogenetic relationships in the lizard family Pygopodidae: an evaluation of theory, methods and data. Miscellaneous Publications University of Michigan, Museum of Zoology 152: 1–72.

KLUGE, A. G. 1991. Checklist of gekkonoid lizards. Smithsonian Herpetological Information Service 85:1–35.

KLUGE, A. G. 1995. Cladistic relationships of sphaerodactyl lizards. American Museum Novitates 3139:1–23.

KLUGE, A. G. 2001. Gekkotan lizard taxonomy. Hamadryad 26:1–209.

KLUGE, A. G., AND R. A. NUSSBAUM. 1995. A review of African-Madagascan gekkonid lizard phylogeny and biogeography (Squamata). Miscellaneous Publications University of Michigan, Museum of Zoology 183:1–20.

KOOPMAN, K., AND R. RUIBAL. 1955. Cave fossil vertebrates from Camaguey, Cuba. Breviora 46:1–8.

LAKJER, T. 1927. Studien über die Gaumenregion bei Sauriern im Vergleich mit Anamniern und primitiven Sauropsiden. Zoologische Jahrbücher. Abteilung für Anatomie und Ontogenie der Tiere 49:57–356.

LANFEAR, R., B. CALCOTT, S. Y. HO, AND S. GUINDON. 2012. PartitionFinder: combined selection of partitioning schemes and substitution models for phylogenetic analyses. Molecular Biology and Evolution 29:1695–1701.

LANGEBARTEL, D. 1953. Faunal and archeological researches in Yucatan caves, part 4. The reptiles and amphibians. Cranbrook Institute of Science Bulletin 33:97–108.

LEE, M. S. Y. 1998. Convergent evolution and character correlation in burrowing reptiles: towards a resolution of squamate relationships. Biological Journal of the Linnean Society 65:369–453.

LEE, M. S. Y., AND M. W. CALDWELL. 2000. Adriosaurus and the affinities of mosasaurs, dolichosaurs, and snakes. Journal of Paleontology 74:915–937.

LEVITON, A. E., R. H. GIBBS JR., E. HEAL, AND C. E. DAWSON. 1985. Standards in herpetology and ichthyology: part I. Standard symbolic codes for institutional resource collections in herpetology and ichthyology. Copeia 1985:802–832.

LIONS, M. L., R. H. AGUIRRE, J. A. CESPEDEZ, AND B. B. ALVAREZ. 1997. Reptiles de las áreas protegidas del Oeste de la Provincia de Formosa, Argentina. Facena 13:43–48.

LOSOS, J. B., D. M. HILLIS, AND H. W. GREENE. 2012. Who speaks with a forked tongue? Science 338:1428–1429.

MARQUET, P. A., F. BOZINOVI, R. G. MEDEL, Y. L. WERNER, AND F. M. JAKSI. 1990. Ecology of Garthia gaudichaudi, a gecko endemic to the semiarid region of Chile. Journal of Herpetology 24:431–434.

MARTORI, R., AND L. AUN. 1994. Análisis comparativo de la composición de tres comunidades de Squamata de la Sierra Grande de Córdoba, Argentina. Cuadernos de Herpetología 8:97–103.

MCDOWELL, S. B. J., AND C. M. BOGERT. 1954. The systematic position of Lanthanotus and the affinities of the anguinomorphan lizards. Bulletin of the American Museum of Natural History 105:1–142, 16 pls.

MCGUIRE, J. A. 1996. Phylogentic systematics of crotapytid lizards (Reptilia: Iguania: Crotaphytidae). Bulletin of the Carnegie Museum of Natural History 32:1–143.

MESZOELY, C. A. M. 1970. North American fossil anguid lizards. Bulletin of the Museum of Comparative Zoology 139:87–150.

MILLER, M. A., W. PFEIFFER, AND T. SCHWARTZ. 2010. Creating the CIPRES Science Gateway for inference of large phylogenetic trees. In Proceedings of the Gateway Computing Environments Workshop (GCE), New Orleans, pp. 1–8. Institute of Electrical and Electronics Engineers, USA.

MORANDO, M., C. D. MEDINA, L. J. AVILA, C. H. F. PEREZ, A. BUXTON, AND J. W. SITES JR. 2014. Molecular phylogeny of the New World gecko genus Homonota (Squamata: Phyllodactylidae). Zoologica Scripta 43:249–260.

MURPHY, R. W., C. BLAIR, AND F. MENDEZ DE LA CRUZ. 2009. A new species of leaf-toed gecko, genus Phyllodactylus (Squamata: Gekkota: Phyllodactylidae) from Guerrero, Mexico. South American Journal of Herpetology 4:17–24.

NORELL, M. A., AND K. GAO. 1997. Braincase and phylogenetic relationships of Estesia mongoliensis from the Late Cretaceous of the Gobi Desert and the recognition of a new clade of lizards. American Museum Novitates 3211:1–25.

PELEGRIN, N., AND E. H. BUCHER. 2009. Long-term effects of a wildfire on a lizard assemblage in the Arid Chaco Forest. Journal of Arid Environments 74:368–372.

PETERS, J. A., AND R. DONOSO-BARROS. 1970. Catalogue of the Neotropical Squamata: part II. Lizards and amphisbaenians. United States National Museum Bulletin 297:1–293.

PIANTONI, C., N. IBARGÜENGOYTÍA, AND V. E. CUSSAC. 2006. Growth and age of the southernmost distribuited gecko of the world (Homonota darwini) studied by skeletochronology. Amphibia-Reptilia 27:393–400.

PINCHEIRA-DONOSO, D. 2006. The Geckos of Chile (Scleroglossa, Gekkonidae, Gekkoninae). Part I. Synthesis of taxonomic and systematic studies. Noticiario Mensual Museo Nacional de Historia Natural 358:3–11.

POUGH, F. H., R. M. ANDREWS, M. L. CRUMP, A. H. SAVITZKY, K. D. WELLS, AND M. C. BRANDLEY. 2016. Herpetology. 4th ed. Sinauer Associates, USA.

RAGE, J.-C. 1976. Les Squamates du Miocène de Bèni Mellal, Maroc. Géologie Méditerranéenne 3:57–70.

RIEPPEL, O. 1980a. The phylogeny of anguinomorph lizards. Birkhäuser Verlag Basel, Switzerland.

RIEPPEL, O. 1980b. The trigeminal jaw adductors of primitive snakes and their homologies with the lacertilian jaw adductors. Journal of Zoology (London) 190:447–471.

RIEPPEL, O. 1984a. The structure of the skull and jaw adductor musculature of the Gekkota, with comments on the phylogenetic relationships of the Xantusiidae (Reptilia: Lacertilia). Zoological Journal of the Linnean Society 82:291–318.

RIEPPEL, O. 1984b. Miniaturization of the lizard skull: its functional and evolutionary implications. Pp. 503–520 in M. W. J. Ferguson (ed.), The Structure, Development and Evolution of Reptiles. The Zoological Society of London, Academic Press, England.

RIEPPEL, O., AND H. ZAHER. 2000. The braincase of mosasaurs and Varanus, and the relationships of snakes. Zoological Journal of the Linnean Society 129:489–514.

RIEPPEL, O., J. GAUTHIER, AND J. A. MAISANO. 2008. Comparative morphology of the dermal palate in squamate reptiles, with comments of phylogenetic implications. Zoological Journal of the Linnean Society 152:131–152.

RÖSLER, H. 1995. Geckos der Welt: Alle Gattungen. Urania–Verlag, Germany.

RÖSLER, H. 2000. Kommentierte liste der rezenten, subrezenten und fossilen Gecko–taxa (Reptilia: Gekkonomorpha). Gekkota 2:28–153.

ROTHIER, P. S., R. BRANDT, AND T. KOHLSDORF. 2017. Ecological associations of autopodial osteology in Neotropical geckos. Journal of Morphology 278:290–299.

RUSSELL, A. P. 1972. The foot of gekkonid lizards: a study in comparative and functional anatomy. Unpubl. Ph.D. diss., University of London, England.

RUSSELL, A. P. 1979. Parallelism and integrated design in the foot structure of gekkonine and diplodactyline geckos. Copeia 1979:1–21.

RUSSELL, A. P., AND A. M. BAUER. 2002. Underwood's classification of the geckos: a 21st century appreciation. Bulletin of the Natural History Museum, Zoology 68:113–121.

SABAJ PÉREZ, M. 2014. Standard symbolic codes for institutional resource collections in herpetology and ichthyology, version 5.0. Available at http://www.asih.org/resources/standard-symbolic-codes-institutional-resource-collections-herpetology-ichthyology. Archived by WebCite at http://www.webcitation.org/6krk3UoWm.

STAMATAKIS, A. 2014. RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. Bioinformatics 10:1093.

SUMIDA, S. S., AND R. W. MURPHY. 1987. Form and function of the tooth crown structure in gekkonid lizards (Reptilia, Squamata, Gekkonidae). Canadian Journal of Zoology 65:2886–2892.

SWOFFORD, D. L. 1991. When are phylogeny estimates from molecular and morphological data incongruent? Pp. 295–333 in M. M. Miyamoto and J. Cracraft (eds.), Phylogenetic Analysis of DNA Sequences. Oxford University Press, USA.

TCHERNOV, E., O. RIEPPEL, H. ZAHER, M. J. POLCYN, AND L. L. JACOBS. 2000. A fossil snake with limbs. Science 287:2010–2012.

TRONCOSO-PALACIOS, J. 2014. Nueva lista actualizada de los reptiles terrestres de la Región de Atacama, Chile. Boletín Chileno de Herpetología 2014:1–4.

UETZ, P., P. FREED, AND J. HOŠEK. 2016. The reptile database. Available from: http://www.reptile-database.org.

UNDERWOOD, G. 1954. On the classification and evolution of geckos. Proceedings of the Zoological Society of London 124:469–492.

VANZOLINI, P. E. 1968. Geography of the South American Gekkonidae (Sauria). Arquivos de Zoologia (São Paulo) 17:85–112.

VANZOLINI, P. E., AND R. DONOSO-BARROS. 1966. Garthia, a new genus for Gymnodactylus gaudichaudii Duméril & Bibron (Sauria, Gekkonidae). Papéis Avulsos de Zoologia (São Paulo) 18:129–131.

VIDAL, M. A., M. ITURRA-CID, AND J. C. ORTIZ. 2008. Clasificación de anfibios y reptiles. Pp. 79–106 in M. A. Vidal Maldonado and A. Labra Lillo (eds.), Herpetología de Chile. Science Verlag, Chile.

VITT, L. J., AND J. P. CALDWELL. 2014. Herpetology, fourth edition: an introductory biology of amphibians and reptiles. Academic Press, England.

WEEKS, D. M., AND R. E. ESPINOZA. 2013. Lizards on ice: Comparative thermal tolerances of the world's southernmost gecko. Journal of Thermal Biology 38:225–232.

WEISS, A. J., AND S. B. HEDGES. 2007. Molecular phylogeny and biogeography of the Antillean geckos *Phyllodactylus wirshingi*, *Tarentola americana*, and *Hemidactylus haitianus* (Reptilia, Squamata). Molecular Phylogenetics and Evolution 45:409–416.

WERNECK, F. P., T. GAMBLE, G. R. COLLI, M. T. RODRIGUES, AND J. W. SITES. 2012. Deep diversification and long-term persistence in the South American 'dry diagonal': integrating continent-wide phylogeography and distribution modeling of geckos. Evolution 66:3014–3034.

WERNER, Y. L., N. CARRILLO DE ESPINOZA, R. B. HUEY, D. ROTHENSTEIN, A. W. SALAS, AND F. VIDELA. 1996. Observations on body temperatures of some Neotropical desert geckos (Reptilia: Sauria: Gekkonidae). Cuadernos de Herpetología 10:59–70.

WIENS, J. J., C. A. KUCZYNSKI, T. M. TOWNSEND, T. W. REEDER, D. G. MULCAHY, AND J. W. SITES JR. 2010. Combining phylogenomics and fossils in higher-level squamate reptile phylogeny: molecular data change the placement of fossil taxa. Systematic Biology 59:674–688.

APPENDIX 1

List of Specimens

Codes for institutional resource collections follow Sabaj Pérez (2014) and preparation type is indicated according to the following key: [C&S] cleared and stained, [EtOH] ethanol-preserved specimens, [Sk] dry skeleton, [XR] X-ray, [HRCT] high-resolution X-ray computed tomography. Phyllodactylidae: *Asaccus elisae*: NHMUK uncataloged [Sk], CAS 218137 [HRCT]. *Garthia gaudichaudii*: FML 01558, 23469 [C&S], UMMZ 111574 [HRCT], USNM 165643 [XR]. *Garthia penai*: MZSP 60938 [C&S], FML 01547, 23470 [C&S], USNM 165598 [XR]. *Gymnodactylus geckoides*: CAS 49397 [HRCT]. *Haemodracon riebeckii*: MCZ A–27255 [HRCT]. *Homonota andicola*: FML uncataloged, 01816, 02608, 06101, 08304, 08315, 08318, 08331, 08332, 08403–08405, 08407, 08576, 10384, 13607–13609, 13610–13612, 17595 [C&S]. *Homonota borellii*: FML 00052, 00082, 00114, 00196, 00319, 00320, 00438, 00475, 00512–00516, 00560, 00562, 00563, 00618, 00717, 00727, 00767, 00866, 00933, 01118, 01141, 01145, 01156, 01180, 01183, 01747, 01799, 02107, 02140, 02164, 02387, 02409, 02414, 02543, 03066, 03180, 03255, 03256, 03353, 06088, 06757, 07666, 07761, 10383, 13670, 15860, 16235, 17601, 18384, 22647 [C&S]. *Homonota darwini*: FML uncataloged, 00640, 00794, 01042, 01828, 02131–02133, 08305, 08310, 08402, 08406, 08408, 08409, 17596–17598, 17746, 17747, 21127–21130, 21451, 21496, 22067–22070 [C&S]. *Homonota fasciata*: CAS 84771 [HRCT], JFBM 15827 [Sk], FML 00002, 00006, 00011, 00033, 00040, 00041, 00050, 00062, 00065, 00095, 00097, 00102, 00106, 00111, 00115, 00125, 00130, 00132, 00133, 00135, 00139, 00142, 00144, 00167, 00220, 00225, 00241, 00297, 00301, 00308, 00448, 00476, 00561, 00595, 00621, 00645, 00777, 00863, 00915, 01114, 01142, 01311, 01475, 01491–01495, 01506, 01576, 01748, 01751, 02033, 02105, 02108, 02109, 02137, 02159, 02415, 02422, 02431, 02460, 02479, 02773, 03057, 03150, 03201, 03251, 03257–03302, 03555, 03601, 03643, 03684, 03691, 03693, 03752, 03758, 03760, 03764, 03773–03775, 03777, 06115, 06119, 06157, 06314, 06551–06553, 06556, 06569, 06576, 06577, 06740, 07559, 07560, 07934, 08293, 08299, 08308, 08347, 09253, 09282, 09287, 09288, 10381, 10554–10594, 11972–11998, 12001–12015, 12396–12408, 13388, 18476, 20356–20383, 22462 [C&S]. *Homonota underwodi*: FML uncataloged, 00691, 01310, 01353, 01479, 01490, 01684, 01726, 01813, 02031, 02106, 02598, 02734, 03716, 03717, 07503, 08296, 08297, 08300–08303, 08327, 10382, 16184, 19819 [C&S]. *Homonota uruguayensis*: FML uncataloged, 01745, 01746, 01749, 01750 [C&S]. *Homonota whitii*: FML 02904, 03546, 03547, 03751 [C&S]. *Phyllodactylus angustidigitus*: USNM 38570 [XR]. *Phyllodactylus baurii*: CAS 09501 [XRCT]. *Phyllodactylus microphyllus*: USNM 38571 [XR]. *Phyllodactylus tuberculosus*: AMNH R–15953 [Sk]; NHMUK 1906.6.1.220 [Sk]. *Phyllodactylus xanti*: AMNH R–141106 [Sk]. *Phyllodactylus wirshingi*: RT 13860 [C&S], CAS 175498 [C&S]. *Phyllopezus lutzae*: MCZ R–46191 [HRCT]. *Phyllopezus pollicaris*: JFBM 15822 [Sk], FML 02313 [C&S], USNM 34104 [XR]. *Ptyodactylus hasselquistii*: NHMUK 1900.9.22.15 [Sk]; FMNH 210095 [Sk]; CAS 228536 [XRCT]. *Tarentola americana*: AMNH R–17726 [Sk]. *Tarentola mauritanica*: AMNH–R 71591, 144408, 144410 [Sk]; NHMUK 1913.7.3.36 [Sk]; CAS 87112 [XRCT]; JFBM 15824 [Sk], MVZ 178184 [Sk]. *Thecadactylus rapicauda*: AMNH–R 59722, 75824, 85311, 85312 [Sk]; NHMUK 59.9.6.436 [Sk]; CAS 95146 [XRCT]; FMNH 13006, 22212, 209454, 209456 [Sk]. Gekkonidae: *Gekko gecko*: AMB uncataloged [C&S]; SHSVMH-0002-2014–SHSVMH-0003-2014 [EtOH]; AMNH R-118697, 140787, 141120 [Sk], FMNH 4448, 209438, 213417, 216495, 216516, 31013 [Sk]; USNM 163787–163791 [XR]; FMNH 186818, SHSVMH-0001-2014 [HRXCT]. Diplodactylidae: *Correlophus belepensis*: CAS 25086 [HRCT]. *Rhacodactylus auriculatus*: NHMUK 86.3.11.10 [Sk].