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Molecular systematics of terraranas (Anura: Brachycephaloidea) with an assessment of the effects of alignment and optimality criteria

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Table of contents

Abstract

Brachycephaloidea is a monophyletic group of frogs with more than 1000 species distributed throughout the New World tropics, subtropics, and Andean regions. Recently, the group has been the target of multiple molecular phylogenetic analyses, resulting in extensive changes in its taxonomy. Here, we test previous hypotheses of phylogenetic relationships for the group by combining available molecular evidence (sequences of 22 genes representing 431 ingroup and 25 outgroup terminals) and performing a tree-alignment analysis under the parsimony optimality criterion using the program POY. To elucidate the effects of alignment and optimality criterion on phylogenetic inferences, we also used the program MAFFT to obtain a similarity-alignment for analysis under both parsimony and maximum likelihood using the programs TNT and GARLI, respectively.

Although all three analytical approaches agreed on numerous points, there was also extensive disagreement. Tree-alignment under parsimony supported the monophyly of the ingroup and the sister group relationship of the monophyletic marsupial frogs (Hemiphractidae), while maximum likelihood and parsimony analyses of the MAFFT similarity-alignment did not. All three methods differed with respect to the position of *Ceuthomantis smaragdinus* (Ceuthomantidae), with tree-alignment using parsimony recovering this species as the sister of *Pristimantis* + *Yunganastes*. All analyses rejected the monophyly of Strabomantidae and Strabomantinae as originally defined, and the tree-alignment analysis under parsimony further rejected the recently redefined Craugastoridae and Pristimantinae.

Despite the greater emphasis in the systematics literature placed on the choice of optimality criterion for evaluating trees than on the choice of method for aligning DNA sequences, we found that the topological differences attributable to the alignment method were as great as those caused by the optimality criterion. Further, the optimal tree-alignment indicates that insertions and deletions occurred in twice as many aligned positions as implied by the optimal similarity-alignment, confirming previous findings that sequence turnover through insertion and deletion events plays a greater role in molecular evolution than indicated by similarity-alignments. Our results also provide a clear empirical demonstration of the different effects of wildcard taxa produced by missing data in parsimony and maximum likelihood analyses. Specifically, maximum likelihood analyses consistently (81% bootstrap frequency) provided spurious resolution despite a lack of evidence, whereas parsimony correctly depicted the ambiguity due to missing data by collapsing unsupported nodes.

We provide a new taxonomy for the group that retains previously recognized Linnaean taxa except for Ceuthomantidae, Strabomantidae, and Strabomantinae. A phenotypically diagnosable superfamily is recognized formally as Brachycephaloidea, with the informal, unranked name terrarana retained as the standard common name for these frogs. We recognize three families within Brachycephaloidea that are currently diagnosable solely on molecular grounds (Brachycephalidae, Craugastoridae, and Eleutherodactylidae), as well as five subfamilies (Craugastorinae, Eleutherodactylinae, Holoadeninae, Phyzelaphryninae, and Pristimantinae) corresponding in large part to previous families and subfamilies. Our analyses upheld the monophyly of all tested genera, but we found numerous subgeneric taxa to be non-monophyletic and modified the taxonomy accordingly.

Key words: Brachycephalidae, Craugastoridae, dynamic homology, direct optimization, Eleutherodactylidae, maximum likelihood, missing data, Neotropics, parsimony, phylogeny, rogue taxa, sparse supermatrix, taxonomy, terrarana, wildcard

Introduction

With more than 1000 species, the clade of New World direct-developing frogs, Brachycephaloidea[1], comprises around 33% of all New World frog species and nearly 17% of named anuran species worldwide (Frost, 2014). Species of this clade are found natively over a large portion of the Americas, extending from the southwestern USA to northern Argentina through a broad variety of habitats, including the cold páramos of the Andes up to 4500 m elevation, cloud forests, and lowland rainforests, as well as dry tropical scrub and even semi-arid and arid areas. These frogs are often important components of ecological communities in terms of both species composition and individual abundance (*e.g.*, Duellman, 1978; Lynch & Duellman, 1997; Hedges *et al.*, 2008a; Crawford *et al.*, 2010a). As an example, in Amazonia up to 20 species of these frogs have been found at a single locality (Cisneros-Heredia, 2006).

For decades, most terraranas were considered either a tribe (Eleutherodactylini; Lynch, 1971) or subfamily (Eleutherodactylinae; Heyer, 1975; Laurent, 1986) within the disparate collection of arciferal, procoelous taxa referred to Leptodactylidae (*e.g.*, Lynch, 1971, 1973; Heyer, 1975). The bulk of Eleutherodactylinae was grouped under the large genus *Eleutherodactylus* (also including most of the species now included in the nominal brachycephaloid families) but Ardila-Robayo (1979) found a paraphyletic *Eleutherodactylus* that would also need to include at least *Barycholos*, *Geobatrachus*, *Ischnocnema*, and *Phrynopus* to be rendered monophyletic. Izecksohn (1988) later suggested that Eleutherodactylinae was also likely paraphyletic with respect to Brachycephalidae (at that time restricted to *Brachycephalus* and *Psyllophryne*), and in support of that hypothesis Pombal (1999) noted that the only frogs known to possess an egg tooth were eleutherodactylines and *Brachycephalus*. Subsequently, Darst & Cannatella (2004) inferred via molecular data that the "leptodactylid" subfamily Eleutherodactylinae was indeed paraphyletic with respect to Brachycephalidae (*i.e.*, *Brachycephalus* [by that time including *Psyllophryne*]), although they explicitly did not make the nomenclatural remedy. It was Dubois (2005a), following Darst & Cannatella's (2004) results, who first united eleutherodactylines and *Brachycephalus* into a single family-group, placing Eleutherodactylinae into the synonymy of a subfamily of Leptodactylidae: Brachycephalinae.

Although Dubois' (2005a) action resolved the paraphyly of Eleutherodactylinae, it perpetuated the non-monophyly of Leptodactylidae. Based on an analysis of previously published evidence combined with a large amount of new DNA sequences from species now placed in the genera *Barycholos*, *Brachycephalus*, *Craugastor, Eleutherodactylus*, *Haddadus*, *Ischnocnema*, *Oreobates*, *Psychrophrynella*, and *Pristimantis*, Frost *et al.* (2006) removed all terraranas from Leptodactylidae and recognized them as Brachycephalidae. Their results provided decisive support for the monophyly of the group, as previously evidenced by the phenotypic synapomorphies of

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[1] We herein refer the clade of New World direct-developing frogs to Brachycephaloidea Günther, 1858 (equivalent in diagnosis and content to Brachycephalidae *sensu* Frost *et al.,* 2006) and use terrarana (pl. terraranas) of Hedges *et al.* (2008a) as the common name for frogs in this clade.

direct development (Lutz, 1954; Gallardo, 1965; Lynch, 1971), the presence of a single, bicuspid, keratinized egg tooth in embryos (Sampson, 1904; Noble, 1926; Pombal, 1999), and T-shaped terminal phalanges (Lynch, 1971). More recently, the monophyly of the group has again received substantial support from morphology in the form of seven additional synapomorphies in the urogenital and vascular anatomy (Taboada *et al.*, 2013).

The monophyly of terraranas has been most decisively tested, and corroborated, by extensive analyses of DNA sequences for a large proportion of the group in the studies of Heinicke *et al.* (2007) and Hedges *et al.* (2008a), with 276 and 346 terminal species of terraranas, respectively. Hedges *et al.* (2008a) provided a new family-level taxonomy designed to make the taxonomy of Brachycephalidae of Frost *et al.*, (2006) (> 850 species at the time) "more manageable by splitting the group into four families" (p. 11). Rather than employ the available family-group name Brachycephaloidea Günther, 1858 for the clade containing the new families, Hedges *et al.* (2008a) proposed the new unranked name Terrarana explicitly "to avoid putting in place yet another formal name (superfamily rank)… and the potential problems it might raise in dealing with existing superfamily names (*e.g.*, Hyloidea) that may apply to this group" (p. 11). We do not find these arguments to be compelling for the following reasons.

First, with nearly half of all frogs (> 3600 of ca. 7200 species and ca. 20 families) currently placed within Hyloidea, the usefulness of the superfamilial taxonomy of frogs employed by Hedges *et al.* (2008a) is limited due to the over inclusiveness of regulated family-group names. Hyloidea has been redelimited several times as opinions changed (*e.g.*, Duellman, 1975 [as Bufonoidea], Darst & Cannatella, 2004; Pyron & Wiens, 2011) and remains a huge and unstably delimited taxon whose rank formality precludes the nomenclatural recognition needed for groups between it and the large number of formal families that it contains. A solution to this problem was provided by Frost *et al.* (2006), who explicitly deployed a number of unranked above-family-group taxon names in order to provide taxonomists with room for maneuver so that a stable family-group taxonomy could be built from the ground up[2]. We therefore fail to see the benefit of avoiding a formal family-group name for this important and universally recognized group. Indeed, Hedges *et al.* (2008a) went on to treat terraranas formally as a "New Taxon" (see also Hedges *et al.*, 2008b; Heinicke *et al.*, 2009) and, as such, the consequence of this act was not to provide an *informal* name for this group, but rather a formal but *unregulated* and *unranked* name, Terrarana, even though (or perhaps because) the regulated family-group name Brachycephaloidea was already available.

Second, problems in dealing with existing taxa are by no means avoided by naming a taxon in a way that avoids regulation by the International Code of Zoological Nomenclature (1999). Indeed, the Code and its Commission exist precisely to resolve problems, should they arise. This is not to say that we think all unregulated names are undesirable or that the Code should regulate above-family-group taxa[3]. To the contrary, we believe unregulated names play an important role in allowing workers to discuss species and their relationships. Whether ranked or unranked, unregulated names for more inclusive clades are necessary once family-group names have been exhausted at less inclusive hierarchic levels, and they can be extremely useful even when family-group names have not been exhausted. For example, standard vernacular names provide stability as scientific hypotheses are proposed and refuted (Crother, 2009), and informal groups (*e.g.*, species groups) can allow systematists to recognize and discuss groups tentatively as evidence accumulates without proliferating taxonomy with "yet another formal name." Indeed, given the recentness and limited and conflicting evidence for the major lineages within this clade, it would have been understandable if Hedges *et al.* (2008a) had used informal, unregulated names for the putative major lineages within the clade instead of dividing them into four formal families (two of which have already been combined; Pyron & Wiens, 2011).

In contrast, recognition of the Brachycephaloidea clade is by no means tentative. The group has been recognized more-or-less universally since Lynch (1971) modified earlier proposals by Lutz (1954) and Gallardo (1965), the only noteworthy recent change being the inclusion of *Brachycephalus*, which is why Hedges *et al.* (2008a) were warranted in applying a formal name to the inclusive group, their choice being the unranked Terrarana (instead of Brachycephalidae or Brachycephaloidea).

Concerning the division of the group into several families, Hedges *et al.* (2008a) restricted Brachycephalidae to

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[2] We reject the use of the family-group name Hyloidea for a taxon otherwise equating to the above-family-group name Notogaeanura of Frost *et al.* (2006), which equates to Hyloidea of Pyron & Wiens (2011), and differs in content from Hyloides of Frost *et al.,* (2006), only in the latter's exclusion of Sooglossidae and Nasikabatrachidae.

[3] We do not adopt the suggested rules for regulating above-family-group names by Dubois (2005b, 2006), which in our view are problematic and, moreover, have no force pending discussion and adoption by the International Commission of Zoological Nomenclature.

the clade composed of *Brachycephalus* and *Ischnocnema* and extracted another three families and four subfamilies from Brachycephalidae *sensu* Frost *et al.* (2006), all posited on molecular grounds to be monophyletic: Craugastoridae, Eleutherodactylidae (including Phyzelaphryninae and Eleutherodactylinae), and Strabomantidae (including Holoadeninae and Strabomantinae). Subsequently, Heinicke *et al.* (2009) named a species from the Guiana Shield previously thought to be related to species of *Pristimantis* but recovered as the sister of all other terraranas by Hedges *et al.* (2008a; listed by them as "Unknown anuran sp"). In order to preserve the families Hedges *et al.* (2008a) had just recognized, Heinicke *et al.* (2009) named the genus *Ceuthomantis* and family Ceuthomantidae to accommodate that species (*C. smaragdinus*) and two others previously referred to *Pristimantis* but assumed on the basis of morphological similarity to be closely related.

In their large study of legacy DNA sequences, Pyron & Wiens (2011) recovered a topology that required a number of changes to the taxonomy proposed by Hedges *et al.* (2008a), the most conspicuous being that Strabomantidae of Hedges *et al.* (2008a) was non-monophyletic with part (*Strabomantis*) more closely related to Craugastoridae (*Craugastor* and *Haddadus*). To avoid partitioning terraranas into additional families, Pyron & Wiens (2011) placed Strabomantidae into the synonymy of Craugastoridae, rendering Strabomantinae a monotypic subfamily (containing only the genus *Strabomantis*) and proposed the *nomen nudum* Pristimantinae [later diagnosed and validated by Ohler & Dubois (2012)] for the clade of *Lynchius*, *Oreobates*, *Phrynopus*, and *Pristimantis,* but excluding *Yunganastes*. Under this new arrangement, four families were recognized: Brachycephalidae, Ceuthomantidae, Craugastoridae, and Eleutherodactylidae.

Craugastoridae sensu Pyron & Wiens (2011) was not recognized by Blackburn & Wake (2011), who retained the scheme of Hedges *et al.* (2008a), arguing that “because of low support values among basal nodes in this larger clade, the analysis of Pyron & Wiens (2011) does not reject the hypothesis that Craugastoridae is sister to the Strabomantidae” (p. 41, fn. 24). However, insofar as that clade is absent from their optimal maximum likelihood tree, the analysis of Pyron & Wiens (2011) does reject that hypothesis, regardless of the bootstrap values. Further, in the Hedges *et al.* (2008a) results Strabomantidae and Strabomantinae present bootstrap frequencies < 70% in all analyses, and the sister relationship of Craugastoridae and Strabomantidae was rejected in two of their three analyses (the 362- and 216-taxa analyses; 54% bootstrap in likelihood and unsupported in parsimony in the third one, the 80-taxon analysis). Despite increased character sampling, resampling values were even lower in the tree proposed by Heinicke *et al.* (2009), which also recovered Strabomantinae *sensu* Hedges *et al.* (2008a) as non-monophyletic. As such, it was no surprise that the denser taxon sampling of Pyron & Wiens (2011) would result in topological changes, and it is evident that Blackburn & Wake’s (2011) preference of the taxonomy of Hedges *et al.* (2008a) over that of Pyron & Wiens (2011) was not due to rejection of clades with low resampling values per se, but something else.

In summary, in less than a decade the taxonomy of terraranas has shifted from having its parts placed in two distantly related families (Brachycephalidae [composed only of *Psyllophryne* and *Brachycephalus*] and Leptodactylidae [the subfamily Eleutherodactylinae, with more than 700 species in a single genus, *Eleutherodactylus*]), to being merged into a single large, but monophyletic subfamily (Brachycephalinae; Dubois, 2005a) and then family (Brachycephalidae; Frost *et al.*, 2006), then referred to the unranked taxon Terrarana and partitioned into four families (Hedges *et al.*, 2008a), then five (Heinicke *et al.*, 2009), then four (Pyron & Wiens, 2011), and then five again (Blackburn & Wake, 2011). Additionally, five subfamilies were proposed during this period, and species have been transferred across families as DNA sequences have accumulated (*e.g.*, Canedo & Haddad, 2012). Few groups of amphibians have enjoyed such dramatic taxonomic instability in recent times.

Beyond the family-group changes promoted by new data, new analyses, and conflicting views on best taxonomic practice, both understanding and conflict have increased among genera as well. *Adelophryne*, *Holoaden*, *Noblella*, *Phyzelaphryne* (Heinicke *et al.*, 2007; Hedges *et al.*, 2008a), *Yunganastes* (Padial *et al.*, 2009), and *Euparkerella* (Canedo & Haddad, 2012) were corroborated as terraranas, and six more genera (*Bryophryne, Diasporus, Haddadus, Psychrophrynella, Isodactylus* [preoccupied by *Isodactylus* Gray, 1845; replaced by *Hypodactylus* Hedges *et al.*, 2008b], and *Lynchius*) were proposed by Hedges *et al.* (2008a), partitioning and redelimiting the large South American groups of “*Eleutherodactylus*” and *“Phrynopus”* of earlier authors (*e.g.,* Lynch, 1971, 1975; Lynch & Duellman, 1997; Frost *et al.*, 2006).

Despite the advances brought by molecular data in understanding amphibian higher systematics, the position of terraranas within Nobleobatrachia remains conflicted. Faivovich *et al.* (2005) and Frost *et al.* (2006) found Brachycephaloidea to be the sister taxon of a large clade including Hemiphractidae (in the case of Frost *et al.*, 2006, all except *Hemiphractus*), Hylidae, Bufonidae, Leptodactylidae, and others. Roelants *et al.* (2007), using different and fewer terminals, substantially different molecular data, and analyzing a similarity-alignment with a maximum likelihood method, found terraranas to be embedded within hylids. Wiens *et al.* (2005), employing Bayesian and parsimony analyses of a combined morphology and DNA dataset, found hemiphractids (*Cryptobatrachus*, *Flectonotus*, *Gastrotheca, Hemiphractus*, and *Stefania*) to form the sister group of a clade of terraranas, including the genera *Oreobates, Pristimantis*, *Lynchius,* and *Strabomantis* (following the current taxonomy). Heinicke *et al.* (2009) subsequently included representatives of 13 genera of brachycephaloids, three genera of hemiphractids (*Flectonotus, Hemiphractus*, and *Stefania*), and representatives of all other families of Nobleobatrachia of Frost *et al.* (2006) and again recovered hemiphractids and brachycephaloids as sister groups (both under parsimony and maximum likelihood), forming the most derived clade of Nobleobatrachia Frost *et al.* (2006), a relationship that they formalized with the unranked name Orthobatrachia. More recently Pyron & Wiens (2011) found Brachycephaloidea to be the sister of all other nobleobatrachians in their maximum likelihood analysis, a result concordant with the results of the much smaller study of Darst & Cannatella (2004).

Pyron & Wiens (2011) performed the largest phylogenetic (maximum likelihood) analysis of Brachycephaloidea to date and provided a jumping-off point for additional phylogenetic work. Nevertheless, several loci sampled by Frost *et al.* (2006), Hedges *et al.* (2008a), and Heinicke *et al.* (2009) were not included by them, several terminals were excluded, erroneous identifications of GenBank sequences were perpetuated or evidenced in their analyses (*e.g.*, Blotto *et al.*, 2012; see also below), and a substantial number of new sequences for additional taxa have accumulated subsequently. What is more important than these kinds of shortcomings, for which any large study can be criticized, is that the degree to which the similarities and differences between their results and those of previous studies depend on the underlying assumptions of each of the methods of optimization and sequence-alignment is unclear.

Objectives of this study

The primary objective of this study is to identify the optimal phylogenetic explanation of the species diversity of Brachycephaloidea. To provide the strongest possible test of the monophyly of Brachycephaloidea and its component subclades, we analyzed published (and, where necessary, reidentified) DNA sequences for all species listed in GenBank as of February 2012. Because all terminals and all molecular data used by previous workers (*e.g.*, Heinicke *et al.*, 2007; Hedges *et al.*, 2008a, Heinicke *et al.*, 2009; Pyron & Wiens, 2011) are included, our study represents a test of all previous large-scaled molecular-based hypotheses of relationship. New sequences from two recent large studies focusing on parts of the group (Canedo & Haddad, 2012; Pinto-Sánchez *et al.*, 2012), studies focusing on smaller parts of the terrarana tree (Amaro *et al.*, 2013; Barrio-Amorós *et al.* 2013; Fouquet *et al.*, 2012; Fusinatto *et al.*, 2013; Rodríguez *et al.*, 2013; Zhang *et al.*, 2013), dealing with species-level taxonomy (Brusquetti *et al.*, 2013; Gehara *et al.*, 2013; Hertz *et al.*, 2013: Fouquet *et al.*, 2013a; García-R. *et al.*, 2014; Pereyra *et al.*, 2014) or phylogeography (Rodríguez *et al.*, 2012; García-R. *et al.*, 2012; Kieswetter & Schneider, 2013) were not available in time for this study. Nonetheless, they differ little or not at all from our results, which we address in detail below.

A secondary, albeit equally important, objective of this study is to discern the effects that increasing assumptions about both nucleotide homology and evolutionary processes have on phylogenetic inferences. Specifically, we compare the results of tree-alignment under parsimony (the optimality criterion being the minimization of hypothesized changes required to explain the observed variation in DNA sequences, also referred to as direct optimization or dynamic homology; Sankoff, 1975; Wheeler, 1996, 2001; Wheeler *et al.*, 2006; Grant & Kluge, 2009) with results from state-of-practice maximum likelihood analyses that extend from a prior, similarity-based alignment and assume a probabilistic model of molecular evolution (see Felsenstein, 2004). In order to distinguish between effects of alignment and tree selection criteria, we also analyze the same similarity-based alignment under parsimony. Nevertheless, for reasons discussed below, we consider the tree-alignment + parsimony solution to be optimal and use it for taxonomic decisions.

Material

Locus sampling

Phylogenetic analyses in this study employ DNA sequences of terraranas for 22 loci available in GenBank as of February 1, 2012, and which represent all loci used by previous studies to infer relationships of Brachycephaloidea. Non-coding mtDNA genes include rRNA genes of the heavy strand transcription unit 1 fragment (12S, 16S and the intervening $\mathrm{tRNA}^{\mathrm{valine}}$, and $\mathrm{tRNA}^{\mathrm{leucine}}$ segments). Protein-coding mtDNA genes include cytochrome b (cytb), cytochrome c oxidase subunit I (COI), and NADH dehydrogenase subunit I (ND1) and subunit II (ND2), and intervening $\mathrm{tRNA}^{\mathrm{cyst}}$. Nuclear protein-coding genes include two exons of cellular myelocytomatosis (c-myc), chemokine receptor 4 (CXCR4), histone H3 (HH3), sodium-calcium exchanger 1 (NCX1), propiomelanocortin A (POMC), recombination-activating protein 1 (RAG1), rhodopsin (Rhod), seven-in-absentia (SIA), solute carrier family 8 member 3 (SLC8A3), and tyrosinase precursor (Tyr). Non-coding nuclear genes include 28S and the intron region of the cellular myelocytomatosis gene (c-myc). Accession numbers for all sequences used in this study are listed in Appendix 1.

Taxon sampling

DNA sequences represent 456 terminals (Appendix 1), of which 25 are treated as outgroup taxa. Outgroup sampling was guided by results of the following recent phylogenetic analyses: Darst & Cannatella's (2004) parsimony analyses recovered terraranas as the sister group of their sample of Nobleobatrachia, while in their maximum likelihood analyses they were embedded within Nobleobatrachia in an unresolved position. Faivovich *et al.* (2005) found hemiphractids to be paraphyletic with respect to Brachycephaloidea because two species of *Eleutherodactylus* (now *Pristimantis pharangobates* and *P. thymelensis*) formed the sister group of *Hemiphractus helioi*, and the inclusive clade was placed with *Brachycephalus ephipppium* and *Phrynopus* sp. (now *Psychrophrynella guillei*). Wiens *et al.* (2005) found hemiphractids (*Cryptobatrachus*, *Hemiphractus*, *Flectonotus*, *Gastrotheca,* and *Stefania*) to be sister to a clade of terraranas including, following the current taxonomy, the genera *Lynchius, Oreobates, Pristimantis,* and *Strabomantis*. Frost *et al.* (2006) found terraranas to be the sister of all nobleobatrachians except *Hemiphractus helioi* (and excluding other species now included in Hemiphractidae), a clade they formally recognized as Meridianura. Roelants *et al.* (2007) found Brachycephaloidea to be embedded within hylids. Heinicke *et al.* (2009) sampled 13 genera of terraranas, three genera of hemiphractids (*Flectonotus, Hemiphractus*, and *Stefania*), and an ample representation of genera of the Nobleobatrachia and Australobatrachia of Frost *et al.* (2006), and again recovered Hemiphractidae and Brachycephaloidea as sister groups. Pyron & Wiens (2011) recovered Brachycephaloidea as the sister of all other nobleobatrachians, a result concordant with the parsimony analyses of Darst & Cannatella (2004). The analyses by Zhang *et al.* (2013) of nearly complete mtDNA genomes found three brachycephaloid terminals (*Craugastor augusti*, *Eleutherodactylus atkinsi*, and *Pristimantis thymelensis*) as the sister group of nobleobatrachians. Fouquet *et al.* (2013b) found a clade with representatives of six genera of terraranas (*Brachycephalus*, *Craugastor*, *Eleutherodactylus*, *Oreobates*, *Phyzelaphryne*, and *Pristimantis*) as either the sister group of a diverse array of nobleobatrachians in Bayesian analyses or embedded within Nobleobatrachia as the sister of a group of hemiphractids (*Gastrotheca*, *Hemiphractus*, and *Stefania*) in maximum likelihood analyses. The same study used a larger array of terraranas (*Brachycephalus ephippium*, *Ceuthomantis smaragdinus*, *Eleutherodactylus marnockii*, *Haddadus binotatus*, *Phyzelaphryne miriamae*, and *Pristimantis pharangobates* misidentified as *P. pluvicanorus* [now in *Yunganastes*]) for their maximum parsimony and tree-alignment inferences and found terraranas to be paraphyletic, with *Ceuthomantis* as the sister group to all other terraranas and nobleobatrachians. Accordingly, we included 23 species of Nobleobatrachia representing all of the groups previously hypothesized to be closely related to Brachycephaloidea (13 species of hemiphractids, 8 species of hylids, and 2 species of leptodactylids) plus the distantly related *Calyptocephalella gayi* (Calyptocephalellidae) and *Xenopus laevis* (Pipidae) as the root. The identities of three outgroup terminals were corrected (Table 1).

The ingroup includes 431 terminals representing 19 nominal genera (*Barycholos*, *Brachycephalus*, *Bryophryne*, *Diasporus*, *Ceuthomantis*, *Craugastor*, *Eleutherodactylus*, *Haddadus*, *Holoaden*, *Hypodactylus*, *Ischnocnema*, *Lynchius*, *Noblella*, *Oreobates*, *Phrynopus*, *Pristimantis*, *Psychrophrynella*, *Strabomantis*, and *Yunganastes*), 408 nominal species and 23 unidentified species. Due in part to the difficulties involved in identifying terraranas and in part to the rapid evolution of understanding of the group, the identities of numerous samples used in previous phylogenetic analyses had to be corrected. Of the 431 terminals, 24 GenBank sequences required re-identification (Table 1) and another 23 could not be identified beyond the generic level (Appendix 1). Corrections were made by cross-checking GenBank identifications with updated determinations provided in the publications for which sequences were originally submitted, new identifications provided in subsequent literature, and by direct examination of voucher specimens by the first author, and in one case based on the results of our phylogenetic analyses. Unfortunately, in this process we overlooked two nominal species of *Eleutherodactylus* (*E. diplasius*, *E. notitodes*) that were elevated from subspecies to species by Hedges *et al.* (2008a) because corresponding sequences were deposited in GenBank under their older covering-species names *E. wetmorei* and *E. audanti*. Similarly, we overlooked *E. varians* because among the several sequences deposited in GenBank under this name several correspond to *E. olibrus* (formerly a subspecies of *E. varians*) and we only sampled those.

TABLE 1. Updated terminal species names of GenBank sequences re-identified for the purposes of this study.

Terminal name	Original name and rationale for re-identification
Adelophryne patamona	*Adelophryne adiastola* (ROM 39578) of Hedges *et al.* (2008a) is *A. patamona* according to Fouquet *et al.* (2012, p. 555).
Craugastor cf. *augusti*	*Craugastor augusti* from Alamos, southern Sonora, Mexico (DQ283271) of Frost *et al.* (2006) is treated here as *C.* cf. *augusti* in contrast to another terminal, *C. augusti* from Jalisco (UTACV A-12980), which comes from a population geographically much closer to the type locality (Guanajuato, Mexico) than to the Sonoran locality, and this nominal species likely represents a species complex (Goldberg *et al.*, 2004).
Craugastor cf. *longirostris*	*Craugastor* cf. *longirostris* (FMNH 257678) of Streicher *et al.* (2009) and *Craugastor* aff. *longirostris* (AJC-2009) of Crawford *et al.* (2010a) are considered conspecific following Crawford *et al.* (2010a), with sequences of both specimens being used for our terminal *C.* cf. *longirostris*.
Craugastor montanus	Sequences of *Craugastor sartori* (EF493530, EF493478, EF493453, AY273121, and AY211308) are re-identified as *C. montanus* because the former—originally a replacement name for *Microbatrachylus montanus* Taylor, 1942 (when *Microbatrachylus montanus* was *Eleutherodactylu*s)—is now considered a junior synonym of the later (see Frost, 2014).
Cryptobatrachus fuhrmanni	*Cryptobatrachus* sp. (JDL14865) of Darst and Cannatella (2004) is *Cryptobatrachus fuhrmanni* (S. Castroviejo, personal commun.; J. D. Lynch in litt. to W.E. Duellman, the latter in litt. to S. Castroviejo)
Diasporus citrinobaephus	*Diasporus* aff. *diastema* of Crawford *et al.* (2010a) is considered here as *D. citrinobaephus* because Hertz *et al.* (2012, p. 33) found the former to be sister to topotypic populations of the latter, show differences of 1.8% in base composition in 16S sequences, and they occur within the same habitat.
Fritziana aff. *fissilis*	*Flectonotus* sp. (CFBH5726 [the number CFBH5720 listed in GenBank and the original publication is erroneous]) of Faivovich *et al.* (2005) is a species of *Fritziana* following the partition of *Flectonotus* by Duellman *et al.* (2011, p. 25), and according to C. F. B. Haddad (personal commun.) it represents an unnamed species related to *F. fissilis*.
Gatrotheca piperata	*Gastrotheca* cf. *marsupiata* (MNK 5286) of Faivovich *et al.* (2005) was re-determined as *G. piperata* by Duellman and Köhler (2005).
Oreobates saxatilis	*Ischnocnema* sp. (DQ284091, DQ283788, DQ282661) of Frost *et al.* (2006) is *Oreobates saxatilis* according to Padial *et al.* (2012, p. 11).
Phrynopus auriculatus	*Phrynopus* sp. (KU 291633) of Heinicke *et al.* (2007) is reidentified as *P. auriculatus* following Duellman and Hedges (2007).
Phrynopus tribulosus	*Phrynopus* sp. (KU 291630) of Hedges *et al.* (2008a) is herein reidentified as *P. tribulosus* (see Duellman and Hedges, 2007).
Pristimantis achuar	*Pristimantis ockendeni* (QCAZ 25273) corresponds to *P. achuar* (see Elmer and Cannatella, 2008).

......continued on the next page

TABLE 1. (Continued)

Terminal name	Original name and rationale for re-identification
Pristimantis adiastolus	*Eleutherodactylus* sp. (KU 291681) of Hedges *et al.* (2008a) corresponds to *Pristimantis adiastolus* (see Duellman and Hedges, 2007).
Pristimantis albertus	*Pristimantis* sp. SBH-2008 (KU 291675) of Hedges *et al.* (2008a) corresponds to *P. albertus* (see Duellman and Hedges, 2007).
Pristimantis altamnis	*P. ockendeni* (QCAZ 25439) corresponds to *P. altamnis* (see Elmer and Cannatella, 2008).
Pristimantis aniptopalmatus	Sequences available in GenBank as "*Pristimantis* sp. SBH-2008 voucher KU 291666" are here identified as *P. aniptopalmatus* because they cluster in our analyses with a paratype of *P. aniptopalmatus* and are topotypic. These sequences are listed in GenBank as produced by Hedges *et al.* (2008a), but there is no reference to that terminal or its accession numbers in Hedges *et al.* (2008a). Duellman and Hedges (2005) described and named *P. aniptopalmatus,* produced sequences for one paratype and two referred specimens for their molecular phylogenetic analyses, but did not deposit sequences in GenBank. Later Heinicke *et al.* (2007) used sequences of one paratype and deposited sequences in GenBank (identified as "*Pristimantis aniptopalmatus* voucher KU 291627" in GenBank), which are also used herein. Therefore, two terminals in our trees correspond to *P. aniptopalmatus*.
Pristimantis cruciocularis	*Pristimantis* sp. SBH-2008 (KU 291673) of Duellman and Hedges (2005) corresponds *P. cruciocularis* (see Lehr *et al.*, 2006).
Pristimantis festae	*Pristimantis trepidotus* of Heinicke *et al.* (2007) has been considered a synonym of *P. festae* since Lynch (1974) and we use the latter name.
Pristimantis kichwarum	*P. ockendeni* (QCAZ 18069) corresponds to *P. kichwarum* (see Elmer and Cannatella, 2008).
Pristimantis minutulus	*Pristimantis* sp. SBH-2008 (KU 291677) of Hedges *et al.* (2008a) corresponds to *P. minutulus* (see Duellman and Hedges, 2007).
Pristimantis ornatus	*Pristimantis* cf. *rhabdolaemus* SBH-2008 (MTD 45073) of Duellman and Hedges (2005) corresponds *P. ornatus* (see Lehr *et al.*, 2006).
Pristimantis pharangobates	*Yunganastes pluvicanorus* (AMNH-A 165195) of Faivovich *et al.* (2005) was reidentified as *P. rhabdolaemus* by Padial *et al.* (2007, p. 235), but the corresponding population is now assigned to *P. pharangobates* according to Duellman and Lehr (2009, p. 215), who removed it from the synonym of *P. rhabdolaemus* where it had been placed by Lynch and McDiarmid (1987).
Pristimantis reichlei	*Pristimantis peruvianus* of Hedges *et al.* (2008a) is *P. reichlei* according to our examination of the voucher specimen (MHNSM 9267) (see also Padial and De la Riva, 2009).
Pristimantis saltissimus	*Pristimantis* sp. SBH-2008 (ROM 43310) of Hedges *et al.* (2008a) corresponds to *P. saltissimus* (see Means and Savage, 2007).
Pristimantis simonsii	*Phrynopus simonsii* (KU 212350) of Wiens *et al.* (2005) is *Pristimantis simonsii* according to Hedges *et al.* (2008a, p. 125).
Pristimantis sp. (ROM 43978)	*Pristimantis zeuctotylus* of Hedges *et al.* (2008a) is here treated as *Pristimantis* sp. (ROM 43978) based on examination of the voucher.
Psychrophrynella guillei	*Phrynopus* sp. (AMNH-A 165108) of Faivovich *et al.* (2005) is *Psychrophrynella guillei* (see De la Riva 2007, p. 258).
Psychrophrynella saltator	*Phrynopus* sp. GF-La_Paz-Phr1 of Lehr *et al.* (2005) is *Psychrophrynella saltator* according to the results of De la Riva *et al.* (2008).
Psychrophrynella usurpator	*Phrynopus peruvianus* (KU 173495) of Heinicke *et al.* (2007) is *Psychrophrynella usurpator* according to the results of De la Riva *et al.* (2008).

Methods

Overview and goals

We are in a period of enormous growth of phylogenetic knowledge. To a large degree, this growth has been driven by technological advances in obtaining and analyzing DNA sequences that enable workers to perform sophisticated analyses without requiring that they understand the underlying logical and theoretical foundations of those analyses. The positive aspects of the resulting increased population of workers cannot be overstated. It is good that more people are generating data and publishing trees, even in a rough-and-ready form. The downside, however, is that in such a climate it is social trends, instead of intellectual discussion, that largely govern which techniques are popular and "correct" (Kuhn, 1962), and much of the discourse moves away from science and towards propaganda and sloganeering. Sober (2004) drew attention to this in regards to the misconception that maximum likelihood is for DNA and parsimony is for phenotypic characters, but otherwise such sociological aspects of systematics are rarely discussed in scientific circles (but see Frost *et al.*, 2008).

The effect of social pressures is perhaps best exemplified by the trend of empirical papers to base conclusions on the combined or cherry-picked results of whatever methods (*e.g.*, maximum likelihood, Bayesian inference, parsimony) and software are currently popular, despite their incongruent assumptions and without explaining why other, previously popular methods (*e.g.*, neighbor joining, UPGMA) or variations (*e.g.*, implied weighting in parsimony) were not "explored" as well. To be clear, where the objectives are methodological, comparisons of results from different methods can provide insights into the effects methods and their assumptions have on empirical inferences (*e.g.*, the extent to which increased assumptions cause results to depart from the most parsimonious explanation). That is, like numerical simulations (Oreskes *et al.*, 1994), such comparisons are heuristic, but they do not constitute empirical tests because there is no logical basis for employing congruence or incongruence of results across analytical methods as an optimality criterion (Grant & Kluge, 2003). Unfortunately, this path seems most often to be taken in order to avoid having to choose and defend a particular method and, thus, controversy. Regardless, both philosophically and methodologically, by deciding not to choose, a choice still has been made.

As noted above, one of our objectives is to relate the similarities and differences of the trees that result from different methods of phylogenetic analysis to the underlying assumptions and procedures of these approaches. Specifically, we compare the trees selected through tree-alignment (here used as synonymous with dynamic homology analysis: Sankoff, 1975; Wheeler *et al.*, 2006; Varón & Wheeler, 2012) under the optimality criterion of parsimony with those found through analysis of a prior, static, similarity-based alignment analyzed under both the maximum likelihood and parsimony optimality criteria. Although we attribute incongruence to specific analytical causes as precisely as possible, to identify the exact cause of each and every difference would require analytical manipulations of each assumption and combination of assumptions of each method, which is beyond the scope of this paper due to the size of the dataset and available computational resources. Instead, we draw attention to the importance of these assumptions through a comparison of three broadly different but overlapping methods of analysis. Similarly, much of our discussion below applies equally to Bayesian phylogenetic inference, but for simplicity we limit our comparisons to parsimony and maximum likelihood.

Below we clarify the philosophical and theoretical foundations of the competing approaches with special reference to 1) parsimony and maximum likelihood optimality criteria; 2) tree-alignment and phylogenetic analysis of similarity-alignments; and 3) the use of models of molecular evolution to infer historical events.

Optimality criteria

Although optimality criteria are usually discussed in terms of the objective functions they minimize or maximize, their preference is based on underlying philosophical and theoretical foundations. As employed in phylogenetics, parsimony and maximum likelihood extend from fundamentally different foundations, despite their numerical equivalence in certain situations (*e.g.*, Goloboff, 2003). Parsimony is a non-statistical, non-parametric, evidentially conservative approach to scientific inference that aims to maximize explanatory power by minimizing assumptions about both the process of character evolution and the quantity of evolutionary events needed to explain the data (Eernisse & Kluge, 1993; Kluge & Grant, 2006; Grant & Kluge, 2009). As a scientific method, its justification is based on refutationism sensu Popper (1959, 1963, 1972, 1983; for its application to phylogenetic inference see Wiley, 1975; Farris, 1983; Farris *et al.*, 2001; Kluge, 2001, 2009) as applied to historical inferences, whereby the least refuted hypothesis is selected as optimal. Operationally, the nested patterns of homologs are interpreted as a retrodictive map of history, with the optimal tree being that which requires the fewest transformation events to explain the evidence in light of background knowledge (Kluge & Grant, 2006; Grant & Kluge, 2009). Background knowledge in this context is limited only to those assumptions that are necessary to make an inference of common ancestry, *i.e.*, descent with modification (Hennig, 1966; Kluge, 1999).

In contrast, maximum likelihood is a statistical, parametric, evidentially ambivalent approach that aims to maximize accuracy by incorporating a potentially unlimited number and diversity of assumptions about the process of evolution (*e.g.,* Felsenstein, 2004). Given that evolutionary history is unknown, the accuracy of hypothesized phylogenetic hypotheses cannot be assessed. However, an enormous number of numerical simulation studies have been undertaken to *prove* the accuracy of maximum likelihood methods for phylogenetic inference (*e.g.*, Hillis, 1995; Huelsenbeck, 1995; Philippe *et al.*, 2005; Swofford *et al.*, 2001; but see *e.g.*, Siddall, 1998; Farris, 1999; Pol & Siddall, 2001; Kolaczkowski & Thornton, 2004; Kück *et al.*, 2012), the results of which are extended by induction to empirical studies, despite the well established pitfalls of such reasoning (*e.g.*, Oreskes *et al.*, 1994; Grant, 2002; Grant & Kluge, 2003). As such, in phylogenetics, maximum likelihood's justification falls within the realm of verificationism (Siddall & Kluge, 1997), although, in practice, it often shifts to instrumentalism (see below).

Parsimony and maximum likelihood also entail contradictory views of history and historical inference. Historical inference under parsimony is idiographic in that it aims to infer particular events rather than universal trends or laws and, as such, treats all hypothesized homologs and evolutionary transformations as unique, concrete, and singular (*i.e.*, as ontological individuals; Grant & Kluge, 2004, 2009; Kluge & Grant, 2006). Insofar as infrequent events must have occurred in the past, the frequency of a class of events (*e.g.*, transitions) has no bearing on the inference of a particular historical event (*e.g.*, a transition in position 384 of the cytochrome *b* gene in the most recent common ancestor of *Pristimantis*). By using the overall frequency of classes of events (within some arbitrarily circumscribed universe) to infer the past occurrence of particular events, maximum likelihood necessarily assumes that evolutionary history can be reduced to universal probabilistic laws applied to classes of events (*e.g.*, transitions, transversions, insertions, deletions; for general discussions of this fallacy and its effects outside systematics see Popper, 1959; Taleb, 2007). Moreover, maximum likelihood conflates the probability that a class of event *could have occurred* with the probability that a particular event *did occur*. Making matters more complicated, the frequency of events can only be estimated *a posteriori* once all the particular events have been counted. In other words, the frequency of events is a result of phylogenetic analysis, not a premise (Sankoff *et al.*, 1973; 1976; Farris, 1983) and, hence, this frequentist approach to historical inference is logically flawed.

Despite the contradictory logical foundations of parsimony and maximum likelihood, much effort has gone into portraying parsimony as if it were a parametric statistical method by identifying the assumptions under which the maximum likelihood solution is identical to the parsimony solution. The resulting "parsimony-equivalent" likelihood models (reviewed and discussed by Holder *et al.*, 2010; Steel, 2011) purport to expose parsimony's implicit statistical assumptions about the evolutionary process. Although this line of reasoning has a long and impressive pedigree dating back at least four decades (Farris, 1973; Felsenstein, 1973) and has played a major role in methodological debates, in the final analysis it has generated much more heat than light, principally because it rests on the false premise that all quantitative, numerical methods are *necessarily* statistical, even if only implicitly. To the contrary, finding that a maximum likelihood solution under a particular model (be it simple or complex) matches a parsimony solution has no logical bearing on the justification of the non-probabilistic method of parsimony and its assumptions. (Similarly, mathematical formulas generating, respectively, a parabola and a straight line on a Cartesian plane cannot be judged identical even if they produce the same formulaic results at two points of intersection.) Further, the fact that both extremely complex (*e.g.*, Farris, 1973; Tuffley & Steel, 1997) and simple (*e.g.*, Goldman, 1990) "parsimony-equivalent" models have been identified (and more undoubtedly exist; Sober, 2004) demonstrates the futility of this approach, even if parsimony is interpreted as a statistical method (Goloboff, 2003).

Nucleotide homology: similarity-alignment vs. tree-alignment

The importance of alignment in the phylogenetic analysis of DNA sequences cannot be overstated; it truly is the elephant in the room with respect to molecular phylogenetics. The number of possible alignments for even a tiny number of terminals and nucleotides is staggering and increases faster than the number of possible trees (Slowinski, 1998). Many methods to select optimal alignments have been proposed, and different alignment methods can lead to different alignments and different alignments can lead to different phylogenetic trees

(Wheeler, 1994; Morrison & Ellis, 1997; Whiting *et al.*, 2006; Wong *et al.*, 2008; Blackburne & Whelan, 2012). As we argue below, which method is best depends on the investigator's goals.

Computational biologists have long recognized that the problem of aligning nucleotides into homologous characters is inseparable from the problem of phylogenetic inference. Indeed, Sankoff's (1975; for a historical overview see Sankoff, 2000) tree-alignment algorithm was the first formal algorithm for both multiple sequence alignment and "generalized parsimony" (Swofford & Maddison, 1992). Unfortunately, when systematists began analyzing DNA sequences in the 1980s, the full implications of that seminal paper were overlooked by most workers (but not all[4]), and, instead of viewing phylogeny and alignment as two parts of one problem (*i.e.*, the generalized tree-alignment problem), they applied a two-step procedure similar to the one they were accustomed to using in analyses of phenotypic characters. In the first step, the homology of nucleotide characters is fixed, either manually or algorithmically, by inserting gaps to make all sequences the same length, and the aligned nucleotides are displayed as a matrix. In the second step, searches are performed to find the tree that best explains variation in the matrix according to the chosen optimality criterion (*e.g.*, parsimony, maximum likelihood) and evolutionary assumptions.

Insofar as the first step is intended to be independent of the second (Simmons, 2004), nucleotide correspondences are based on similarity and judged by structural or functional criteria (*e.g.*, conservation of structural or functional properties across the aligned sequences). Manual similarity-alignments can be based on either human pattern recognition or assumptions about evolutionary mechanisms (*e.g.*, RNA secondary structure, codon structure), but in either case a fundamental weakness is the inability to measure objectively the quality of alternative alignments. As such, objective comparison among the many possible alignments is difficult or impossible, making the preference for manual alignments notoriously subjective. Algorithmic approaches overcome this weakness by aligning sequences according to objective functions that minimize edit cost or maximize identity (Chan *et al.*, 1992). However, insofar as the aim is to define structural or functional correspondences, the resulting similarity-alignments are often found lacking and adjusted manually, which re-introduces subjectivity and invalidates the objective function. A further complication is that different objective functions (*e.g.*, sum-of-pairs functions, consensus functions; for review see Wheeler, 2012) can result in different optimal alignments, even under the same biological assumptions (*e.g.*, transition, transversion, indel opening, and indel extension costs), and the basis for choosing among them is unclear. In the two-step approach, the biological assumptions used in the alignment and tree-searching steps are seldom the same, and the optimality criteria always differ. Furthermore, popular phylogenetic software for maximum likelihood (*e.g.*, RAxML, GARLI) treats gaps as nucleotides of unknown identity (Ns; a possibly unique case in which evidence of absence is treated as absence of evidence), which excludes an entire class of evidence and can significantly distort phylogenetic results (Denton & Wheeler, 2012).

In tree-alignment, alignments are evaluated in reference to phylogenetic trees, either by optimizing sequences directly onto trees (*e.g.*, Sankoff, 1975; Wheeler, 1996; Varón & Wheeler, 2012, 2013) or, as a heuristic approximation, by iteratively aligning sequences using a guide tree, reporting the alignment as a matrix, searching for the optimal tree for that matrix, and using the new tree to guide a new alignment (*e.g.*, Hogeweg & Hesper, 1984; Wheeler & Gladstein, 1994; Liu *et al.* 2009, 2012). Because both the alignment and the tree are evaluated simultaneously under the same optimality criterion (*e.g.*, parsimony, maximum likelihood) and biological assumptions, nucleotide correspondences relate directly and explicitly to evolutionary transformation events, *i.e.*, homology (note that this does not hold in the approximation of Liu *et al.*, 2009, 2012; see Denton & Wheeler, 2012). Accordingly, tree-alignment can identify phylogenetic hypotheses that are significantly more optimal than the two-step procedure (*e.g.*, Wheeler, 1994, 1996, 2007; Whiting *et al.*, 2006; Wheeler & Giribet, 2009). As with other methods of alignment, it is possible to display aligned nucleotides as a matrix (Wheeler, 2003); however, this

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[4] Felsenstein (1988, p. 525): "Sankoff *et al.* [1973] applied a method, later described by Sankoff & Rousseau [1975] and Sankoff [1975], that performs alignment of sequences at the same time as it estimates the phylogeny by minimizing a weighted count of substitutions and deletion/ insertion events…This process is computationally intensive but will receive more attention when sequence aligners realize, as they must, that multiple-sequence alignment is best carried out with explicit reference to the phylogeny and that one cannot simply treat all sequences symmetrically, when some may be near-duplicates of others. The realization of this will have a large impact on multiple-sequence alignment and may cause some embarrassment when it is noted that David Sankoff and his colleagues understood the matter clearly in 1973."

so-called "implied alignment" differs fundamentally from those discussed above in that it depicts the historical, evolutionary relationships among nucleotides, not their structural or functional similarity (Wheeler, 2003; Giribet, 2005).

Failure to recognize the distinction between similarity-alignments and tree-alignments can lead to serious logical errors, and it is incorrect to assess either approach by the other's criteria (as exemplified by Hickson *et al.*, 2000). For example, similarity-alignments are often constrained to preserve structural and/or functional characteristics such as codon reading frames. If the goal is to visualize structural or functional similarity across extant taxa, then this constraint is appropriate. However, if the goal is to explain shared structural or functional similarity by identifying homologous nucleotides related through evolutionary transformation events, then it is not. Gaps are not nucleotides of unknown identity (Ns), as they are treated by most phylogenetic software; they are symbolic representations of the absence of any nucleotide (*i.e.*, they do not exist) and serve as mere placeholders to allow homologous nucleotides to be visualized in matrix format. As such, gaps have no bearing on the structural or functional viability of the extant sequences; to understand the structural or functional implications of a given alignment, the hypothetical ancestral sequences must be examined for the effects of both indels, which can alter reading frame and secondary structure, and substitutions, which can also result in missense and nonsense codons and alter secondary structure (*e.g.*, non-Watson-Crick pairing within stems). Tree-alignment matrices commonly place gaps within functional blocks, indicating that indel events contributed to the evolution of those blocks. As Löytynoja & Goldman (2008, p.1635) summarized succinctly, "the resulting alignments may be fragmented by many gaps and may not be as visually beautiful as the traditional alignments, but if they represent correct homology, we have to get used to them."

Similarly, because matrix representations of tree-alignments depict evolutionary transformation series, they are not necessarily effective at identifying structural and functional similarities across terminals. Structural patterns can be less evident due to gaps within functional blocks in tree-alignment matrices. Further, nucleotides in the same sequence position that are separated evolutionarily by indels form non-homologous transformation series in tree-alignments and, therefore, are correctly depicted in different columns in the tree-alignment matrix (Figure 1); however, this separation in the matrix obscures the structural and functional equivalence of these nucleotides, which is correctly depicted by merging the separate, non-homologous transformation series into a single column, as shown in the similarity-alignment matrix. Consequently, workers must consider their objectives carefully when choosing an alignment method: similarity-alignment for visualizing structural and functional similarities among terminals, tree-alignment for discovering the evolutionary transformation events that gave rise to (and therefore explain) those structural and functional similarities.

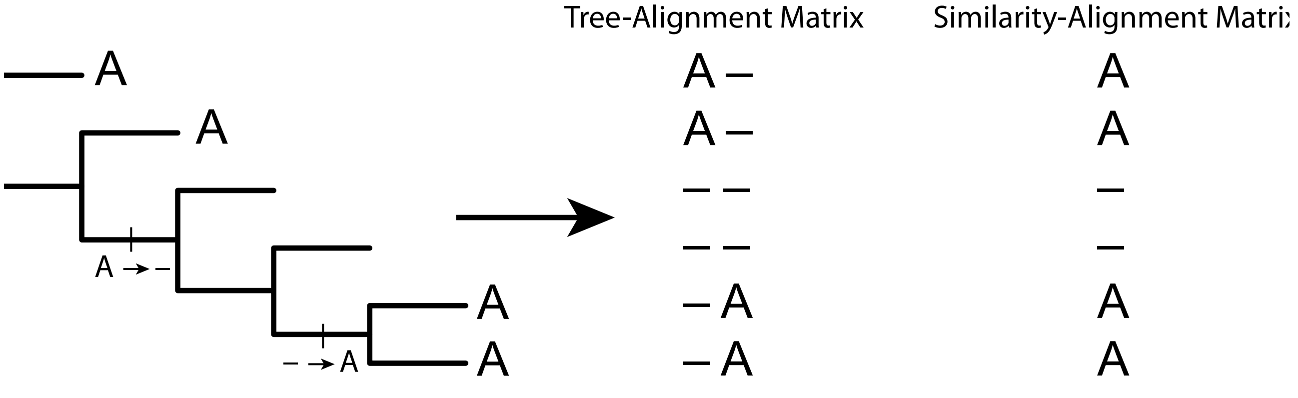

FIGURE 1. An example showing one of the differences between similarity- and a tree-alignments of the same data. Nucleotides in the same sequence position but separated evolutionarily by insertion/deletion events are non-homologous but functionally equivalent. The tree-alignment matrix depicts the homology relationship of the nucleotides clearly but obscures their functional equivalence, whereas the similarity-alignment matrix depicts the functional equivalence of the nucleotides clearly but obscures their homology relationship.

Models and model selection

The idea that some characters are better than others for discovering relationship has a long pedigree that descends directly from Owen's (1843) pre-evolutionary notions of analogy and homology. We identify two ways in which the quality of characters is commonly assessed and used in phylogenetic analysis. First, quality is assessed in terms of the observer's ability to unambiguously individuate character-states and group them into transformations series. Accordingly, "good" characters in frogs would include the presence/absence of direct development, tadpole transport by parental nurse frogs, and teeth, whereas those that are more ambiguously individuated (*e.g.*, shape of the frontoparietal fontanelle; relative length of toes III and V, wherein the same states could arise through different transformations) or grouped into homologous transformation series (*e.g.*, the various morphologies of the supplementary elements of the submandibular musculature) are "less good". It was this line of reasoning that formed the basis for Neff's (1986; see also Haszprunar, 1998; Vogt, 2002) proposal to weight characters by asking, "how much do we think we know about this character?" rather than "how much is this character intrinsically capable of telling us?" However, its unavoidable subjectivity, both philosophically (the focus is not on the objective ability of evidence to refute hypotheses, but instead on what has been learned about the evidence) and operationally (the determination of specific values to quantify how much we think we know) has prevented it from being widely adopted.

The second way character quality is commonly assessed and applied in phylogenetic analysis is by assessing a character's intrinsic reliability. *A priori* weighting, whereby more reliable characters or changes are attributed greater weight than less reliable ones, was criticized early and often due to its subjectivity (*e.g.*, Sokal & Sneath, 1963; Kluge & Farris, 1969) and several efforts have aimed to objectify the approach[5]. It has often been argued that complexity and functional or adaptive importance indicate how easy or difficult it is for characters or character-states to arise or change (*e.g.*, Le Quesne, 1974; Hecht & Edwards, 1976). However, it is well established that simple genetic mutations can have highly complex and major phenotypic consequences such that apparently complex and functionally important changes may be achieved quite simply (*e.g.*, Eizirik *et al.*, 2003; Theissen, 2009; Uy *et al.*, 2009; Nadeau & Jiggins, 2010). Cracraft (1981) discussed in detail the subjectivity and irrelevance of using functional and adaptive criteria for discriminating characters for phylogenetic inference. Similarly, even though functional constraints on some genes and sequence positions might make certain changes implausible, many such assumptions are rejected by an ever-increasing variety of mechanisms that permit exceptions, including post-transcriptional editing (Bock, 2000), altered genetic codes (Abascal *et al.*, 2012), frameshift tolerance (Russell & Beckenbeck, 2008; Masuda *et al.*, 2010), network rewiring (Kim *et al.*, 2012), and wobbling and superwobbling (Alkatib *et al.*, 2012), among many others.

Alternatively, Farris (1966, 1970; see also Kluge and Farris, 1969) proposed to weight characters inversely according to their within-population variation, the argument being that traits that vary extensively within a population are more likely to evolve at a higher rate and vary among species, whereas traits that are more conserved within a population are likely to evolve more slowly and be more conserved among species, thereby constituting more reliable characters. Although this potentially offers an objective, data-driven method for *a priori* character weighting, the necessary data are rarely available and, more importantly, even if on average a correlation exists between variation within and among groups (Kluge & Kerfoot, 1973), there is no biological or evolutionary law that requires a given trait to maintain the same amount of within-population variation over time and across lineages. Given its many drawbacks in both theory and practice, *a priori* reliability weighting was overwhelmingly rejected in parsimony analyses.

Despite the many criticisms of methods that differentially weight characters based on their intrinsic reliability, maximum likelihood methods weight according to reliability by modeling the process of character evolution. The putative problem of superimposed substitutions (multiple hits, saturation) in DNA sequences has probably received most attention (*e.g.*, Simon *et al.*, 1994; Swofford *et al.*, 1996; Xia *et al.*, 2003; see also Wenzel & Siddall, 1999), but modeling extends well beyond this to accommodate potentially any problem of so-called non-phylogenetic signal (Philippe *et al.*, 2011). Whether statistical models are mechanistic, specifying parameter values based on empirical data obtained previously, or empirical, estimating values directly from the data to be analyzed, the

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[5] Another approach is to assess and weight reliability according to homoplasy (Farris, 1969; Goloboff, 1993) or support (Farris, 2001). However, these methods are rarely applied to molecular data and therefore we do not address them beyond noting that the results of these methods can only deviate from those obtained under equal weights by increasing the amount of homoplasy and number of *ad hoc* hypotheses of transformation, *i.e.*, by selecting a less parsimonious tree.

parameters included in a given model are specified *a priori* on the basis of external knowledge claims, wherein lies modeling's major operational shortcoming as objectively assessing character reliability. Instead of developing models from painstaking empirical research into, for example, the chemical laws that govern mutations and molecular interactions, DNA repair efficiency, metabolic rate, generation time, body size, population size, and selection pressures, phylogenetic models are merely "biologically inspired" (Huelsenbeck *et al.*, 2011)—speculations based on what people believe to be more-or-less plausible. One need only reflect on the complexity of the human genome and the results that are emerging from the ENCODE Project Consortium (Dunham *et al.*, 2012) to see the futility and inherent subjectivity of "biological inspiration."

Indeed, although biological realism has been claimed as a critical strength of modeling (*e.g.*, Huelsenbeck & Crandall, 1997; Huelsenbeck & Rannala, 1997) it has never been more than a slogan; models have always been defined more by the simplicity of mathematical calculations and avoidance of statistical inconsistency than biological realism (Farris, 1999). The lack of concern for realism is perhaps best illustrated by the fact that to this day the most popular methods and software for model selection (*e.g.*, ModelTest) and statistical phylogenetic analysis (*e.g.*, RAxML, GARLI) fail to model indels and instead treat gaps as if they were nucleotides of unknown identity, despite the well-recognized evolutionary importance of indels (*e.g.*, Britten *et al.*, 2003; Wetterbom *et al.*, 2006). Although some authors remain skeptical and acknowledge that models rely on false or at best untested assumptions (*e.g.*, Fontanillas *et al.*, 2007; Ho, 2009; Ho *et al.*, 2011), such fine print is usually overlooked by end users. A generation ago, systematists rejected this kind of *a priori* subjectivism as being inconsistent with core scientific principles, and the fact that it has gained such popularity is more a reflection of the degree to which those principles have been set aside than progress in understanding of molecular evolution.

In the absence of objective model specification, the field has turned to model selection criteria to objectively choose among the subjectively formulated models. It is important to note that model selection methods optimize statistical selection criteria (in essence, balancing the tradeoff between bias and variance through the parsimonious inclusion of parameters) regardless of the statistical adequacy or biological legitimacy of the candidate models, which is why statisticians are careful to caution "*If a particular model (parameterization) does not make biological sense, it should not be included in the set of candidate models*" (Burnham & Anderson, 1998, p. 8, italics in original) and recommend extensive *a priori* probing. This is especially germane considering that the practical effect of "biologically inspired" models (Huelsenbeck *et al.*, 2011) is to impose constraints on Tuffley & Steel's (1997) No-Common-Mechanism model—one of the "parsimony-equivalent" likelihood models. Moreover, given that "indel formation is likely the most rapid and significant form of sequence change (mutation) in eukaryotic evolution and probably bacterial evolution" (Britten *et al.*, 2003, p. 4665), any model that ignores this class of event or, worse still, treats gaps as nucleotides of unknown identity clearly "does not make biological sense." In addition to empirical evaluation of model constraints, we suggest that *a priori* probing also address such considerations as the uniqueness of history, the applicability of models to idiographic problems, and the role of subjectively defined models in science, as well as the philosophical foundations of model testing itself (cf. Burnham & Anderson, 2004). As George Box counseled, "It is inappropriate to worry about mice when there are tigers abroad" (Box, 1976, p. 792).

Central to the philosophy of model testing is the assertion that there are no true models (Burnham & Anderson, 2004), a sentiment captured succinctly by George Box's more famous quote (usually attributed to the same 1976 paper) "all models are wrong, but some are useful" and echoed by systematists (*e.g.*, Posada & Buckley, 2004; Sullivan & Joyce, 2005). Consequently, by embracing this approach to science, systematists abandon scientific realism in favor of instrumentalism, an anti-realist view that rejects scientific theories as candidates for truth or reference and construes methods and hypotheses as mere instruments that are more or less useful. Instrumentalism is potentially appealing because it avoids problems that realism must face square on; however, in failing to resolve the problems faced by realism, the resulting knowledge lacks any claim to reality and must instead be defended by answering the question "useful for what?" without resorting to tautology or parochial goals (*e.g.*, publishing). In applied sciences like economics, engineering, and medicine, the answer is clear. However, what does "useful" mean in a science that aims to discover unique historical events, and why should parsimony in the tradeoff between bias and variance take precedence over parsimony in the postulation of events?

Maximum likelihood and Brachycephaloidea

The gulf between the statistical rhetoric of theoretical papers and the reality of most empirical studies is vast, as exemplified by the recent maximum likelihood analyses used to erect the current taxonomy of terraranas, specifically Heinicke *et al.* (2007, 2009), Hedges *et al.* (2008a), Padial *et al.* (2009), Pyron & Wiens (2011), Canedo & Haddad (2012), and Pinto-Sánchez *et al.* (2012). In examining these studies, we have identified five fundamental analytical problems that contravene the theoretical foundations of maximum likelihood inference.

1. Application of the optimality criterion.—Heinicke *et al.* (2007) and Hedges *et al.* (2008a) based their inferences on analyses of three overlapping datasets. Analysis 1 had the most terminals (280 and 350, respectively) scored for 350 bp of 12S and 800 bp of 16S, analysis 2 had fewer terminals (146 and 216) scored for the entire 2.5 kb heavy strand transcription unit 1 fragment (12S + tRNA^{val} + 16S; H1), and analysis 3 had the fewest terminals (65 and 80) sequenced for the most data (H1, and the two nuclear genes Rag-1 and Tyrosinase). However, they never combined all their data into a single analysis, which means they never actually searched for the maximum likelihood solution for their data. Neither Heinicke *et al.* (2007) nor Hedges *et al.* (2008a) offered a justification for this procedure, but decreased accuracy due to missing data does not seem to have been the motivation, as Hedges *et al.* (2008a, p. 9) clarified that some of the species included in their analyses lacked "substantial amounts" of data. Nor did Heinicke *et al.* (2007) or Hedges *et al.* (2008a) provide a rule for resolving conflict between the different results, stating only that "the species-rich analyses [1 and 2] provided guidance for taxonomic decisions at lower levels (*e.g.*, species groups and series) whereas the gene-rich analyses [2 and 3] provided guidance for decisions at higher levels, although all three analyses were consulted in many cases" (Hedges *et al.* 2008a, p. 11), meaning that results that did not conform to expectations could be waved away in favor of one of the other analyses. For example, *Haddadus* is the sister of Eleutherodactylidae in analysis 1 but is the sister of *Craugastor* in analyses 2 and 3. Without comment, Hedges *et al.* (2008a) referred *Haddadus* to Craugastoridae instead of Eleutherodactylidae and then used its phylogenetic position to interpret the role of ancestral body size in large adaptive radiations (p. 137). Not only does this violate basic statistical assumptions, it is also precisely this sort of subjective cherry-picking among hypotheses that explicit optimality criteria are meant to avoid.

In order to assess whether Hedges *et al.*'s (2008a) partitioning of the data into different datasets led them to recognize taxa not supported by the overall evidence, we combined their three datasets and analyzed them in GARLI (Zwickl, 2006; for more details about the procedure followed for maximum likelihood inferences in GARLI see below). The optimal topology (log likelihood = -203567.0836; TreeBase accession http://purl.org/phylo/treebase/phylows/study/TB2:S15350) is largely congruent with Hedges *et al.*'s (2008a) analysis 3 with respect to the family-group taxa (including the placement of *Haddadus* as sister to *Craugastor*) and analysis 1 and 2 with respect to genera, subgenera, and species groups and series. All their family-group taxa are monophyletic, including Strabomantidae and Strabomantinae, as are all their genus-group taxa except the subgenus *Pristimantis*, because *P. dendrobatoides*, *P. rozei*, and *P. urichi* are the sister taxon of *Hypodictyon* and the rest of species of the subgenus *Pristimantis*. The most egregious difference that results from the combined analysis is the placement of *Ceuthomantis smaragdinus* (as unknown anuran sp.), which is placed outside the Brachycephaloidea as the sister of *Dendrobates sylvaticus* (presently *Oophaga sylvatica*; Grant *et al.*, 2006). Given that the maximum likelihood solution for the entire dataset supports Hedges *et al.*'s (2008a) major conclusions, whatever concerns led those authors to sacrifice analytical principles to base their conclusions exclusively on separate analyses seem unwarranted.

2. Alignment.—Despite tree-alignment's clear advantages over similarity-alignment for phylogenetic inference and the wide availability of software for both parsimony and statistical optimality criteria (*e.g.*, Hogeweg & Hesper, 1984; Wheeler & Gladstein, 1993; Wheeler, 1996; Edgar & Sjölander, 2003; Lunter *et al.*, 2003; Wheeler *et al.*, 2003; Fleißner *et al.*, 2005; Redelings &Suchard, 2005; Novák *et al.*, 2008; Rivas &Eddy, 2008; Yue *et al.*, 2009; Varón *et al.*, 2010), none of the recent papers on the phylogeny of terraranas employed this approach. Without discussion or justification, Heinicke *et al.* (2007), Hedges *et al.* (2008a), and Canedo & Haddad (2012) used Clustal (Thomson *et al.*, 1994; Larkin *et al.*, 2007), Heinicke *et al.* (2009) used MUSCLE (Edgar, 2004), Pyron & Wiens (2011) used Clustal and MUSCLE, and Padial *et al.* (2009) and Pinto-Sánchez *et al.* (2012) used MAFFT (Katoh *et al.*, 2005); all of these methods seek to minimize the weighted pairwise distance summed over all sequence pairs in the multiple sequence alignment. And all of these studies except Padial *et al.* (2009), which only used ribosomal DNA, forced gaps to correspond with codon reading frame of the observed sequences, even though gap placement has no bearing on the reading frame of extant sequences and hypothetical ancestral sequences were not examined for missense or nonsense codons in any of the studies. Moreover, all of the studies except Padial *et al.* (2009) performed manual adjustments of their algorithmic alignments, often removing "poorly conserved" regions. Perhaps most importantly, all of these studies used model selection and tree searching software that fails to model indel evolution and instead treats gaps as nucleotides of unknown identity (Ns).

3. Model selection.—Although the importance of model selection in statistical phylogenetic inference is widely recognized (*e.g.*, Johnson & Omland, 2004; Posada & Buckley, 2004; Sullivan & Joyce, 2005), Heinicke *et al.* (2007), Hedges *et al.* (2008a), and Pyron & Wiens (2011) did not perform any analysis to select the optimal models for their data. Padial *et al.* (2009) used the Akaike Information Criterion (AIC) in ModelTest v.3.7 (Posada & Crandall, 1998) to identify the best model (general-time-reversible + gamma + proportion of invariant sites; GTR + GAMMA + I), which they applied in their phylogenetic analysis. Heinicke *et al.* (2009), Canedo & Haddad (2012), and Pinto-Sánchez *et al.* (2012) used ModelTest v.3.7 or jModelTest (Posada, 2008) to identify the best models (usually GTR + GAMMA + I), but none of the studies actually used the selected models in their maximum likelihood analyses. Instead, they used the GTR + GAMMA model (or approximations). If the authors were opposed to GTR + GAMMA + I *a priori* due to theoretical objections (*e.g.*, Stamatakis, 2008), then those objections should have been provided and the model should have been excluded from the set of candidates. Otherwise, the model that best accounts for their data should have been used. In addition to using an underparameterized model, Canedo & Haddad (2012, p. 612) justified using GTR + GAMMA when it was an overparameterized model by citing Lemmon & Moriarty (2004) and Kelchner & Thomas (2007) that "overparameterization may have little influence on the resulting topology", despite the cited authors' clear warnings that the potential impacts of estimating more parameters than warranted should not be ignored. Under- and over-parameterization also obtain when data are partitioned into too few or too many partitions (McGuire *et al.*, 2007; Li *et al.*, 2008; Lanfear *et al.*, 2012; Leavitt *et al.*, 2013). However, Pinto-Sánchez *et al.* (2012) were the only authors who statistically evaluated their *a priori* partition schemes. All other studies simply assumed a single partition scheme. Finally, none of the studies evaluated model adequacy, meaning that the selected models might be relatively better than others but still not provide a significantly good fit to the data (Ripplinger & Sullivan, 2010).

4. Heuristic searches.—The statistical strengths of maximum likelihood dissolve if heuristic searches are unable to find the maximum likelihood solution—a non-trivial consideration given that maximum likelihood tree searches are thousands of times slower than parsimony tree searches (Sanderson & Kim, 2000). Given the large numbers of terminals in most of these studies, the heuristic searches were extremely superficial and are unlikely to have discovered global optima—the sole exception being those of Heinicke *et al.* (2009), which analyzed only 46 terminals. Despite the differences in datasets sizes (46–362 terminals), Heinicke *et al.* (2007), Hedges *et al.* (2008a), Heinicke *et al.* (2009), and Canedo & Haddad (2012) all performed the same maximum likelihood search of 100 runs in RAxML (Stamatakis *et al.*, 2006), each run consisting of an initial random addition sequence parsimony tree swapped using the "Lazy Subtree Rearrangements" algorithm (lazy SPR; Stamatakis *et al.*, 2005, 2007), which confines SPR swapping to the vicinity of the clipped branch instead of performing global SPR swapping. No reason was given by any of the authors for using the 100-replicate lazy SPR search strategy as their standard, and although such procedures may be effective as components of an overall search strategy (*e.g.*, Goloboff, 1999), on their own they are quite unreliable (Morrison, 2007). Pyron & Wiens (2011) and Pinto-Sánchez *et al.* (2012) used the Rapid ML Search procedure (Stamakis *et al.*, 2008), which performs lazy SPR on every 5th bootstrap replicate tree (totaling 20 trees) using the GTR + CAT model (a GAMMA approximation using a fixed number of rate categories; Stamatakis *et al.*, 2006), rediagnoses the resulting trees using GTR + GAMMA and swaps the best 10 trees again (similar to a reweighting step in the parsimony ratchet; Nixon, 1999), and then swaps the best of the resulting trees using less-lazy lazy SPR. Although that heuristic is more effective for large datasets than standard lazy SPR searches (Stamakis *et al.*, 2008), given the size of the Pyron & Wiens (2011) and Pinto-Sánchez *et al.* (2012) datasets, its adequacy is questionable. Similarly, Padial *et al.* (2009) ran 100 replicates in GARLI (Zwickl, 2006), which, under default parameters, also implements stepwise addition and local SPR searches with reattachments restricted to a maximum of six nodes from the original location of a pruned branch.

5. Support.—Inadequate heuristic searches also affect estimates of support. All recent studies of Brachycephaloidea exclusively used non-parametric bootstrap resampling frequencies (Efron, 1979; Felsenstein, 1985) as clade support measures in maximum likelihood. Heinicke *et al.* (2007, 2009), Hedges *et al.* (2008a), and Canedo & Haddad (2012) calculated bootstrap frequencies by swapping 1000 pseudoreplicates with the same lazy SPR algorithm. Padial *et al.* (2009) performed 200 bootstrap pseudoreplicates in GARLI using the weak version of SPR performed by this program. Pyron & Wiens (2011) and Pinto-Sánchez *et al.* (2012) used RAxML's "rapid bootstrap algorithm" (Stamatakis *et al.*, 2008). The speed-up is achieved by using an even lazier lazy SPR to swap pseudoreplicate matrices, with the first and every 10th pseudoreplicate starting from the most parsimonious tree derived from the original, non-resampled dataset and all other replicates starting from the tree from the previous pseudoreplicate. As Siddall (2010), Simmons & Norton (2013), and Simmons & Goloboff (2013) pointed out, this autocorrelated and superficial swapping biases searches toward finding the tree obtained from the non-resampled data, resulting in inflated resampling values. Even though Canedo & Haddad (2012) used the "thorough" (standard) RAxML bootstrap algorithm, the effects of the more exhaustive parsimony analysis (1000 pseudoreplicates, 100 random addition sequences per replicate followed by sectorial searching, ratcheting, drifting, and fusing) are evident in their results; of the 115 nodes that are shared by the maximum likelihood and parsimony trees and differ in bootstrap frequency, 113 (98%) are higher for maximum likelihood than parsimony, including several nodes > 95% for maximum likelihood and < 70% for parsimony.

Although all of these studies exclusively used bootstrap frequencies to measure clade support, the use of bootstrap resampling in maximum likelihood has been criticized from a variety of perspectives (*e.g.*, Goldman, 1993; Holmes, 2003; Soltis & Soltis, 2003; Anisimova & Gascuel, 2006; Grant & Kluge, 2008a). Minimally, the use of multiple data partitions with separate models seems to be an admission that the basic assumption of the bootstrap that the data are independent of each other and all drawn from the same probability distribution (Efron *et al.*, 1996) is violated. Alternatively, likelihood ratios are a natural measure of strength of evidence (Hacking, 1965) that avoid the assumptions of the bootstrap and are easily applied in phylogenetics as a measure of clade support (Meireles *et al.*, 1999; Wheeler, 2006, 2010; Grant & Kluge, 2008a). As a descriptive statistic, the ratio of likelihoods measures the degree to which evidence favors one model (in this case, the maximum likelihood tree) relative to another (the most likely tree lacking a given clade), thereby providing an estimate of the size of the effect of the two models. The support for a given clade in the maximum likelihood tree is simply the difference between the log likelihoods of the maximum likelihood tree and the most likely tree that lacks that clade (Grant & Kluge, 2008a). A cut-off (*e.g.*, likelihood ratio > 4) or null distribution and significance level must be assumed for inferential statistics (*e.g.*, Huelsenbeck *et al.*, 1996; Anisimova & Gascuel, 2006), but not to interpret the likelihood ratio as a measure of support. Although this approach is also sensitive to tree searching, by targeting specific nodes of interest (*e.g.*, those most relevant to specific taxonomic or evolutionary questions) the total number of searches can be greatly reduced.

Methods applied in this study

Tree-alignment + parsimony analysis

Homologous fragments were identified and formatted following Grant *et al.* (2006, p. 56), and exactly the same dataset was subsequently used to generate the similarity-alignment for parsimony and maximum likelihood analyses (see below). Tree-alignment was performed under parsimony with equal weights for all classes of transformations using the direct optimization (DO; Wheeler, 1996; Wheeler *et al.*, 2006) and iterative-pass optimization (IPO; Wheeler, 2003) algorithms in POY 4.1.2 and POY5_beta (Varón *et al.*, 2010). Tree searches were first conducted using DO and the "search" command of POY, which implements a driven search composed of random addition sequence Wagner builds, subtree pruning and regrafting and tree bisection and reconnection branch swapping (see Goloboff, 1996, 1999), parsimony ratcheting (Nixon, 1999), and tree fusing (Goloboff, 1999), running consecutive rounds of searches within a specified run-time, storing the shortest trees of each independent run and performing a final round of tree fusing on the pooled trees. A total of 56 days of "search" was carried out using either 60 parallel processors at the American Museum of Natural History's high performance computing cluster Demeter (a cluster of 127 Intel Xeon 2.8GHz dual-core, 256 processors, diskless nodes, 4GB RAM per node and 32-bit) or 32 processors on Enyo (a cluster of 33 Intel Xeon 3.0GHz dual-core, 128 dual-processors, L2 cache, 64-bit and 1TB shared storage, and 16GB RAM per node). We performed 22 independent rounds of driven searches using the command "search" lasting 7–12 days each. Optimal trees obtained from each search were fed to subsequent analyses together with the resulting optimal trees from maximum likelihood analysis. This procedure was repeated until five consecutive 7-day searches did not render a shorter tree. The optimal topology was then submitted to 16 rounds of fusing (20,000–1,000,000 iterations) using the command "fuse" and 20–60 processors and four rounds of time-constrained swaps using 4–8 processors. None of these strategies found a more optimal tree. The optimal tree was then submitted to an additional 9-day driven search using 32 processors in Enyo that also included the best trees from previous searches. Since a more optimal tree was not found, that optimal tree was submitted to iterative pass optimization (Wheeler, 2003). The optimal alignment from iterative pass optimization was then converted to a matrix and driven searches were conducted in TNT (Goloboff *et al.*, 2008; equal costs for all transformations, gaps treated as fifth state) until a stable strict consensus was reached at least five times.

Given the heterogeneous coverage of the dataset, we expected some terminals to be highly unstable “wildcards” or “rogues” due to a lack of corresponding loci in related taxa (reviewed by Simmons, 2012; Simmons & Norton, 2013). Although the strict consensus of optimal trees correctly excludes all clades that are not supported by the available evidence, it does not distinguish between lack of support due to missing data and lack of support due to evidential conflict and/or lack of variation (Kearney, 2002). Insofar as these two explanations heuristically point to different solutions (*e.g.*, obtaining missing sequences for wildcards versus adding new markers for all terminals), it is a valuable distinction to make (Grant & Kluge, 2003). As such, to identify wildcards we used TNT to prune terminals from the set of most parsimonious trees and recalculate the strict consensus. We present both the strict consensus including all terminals as the summary of all clades supported by the available evidence and the strict consensus of the pruned trees to reveal the effect of the wildcard terminals.

We calculated Goodman-Bremer (GB) values (Goodman *et al.*, 1982; Bremer, 1988; see Grant & Kluge, 2008b) for each supported clade in TNT using the optimal tree-alignment matrix and the parameters specified in the bremer.run macro (available at http://www.lillo.org.ar/phylogeny/tnt/), which begins by searching for trees N steps longer than the optimum (10 random addition sequence Wagner builds and TBR swapping saving two trees per replicate) and then using inverse constraints for each node of the most parsimonious tree. Swapping of each constrained search was limited to 20 minutes and constrained searches were repeated 100 times rather than the three times specified as default in bremer.run macro. Groups that are absent in the strict consensus are unsupported by the evidence and therefore have GB ≤ 0; however, because wildcards affect GB support in the same way that they affect the strict consensus (Wilkinson *et al.*, 2000; Grant & Kluge, 2003), we performed the GB analysis of the tree-alignment matrix excluding wildcard terminals and identify nodes unsupported in the complete analysis with dashed lines.

In order to facilitate comparisons with previous studies and the similarity-alignment + maximum likelihood analyses (see below), we also calculated parsimony jackknife frequencies (Farris *et al.*, 1996) for each supported clade. Given that nucleotide correspondences are not established *a priori* in tree-alignment, it is impossible to construct pseudoreplicate datasets by resampling individual characters. The first alternative is to construct pseudoreplicate datasets by resampling whole fragments (partitions, fractions, loci) of unaligned sequences (Wheeler *et al.*, 1996–2003; Wheeler *et al.*, 2006; Varón *et al.*, 2010). Siddall (2010) recently argued that fragment resampling might be more statistically defensible than standard bootstrapping of similarity-alignment matrices because the assumption of sample independence is less likely to be violated. However, it is not clear that fragments are appropriate sampling units for statistical analysis. Fragments can vary greatly in length, and unless fragment length is standardized or corrected (*e.g.*, by weighting according to maximum sequence length or number of aligned basepairs), the sampling units are not equivalent, and the effect this has on clade frequencies has not been studied. Furthermore, our reason for reporting clade frequencies is to facilitate comparison with the results of previous studies of terraranas, all of which constructed pseudoreplicate datasets by resampling columns, not fragments.

The second alternative is to construct pseudoreplicates by resampling the tree-alignment matrix, which is the procedure we follow in the present study. We caution that, as in analyses of similarity-alignment matrices, the resulting clade frequencies are conditional on this particular alignment and not the data themselves. Also, given that the tree-alignment matrix is derived from the optimal tree, the resulting clade frequencies are expected to be higher than would be obtained from matrices aligned according to different guide trees (*e.g.*, a UPGMA or neighbor-joining tree, as in MAFFT and Clustal, respectively). We calculated jackknife frequencies from 1000 pseudoreplicates searched with 100 RAS + TBR and a maximum of 10 trees saved per replicate, gaps treated as fifth state, and removal probability of 0.36 ($\approx e^{-1}$), which purportedly renders jackknife and bootstrap values comparable (Farris *et al.*, 1996). We performed this analysis for both the complete dataset (which is equivalent to our maximum likelihood bootstrap analyses; see below) and the dataset lacking wildcards.

Similarity-alignment + parsimony analysis

Similarity-alignments for parsimony and maximum likelihood analyses of static matrices were performed in MAFFT online version 6 using the G-INS-i strategy, which is considered appropriate for alignments that consist of large numbers of sequences (Katoh *et al.,* 2005). Like other alignment software used in recent studies of Brachycephaloidea, MAFFT seeks to minimize the weighted pairwise distance summed over all sequence pairs, but also sums a score for the consistency (COFFEE-like score) between the multiple alignment and pairwise alignments in the objective function (weighted sum of pair score, WSP). The G-INS-i strategy performs global alignment with a Fast Fourier Transform approximation progressively on a modified UPGMA guide tree followed by iterative edge refinement that evaluates the consistency between the multiple alignment and pairwise alignments. The iterative refinement is repeated until no improvement is observed in the WSP score or 1000 cycles are completed (maxiterate = 1000). We applied the default transition:transversion cost ratio of 1:2 but changed the gap opening penalty from 3 times substitutions to 1 times substitutions to avoid penalizing insertions and deletions more than we did in the tree-alignment analysis.

For parsimony analyses of the MAFFT similarity-alignment, we weighted all transformations equally and treated gaps as a fifth state. We used TNT (Goloboff *et al.*, 2008) to perform the same analyses described above for the tree-alignment matrix, including driven searches until a stable strict consensus was reached at least five times, identification of wildcard terminals, Goodman-Bremer support analysis of the dataset lacking wildcards, and calculation of jackknife frequencies (1000 pseudoreplicates, 100 RAS + TBR, maximum of 10 trees saved per replicate, removal probability of 0.36) for both the complete dataset and the dataset lacking wildcards.

Similarity-alignment + maximum likelihood analysis

Model selection for maximum likelihood analyses was performed in two phases. First, we used jModelTest 0.1.1 (Posada & Crandall, 1998) run on an iMac with dual 3.2GHz quad-core Intel Core i5 processors and 8GB of RAM to select optimal substitution models under the Akaike Information Criterion (Akaike, 1974) for an 18-partition dataset composed of (1) 12S, 16S the intervening tRNA^{val}, and tRNA^{L}; (2) 28S; (3) c-myc exon 2; (4) c-myc exon 4; (5) c-myc intron; (6) cytochrome *c* oxidase I; (7) CXCR4; (8) cytochrome *b*; (9) HH3; (10) NCX1; (11) ND1; (12) ND2 and tRNA^{cys}; (13) POMC; (14) RAG-1; (15) RHO; (16) seven in absentia; (17) SLC8A3; and (18) tyrosinase. We then performed a 32-replicate maximum likelihood analysis in GARLI 2.0 (Zwickl, 2006) using the parameters described below and the optimal substitution models for each partition. Next, we used PartitionFinderV1.0.1 (Lanfear *et al.*, 2012) to select the optimal partition scheme and substitution models for our dataset assuming the tree from the 18-partition analysis. Due to computational limitations related to the size of our dataset, comparisons were limited to three partitions schemes: (1) data combined into a single partition, (2) a 2-partition, mtDNA/nuDNA, scheme, and (3) the 18-partition scheme described above; additional partition schemes were attempted but the software crashed during the evaluation of more diverse partition schemes both under a greedy heuristic search (Lanfear *et al.* 2012) and during greedy searches restricted to a set of 54 partitions that resulted from considering codon positions.

Maximum likelihood analyses (maximum average likelihood in the sense of Barry and Hartigan, 1987) using the optimal partition scheme and substitution model were performed in GARLI 2.0 (Zwickl, 2006), which was preferred because it allows more thorough searching of the tree space than RAxML (Stamatakis, 2006; Morrison, 2007). Analyses were run on the Museu de Zoologia da Universidade de São Paulo's high-performance computing cluster Ace, which consists of 12 quad-socket AMD Opteron 6376 16-core 2.3-GHz CPU, 16MB cache, 6.4 GT/s compute nodes (= 768 cores total), eight with 128 GB RAM DDR3 1600 MHz (16 x 8GB), two with 256 GB (16 x 16GB), and two with 512 GB (32 x 16GB), and QDR 4x InfiniBand (32 GB/s) networking. Tree searches ran 166 replicates of an enhanced strategy consisting of the modification of a set of default parameters that, according to Zwickl (2006), should improve tree searches, albeit at the expense of computational time: random addition sequence starting trees (streefname = random; default = stepwise) with 1000 attachments per terminal (attachmentspertaxon = 1000; default = 50) or a specified starting tree (see below), run termination threshold of 100000 generations without topology improvement (genthreshfortopoterm = 100000; default = 20000), and maximum SPR distance of 30 branches away from original location (limsprrange = 30; default = 6).

We calculated bootstrap frequencies from 500 pseudoreplicate analyses using the same search parameters used to find the optimal tree (one search replicate per pseudoreplicate). To better evaluate support for taxonomically relevant nodes, we performed 32-replicate searches using the same search parameters and optimal partition scheme and substitution model under inverse constraints to calculate the ratios of the likelihoods of the maximum likelihood tree and the best tree lacking each of the following clades: (1) the clade including the terrarana *Ceuthomantis smaragdinus* and the egg-brooding frog *Cryptobatrachus fuhrmanni*, (2) the relationship of *Strabomantis* with *Craugastor* and *Haddadus*, (3) the sister relationship between Brachycephalidae (*Brachycephalus* and *Ischnocnema*) and Eleutherodactylidae, and (4) the consistent placement of *E. dilatus* in the maximum likelihood analyses (see below). Finally, for comparison we also ran a 32-replicate analysis of the unpartitioned dataset under GTR + G + I.

Comparison of methods

To evaluate the effects of the different analytical approaches, we compared the size (number of aligned positions) of the optimal tree-alignment and similarity-alignment matrices, as well as the proportion of aligned positions that contain gaps in each alignment. We also compared the topologies that resulted from the tree-alignment + parsimony, similarity-alignment + parsimony, and similarity-alignment + maximum likelihood analyses by examining the occurrence of specific clades and by calculating the pairwise rooted SPR distances between topologies using the heuristic method of Goloboff (2008; replicates = 50, stratification level = 20) in TNT (Goloboff *et al.*, 2008). The large number of most parsimonious trees prevented us from calculating all pairwise rooted SPR distances, so we calculated the distances between trees sampled at disparate points of each search (trees 0, 50, 100, and 200 of the similarity-alignment analysis and trees 50, 100, 200, 300, 400, and 500 of the tree-alignment analysis). We also compared the bootstrap and jackknife clade frequencies and support (Goodman-Bremer index for parsimony, likelihood ratio for maximum likelihood) for key clades.

Results

Tree-alignment + parsimony

Driven searches under the direct optimization algorithm performed 99 rounds of random addition sequence Wagner builds and alternating SPR and TBR swapping, 88 rounds of fusing, and 33 rounds of ratcheting. These searches identified a single optimal tree of 94760 steps (found twice). A final round of swapping under iterative pass optimization followed by driven searches of the tree-alignment matrix did not alter the topology but reduced the length of this tree to 94413 steps. The tree-alignment matrix included 23241 aligned positions, of which 9618 (41%) contain gaps. A stable strict consensus composed of 319 nodes (Figures 2–7) was reached seven times and included 536 most parsimonious trees (TreeBase accession: http://purl.org/phylo/treebase/phylows/study/TB2:S15350).

The tree-alignment analyses (Figures 2–7) recovered Brachycephaloidea as the monophyletic sister of a monophyletic Hemiphractidae, the inclusive clade forming Orthobatrachia of Heinicke *et al.* (2009). Within Hemiphractidae, *Gastrotheca* is the monophyletic sister taxon of *Stefania*, together forming the sister of a clade composed of a polyphyletic *Cryptobatrachus*, with *C. fuhrmanni* and *C. boulengeri* separated by, in sequence, *Fritziana*, *Flectonotus,* and a clade composed of *C. boulengeri* forming a polytomy with *Hemiphractus* species. Hylids are monophyletic and the sister of Orthobatrachia. As expected (*e.g.*, Faivovich *et al.*, 2005), Phyllomedusinae and Pelodryadinae form a clade that is the sister of a monophyletic Hylinae. The subsequent sister group is *Leptodactylus*, with *Calyptocephalella gayi* and Pipidae at the root.

Brachycephaloidea is divided basally into two clades (Figures 2–7; Figure 8). The first corresponds to Eleutherodactylidae sensu Hedges *et al.* (2008a). Much of the structure within Eleutherodactylidae is collapsed in the strict consensus of most parsimonious trees, suggesting a lack of evidence for the monophyly of Eleutherodactylinae and Phyzelaphryninae. However, the lack of this strict consensus structure is due almost entirely to a single terminal, *E. dilatus*. Following pruning of *E. dilatus*, the strict consensus of the 536 most parsimonious trees resulted in an almost completely bifurcated Eleutherodactylidae, the only remaining polytomy being the clade of *E. abbotti*, *E. audanti*, *E. haitianus*, and *E. parabates* (Figure 2). Although the *E. dilatus* terminal was scored for > 1200 bp, the data derive exclusively from c-myc, a nuclear gene that was available for only two other eleutherodactylids, *Adelophryne patamona* and *E. pantoni*. Because these two latter terminals were both scored for additional loci, they were decisively placed in distantly separated eleutherodactylid clades, leaving the placement of *E. dilatus* ambiguous. Although additional polytomies occur in *Craugastor* and *Pristimantis* (see below), resolution of the strict consensus was not improved by pruning any of the terminals involved, including those with limited data. Removal of *E. dilatus* from the tree-alignment matrix and optimal trees reduced the tree length to 94322 steps; searches using the pruned matrix failed to find shorter trees.

The strict consensus of the pruned most parsimonious trees recovers Phyzelaphryninae Hedges *et al.* (2008a), composed of the sister genera *Adelophryne* and *Phyzelaphryne*, and Eleutherodactylinae of Hedges *et al.* (2008a), containing the monophyletic sister genera *Diasporus* and *Eleutherodactylus* (Figure 2). Within *Eleutherodactylus*, the subgenera *Eleutherodactylus, Euhyas*, *Pelorius*, and *Syrrhophus* are all monophyletic, with one clade formed by *Pelorius* as the sister of a clade formed by monotypic subgenus *Schwartzius* and *Eleutherodactylus* (Figure 2) and a second clade formed by *Syrrhophus* and *Euhyas* (Figure 3). Among the species series, groups, and subgroups recognized by Hedges *et al.* (2008a) within the genus *Eleutherodactylus*, the *E. bakeri* species group and the *E. antillensis* subgroup of the otherwise monophyletic *E. antillensis* group are non-monophyletic. Moreover, the more inclusive *E. antillensis* series is paraphyletic with respect to the *E. varians* and *E. auriculatus* series. Additionally, the monophyly of all of the non-monotypic subgroups of the *E. luteolus* group was refuted.

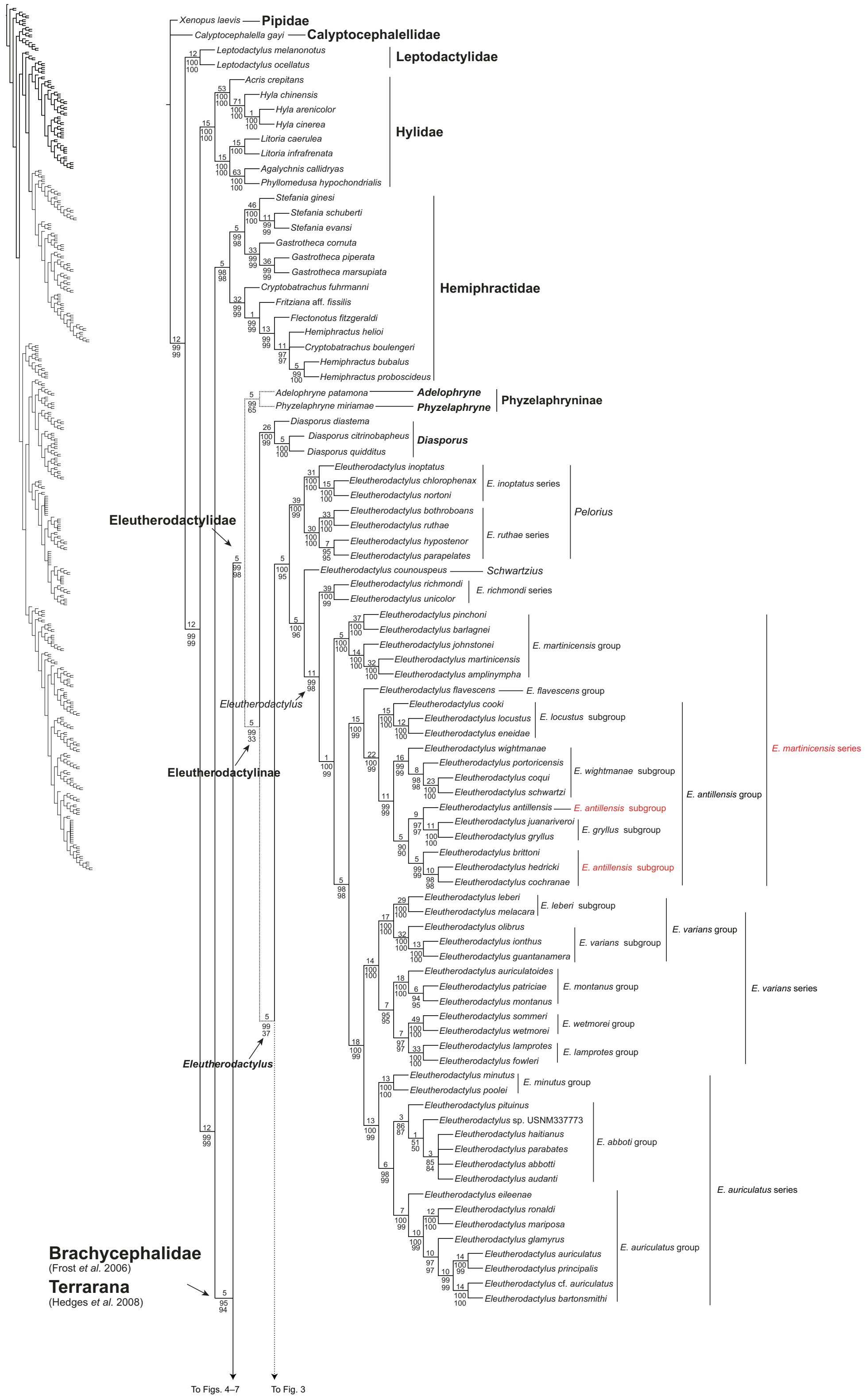

FIGURE 2. Tree-alignment + parsimony: strict consensus of 536 most parsimonious trees of 94413 steps showing relationships among 430 terminals of Brachycephaloidea and 25 outgroup taxa. Dashed branches indicate clades that collapse due to the wildcard *Eleutherodactylus dilatus*. Numbers above branches are Goodman-Bremer values excluding *E. dilatus* and those below branches are jackknife percentages excluding (upper) and including (lower) *E. dilatus*. Linnaean taxa follow previous studies except when otherwise indicated. Non-monophyletic taxa are highlighted in red (monophyletic taxa within paraphyletic groups remain in black).

FIGURE 3. Tree-alignment + parsimony: strict consensus of 536 most parsimonious trees of 94413 steps showing relationships among 430 terminals of Brachycephaloidea and 25 outgroup taxa. Dashed branches indicate clades that collapse due to the wildcard *Eleutherodactylus dilatus*. Numbers above branches are Goodman-Bremer values excluding *E. dilatus* and those below branches are jackknife percentages excluding (upper) and including (lower) *E. dilatus*. Linnaean taxa follow previous studies except when otherwise indicated. Non-monophyletic taxa are highlighted in red (monophyletic taxa within paraphyletic groups remain in black).

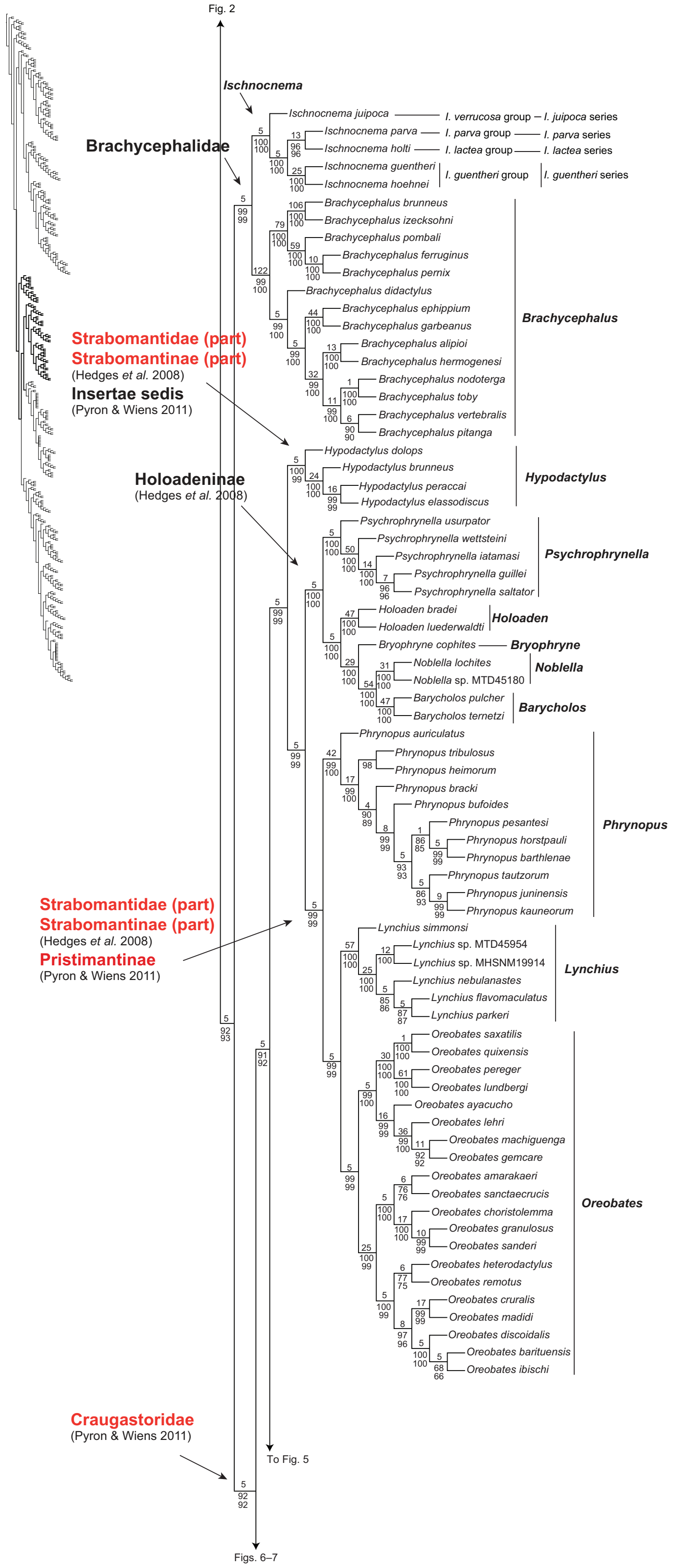

FIGURE 4. Tree-alignment + parsimony: strict consensus of 536 most parsimonious trees of 94413 steps showing relationships among 430 terminals of Brachycephaloidea and 25 outgroup taxa. Dashed branches indicate clades that collapse due to the wildcard *Eleutherodactylus dilatus*. Numbers above branches are Goodman-Bremer values excluding *E. dilatus* and those below branches are jackknife percentages excluding (upper) and including (lower) *E. dilatus*. Linnaean taxa follow previous studies except when otherwise indicated. Non-monophyletic taxa are highlighted in red (monophyletic taxa within paraphyletic groups remain in black).

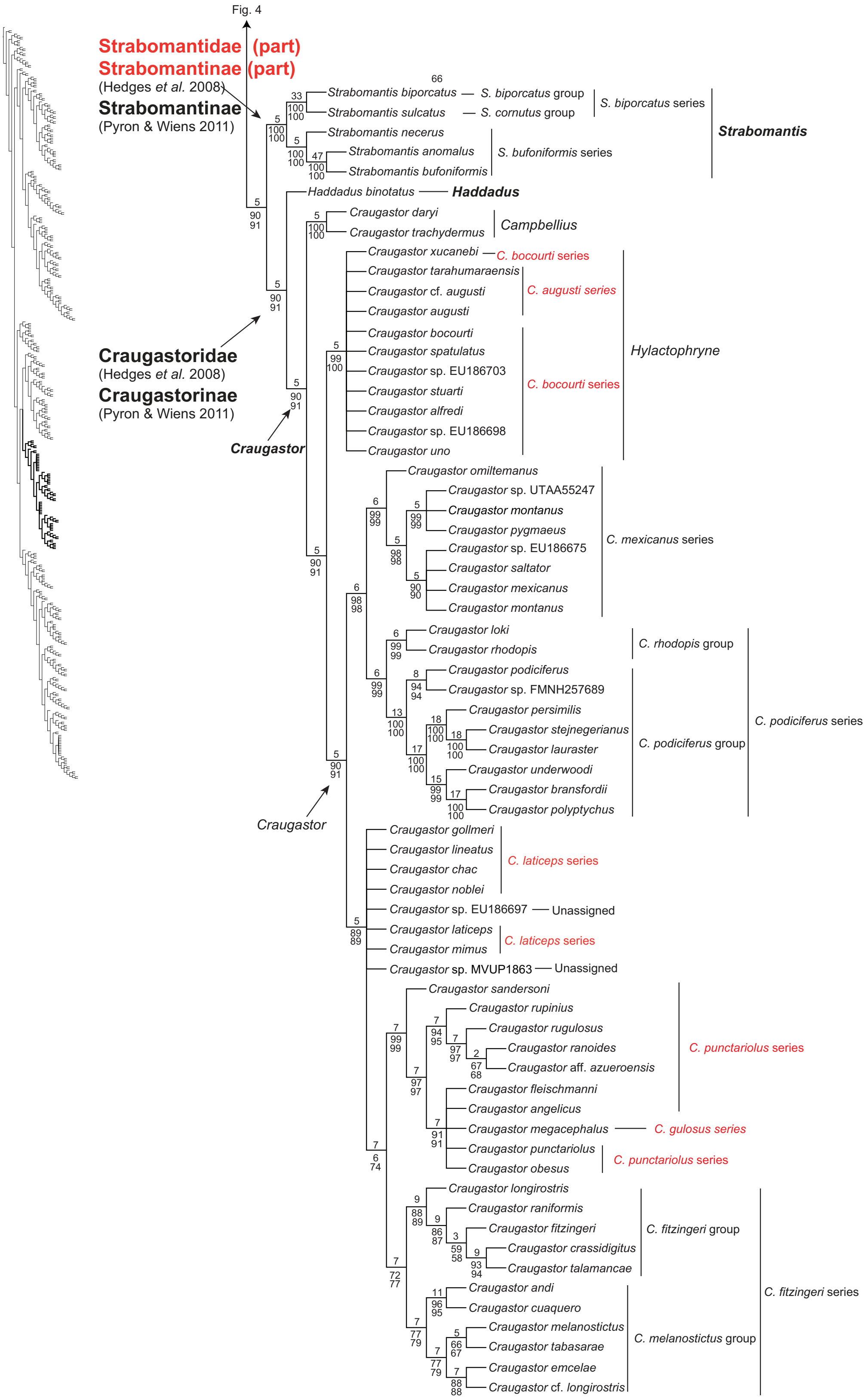

FIGURE 5. Tree-alignment + parsimony: strict consensus of 536 most parsimonious trees of 94413 steps showing relationships among 430 terminals of Brachycephaloidea and 25 outgroup taxa. Dashed branches indicate clades that collapse due to the wildcard *Eleutherodactylus dilatus*. Numbers above branches are Goodman-Bremer values excluding *E. dilatus* and those below branches are jackknife percentages excluding (upper) and including (lower) *E. dilatus*. Linnaean taxa follow previous studies except when otherwise indicated. Non-monophyletic taxa are highlighted in red (monophyletic taxa within paraphyletic groups remain in black).

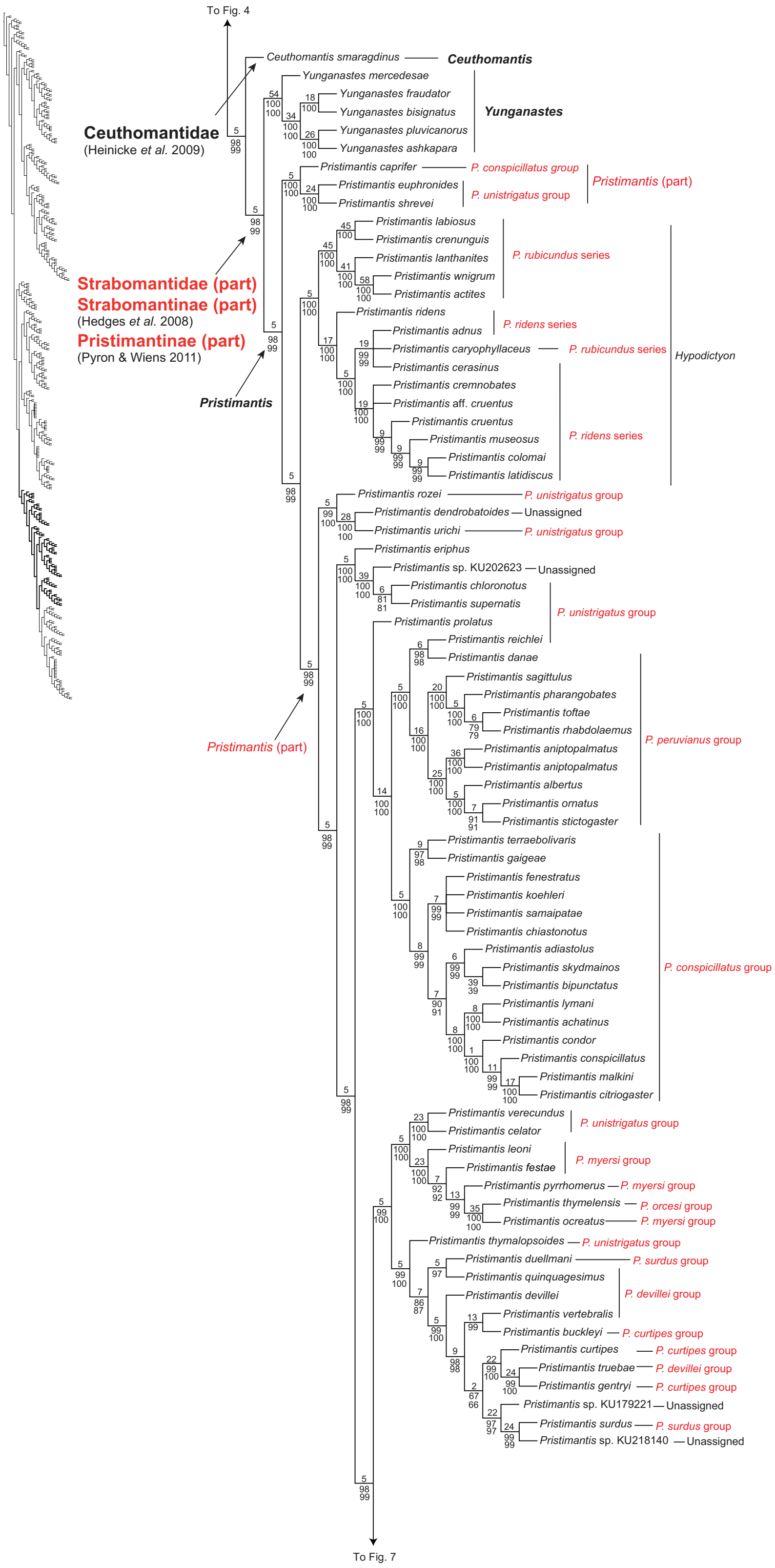

FIGURE 6. Tree-alignment + parsimony: strict consensus of 536 most parsimonious trees of 94413 steps showing relationships among 430 terminals of Brachycephaloidea and 25 outgroup taxa. Dashed branches indicate clades that collapse due to the wildcard *Eleutherodactylus dilatus*. Numbers above branches are Goodman-Bremer values excluding *E. dilatus* and those below branches are jackknife percentages excluding (upper) and including (lower) *E. dilatus*. Linnaean taxa follow previous studies except when otherwise indicated. Non-monophyletic taxa are highlighted in red (monophyletic taxa within paraphyletic groups remain in black).

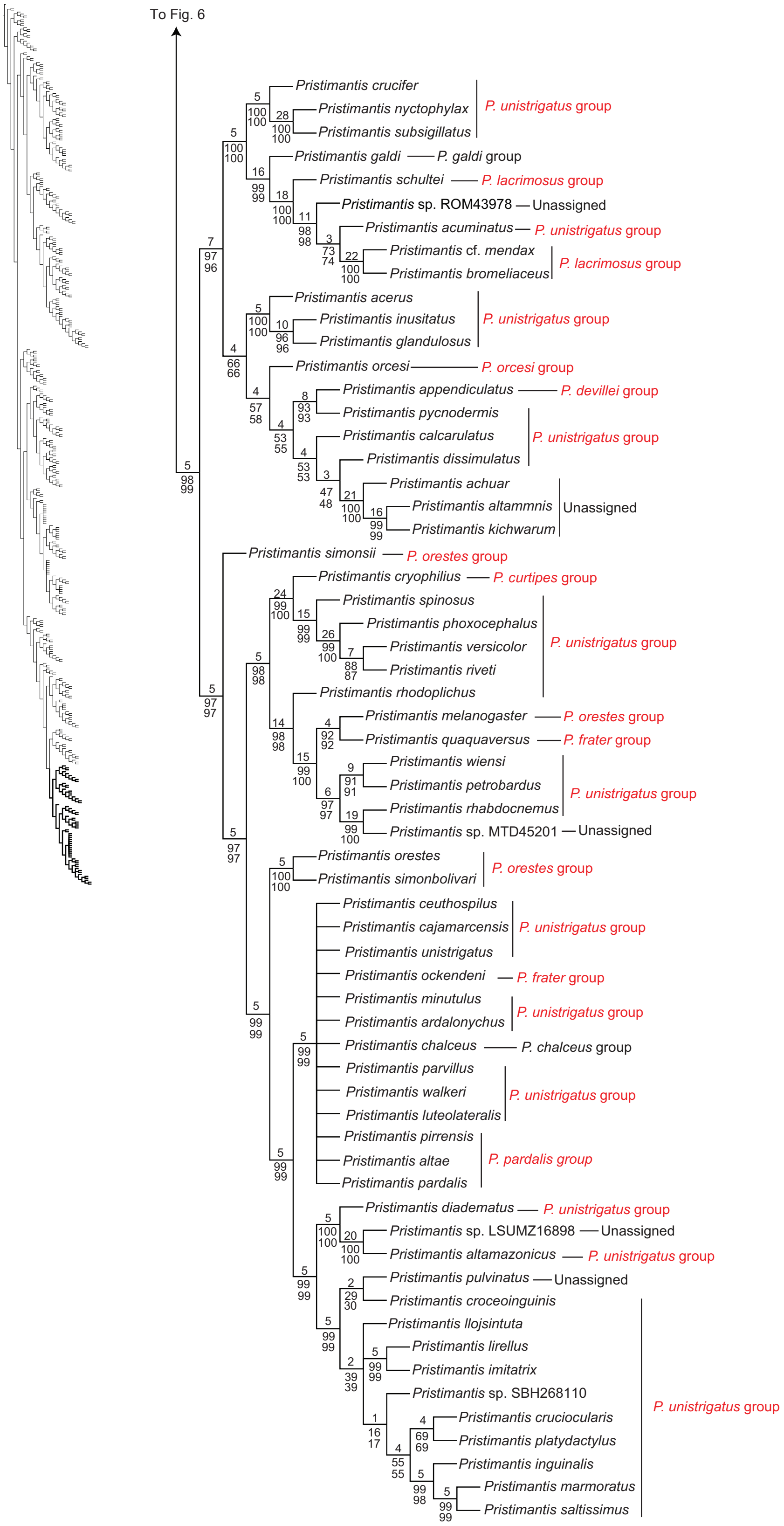

FIGURE 7. Tree-alignment + parsimony: strict consensus of 536 most parsimonious trees of 94413 steps showing relationships among 430 terminals of Brachycephaloidea and 25 outgroup taxa. Dashed branches indicate clades that collapse due to the wildcard *Eleutherodactylus dilatus*. Numbers above branches are Goodman-Bremer values excluding *E. dilatus* and those below branches are jackknife percentages excluding (upper) and including (lower) *E. dilatus*. Linnaean taxa follow previous studies except when otherwise indicated. Non-monophyletic taxa are highlighted in red (monophyletic taxa within paraphyletic groups remain in black).

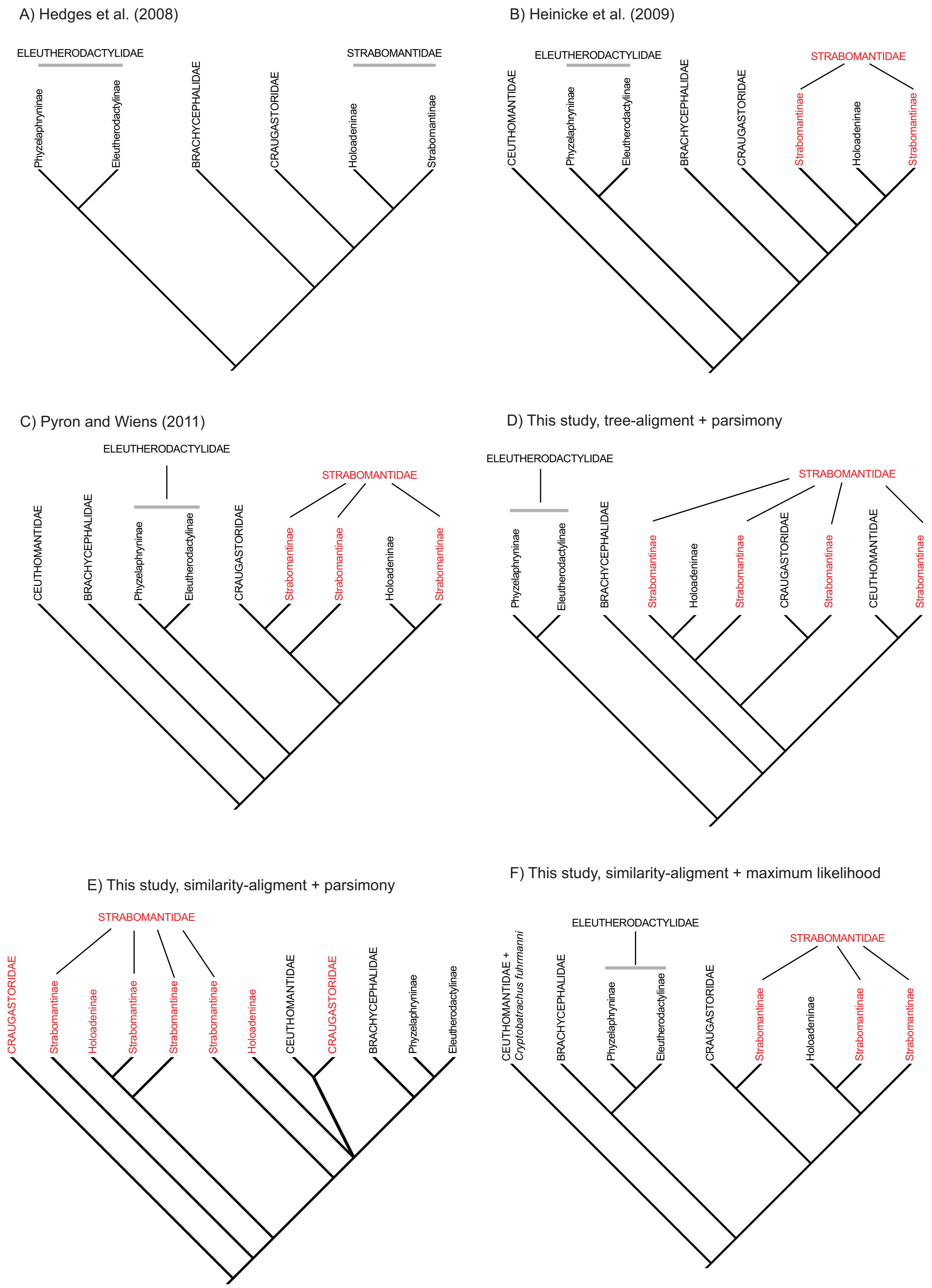

FIGURE 8. Relationships among families and subfamilies of Brachycephaloidea recognized by Hedges *et al.* (2008a): (A) similarity-alignment + maximum likelihood of analysis 3 of Hedges *et al.* (2008a); (B) similarity-alignment + maximum likelihood of the 17-gene analysis of Heinicke *et al.* (2009); (C) similarity-alignment + maximum likelihood of total evidence analysis of Pyron & Wiens (2011); (D) tree-alignment + parsimony, this study; (E) similarity-alignment + parsimony, this study; (F) similarity-alignment + maximum likelihood, this study. Non-monophyletic taxa are highlighted in red.

All recognized species of *Yunganastes* were sampled and found to be the monophyletic sister of the genus *Pristimantis* (Figure 6). Neither of the subgenera of *Pristimantis* was found to be monophyletic. *Pristimantis* (*Hypodictyon*) sensu Hedges *et al.* (2008a) is polyphyletic because *P.* (*H.*) *altae*, *P.* (*H.*) *pardalis,* and *P.* (*H.*) *pirrensis* are deeply nested within *Pristimantis* (*Pristimantis*) (Figure 6); nonetheless, *Pristimantis* (*Hypodictyon*) sensu Crawford *et al.* (2010b) is monophyletic because they transferred these three species to the subgenus *Pristimantis*. Regardless, *Pristimantis* (*Pristimantis*) is paraphyletic with respect to the remaining species of *Pristimantis* (*Hypodictyon*), which separate the clade of *P.* (*P.*) *caprifer*, *P.* (*P.*) *euphronides*, and *P.* (*P.*) *shrevei* from the remainder of the subgenus. Within these subgenera, the monophyly of the two species series recognized by Hedges *et al.* (2008a) within *Hypodictyon* was rejected, with *P.* (*H.*) *caryophyllaceus* of the *P.* (*H.*) *rubicundus* series embedded within the *P.* (*H.*) *ridens* series. Within *Pristimantis* every currently recognized species group for which there was more than a single representative species was found to be non-monophyletic.

Similarity-alignment + parsimony

The optimal MAFFT similarity-alignment comprises 17233 aligned positions (TreeBase accession: http://purl.org/phylo/treebase/phylows/study/TB2:S15350), of which 3055 (18%) contain gaps. Driven searches in TNT reached a stable strict consensus of 376 nodes five times and included 205 optimal trees of 105810 steps (Figures 9–14). Orthobatrachia is corroborated (Figure 9); however, Hemiphractidae and Brachycephaloidea are not because the hemiphractid Cryptobatrachus fuhrmanni is nested within Brachycephaloidea as sister to Ceuthomantis smaragdinus, and this clade is sister to Haddadus and Craugastor (Craugastoridae sensu Hedges *et al.*, 2008a). Within the clade formed by the remaining hemiphractids, Gastrotheca is paraphyletic, with Cryptobatrachus boulengeri and G. cornuta as sister taxa. Fritziana is sister of a clade formed by Flectonotus and a monophyletic Hemiphractus. Hylidae is paraphyletic, with Phyllomedusinae and Pelodryadinae forming the sister group of a clade formed by Orthobatrachia and Hylinae. The subsequent sister group is Leptodactylus, with Calyptocephalella gayi and Pipidae at the root.

Craugastor omiltematus is the sister of all other terraranas (and *Cryptobatrachus fuhrmanni*), which are divided into two basal clades (Figure 8, Figures 9–14). The first clade includes the monophyletic genera *Pristimantis* and *Yunganastes* as sister groups, and this clade is sister to a clade that includes three of the four sampled species of *Hypodactylus* (Figure 9). Within *Pristimantis*, *Hypodictyon* sensu Crawford *et al.* (2010b) is monophyletic but is deeply nested within the subgenus *Pristimantis*. Among all the species groups of the subgenus *Pristimantis* for which we sampled more than one species, only the *Pristimantis peruvianus* group is monophyletic (Figures 9–10).

The second clade is subdivided into several major subclades that include all of the sampled species of Brachycephalidae, Eleutherodactylidae, Strabomantidae, Holoadeninae, and Strabomantinae *sensu* Hedges *et al.* (2008a) (Figure 8, Figures 11–14). The fourth species of *Hypodactylus*, *H. dolops*, is the sister of the remainder of this second major clade, which is comprised of a trichotomy formed by (1) *Barycholos*, *Bryophryne*, *Holoaden,* and *Noblella* (Figure 12), (2) *Ceuthomantis smaragdinus* + *Cryptobatrachus fuhrmanni* and Craugastoridae *sensu* Hedges *et al.* (2008a) (Figure 12), and (3) Brachycephalidae and Eleutherodactylidae (Figures 13–14).

The basal structure within the Brachycephalidae clade is collapsed in the strict consensus of most-parsimonious trees, suggesting a lack of evidence for the monophyly *Brachycephalus* and *Ischnocnema* and the possible non-monophyly of the families. However, as in the tree-alignment + parsimony analysis, the lack of structure is due entirely to a single wildcard, *E. dilatus*. Pruning of *E. dilatus* increases the number of nodes in the strict consensus to 393 and results in the monophyly of both Brachycephalidae, with *Brachycephalus* and *Ischnocnema* as sister groups (Figure 13). *Phyzelaphryne* and *Adelophryne* are sister groups, and this clade is sister to monophyletic *Eleutherodactylus* and *Diasporus* (Figure 13). The subgenus *Schwartzius* forms a polytomy with *E.* (*Eleutherodactylus*) *unicolor* and the remaining species of the subgenera *Eleutherodactylus* and *Pelorius*. *Pelorius* is monophyletic but is nested within the subgenus *Eleutherodactylus* (Figure 13). The species of *Euhyas* and *Syrrhophus* form a clade, but *Syrrhophus* is paraphyletic with respect to *Euhyas* (Figure 14).

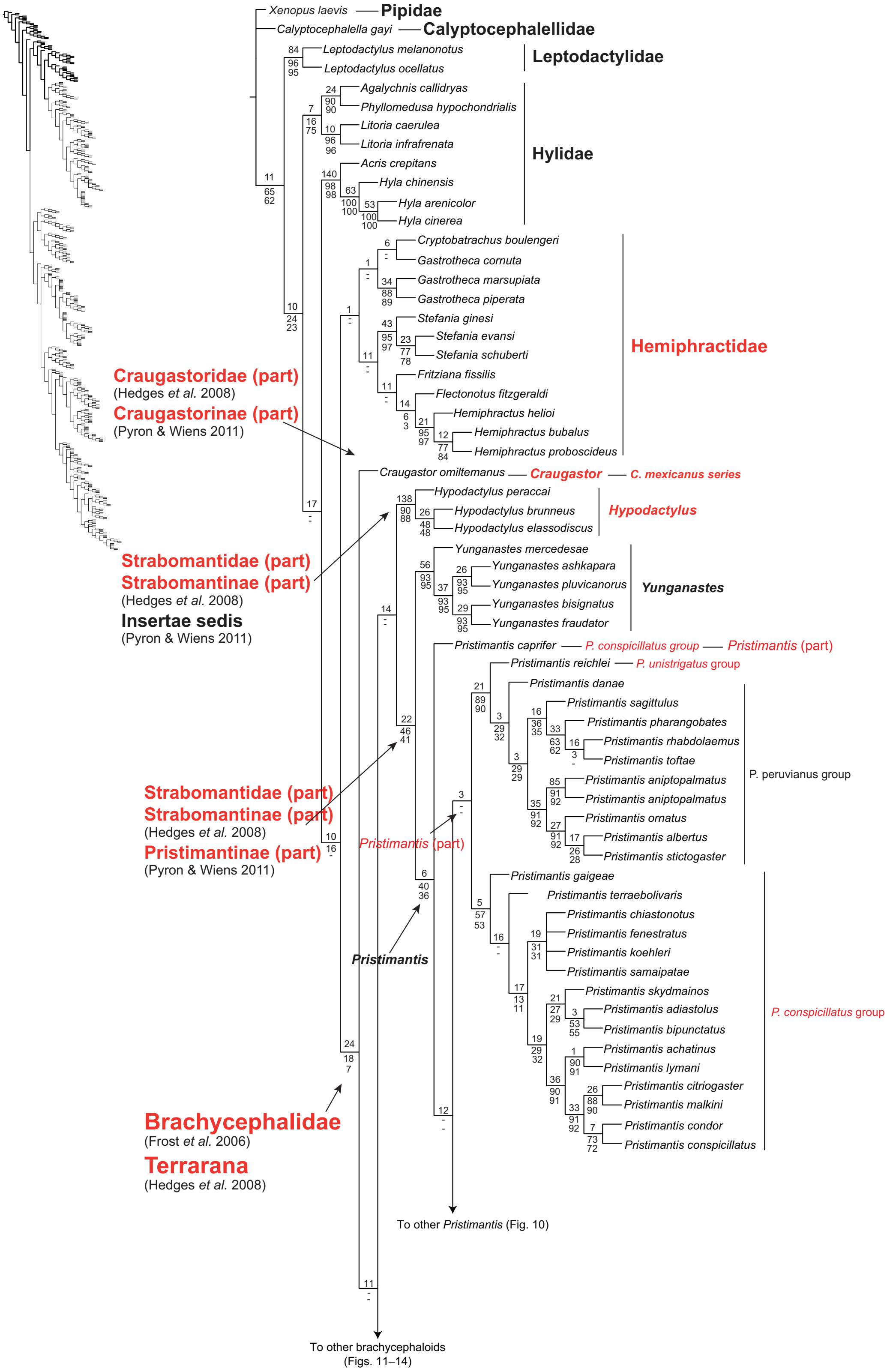

FIGURE 9. Similarity-alignment + parsimony: strict consensus of 205 most parsimonious trees of 105810 steps for a dataset of 17233 aligned sites of mitochondrial and nuclear DNA showing relationships among 430 terminals of Brachycephaloidea and 25 outgroup taxa. Dashed branches indicate clades that collapse due to the wildcard *Eleutherodactylus dilatus*. Numbers above branches are Goodman-Bremer values excluding *E. dilatus* and those below branches are jackknife percentages excluding (upper) and including (lower) *E. dilatus*; jackknife values reported as a dash (-) were recovered in < 5 pseudoreplicates. Non-monophyletic taxa of other authors or differing from the results of our similarity-alignment + parsimony are highlighted in red (monophyletic taxa within paraphyletic groups remain in black).

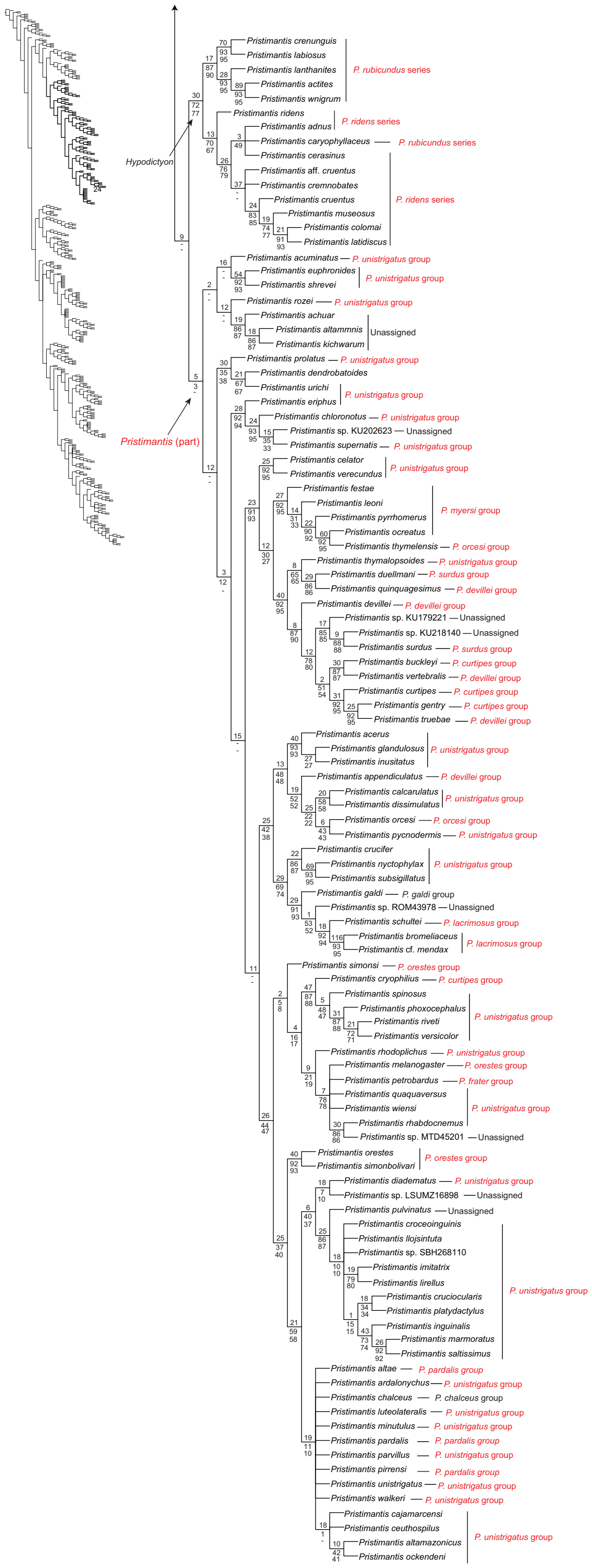

FIGURE 10. Similarity-alignment + parsimony: strict consensus of 205 most parsimonious trees of 105810 steps for a dataset of 17233 aligned sites of mitochondrial and nuclear DNA showing relationships among 430 terminals of Brachycephaloidea and 25 outgroup taxa. Dashed branches indicate clades that collapse due to the wildcard *Eleutherodactylus dilatus*. Numbers above branches are Goodman-Bremer values excluding *E. dilatus* and those below branches are jackknife percentages excluding (upper) and including (lower) *E. dilatus*; jackknife values reported as a dash (-) were recovered in < 5 pseudoreplicates. Non-monophyletic taxa of other authors or differing from the results of our similarity-alignment + parsimony are highlighted in red (monophyletic taxa within paraphyletic groups remain in black).

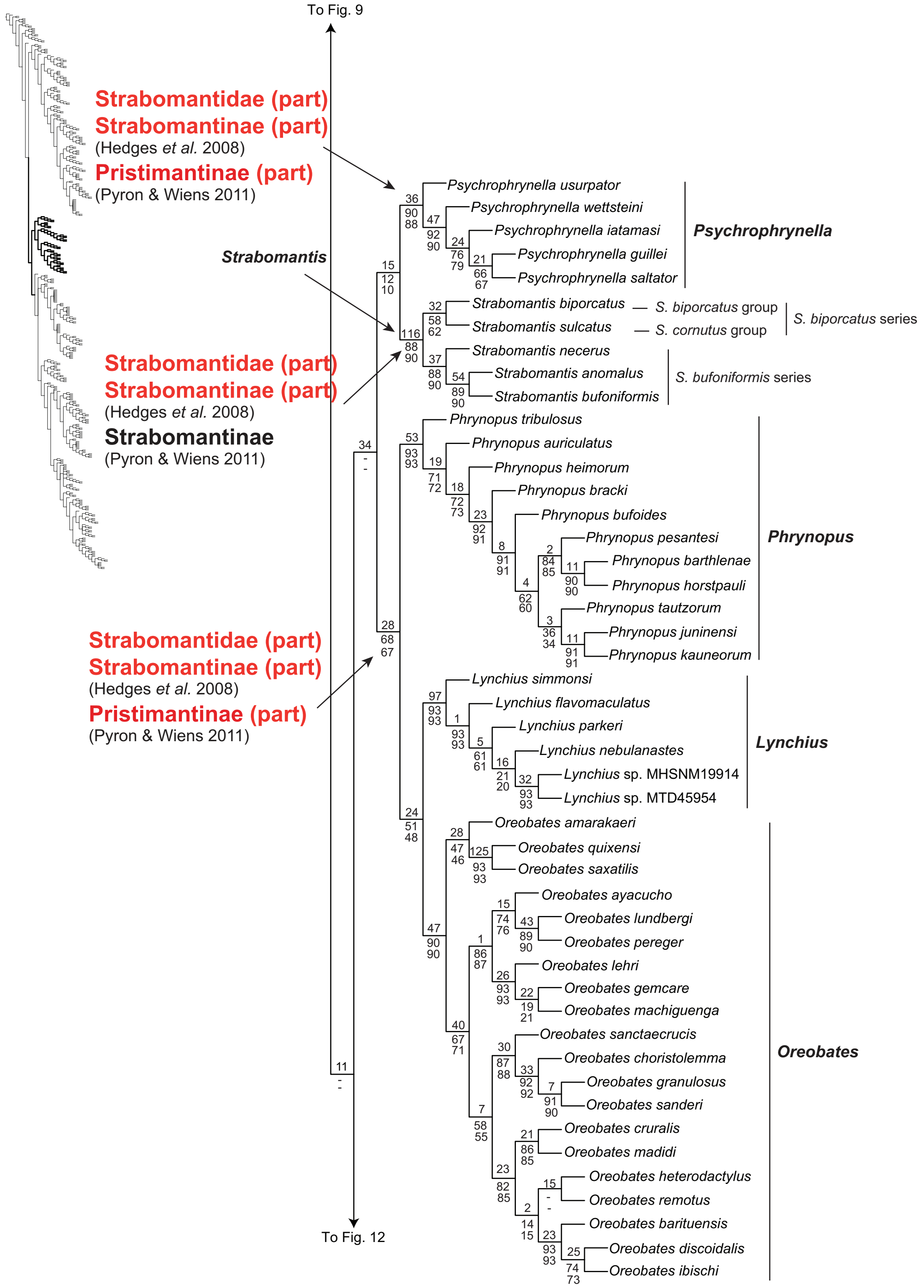

FIGURE 11. Similarity-alignment + parsimony: strict consensus of 205 most parsimonious trees of 105810 steps for a dataset of 17233 aligned sites of mitochondrial and nuclear DNA showing relationships among 430 terminals of Brachycephaloidea and 25 outgroup taxa. Dashed branches indicate clades that collapse due to the wildcard *Eleutherodactylus dilatus*. Numbers above branches are Goodman-Bremer values excluding *E. dilatus* and those below branches are jackknife percentages excluding (upper) and including (lower) *E. dilatus*; jackknife values reported as a dash (-) were recovered in < 5 pseudoreplicates. Non-monophyletic taxa of other authors or differing from the results of our similarity-alignment + parsimony are highlighted in red (monophyletic taxa within paraphyletic groups remain in black).

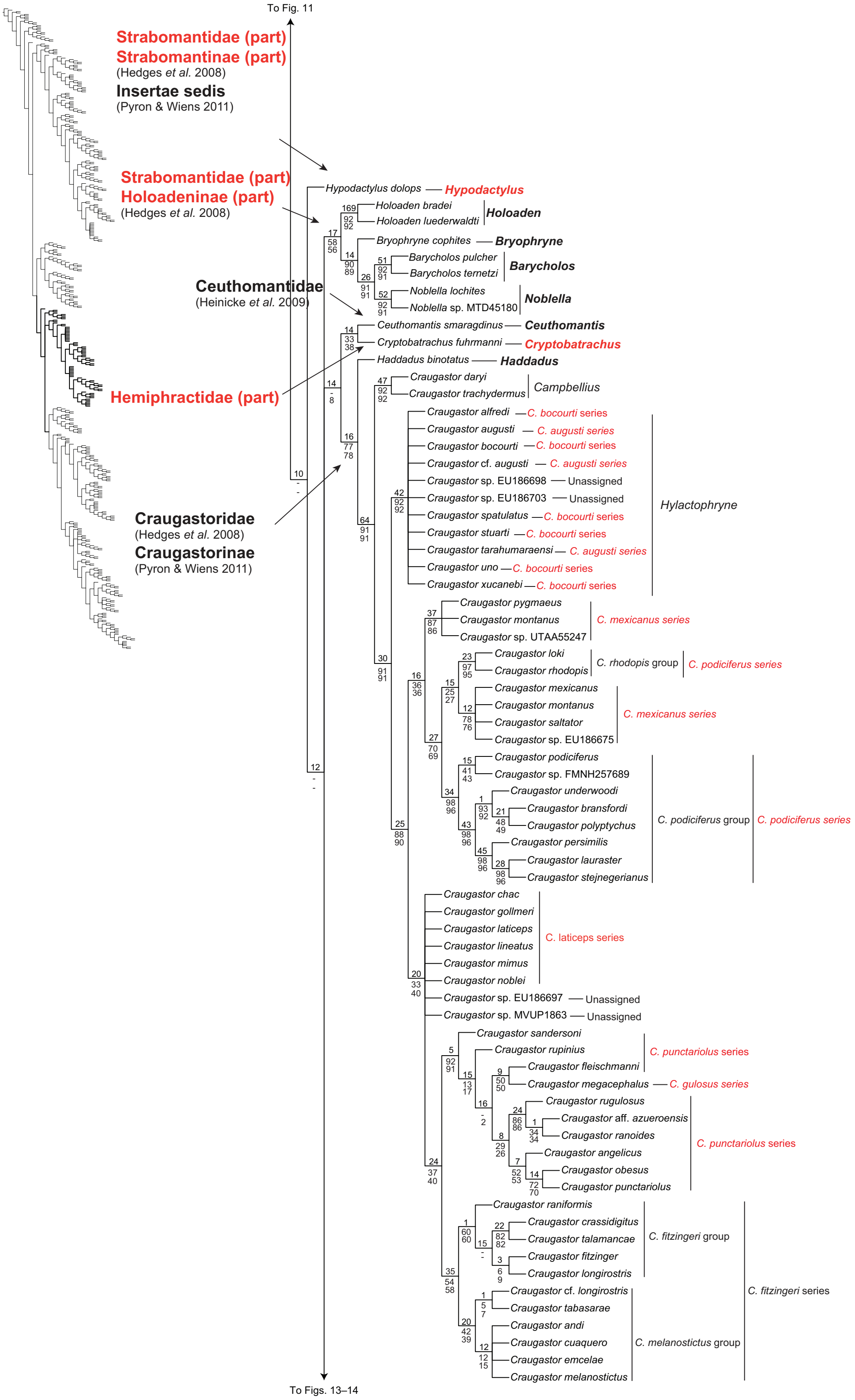

FIGURE 12. Similarity-alignment + parsimony: strict consensus of 205 most parsimonious trees of 105810 steps for a dataset of 17233 aligned sites of mitochondrial and nuclear DNA showing relationships among 430 terminals of Brachycephaloidea and 25 outgroup taxa. Dashed branches indicate clades that collapse due to the wildcard *Eleutherodactylus dilatus*. Numbers above branches are Goodman-Bremer values excluding *E. dilatus* and those below branches are jackknife percentages excluding (upper) and including (lower) *E. dilatus*; jackknife values reported as a dash (-) were recovered in < 5 pseudoreplicates. Non-monophyletic taxa of other authors or differing from the results of our similarity-alignment + parsimony are highlighted in red (monophyletic taxa within paraphyletic groups remain in black).

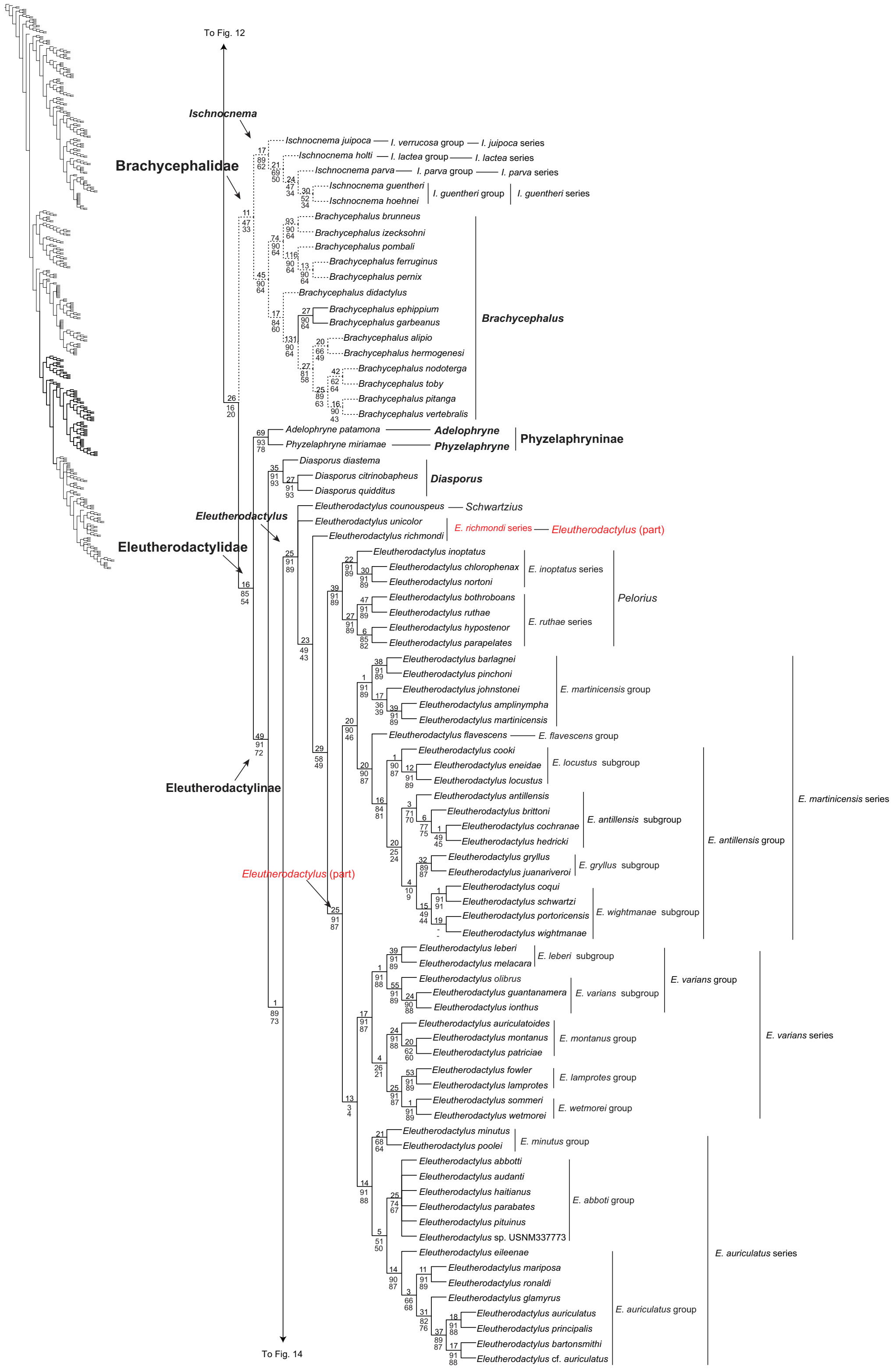

FIGURE 13. Similarity-alignment + parsimony: strict consensus of 205 most parsimonious trees of 105810 steps for a dataset of 17233 aligned sites of mitochondrial and nuclear DNA showing relationships among 430 terminals of Brachycephaloidea and 25 outgroup taxa. Dashed branches indicate clades that collapse due to the wildcard *Eleutherodactylus dilatus*. Numbers above branches are Goodman-Bremer values excluding *E. dilatus* and those below branches are jackknife percentages excluding (upper) and including (lower) *E. dilatus*; jackknife values reported as a dash (-) were recovered in < 5 pseudoreplicates. Non-monophyletic taxa of other authors or differing from the results of our similarity-alignment + parsimony are highlighted in red (monophyletic taxa within paraphyletic groups remain in black).

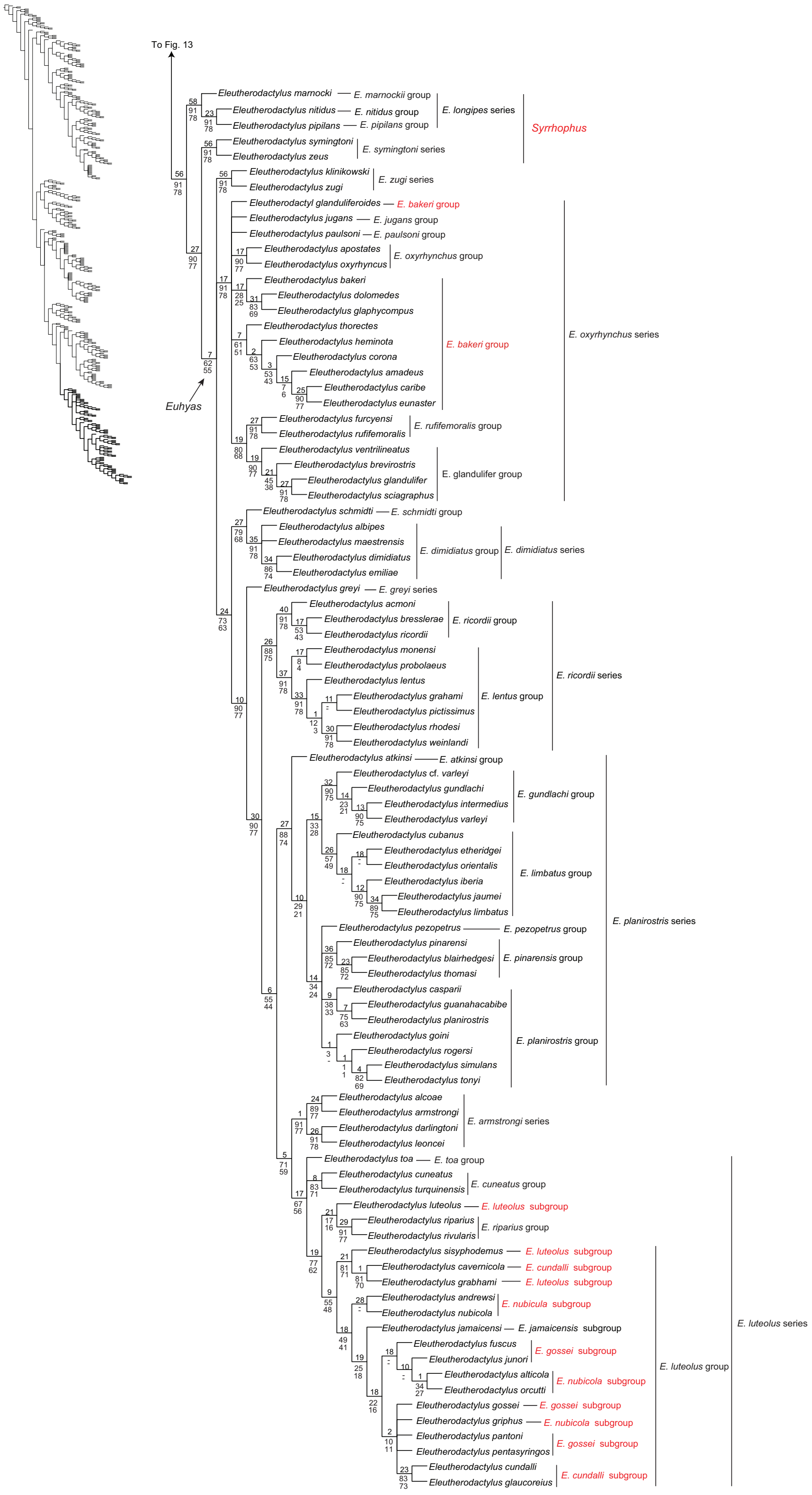

FIGURE 14. Similarity-alignment + parsimony: strict consensus of 205 most parsimonious trees of 105810 steps for a dataset of 17233 aligned sites of mitochondrial and nuclear DNA showing relationships among 430 terminals of Brachycephaloidea and 25 outgroup taxa. Dashed branches indicate clades that collapse due to the wildcard *Eleutherodactylus dilatus*. Numbers above branches are Goodman-Bremer values excluding *E. dilatus* and those below branches are jackknife percentages excluding (upper) and including (lower) *E. dilatus*; jackknife values reported as a dash (-) were recovered in < 5 pseudoreplicates. Non-monophyletic taxa of other authors or differing from the results of our similarity-alignment + parsimony are highlighted in red (monophyletic taxa within paraphyletic groups remain in black).

Strabomantidae sensu Hedges *et al.* (2008a) is not monophyletic (Figure 8, Figures 9–12), being divided into the following clades: (1) *Lynchius*, *Oreobates*, *Phrynopus*, *Psychrophrynella*, and *Strabomantis* (all monophyletic); (2) *Pristimantis*, *Yunganastes* (both monophyletic), and most *Hypodactylus*; (3) *Hypodactylus dolops* forming the monotypic sister lineage of a large clade of brachycephalids, craugastorids, eleutherodactylids, and strabomantids; and (4) *Barycholos*, *Bryophryne*, *Holoaden*, and *Noblella*.

Haddadus is the sister group of *Craugastor* (Figure 12). Within *Craugastor*, *Campbellius* is the sister of all remaining congeners except *Craugastor omiltemanus* (see above). *Hylactophryne* is the monophyletic, but entirely unresolved, sister clade of the subgenus *Craugastor* (minus *C. omiltemanus*). The *C. mexicanus* and *C. podiciferus* series are paraphyletic, with part of the *C. mexicanus* series being nested within the *C. podiciferus* series as the sister of the *C. rhodopis* group and the remaining part (minus *C. omiltemanus*) sister to that clade and the *C. podiciferus* group. The *C. laticeps* series is collapsed in a polytomy with a clade composed of the *C. fitzingeri*, *C. gulosus*, and *C. punctariolus* series. The *C. punctariolus* series includes *C. megacephalus*, the sole representative of the *C. gulosus* series, and is therefore paraphyletic.

Similarity-alignment + maximum likelihood

The same MAFFT alignment used for the similarity-alignment + parsimony analyses was used in the maximum likelihood analyses. For all but four partitions of the 18-partition dataset, GTR + I + G was selected by jModelTest; for CXCR4, Rho, SIA, and Tyr, TrN + I + G, TVM + I + G, K81uf + I + G, and TVM + I + G models were selected, respectively. PartitionFinder identified the 2-partition (mtDNA/nuDNA) scheme with the GTR + G substitution model for both partitions to be the optimal model (Table 2). GARLI searches under the optimal 2-partition + GTR model identified a single maximum likelihood tree (log likelihood = -398630.4935; Figures 15–21; TreeBase accession: http://purl.org/phylo/treebase/phylows/study/TB2:S15350). As expected, this is considerably less than the maximum likelihood score for the 18-partition dataset (-395849.478766) and greater than that of the unpartitioned dataset (-401805.965730).

TABLE 2. Partition schemes evaluated in PartitionFinder and resulting scores for the Akaike Information Criterion (AIC), Corrected Akaike Information Criterion (AICc), and Bayensian Information Criterion (BIC). See section *Similarity-alignment + maximum likelihood analysis* for explanations about criteria and limitations that guided the selection of partition schemes.

Partition Scheme	lnL	parameters	sites	subsets	AIC	AICc	BIC
mtDNA/nuDNA	-397633.716	1836	17233	2	798939.432	799377.563	813176.843
None	-403980.663	918	17233	1	809797.326	809900.751	816916.031
18 partitions	-394185.589	16524	17233	18	821419.179	1592772.568	949555.882

The maximum likelihood analysis did not recover Brachycephaloidea, Hemiphractidae, or Hylidae (Figure 15). Instead, the hemiphractid *Cryptobatrachus fuhrmanni* was recovered within Brachycephaloidea as the sister of the terrarana *Ceuthomantis smaragdinus* and the hemiphractid *Cryptobatrachus boulengeri* was placed within Hylidae as the sister of Phyllomedusinae. The remaining outgroup relationships conform to expectations.

Within Brachycephaloidea, the *Cryptobatrachus fuhrmanni* + *Ceuthomantis smaragdinus* clade is strongly supported (likelihood ratio = 7.6) and is placed as the sister of all other terraranas, which splits into two large clades (Figure 8). The first is a well-supported clade (likelihood ratio = 4.6) composed of Brachycephalidae (composed of monophyletic *Ischnocnema* and *Brachycephalus*) and Eleutherodactylidae, both of which are monophyletic (Figures 15–16). Within Eleutherodactylidae, Phyzelaphryninae and Eleutherodactylinae are both monophyletic, with the latter composed of the monophyletic genera *Diasporus* and *Eleutherodactylus* (Figure 16). The subgenus *Eleutherodactylus* is paraphyletic with respect to *Schwartzius* and *Pelorius*, because *E. unicolor* is sister to these two subgenera and to the subgenus *Eleutherodactylus*, which also renders the *E. richmondi* series polyphyletic (Figure 16). The *E. martinicensis* series is polyphyletic, with the *E. martinicensis* group imbedded within the *E. auriculatus* series, and with *E. poolei* (*E. abbotti* group) + *E. minutus* (*E. minutus* group) forming the sister taxon of the *E. martinicensis* group plus the remainder of the *E. auriculatus* series. The subgenus *Syrrhophus* is also polyphyletic, because *Eleutherodactylus (Syrrhophus) dilatus* is consistently placed (bootstrap frequency = 0.81) as sister of a monophyletic *Euhyas* plus the remaining *Syrrhophus* despite the low support for this inference (likelihood ratio = 2.7) (Figure 17). Within *Euhyas*, the *E. bakeri* species group is monophyletic, but the subgroups within the *E. luteolus* species group are not (Figure 17).

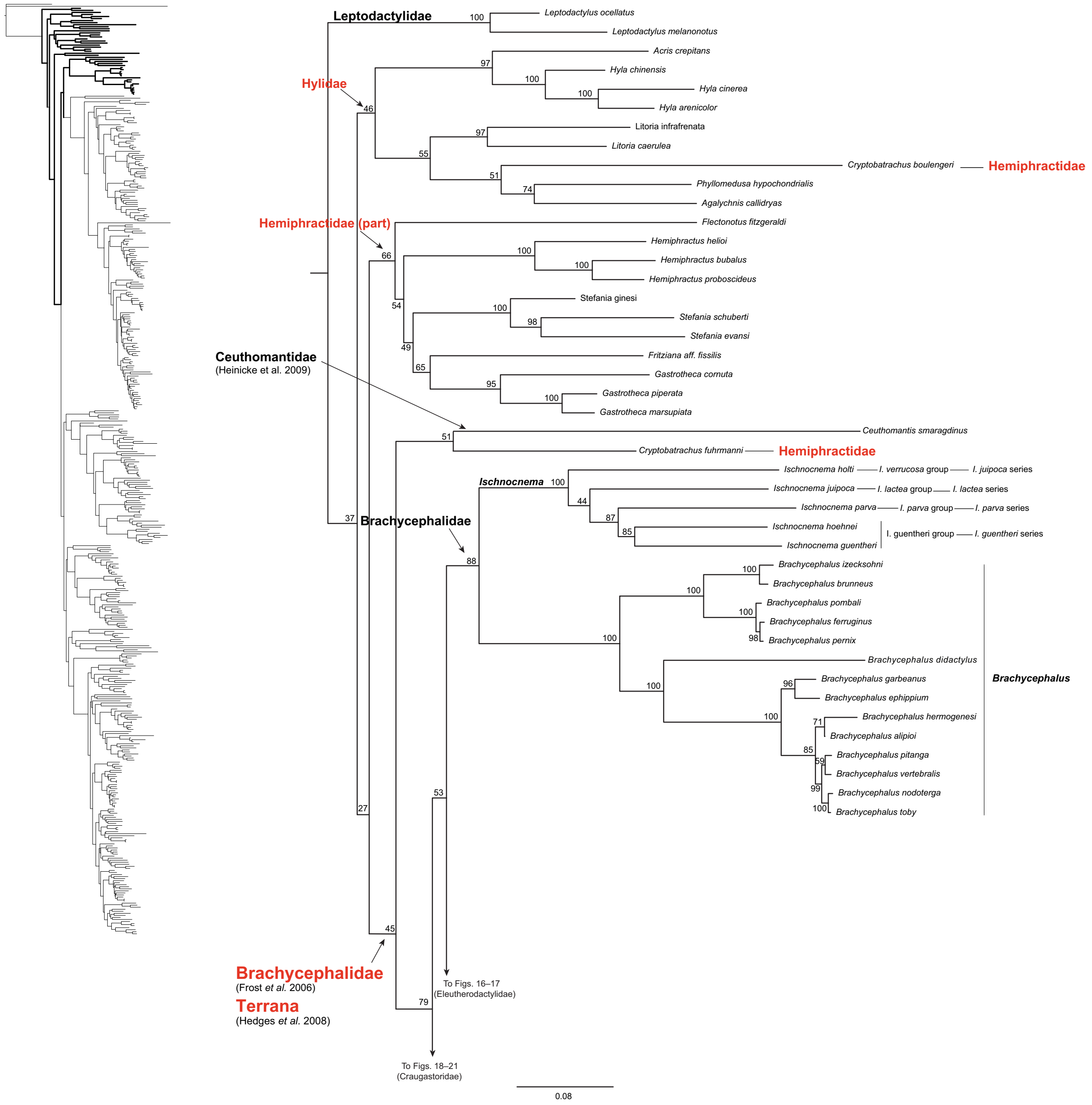

FIGURE 15. Similarity-alignment + maximum likelihood: optimal solution (log likelihood= -398630.4935) showing relationships among 430 terminals of Brachycephaloidea and 25 outgroup taxa scored for 17233 aligned sites of mitochondrial and nuclear DNA assuming mitochondrial and nuclear partitions and the GTR + G substitution model. Numbers above nodes are bootstrap percentages. Non-monophyletic taxa of other authors or differing from the results of our similarity-alignment + parsimony are highlighted in red (monophyletic taxa within paraphyletic groups remain in black).

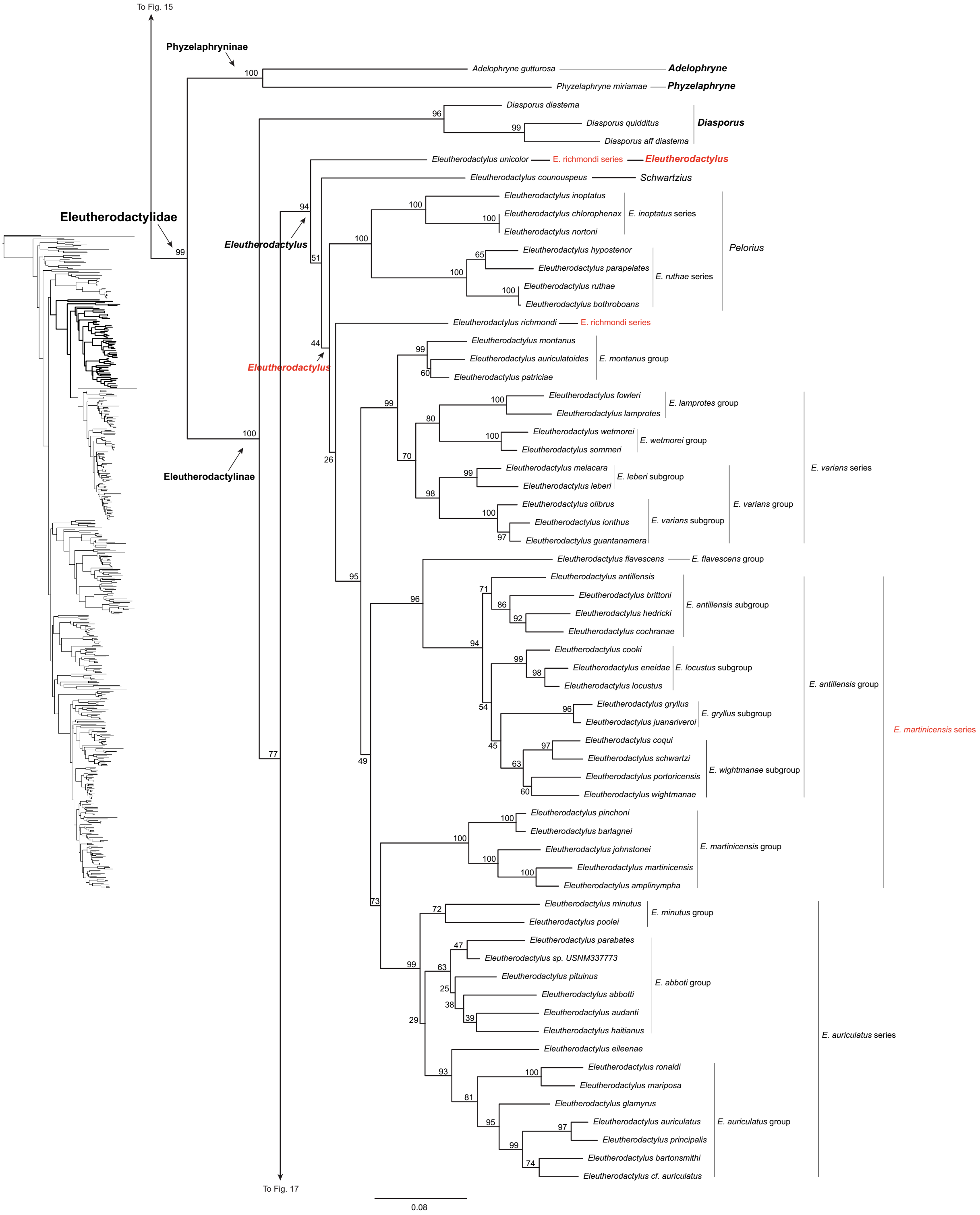

FIGURE 16. Similarity-alignment + maximum likelihood: optimal solution (log likelihood= -398630.4935) showing relationships among 430 terminals of Brachycephaloidea and 25 outgroup taxa scored for 17233 aligned sites of mitochondrial and nuclear DNA assuming mitochondrial and nuclear partitions and the GTR + G substitution model. Numbers above nodes are bootstrap percentages. Non-monophyletic taxa of other authors or differing from the results of our similarity-alignment + parsimony are highlighted in red (monophyletic taxa within paraphyletic groups remain in black).

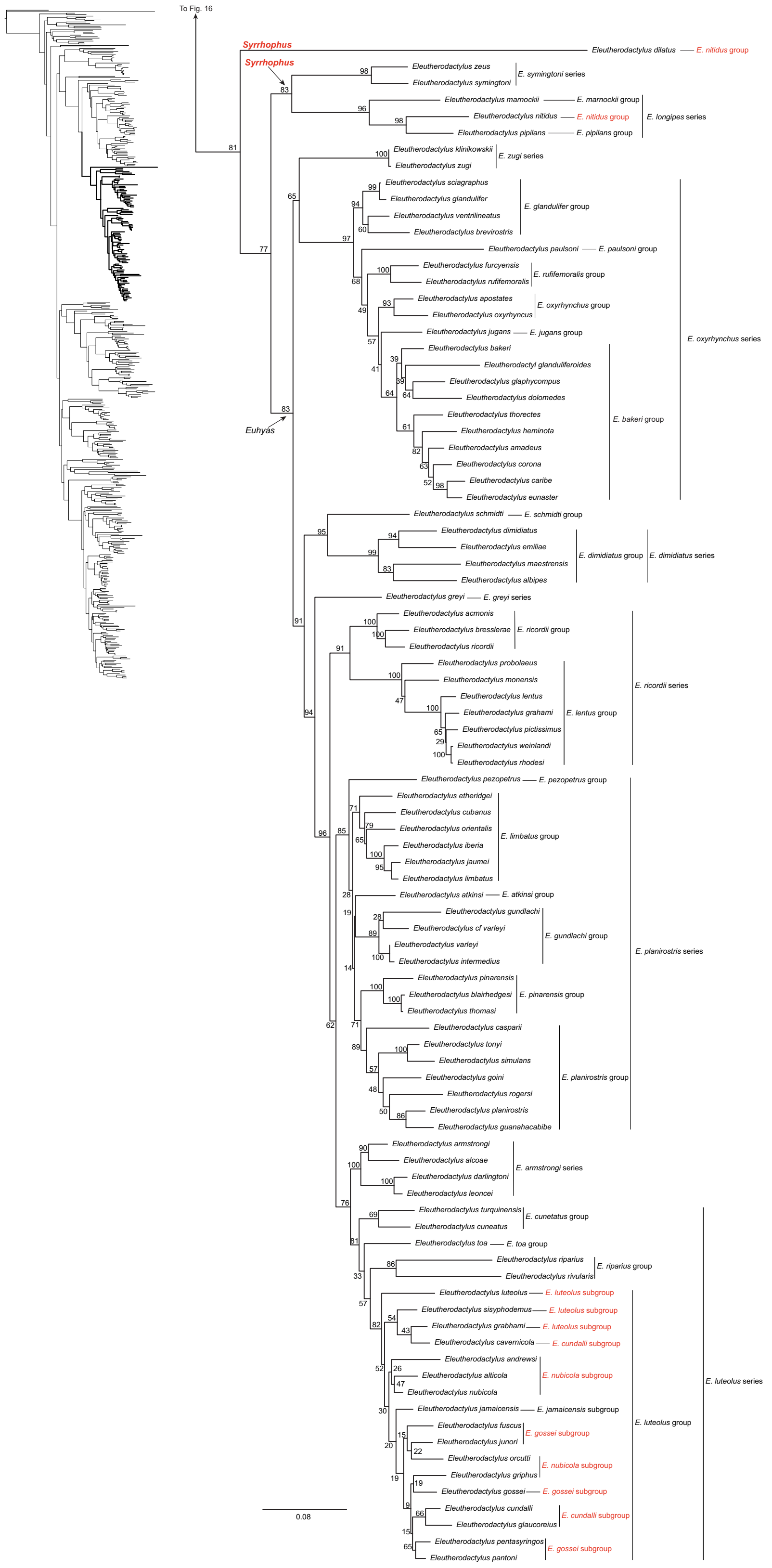

FIGURE 17. Similarity-alignment + maximum likelihood: optimal solution (log likelihood= -398630.4935) showing relationships among 430 terminals of Brachycephaloidea and 25 outgroup taxa scored for 17233 aligned sites of mitochondrial and nuclear DNA assuming mitochondrial and nuclear partitions and the GTR + G substitution model. Numbers above nodes are bootstrap percentages. Non-monophyletic taxa of other authors or differing from the results of our similarity-alignment + parsimony are highlighted in red (monophyletic taxa within paraphyletic groups remain in black).

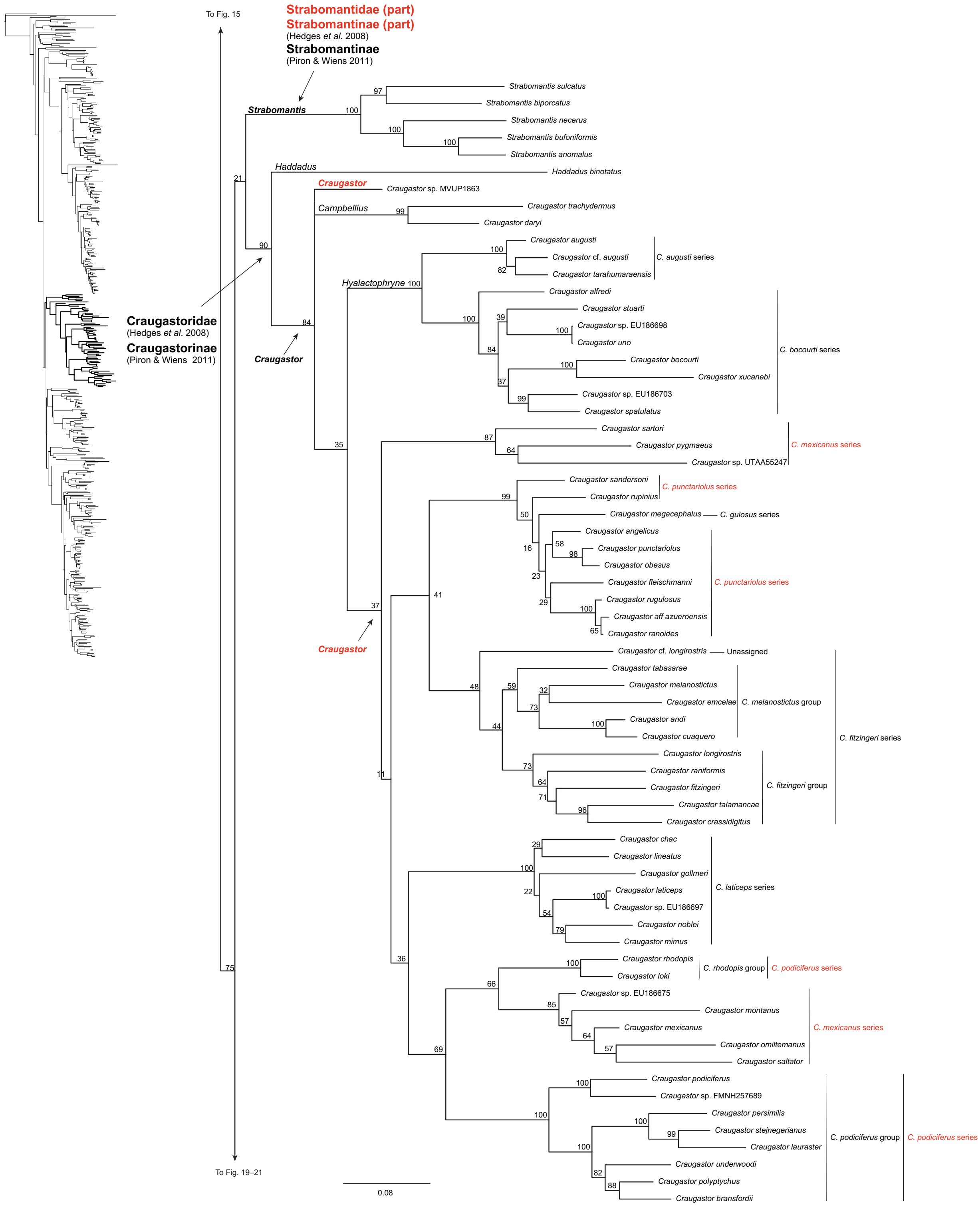

FIGURE 18. Similarity-alignment + maximum likelihood: optimal solution (log likelihood= -398630.4935) showing relationships among 430 terminals of Brachycephaloidea and 25 outgroup taxa scored for 17233 aligned sites of mitochondrial and nuclear DNA assuming mitochondrial and nuclear partitions and the GTR + G substitution model. Numbers above nodes are bootstrap percentages. Non-monophyletic taxa of other authors or differing from the results of our similarity-alignment + parsimony are highlighted in red (monophyletic taxa within paraphyletic groups remain in black).

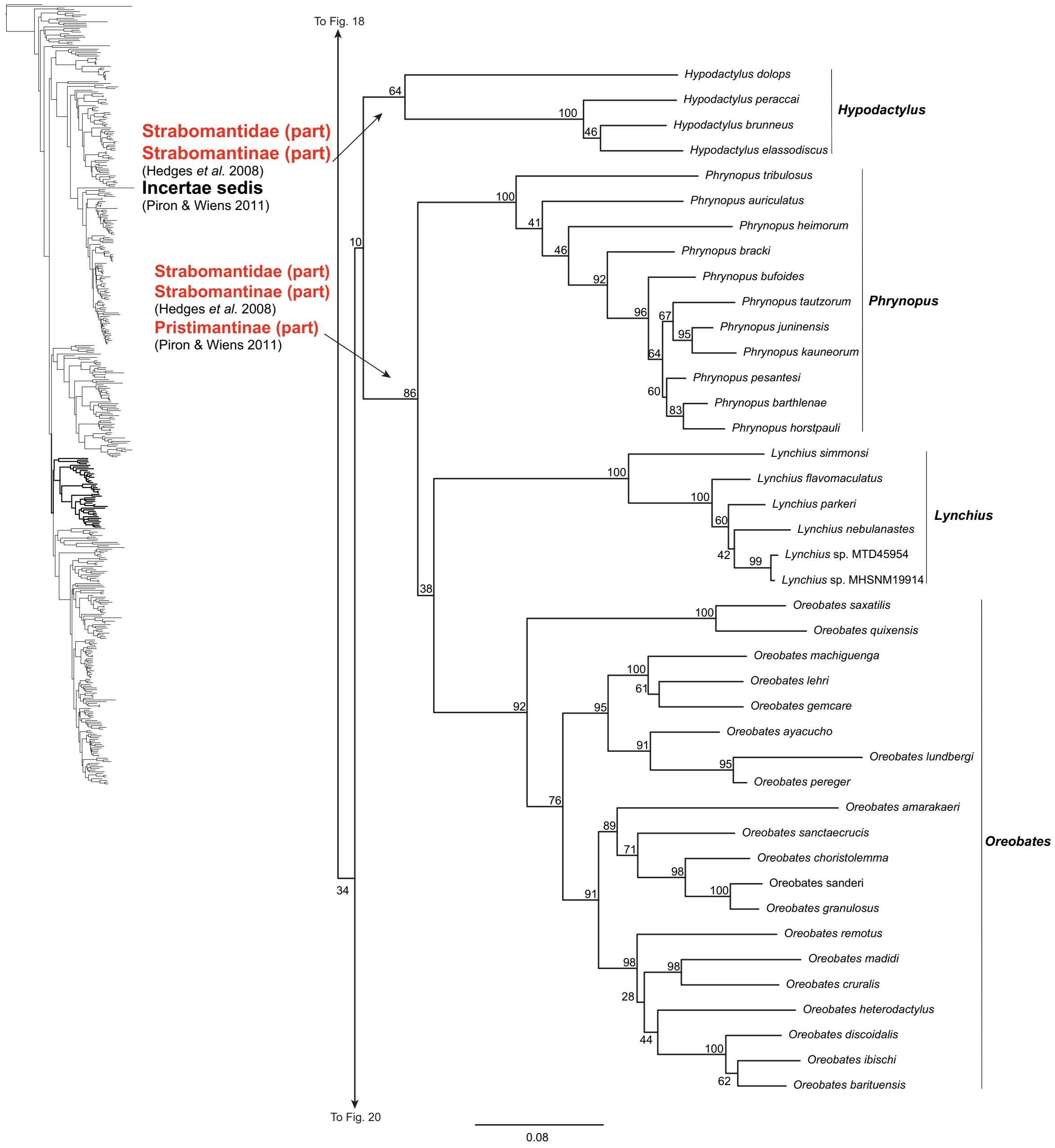

FIGURE 19. Similarity-alignment + maximum likelihood: optimal solution (log likelihood= -398630.4935) showing relationships among 430 terminals of Brachycephaloidea and 25 outgroup taxa scored for 17233 aligned sites of mitochondrial and nuclear DNA assuming mitochondrial and nuclear partitions and the GTR + G substitution model. Numbers above nodes are bootstrap percentages. Non-monophyletic taxa of other authors or differing from the results of our similarity-alignment + parsimony are highlighted in red (monophyletic taxa within paraphyletic groups remain in black).

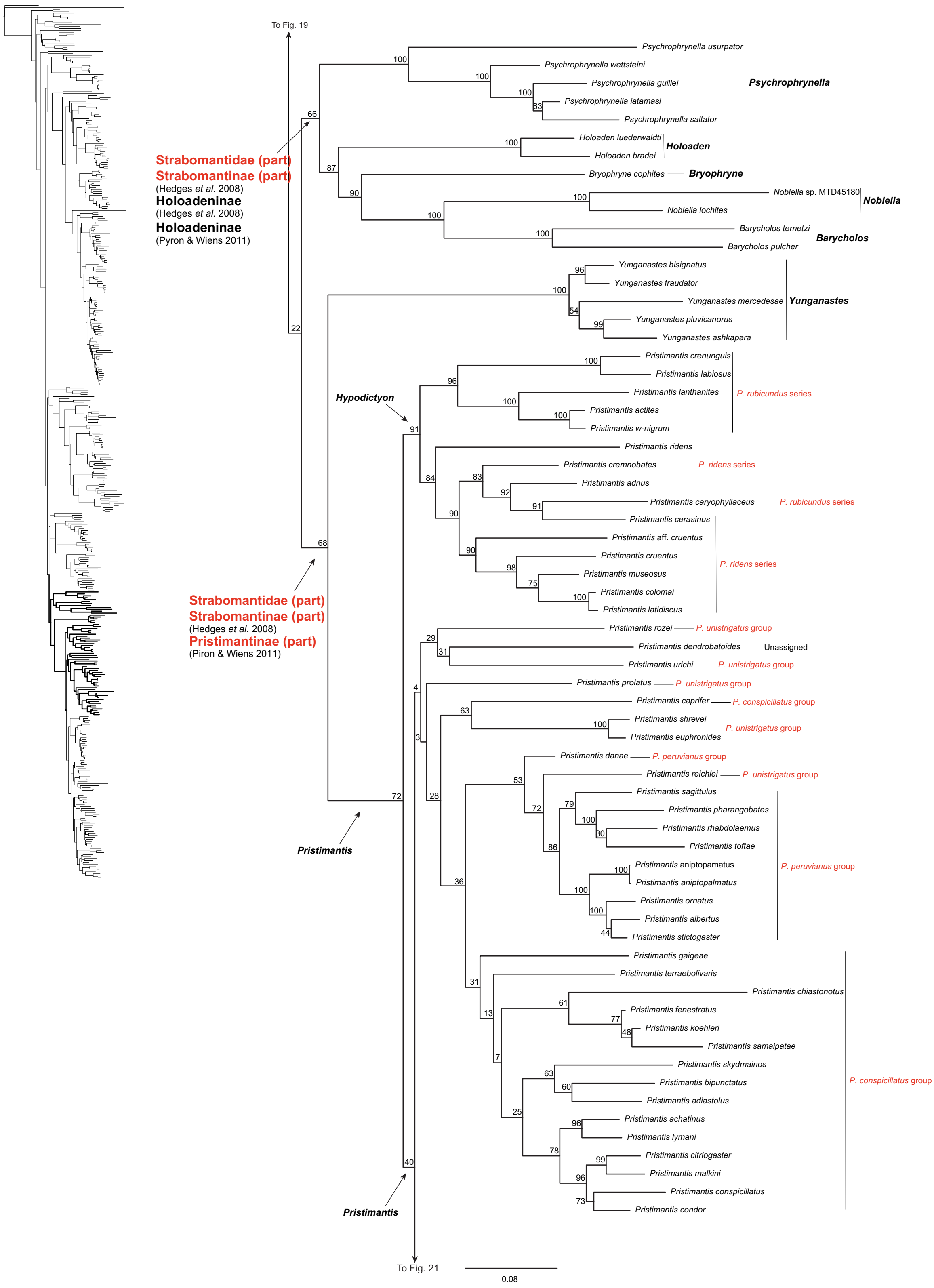

FIGURE 20. Similarity-alignment + maximum likelihood: optimal solution (log likelihood= -398630.4935) showing relationships among 430 terminals of Brachycephaloidea and 25 outgroup taxa scored for 17233 aligned sites of mitochondrial and nuclear DNA assuming mitochondrial and nuclear partitions and the GTR + G substitution model. Numbers above nodes are bootstrap percentages. Non-monophyletic taxa of other authors or differing from the results of our similarity-alignment + parsimony are highlighted in red (monophyletic taxa within paraphyletic groups remain in black).

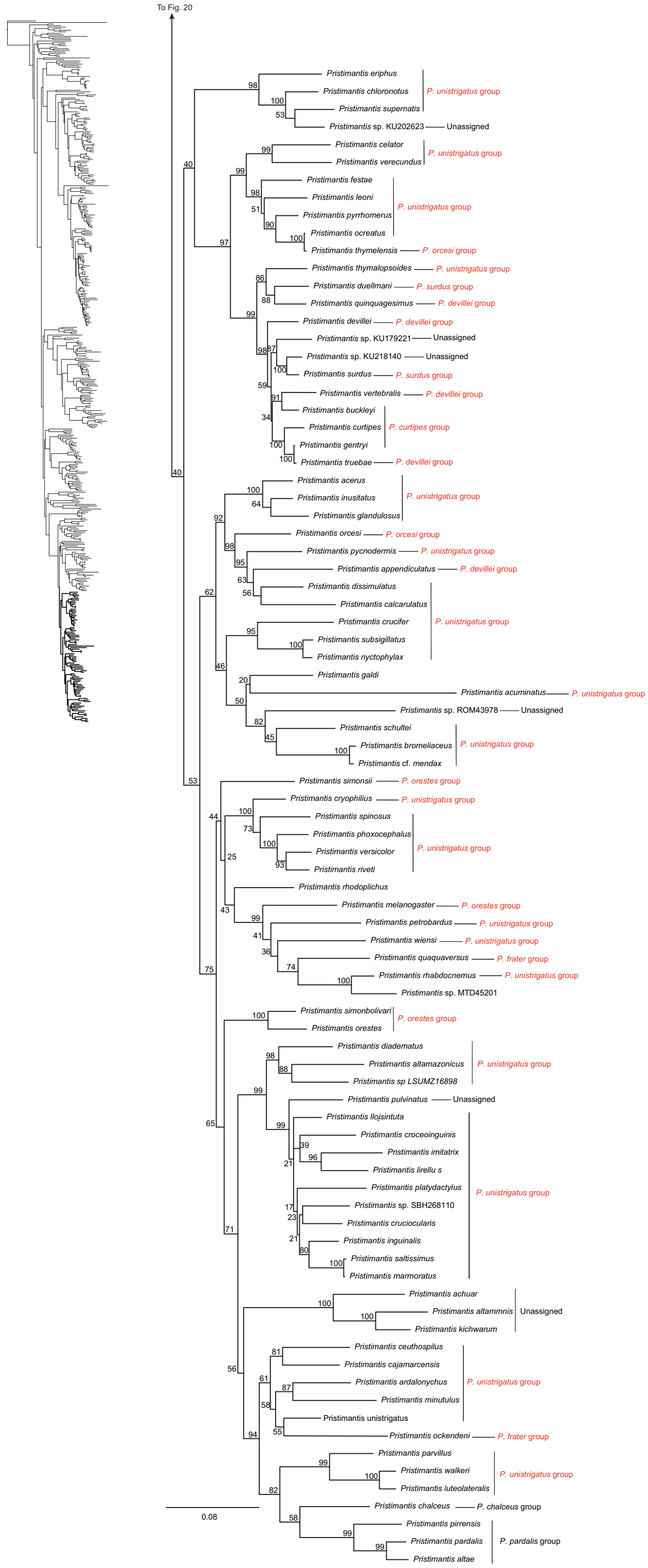

FIGURE 21. Similarity-alignment + maximum likelihood: optimal solution (log likelihood= -398630.4935) showing relationships among 430 terminals of Brachycephaloidea and 25 outgroup taxa scored for 17233 aligned sites of mitochondrial and nuclear DNA assuming mitochondrial and nuclear partitions and the GTR + G substitution model. Numbers above nodes are bootstrap percentages. Non-monophyletic taxa of other authors or differing from the results of our similarity-alignment + parsimony are highlighted in red (monophyletic taxa within paraphyletic groups remain in black).

The second clade of Brachycephaloidea (Figures 4–8) is composed of the remaining families of Hedges *et al.* (2008a) and Heinicke *et al.* (2009). Brachycephalidae, composed of the monophyletic sister genera *Brachycephalus* and *Ischnocnema* (Figure 4), is the sister of a large clade (Figures 4–7) composed of interdigitating Central and South American groups of Ceuthomantidae, Craugastoridae, and Strabomantidae sensu Hedges *et al.* (2008a). This Central–South American clade conforms more-or-less to Craugastoridae sensu Pyron & Wiens (2011), the difference being that it includes Ceuthomantidae. Ceuthomantidae was represented in our analysis only by *Ceuthomantis smaragdinus*, so its monophyly was not tested. Craugastoridae sensu Hedges *et al.* (2008a) was corroborated. In contrast, Strabomantidae formed three independent clades (Figures 4–7, 8D). The first large clade of strabomantids is composed of *Barycholos*, *Bryophryne*, *Holoaden*, *Hypodactylus*, *Lynchius*, *Noblella*, *Oreobates*, *Phrynopus*, and *Psychrophrynella*. The second clade consists only of *Strabomantis*, which is the sister of Craugastoridae sensu Hedges *et al.* (2008a). The remaining massive clade of Strabomantidae is composed of *Yunganastes* and *Pristimantis* and is the sister of Ceuthomantidae. In summary, Strabomantidae and Strabomantinae of Hedges et al (2008a) and Craugastoridae and Pristimantinae of Pyron & Wiens (2011) and Ohler & Dubois (2012) are all paraphyletic (Figure 8).

Within the large and eminently North and Central American genus *Craugastor*, the subgenera *Campbellius*, *Craugastor,* and *Hylactophryne* are monophyletic, although all of the species of *Hylactophryne* collapse into a polytomy in the strict consensus (Figure 5). Also, the *C. punctariolus* series is paraphyletic with respect to the *C. gulosus* series because *C. megacephalus* (*C. gulosus* series) is embedded within the *C. punctariolus* series.

The second large clade corresponds to Craugastoridae sensu Pyron & Wiens (2011) (Figure 18). Craugastoridae sensu Hedges *et al.* (2008a) and Heinicke *et al.* (2009), comprising *Haddadus* and the monophyletic *Craugastor*, is also monophyletic, but it is the sister of *Strabomantis* (albeit with weak support; likelihood ratio = 1.6), which renders Strabomantidae sensu Hedges *et al.* (2008a) paraphyletic. Within *Craugastor*, the unidentified species *Craugastor* sp. MVUP1863 (labeled as *Craugastor* sp. *'podi-noblei'* in GenBank) forms a trichotomy with the subgenus *Campbellius* and a clade composed of the monophyletic remainer (excluding C. sp. MVUP 1863) of the subgenus *Craugastor* and the subgenus *Hylactophryne*. The *C. bocourti* and *C. augusti* series of the subgenus *Hylactophryne* are monophyletic, whereas the *C. mexicanus* series of the subgenus *Craugastor* is polyphyletic with the two recovered groups within the series being far apart phylogenetically. Likewise, the *C. podiciferus* species series of *Craugastor* is paraphyletic, with *C. rhodopis* and *C. loki* forming the clade sister of part of the *C. mexicanus* series. Also, the *C. punctariolus* series is non-monophyletic with respect to the *C. gulosus* series because its member *C. megacephalus* is nested within the *C. punctariolus* series.

Hypodactylus is monophyletic and forms the sister taxon of a group composed of the monophyletic genera *Lynchius, Oreobates,* and *Phrynopus.* This inclusive group is, in turn, the sister of a group composed of Holoadeninae of Hedges *et al.* (2008a) (*Barycholos, Bryophryne, Holoaden, Noblella,* and *Psychrophrynella*), and *Yunganastes* + *Pristimantis* (Figures 19–20). Pristimantinae of Pyron & Wiens (2011) is rendered paraphyletic by position of Holoadeninae as sister to *Pristimantis* + *Yunganastes* (Figures 19–20).

Within *Hypodictyon*, neither of the recognized species series (*C. rubicundus* or *C. ridens*) are monophyletic under this assumption-set. Within the enormous subgenus *Pristimantis*, with the exception of the *P. chalceus* and *P. pardalis* species group, none of the previously recognized species groups are monophyletic (Figures 20–21).

Comparison of methods

The optimal tree-alignment + parsimony (TA + PA), similarity-alignment + parsimony (SA + PA), and similarity-alignment + maximum likelihood (SA + ML) results show a great deal of congruence. However, they also differ in a number of important points that shed light on the effects of using a static similarity-alignment, treating gaps as nucleotides of unknown identity, and assuming common mechanisms of nucleotide evolution under the maximum likelihood criterion.

As a heuristic to accelerate analyses, we calculated Goodman-Bremer (GB) support and resampling frequencies for TA + PA using the optimal tree-alignment matrix. As such, for both the TA and SA trees, the reported values are conditional on the assumed static alignments. That is, they reflect the degree to which the results are supported by those alignments, not by the data themselves. Given the direct relationship between the tree-alignment matrix and the optimal tree, we expected systematically higher GB support values for that matrix. However, we found that the maximum (122), mean (12.4), and median (7) GB values derived from the POY tree-alignment were lower than the maximum (169), mean (24.0), and median (19) values obtained from the MAFFT similarity-alignment. For example, the topology of the *Eleutherodactylus limbatus* group is identical in both parsimony analyses, but all GB values are greater in the SA + PA analysis. The difference applies to clades that are both relatively weakly supported (*e.g.*, *Euhyas*: GB = 5 in TA + PA; GB = 7 in SA + PA) and strongly supported (*e.g.*, *Lynchius*: GB = 57 in TA + PA; GB = 97 in SA + PA). Although some discrepancies might be due to the vagaries of tree searching, it is unlikely that this would generate such a large difference across so many clades. In contrast, jackknife percentages were consistently higher for the TA + PA dataset (mean = 92.6, median = 99) than the SA + PA dataset (mean = 62.5, median = 78).

The matrix representations of the tree-alignment and similarity-alignment differ greatly in number of aligned positions. Whereas the tree-tested optimal POY tree-alignment matrix comprises 23241 aligned positions, of which 9618 (41%) contain gaps, the optimal MAFFT similarity-alignment includes only 17233 aligned positions, of which only 3055 (18%) contain gaps. Whereas the optimal TA + PA solution entails 94413 steps, the minimum tree length for the similarity-alignment matrix is 105850 steps, meaning that the decrease in the number of characters containing gaps required an increase of 11437 evolutionary events to explain variation in DNA sequences—over 12% more than the optimal tree-alignment length.

Optimization of the maximum likelihood topology in POY using equal transformation costs and iterative pass optimization followed by static approximation gives a length of 94808 steps, 395 steps longer than the optimal tree-alignment trees. Similarly, optimization of the optimal tree-alignment topology in GARLI using the optimal 2-parameter partition scheme and GTR + G substitution model for the similarity-alignment returned a log likelihood score of -399496.1274, which is 865 times worse than the optimal maximum likelihood tree.

TABLE 3. Pairwise rooted SPR distances between (1) the maximum likelihood trees obtained from analysis of the MAFFT similarity-alignment using three different partition schemes and substitution models in GARLI, (2) a representative sample of the 205 most-parsimonious trees obtained from the analysis of the MAFFT similarity-alignment in TNT, and (3) a representative sample of the 536 most-parsimonious trees obtained from the tree-alignment analysis in POY and TNT.

	Tree	1	2	3	4	5	6	7	8	9	10	11	12	13
1	MAFFT + GARLI, 0 parts.	–												
2	MAFFT + GARLI, 2 parts. (optimal)	22	–											
3	MAFFT + GARLI, 18 parts.	24	19	–										
4	MAFFT + TNT (tree 0)	82	84	81	–									
5	MAFFT+ TNT (tree 50)	85	85	80	20	–								
6	MAFFT+ TNT (tree 100)	82	84	81	14	14	–							
7	MAFFT+ TNT (tree 200)	81	82	79	20	15	15	–						
8	POY + TNT (tree 50)	88	91	93	80	83	81	81	–					
9	POY + TNT (tree 100)	90	94	94	82	85	81	83	12	–				
10	POY + TNT (tree 200)	89	93	94	81	83	81	81	9	13	–			
11	POY + TNT (tree 300)	91	95	95	81	86	81	84	13	9	11	–		
12	POY + TNT (tree 400)	92	95	97	82	86	81	83	11	11	7	9	–	
13	POY + TNT (tree 500)	92	94	95	80	85	81	82	10	11	10	10	11	–

The rooted SPR distances between the maximum likelihood trees obtained under the three different partition schemes (19–24 moves) are approximately equal to the distances among the SA + PA trees (14–20) and slightly greater than the distances among the TA + PA trees (7–13) (Table 3). That is, the topological variation due to selection of partition schemes and substitution models in maximum likelihood is only slightly greater than the variation observed within sets of most parsimonious trees. The rooted SPR distances between the most parsimonious TA and SA trees was of 80–86 moves and between the maximum likelihood and most parsimonious SA trees was 79–85 moves (Table 3). In other words, the treatment of gaps as nucleotides of unknown identity and incorporation of model assumptions under the maximum likelihood criterion resulted in trees that are just as distant from the results of the parsimony analysis of the same matrix as they are from the tree-alignment results. Indeed, the rooted SPR distances between optimal trees in analyses that differed in both optimality criterion and alignment method were only slightly greater (91–94 moves).

Another way to examine the impact of alignment versus gap treatment and optimality criterion is to consider the specific clades that differ in the three analyses. Because the TA + PA and SA + PA analyses used the same optimality criterion, weights, and gap treatment, differences between their results are directly attributable to the different alignment methods (assuming the heuristic searches identified optimal solutions). Indeed, many of those differences also occur between the TA + PA and SA + ML results, which shows that those differences are due to the alignment and not the optimality criterion, model assumptions, or treating gaps as unknown nucleotides. For example, in the TA + PA results Hylidae, Orthobatrachia, Hemiphractidae, and Brachycephaloidea are all monophyletic; however, none of these groups is monophyletic in the SA + ML results, and only Orthobatrachia is monophyletic in the SA + PA results. In both the SA + PA and SA + ML results, the hemiphractid *Cryptobatrachus fuhrmanni* is nested within Brachycephaloidea as the sister of *Ceuthomantis smaragdinus,* although that clade is placed differently in the two analyses. Similarly, contrary to the results of the TA + PA analysis, both SA analyses grouped Brachycephalidae and Eleutherodactylidae as sister taxa, found *Hemiphractus* and the *Eleutherodactylus antillensis* group to be monophyletic, and placed *Hypodactylus elassodiscus* and *H. brunneus* as sister species. All three analyses agree on the monophyly of *Pelorius*; however, the TA + PA analysis placed *Pelorius* as the sister group of *Eleutherodactylus*, whereas both SA analyses placed *Pelorius* inside *Eleutherodactylus*. The SA results agreed in rejecting the monophyly of several more clades present in the TA + PA trees, including the subgenus *Craugastor*, the *C. mexicanus* series, the *C. podiciferus* series, the *E. richmondi* series, the *E. pezopetrus* group + *E. pinarensis* group clade, and the *E. toa* group + *E. cuneatus* group clade.

Results shared by the TA + PA and SA + PA analyses but not the SA + ML analysis show effects that cannot be attributed to the alignment but are instead due to the combined effects of optimality criterion, model assumptions, and gap treatment. Similarly, contrary to the SA + ML results, in the TA + PA and SA + PA trees the *Craugastor* cf. *longirostris* is placed inside *C. melanostictus* group and not as the sister of the entire *C. fitzingeri* series. Likewise, both parsimony analyses present identical topologies for the *Eleutherodactylus limbatus* group, with *E. cubanus* as sister of the remainder of the clade, *E. etheridgei* and *E. orientalis* as sister species, whereas in the maximum likelihood tree *E. etheridgei* is the sister of the remainder of the group with *E. cubanus* placed between that species and *E. orientalis*.

The most remarkable difference between the maximum likelihood and parsimony results involves the placement of *Eleutherodactylus dilatus*. The only data available for *E. dilatus* are approximately 1200 bp of c-myc, which has been sequenced for only two additional eleutherodactylids (*Adelophryne patamona* and *E. pantoni*) and very few terminals of closely related clades (*i.e.*, among brachycephalids, it is present only for *Brachycephalus ephippium*). Given the lack of variation in c-myc and the cladistic distance that separates the other species sequenced for this marker, the available evidence is clearly inadequate to decisively place *E. dilatus* in the tree. This ambiguity is correctly depicted in the TA + PA and SA + PA results, wherein *E. dilatus* behaves as a wildcard and causes large polytomies in the strict consensuses of both the similarity-alignment and tree-alignment analyses, and removal of this terminal from the set of most parsimonious trees increases resolution greatly. However, despite the lack of evidence, the maximum likelihood analysis decisively placed *E. dilatus* deep within *Eleutherodactylus* immediately outside *Syrrhophus* and *Euhyas* at a point approximately midway between *A. patamona* and *Eleutherodactylus* (*Euhyas*) *pantoni*. Although this placement is weakly supported (likelihood ratio = 2.7), it is highly consistent in the SA + ML results, being present in 81% of the bootstrap replicates.

Curiously, several clades present in both the TA + PA results and the SA + ML results were absent from the SA + PA results. For example, *Gastrotheca* and *Hypodactylus* are both monophyletic in the TA + PA and SA + ML trees but not the SA + PA trees. Likewise, in the TA + PA and SA + ML results *Psychophrynella* is the sister of (*Holoaden* (*Bryophryne* (*Noblella*+*Barycholos*))) and *Strabomantis* is the sister of *Haddadus* + *Craugastor* (*i.e.*, Craugastoridae sensu Hedges *et al.*, 2008a), whereas in the SA+PA results *Psychrophrynella* is the sister of *Strabomantis* in a clade with *Lynchius*, *Oreobates* and *Phrynopus*. Similarly, if *E. dilatus* is excluded (see below), *Syrrhophus* is monophyletic in both the TA + PA and SA + ML trees but paraphyletic in the SA + PA trees. In these examples, alignment effects were overcome by treating gaps as unknown nucleotides, applying model assumptions, and choosing the maximum likelihood tree.

Discussion

Although we can never know with complete certainty the objective truth of any phylogenetic tree, comparison of the results of the tree-alignment + parsimony (TA + PA), similarity-alignment + parsimony (SA + PA), and similarity-alignment + maximum likelihood (SA + ML) analyses provides insights into the effects that choice of alignment method and optimality criterion can have on a large, heterogeneous molecular dataset.

We found that choice of alignment method was just as important as choice of optimality criterion for choosing among trees. The distances between the optimal topologies for the similarity-alignment and tree-alignment using the same optimality criterion (parsimony) were approximately equal to the distances between the optimal topologies using the same similarity-alignment and different optimality criteria (parsimony and maximum likelihood). Further, these topologies entailed taxonomically relevant differences attributable to the alignment method and not the treatment of gaps, inclusion of model assumptions, or choice of optimality criterion. For example, *Cryptobatrachus fuhrmanni* was placed within terraranas as the sister of *Ceuthomantis smaragdinus* in both the parsimony and maximum likelihood analyses of the similarity-alignment, whereas it was placed with other hemiphractids outside Brachycephaloidea in the TA + PA analysis, and Brachycephalidae was the sister of Eleutherodactylidae in both the parsimony and maximum likelihood analyses of the similarity-alignment but sister to Ceuthomantidae, Craugastoridae, and Strabomantidae (sensu Hedges *et al.*, 2008a) in the TA + PA analysis.

Although numerous topological differences attributable to choice of optimality criterion occurred, the most remarkable difference relates to the way parsimony and maximum likelihood treat missing data, as evidenced by the different effect of the wildcard *Eleutherodactylus dilatus* in the results of the parsimony and maximum likelihood analyses. Most discussion of differences between model-based methods and parsimony focus on their different interpretations of observations (*e.g.*, Siddall & Kluge, 1999), but in the present example there are no observations to interpret. Both methods treat missing data as ambiguities (*i.e.*, character-states of unknown identity). However, insofar as parsimony is evidentially conservative, it treats ambiguous data as such, meaning that the empirical concern is not really about the effect of missing data *per se* (missing data have no effect because they do not favor any topology over any other), but rather the decisiveness of the data that are present and the fact that wildcards can obscure otherwise decisive data (Grant & Kluge, 2003). In contrast, the evidential ambivalence of maximum likelihood allows it to conjure up an apparently supported position out of nothing.

Although our results provide a clear empirical example of the different effects of missing data in parsimony and maximum likelihood, they are not unexpected; Lemmon *et al.* (2009), Simmons (2012), Simmons & Norton (2013), and Simmons & Goloboff (2013) thoroughly demonstrated through simulations and manipulations of empirical data that non-randomly distributed missing data can result in spurious resolutions and clade frequencies, especially in model-based analyses but also in restricted parsimony searches. It should be noted that we were able to detect this behavior in in our dataset because the extent and pattern of missing data were so obvious. Given the extent of missing data throughout this dataset, which is compounded by the treatment of gaps as nucleotides of unknown identity in the maximum likelihood analysis, it is likely that other differences between the parsimony and maximum likelihood solutions share the same cause. For example, the *Craugastor laticeps* series and the species of *Hylactophryne* collapse into identical polytomies in both parsimony analyses but are fully resolved with bootstrap values as great as 100% in the maximum likelihood analysis. Although we could not identify any wildcards affecting these relationships, we cannot rule out a more general missing data effect that involves gaps and/or multiple species of these clades. Nevertheless, the extensive agreement between the maximum likelihood and parsimony results suggests that the missing data effects in the maximum likelihood analysis are limited to certain sectors of the tree and/or relate more to support values and branch lengths than selection of the optimal tree.

In this study we are most concerned with the topological implications of the different methods, but our results also have important consequences for understanding molecular evolution. The optimal tree alignment indicates that insertions and deletions occurred in the evolution of twice as many aligned positions as implied by the optimal similarity-alignment, a finding that supports Löytynoja & Goldman's (2008, p. 1635) prediction that "alignment methods specifically designed for evolutionary analyses will give a very different picture of the mechanisms of sequence evolution and show sequence turnover through short insertions and deletions as a more frequent and important phenomenon."

Below, we outline our proposed taxonomy based on the TA + PA topology, which we consider to be optimal for the reasons discussed above. A detailed taxonomy is provided in Appendix 2, and the proposed family- and genus-group taxonomy is summarized in Figure 22. Also, we briefly discuss how the results of our analyses bear on previously recognized taxa.

The relationships and taxonomy of Brachycephaloidea

In supporting the monophyly of Brachycephaloidea, our results corroborated previous molecular phylogenetic studies of less evidence and similar or different sets of assumptions (Darst & Cannatella, 2004; Frost *et al.* 2006; Heinicke *et al.*, 2007; Hedges *et al.* 2008a; Padial *et al.* 2009; Pyron & Wiens, 2011). Although molecular data provide strong evidence of the monophyly of terraranas, almost the same group was recognized for decades on the basis of phenotypic character-states alone (Lynch, 1971; Heyer, 1975; Ardila-Robayo, 1979), including even the supposedly enigmatic *Brachycephalus* (*e.g.,* Izecksohn, 1988). Also, detailed morphological analysis in light of current phylogenetic hypotheses based on molecular data is leading to the discovery of novel synapomorphies for the group. Thus, in addition to direct development (Lutz, 1954, Gallardo, 1965; Lynch, 1971), T-shaped terminal phalanges (Lynch, 1971; Heinicke *et al.*, 2009), and the presence of a single, bicuspid keratinized egg tooth (Sampson, 1904; Noble, 1926; Pombal, 1999), several new synapomorphies in the urogenital and vascular systems were proposed recently by Taboada *et al.* (2013). These include, (i) fusion of Wolffian ducts (ii) in an anterior position, resulting in a common opening in the cloaca, (iii) presence of a posterior dorsolumbar vein that merges with Jacobson's vein near the junction with the common iliac vein at posterior end of the kidney, (iv) absence of the medial dorsolumbar vein, (v) origin of the posterior caval vein in the anterior 1/3 the kidneys, (vi) posterior origin of the dorsolumbar arteries, and (vii) presence of a pelvic lymphatic septum associated with the discoidal fold, as well as several synapomorphies for clades within Brachycephaloidea. We predict that many more morphological synapomorphies will be identified, especially in relation to the distinctive form of direct development in these frogs.

Incertae sedis

We consider the monotypic genera *Atopophrynus* and *Geobatrachus* to be Brachycephaloidea, *incertae sedis*. These genera have not been included in any molecular phylogeny, and available morphological evidence does not allow unambiguous placement in any subsidiary clade. The Colombian *Atopophrynus syntomopus* was described as a new genus and species of Dendrobatidae by Lynch and Ruíz-Carranza (1982). Myers & Ford (1986) failed to discover any dendrobatid synapomorphies and found many similarities with bufonids, although they ultimately proposed a sister group relationship with *Geobatrachus walkeri*.

The relationship between *Atopophrynus* and *Geobatrachus* was hypothesized on the basis of the shared presence of a pair of long, slender anterior processes on each hyale and the "concealment" of the first toe. The homology of the "concealment" of the first toe is questionable. In *A. syntomopus*, the first toe presents a complete phalangeal formula (2-2-3-4-3) and its reduction in size is achieved through "miniaturization of the metatarsal and two phalanges (rather than to shortening and loss)" (Myers & Ford, 1986, p. 13), whereas in *G. walkeri* it is achieved through shortening of the metatarsal and penultimate phalanx and loss of the ultimate phalanx (phalangeal formula = 1-2-3-4-3). As such, the only available synapomorphy between these two taxa is the condition of the hyale.

Despite over 30 years of taxonomic stability, the phylogenetic affinities of *Geobatrachus* remain uncertain. Like *Atopophrynus syntomopus*, *G. walkeri* was described as a new genus and species of Dendrobatidae (Ruthven, 1915). It was later thought to be related to *Rhinoderma* and *Sminthillus* by Noble (1931), and Griffiths (1959) placed it in his Rhinodermatinae, then a subfamily of Leptodactylidae. Lynch (1971, p. 69) excluded it from Leptodactylidae based on a personal communication from C. F. Walker, who considered it to be part of Microhylidae. Ardila-Robayo (1979), in a meticulous analysis of Eleutherodactylini, rejected a relationship of *Geobatrachus* with microhylids and provided phenotypic evidence for its placement in Eleutherodactylini, and moved it back into Leptodactylidae. No subsequent study has compared *Geobatrachus* with other taxa now included in Brachycephaloidea. Hedges *et al.* (2008a) placed *Geobatrachus* and *Atopophrynus* in their Strabomantinae because they present T-shaped terminal phalanges, expanded terminal digits, and digital disks with circumferential grooves. Those character-states are also present in most other families of brachycephaloids and are probably symplesiomorphic. Our examination of the holotype and paratype of *G. walkeri* suggests that it could be allied to *Adelophryne* and *Phyzelaphryne*, with which it shares the presence of expanded terminal discs with incomplete circumferential grooves (only laterally evident) and pointed tips (see Ardila-Robayo, 1979, p. 406). However, the hyalia of Phyzelaphryninae have not been described and the digits of *Atopophrynus* lack the pointed tips and incomplete grooves. As such, given the available evidence, we can only conclude that *Atopophrynus* and *Geobatrachus* might be sister taxa and that their affinities are unclear.

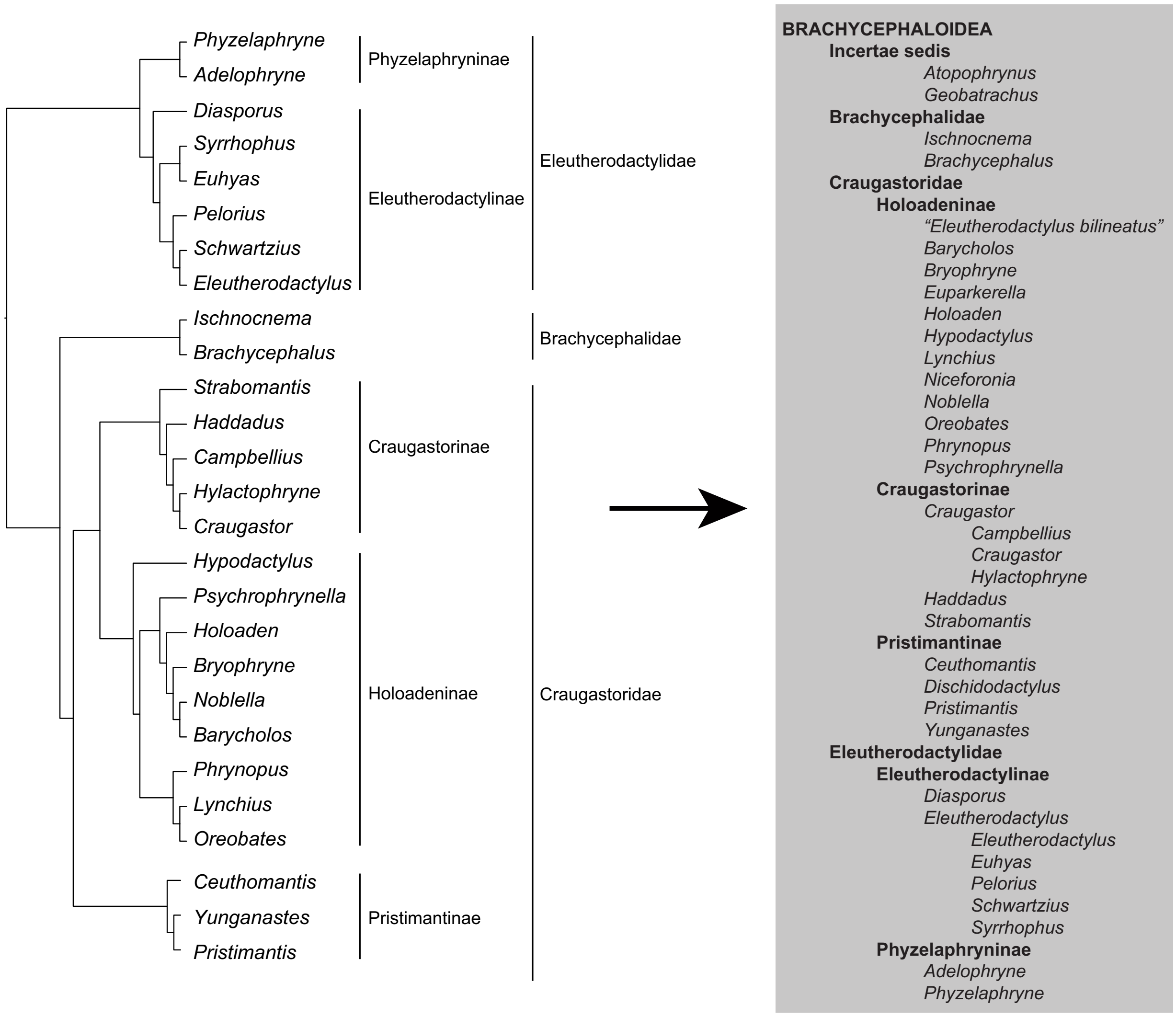

FIGURE 22. Schematic representation of the new family- and genus-level taxonomy of Brachycephaloidea presented in this study as derived from the results of tree-alignment + parsimony phylogenetic analyses of nucleotide sequences. The placement and affinities of *Dischidodactylus* and *Niceforonia* are based on morphological synapomorphies (see text).

Brachycephalidae

This taxon includes the sister taxa *Brachycephalus* and *Ischnocnema*, a relationship first discovered by Heinicke *et al.* (2007), who placed most southeastern Brazilian taxa then referred to "*Eleutherodactylus*" (Frost *et al.*, 2006) in a redelimited *Ischnocnema*. Previously, Caramaschi & Canedo (2006) had restricted *Ischnocnema* to *Ischnocnema verrucosa*, and placed it in the synonymy of *Eleutherodactylus*. A new test of the sister relationship of *Ischnocnema* and *Brachycephalus* was recently provided by Canedo & Haddad (2012), who found the taxa to be reciprocally monophyletic in both maximum likelihood and Bayesian analyses. Interestingly, their parsimony analysis of a similarity alignment placed *Brachycephalus* as the sister of *Haddadus binotatus*, another taxon from southeastern Brazil. Such a relationship had never been proposed, and although it is not corroborated in our analyses, it surely deserves future attention, particularly with regard to the effects of alignment and optimality criterion.

Brachycephalus.—This genus of small, diurnal frogs that usually are brightly colored and contain tetrodotoxin (Pires *et al.* 2005) is endemic to southeastern Brazil. Its unique pectoral girdle has long been recognized as a synapomorphy of the genus (Izecksohn, 1971; Pombal & Gasparini, 2006) and was used to synonymize *Psyllophryne* (*i.e.*, *P. didactyla* and *P. hermogenesi*) with *Brachycephalus* by Kaplan (2002), a synonymy subsequently validated by analyses of DNA sequences that found the two species to be nested among other species of *Brachycephalus* (Clemente-Carvalho *et al.*, 2011; current results). Frost *et al.* (2006), Heinicke *et al.* (2007), Hedges *et al.* (2008a), and Pyron & Wiens (2011) only included *B. ephippium* in their analyses, and Canedo & Haddad (2012) added *B.* cf. *didactylus*. Clemente-Carvalho *et al.* (2011) provided the first extensive molecular phylogenetic analysis of the genus by including 14 of the 18 currently recognized species (Pombal & Izecksohn, 2011). Inadequate outgroup sampling (the tree was rooted on a single terminal of *Ischnocnema*) prevented the monophyly of *Brachycephalus*, the position of *Psyllophryne* within Brachycephaloidea, or the sister relationships with *Ischnocnema* from being tested in that study. Nevertheless, our results agree with Clemente-Carvalho *et al.*'s (2011) Bayesian analysis of the concatenated nuclear and mitochondrial data in recovering two major sister clades, a southern clade formed by locally endemic species restricted to the high and humid Atlantic Forest of Paraná (*B. brunneus*, *B. ferruginus*, *B. izecksohni*, *B. pernix*, and *B. pombali*) and the northern clade, allopatric to the first, distributed from farther north in Paraná to Espírito Santo (*B. alipioi*, *B. didactylus*, *B. ephippium*, *B. garbeanus*, *B. hermogenesi*, *B. nodoterga*, *B. pitanga*, *B. toby*, and *B. vertebralis*), with the two species of the former *Psyllophryne* placed separately in the second clade.

Ischnocnema.—This genus is distributed within the Atlantic Forest of south, southeastern, and northeastern Brazil and Misiones, Argentina (Canedo & Haddad, 2012; Frost, 2014). The monophyly of the genus was hypothesized by Heinicke *et al.* (2007) and Hedges *et al.* (2008a), who analyzed 5 of the 33 species. A more complete test of generic monophyly was recently provided by Canedo & Haddad (2012) in a study that was published while the present manuscript was being written, which unfortunately precluded the use of their data in our analyses. Nevertheless, their taxon sampling of other brachycephalids was large enough (214 species) to provide a strong test of the monophyly of *Ischnocnema*. Their major finding was a polyphyletic *Ischnocnema* sensu Hedges *et al.* (2008a) with three named species (*I. paulodutrai*, *I. ramagii*, and *I. vinhai*) and two unnamed species recovered as part of the *Pristimantis conspicillatus* species group. Also, *Ischnocnema bilineata* was found to be the sister of a clade composed of the genera *Noblella* and *Barycholos* in Holoadeninae. Accordingly, Canedo & Haddad (2012) placed three nominal species of *Ischnocnema* in *Pristimantis*, but left "*Eleutherodactylus*" *bilineatus* Bokermann, 1975 "1974" as *incertae sedis* within Holoadeninae[6] (of Craugastoridae, below). For the remaining species of *Ischnocnema*, they recognized four monophyletic species series and left two species unassigned to any group, although five species were only tentatively assigned to groups based on their morphology. We follow their assignment of species to species series (see Appendix 2).

Craugastoridae

This taxon is equivalent to Craugastoridae of Pyron & Wiens (2011) except for the inclusion of *Ceuthomantis* (see below). The family Craugastoridae was originally named by Hedges *et al.* (2008a) to accommodate a primarily Middle American clade that included most species traditionally assigned to the subgenus *Craugastor*—first recognized as a clade on the basis of molecular evidence by Crawford & Smith (2005) and Frost *et al.* (2006)—plus an unexpected companion from the Atlantic Forest of eastern Brazil as its sister taxon, "*Eleutherodactylus*" *binotatus*, which was placed by Hedges *et al.* (2008a) in their new genus *Haddadus* together with *H. plicifer*. More recently, Pyron & Wiens (2011) found *Strabomantis* to be the sister of *Haddadus* and *Craugastor*. Because *Strabomantis* is the type genus of Strabomantidae (Hedges *et al.* 2008a), in order to rectify the paraphyly of Craugastoridae, Strabomantidae must be considered a junior synonym of Craugastoridae. Our analyses strongly corroborate this finding, with the inclusive Craugastoridae as sister of Brachycephalidae in the TA + PA results. Craugastoridae is composed of three major clades that we recognize as subfamilies Craugastorinae, Holoadeninae, and Pristimantinae (Figure 22).

Craugastorinae

Pyron & Wiens (2011) proposed Craugastorinae for *Haddadus* and *Craugastor* and placed their sister genus *Strabomantis* in a monotypic Strabomantinae (originally proposed to accommodate nearly 500 species in 10 genera; Hedges *et al.*, 2008a). Although we recover the same relationships among the three genera found by Pyron & Wiens (2011), we reformulate Craugastorinae to include *Strabomantis* and treat the otherwise monotypic

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[6] We presume that those authors will soon provide a solution for this taxonomic problem.

subfamily Strabomantinae as a junior synonym of Craugastorinae. Only this study and that by Pyron & Wiens (2011), the two studies of brachycephaloids with the largest taxon and character sampling, have recovered the monophyly of Craugastorinae. Hedges *et al.* (2008a) and Canedo & Haddad (2012) found *Strabomantis* to be associated with taxa now referred to Holoadeninae.

The relationship between *Craugastor* and *Strabomantis* should come as no surprise after a long history of putative relationship among species now placed in these genera. This Central American clade of terraranas with some South American components has long been recognized on the basis of morphology. Lynch's (1971, 1975a) Beta division of Eleutherodactylini (characterized by the frontoparietals and proötic not being fused and the pterygoids overlapping the parasphenoid alae) approximated what is now considered Craugastorinae. Also, Lynch (1986a) identified a condition of the *m. levator mandibulae externus* (muscle undivided, mandibular ramus of trigeminal nerve passing medial to muscle, the so-called "E" condition; Haas, 2001) that turned out to be a synapomorphy for *Craugastor* (Crawford & Smith 2005; Heinicke *et al.*, 2007; Hedges *et al.*, 2008a; this study). Savage (1987) also suggested previously that the ca. 70 Central American species of the subgenus *Craugastor* lack the state of the *m. depressor mandibulae* present in all other subgenera of (then) *Eleutherodactylus*. Although Lynch (1993) disputed in some detail that claim, the group is maintained on the basis of molecular evidence, so it is worth revisiting the character-states proposed by Savage (1987) as they may also be synapomorphic.

Nevertheless, the subgenus *Craugastor* as it was then conceived is not identical to the current delimitation, containing at various times species now referred to *Strabomantis.* In fact, *Strabomantis* roughly coincides with what Lynch (1976a) considered the *Eleutherodactylus biporcatus* group, which was transferred to *Craugastor* by Crawford & Smith (2005). Several species of the broad-headed "*Eleutherodactylus*" in the *C. bufoniformis* and *C. biporcatus* species groups of the subgenus *Craugastor* were transferred to *Limnophys* by Heinicke *et al.* (2007) and later to *Strabomantis*, while others remained within *Craugastor* (Hedges *et al.*, 2008a). Interestingly, Heinicke *et al.* (2007, 2009) and Hedges *et al.* (2008a) discarded the possibility of a close relationship among the species they transferred to *Strabomantis* and *Craugastor* and, thus, rejected previous morphological evidence of evolutionary propinquity. In addition, the only derived morphological condition suggested by Hedges *et al.* (2008a) for Craugastoridae was the first finger longer than second, a condition that is shared by *Craugastor*, *Haddadus*, and *Strabomantis*. Furthermore, the "E" condition of the m. levator mandibulae has so far been only reported for *Craugastor* and *Strabomantis*. Within *Strabomantis*, Lynch (1986a, 1993) recorded the "E" condition in *S. anatipes*, *S. anomalus*, *S. biporcatus*, *S. bufoniformis*, *S. ingeri*, *S. necerus*, *S. ruizi*, *S. sernai*, *S. sulcatus*, and *S. zygodactylus*, while he recorded the S condition for *S. cerastes* and *S. cornutus*—although Lynch (1997) synonymized under *S. cerastes* a species (*S. sernai*) that he diagnosed with the "E" condition (Lynch, 1986a). Only the "S" condition (single muscle, mandibular ramus of trigeminal nerve passing lateral to muscle) has been reported for *Haddadus binotatus* (by Lynch, 1986a) as well as for *H. aramunha* (Cassimiro *et al.,* 2008). Because the "E" condition has proved difficult to assess in some cases and some variants have been discovered (see comments on *Yunganastes* below), a reevaluation of the condition in the Craugastorinae is needed.

The dissonant note within Craugastorinae is *Haddadus*, a taxon historically considered to be related to what is now *Ischnocnema*, although that concept was based solely on biogeographic grounds and not synapomorphy. Nevertheless, *Haddadus* also presents an external morphology barely distinguishable from those of *Strabomantis* or broad-headed *Craugastor*. In fact, *Strabomantis aramunha* (Cassimiro *et al.*, 2008) from southeastern Brazil was placed in *Strabomantis* mainly on the basis of the presence of cranial crests, but is now placed in *Haddadus* on the basis of molecular evidence (Amaro *et al.*, 2013).

Craugastor.—The 60 *Craugastor* species we analyzed form a clade divided into the monophyletic subgenera *Campbellius*, *Craugastor*, and *Hylactophryne*[7]. The internal relationships are largely congruent with those of Hedges *et al.* (2008a), who rearranged species diversity in putatively monophyletic species series. A detailed analysis of the correspondences between the groups and those of Savage (1987, 2002), Lynch & Duellman (1997), and Lynch (2000) was provided by Hedges *et al.* (2008a).

The strict consensus of optimal TA + PA trees collapses all structure within *Hylactophryne*. As such, we do not recognize any species series within this subgenus. Within the subgenus *Craugastor*, we recognize the *C. mexicanus* and *C. podiciferus* series. We found *C. megacephalus* (previously referred to the *C. gulosus* series) to be nested

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[7] We expect that *Campbellius, Craugastor,* and *Hylactophryne* will ultimately be considered genera, but because we cannot diagnose them morphologically, except by enumeration, we refrain from doing so here.

within the *C. punctariolus* series, making the *C. punctariolus* series paraphyletic and, therefore, merge both series into an expanded *C. punctariolus* series. The paraphyly of the *C. punctariolus* series was anticipated by Hedges *et al.* (2008a), who noted that Crawford & Smith (2005) had found *C. megacephalus* as the sister of a species of the *C. punctariolus* series, namely *C. ranoides*, and warned that the distinction between these two series might not hold.

We found *Campbellius* to be the monophyletic sister group of all other species of the genus *Craugastor*. Lynch (2000) hypothesized that *C. greggi* and *C. daryi* are sister species based on the shared fusion of the sacrum and the last presacral vertebra, but Hedges *et al.* (2008a) placed *C. greggi* in the *Craugastor* (*Craugastor*) *laticeps* species series. *Craugastor* (*Campbellius*) *greggi* has not yet been included in any molecular phylogenetic analysis.

Holoadeninae

This taxon includes all genera placed in Holoadeninae by Hedges *et al.* (2008a) (*Barycholos*, *Bryophryne*, *Euparkerella*, *Holoaden*, *Noblella*, and *Psychrophrynella*), plus a clade (*Lynchius*, *Oreobates*, and *Phrynopus*) placed in Strabomantinae by Hedges *et al.* (2008a) and Pristimantinae by Pyron & Wiens (2011), with *Hypodactylus* as sister of all other genera. By including *Hypodactylus*, *Lynchius*, *Oreobates*, and *Phrynopus* in this subfamily, we rectify the non-monophyly of Pristimantinae of Pyron & Wiens (2011) and alter the *incertae sedis* status of *Hypodactylus*. DNA sequences for *Niceforonia* are unavailable. However, Hedges *et al.* (2008a) assigned *Niceforonia* to Strabomantinae on the basis of a synapomorphic character-state (knobbed rather than T-shaped terminal phalanges) that unites it to the *Lynchius*, *Oreobates*, and *Phrynopus* clade, so we also refer *Niceforonia* to Holoadeninae.

Lehr *et al.*'s (2005) maximum likelihood analyses of molecular data first suggested the existence of this inclusive group by recovering a clade containing *Hypodactylus*, *Phrynopus*, *Psychrophrynella*, and *Noblella*. More recently, Canedo & Haddad (2012) found *Euparkerella brasiliensis* to be the sister of *Holoaden* and "*Eleutherodactylus bilineatus*" to be the sister of the clade formed by *Noblella* and *Barycholos* (and, therefore, part of our Holoadeninae). Until recently, "*Eleutherodactylus bilineatus"* was considered a taxon of uncertain affinities (Lynch and Myers 1983; Lynch & Duellman, 1997) and was tentatively placed in *Ischnocnema* by Heinicke *et al.* (2007). Unfortunately, sequences of "*E. bilineatus*" and *Euparkerella* were not available when we undertook the analyses for the present study.

Although no morphological synapomorphies are known to delimit this morphologically diverse group, several of the relationships recovered by molecular evidence within this clade were recognized in early morphological studies. In content, Holoadeninae roughly approximates *Phrynopus* of Lynch (1975), a genus that, besides *Phrynopus sensu stricto*, included species now placed in the genera *Bryophryne*, *Hypodactylus*, *Lynchius, Niceforonia*, *Noblella*, *Oreobates*, *Psychrophrynella*, *Phrynopus*, and *Pristimantis*. Lynch (1971) considered *Euparkerella* to be related to *Holoaden* because they both lack the alary process of the hyoid plate, a relationship later recovered by Ardila-Robayo (1979) and more recently by Canedo & Haddad (2012). Lynch (1973) also suggested that *Leptodactylus mantipus* Boulenger (now *Hypodactylus mantipus*) should be included in *Barycholos* because of the shared presence of a posteriorly bifurcate sternal style. Nevertheless, Heyer (1975) rejected that view based on his morphological observations that suggested that another *Hypodactylus* (*H. nigrovittatus*) and *Barycholos pulcher* were sister taxa. *Hypodactylus nigrovittatus* has yet to be included in a molecular phylogenetic study, and a relationship with *B. pulcher* is still likely. Lynch (1976b) named two species of *Euparkerella*, for which Heyer (1980) later erected the genus *Phyllonastes*, subsequently synonymized by De la Riva *et al.* (2008) with *Noblella*. Lynch (1986b) considered *Phrynopus bagrecito* (now in *Psychrophrynella*) to be closely related to *Phyllonastes heyeri* (now in *Noblella*).

A remarkable characteristic of this clade is the recurrent connection of taxa found in the Atlantic Forest in southeastern Brazil and in the Andes, as suggested by the relationships within *Oreobates* (Andes, Amazonia, and southeastern Brazil) and the clade composed of *Holoaden* (Ecuador and southeastern Brazil), *Euparkerella* (southeastern Brazil), *Bryophryne* (Andes), "*Eleutherodactylus" bilineatus* (southeastern Brazil), *Noblella* (Andes), and *Barycholos* (southeastern Brazil).

Pristimantinae

We apply the name Pristimantinae to the clade composed of the genera *Ceuthomantis*, *Pristimantis*, and *Yunganastes*, and we also include *Dischidodactylus* on the basis of a synapomorphy shared with *Ceuthomantis* (see below). *Ceuthomantis smaragdinus*, the type species of Ceuthomantidae, is the sister taxon of Pristimantinae sensu Pyron & Wiens (2011), a *nomen nudum* validated by Ohler & Dubois (2012). Hedges *et al.* (2008a) provided the first evidence for the position of *Ceuthomantis*, labeled as " Unknown anuran sp." in their analyses. The terminal they analyzed was first identified as a species of *Pristimantis* in the Royal Ontario Museum catalog of the voucher specimen; however, Hedges *et al.*'s (2008a) molecular analysis instead found it to be the sister of all other terraranas or nested within the outgroups, as sister of a clade including *Cryptobatrachus fuhrmanni*, *Pseudis*, *Hyla*, *Litoria*, *Agalychnis*, *Odontophrynus*, *Dendrobates*, *Rhinoderma*, *Melanophryniscus*, *Bufo*, *Leptodactylus*, *Centrolene*, *Ceratophrys*, and *Telmatobius*.

In order to further evaluate the striking position of this "Unknown anuran sp.", Heinicke *et al.* (2009) increased gene sampling (10,739 bp of 17 nuDNA and mtDNA genes) and selected a subset of terraranas (12 genera and four specimens of the " Unknown anuran sp." from the same locality) plus a large array of neobatrachian outgroups, with the goal of minimizing missing data and yet having good representation of both outgroup and ingroup taxa. Their analyses "...revealed that these specimens are not only distinct from Strabomantidae [they were not *Pristimantis*] but represent an evolutionary lineage so distant that its closest relative is the clade containing all terraranas (*i.e.*, 4 families and ~900 species)." (p. 2). According to their results, and to be consistent with their previous partition of terraranas into four families (Hedges *et al.*, 2008a), the "Unknown anuran sp." was named as a new genus and species (*Ceuthomantis smaragdinus*) placed in a new family (Ceuthomantidae) within a now more inclusive clade of terraranas. Two other species, *Eleutherodactylus aracamuni* Barrio-Amorós & Molina, 2006, and *E. cavernibardus* Myers & Donnelly, 1997, both from the tepuis of the Guianan Shield, were transferred from *Pristimantis* to the new genus and family on the basis of morphological similarity, and a fourth species, *Ceuthomantis duellmani* Barrio-Amorós, 2010, was named subsequently. The placement of these frogs as forming the sister of all other terraranas—and, consequently, the justification for their recognition as a new family—was supported under both model-based (maximum likelihood and Bayesian) and parsimony analyses.

Nevertheless, Heinicke *et al.*'s (2009, p. 18) observation that "for most genes, the new family is recovered either as the closest relative of Terrarana or embedded in Terrarana" led us to suspect that their analyses might have overlooked a more optimal solution and, thus, that their own dataset might provide evidence for the placement of *Ceuthomantis* imbedded within brachycephaloids. Further, although Heinicke *et al.*'s (2009) maximum likelihood and Bayesian analyses provided high sampling frequencies for the sister relationship of *Ceuthomantis* with respect to all other brachycephaloids, the parsimony bootstrap frequencies indicated that in 28% of the pseudoreplicate analysis *Ceuthomantis* was not found as sister to other terraranas (bootstrap 72%) and in 57% the group containing all other terraranas was not monophyletic (bootstrap 43%). Therefore, we reanalyzed their 17-gene similarity-alignment under both maximum likelihood and parsimony using the same analytical assumptions (models and weights, search strategy, gap treatment, etc.) as Heinicke *et al.* (2009).

Our maximum likelihood analysis of Heinicke *et al.*'s (2009) alignment in GARLI resulted in an optimal tree (log likelihood = -121122.778) that agrees with them in placing *Ceuthomantis* as the sister of all other terraranas (Figure 23). However, our parsimony reanalyses revealed significant inconsistencies. First, parsimony analysis of Heinicke *et al.'s* (2009) dataset in MEGA 4 (Tamura *et al.* 2007), the same software they used, resulted in a tree that was 49 steps shorter (24468 steps) than the one they reported (24517[8]), and an even more optimal tree (24447 steps, 70 steps shorter than their optimal tree) was quickly found in TNT using driven searches under default parameters. The most parsimonious trees we found using both MEGA 4 and TNT strongly reject the placement of *Ceuthomantis* as the sister of all other terraranas, placing it deep within Brachycephaloidea as sister to *Ischnocnema*. Thus, the apparent robustness of the evidence for the placement of *Ceuthomantis* and recognition of a new family to variation across methods/assumptions was due to having presented a grossly suboptimal parsimony tree. The sensitivity of the placement of *Ceuthomantis* to variation of assumptions is also evident in of our analyses of a greatly expanded dataset, which suggests that not only optimality criteria (maximum likelihood and parsimony) but also taxon sampling and alignment method have considerable influence on the inferred position of *Ceuthomantis*. These noteworthy results should constitute the focus of future tests of the relationships among major taxa of Brachycephaloidea.

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[8] Heinicke *et al.* (2009) did not provide the length of the most parsimonious tree they reported, so we calculated its length using TNT.

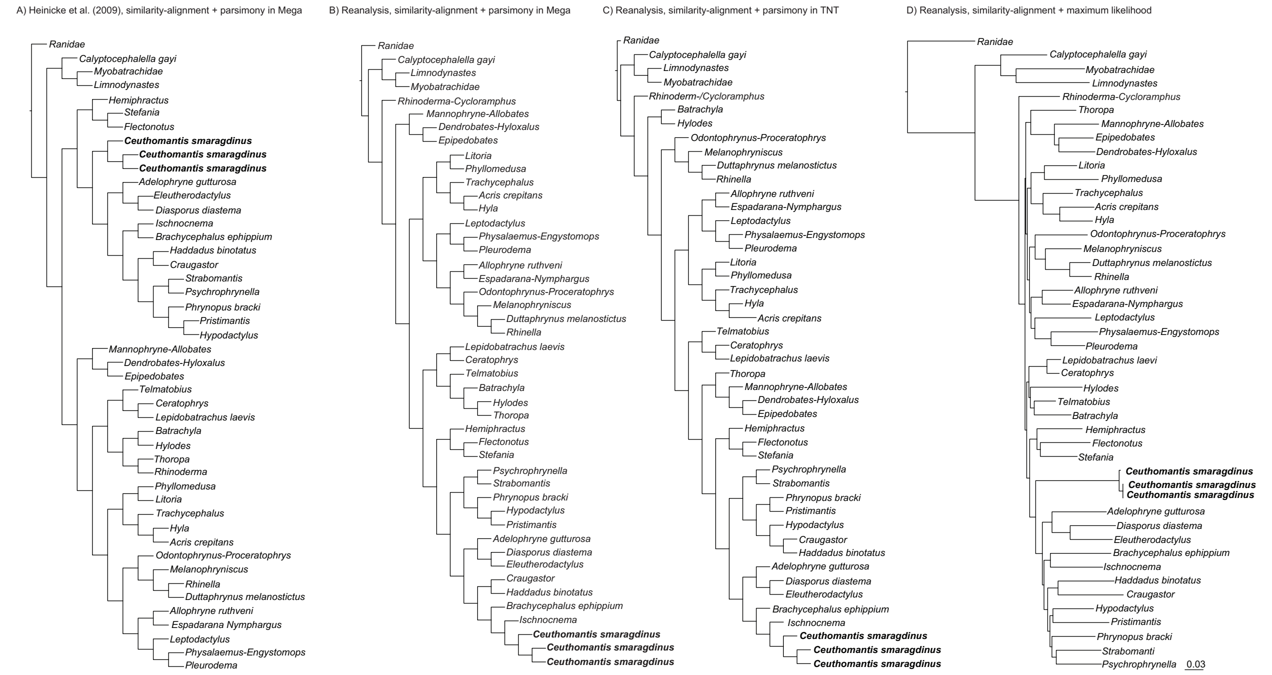

FIGURE 23. Topologies resulting from parsimony and maximum likelihood reanalyses of the 17-gene similarity-alignment of Heinicke *et al.* (2009). (A) The most parsimonious tree (length = 24517) reported by Heinicke *et al.* (2009) in which *Ceuthomantis* is sister to all other terraranas. (B) A shorter tree (length = 24468) found using the same software and parameters as Heinicke *et al.* (2009) showing *Ceuthomantis* to be deeply nested among terraranas as sister to *Ischnocnema*. (C) The most parsimonious tree found using TNT (length = 24447), which continues to show *Ceuthomantis* in the same position deep inside Brachycephaloidea. (D) The maximum likelihood tree found using GARLI (log likelihood = -121122.778), which fully agrees with the maximum likelihood results of Heinicke *et al.* (2009).

The morphological characters Heinicke *et al.* (2009) provided do not constitute compeling evidence for the placement of *Ceuthomantis* as the sister group of all other brachycephaloids either. Despite the "striking" differences reported by Heinicke *et al.* (2009, p.17), and in remarkable agreement with the results of out TA + PA analysis, *C. smaragdinus* was first identified as part of *Pristimantis* based on external morphology, and the two species they referred to Ceuthomantidae based on morphological reseblance (*C. aracamuni* and *C. cavernibardus*) were described as *Eleutherodactylus* (Myers & Donnelly, 1997; Barrio-Amorós & Molina, 2006) and later transferred to *Pristimantis* by Heinicke *et al.* (2007). A close look at the putatively synapomorphic characters used to diagnose the family Ceuthomantidae and the genus *Ceuthomantis* reveals the inconclusiveness of morphological evidence. The family was diagnosed as follows (p. 6):

> A member of Terrarana (Hedges *et al.* 2008) based on direct development of terrestrial eggs (inferred [based only on egg size]), T-shaped terminal phalanges, “S” condition of adductor musculature as defined by Lynch (1986a), and its lacking intercalary elements. It differs from other families in that group in having paired dorsal gland-like protrusions of unknown function in the post-temporal, and sacral regions. Although these protrusions appear to have contained lipids, they are not true glands. Body glands, similar in external appearance to these structures, are present in some species of *Eleutherodactylus* (Eleutherodactylidae) but they are located in the inguinal and flank regions. Also, computed tomography scans of the holotype show that the neurocranium is extraordinarily poorly ossified, and the neopalatine is unusually massive.

Direct development, T-shaped terminal phalanges, “S” condition of jaw adductor musculature, and lack of intercalary elements are widespread or universal among terraranas and were listed to place *Ceuthomantis* within the clade. Similarly, gland-like protrusions occur on the dorsum of many species in practically all clades of brachycephaloids; they are commonly termed warts or tubercles, and sometimes form dorsolateral rows grouped in the occipital, postympanic, sacral, and/or flank regions. Unfortunately, those structures are rarely dissected to determine if they are true macroglands. In addition, nothing unique can be observed concerning the gland-like structures in question in the dorsal skin of the *Ceuthomantis* species examined by us (*C. smaragdinus*, *C. cavernibardus*) or the descriptions of *C. aracamuni* and the subsequently named *C. duellmani* (Barrio-Amorós, 2010). Therefore, the condition is neither demonstrably synapomorphic for the family (and by extension its only genus) nor absent in other terraranas. The two other putative synapomorphies, the neurocranium "extraordinarily poorly ossified" and a neopalatine "unusually massive" are difficult to individuate and lack any value without explicit comparison with other terraranas and assessment of intraspecific variation (comparisons in Heinicke *et al.* 2009 were limited to a single specimen representing each of the genera *Ceuthomantis, Eleutherodactylus*, *Haddadus, Ischnocnema*, and *Pristimantis*). Further, the perceived degree of ossification in CT scans is susceptible to scanning and edition parameters, and Myers & Donnelly (1997) reported a well-ossified neurocranium in *C. cavernibardus* based on cleared and stained specimens.

Nevertheless, the diagnosis of the genus does provide valuable information about the potential phylogenetic position of *Ceuthomantis* (Heinicke *et al.*, 2009, p. 6): "Members of the genus *Ceuthomantis* are unique compared to the strabomantid genera *Dischidodactylus* and *Pristimantis* in the Guiana Highlands by having notched digital discs on the fingers and toes and by lacking dentigerous processes of vomers." Notched digital discs occur in multiple taxa outside of the Guianas, such as *Ischnocnema* (Lynch 1976a, 1979) and, to a lesser degree, some *Pristimantis* (Lynch, 1976a) and *Yunganastes mercedesae* (Padial *et al.*, 2006). However, the ungual flap is almost completely divided in *C. smaragdinus* and is completely divided in some of the fingers of *C. cavernibardus*. The relevance of this character-state is that *D. duidensis* is the only other terrarana known to have a completely divided ungual flap and also inhabits the Guianas, and there is no evidence to reject homology of the condition of the ungual flap in both *Ceuthomantis* and *Dischidodactylus*. Hedges *et al.* (2008a) assigned *D. duidensis* to Strabomantinae due to its expanded terminal disks with circumferential grooves, but they noted (p. 108): "*Dischidodactylus* differs from other strabomantines mainly by having bifurcate discs on the digits. However, at least two species of *Pristimantis* from Tamacuari Tepui in southern Venezuela (*P. cavernibardus* and *P. memorans*) have notably notched anterior margins of the digital discs (Myers & Donnelly 1997)". Although Heinicke *et al.* (2009) reported erroneously that *Pristimantis memorans* has notched ungual flaps (it was never mentioned by Myers & Donnelly 1997, and is not evident in the specimens), they noted the presence of that character in *P. cavernibardus*, a species that they transferred to *Ceuthomantis*.

Another remarkable characteristic *Ceuthomantis* shares with *Dischidodactylus* (both *D. duidensis* and *D. colonnelloi*; Ayarzagüena, 1983) is the structure of the dorsal skin, which is composed of small, flat, pliable (not keratinized) warts that are homogeneous in size and can be arranged in star-like structures (as in *C. duellmani*; Barrio-Amorós, 2010). This kind of warty skin texture has not been described for any other species of Brachycephaloidea, although a similar condition is observed in *Oreobates madidi* and some *Pristimantis* (*e.g.*, *Pristimantis colodactylus*). One less remarkable anatomical characteristic shared by *Ceuthomantis* and *Dischidodactylus* is the absence of nuptial pads in adult males. Although these observations point to a close relationship of *Ceuthomantis* and *Dischidodactylus*, differences also exist. *Dischidodactylus* possesses the dentigerous process of the vomer and *Ceuthomantis* lacks basal toe webbing, which is why we retain them in separate genera. Nevertheless, we conjecture that *Ceuthomantis* and *Dischidodactylus* are closely related and, therefore, place them both in Pristimantinae.

The genera *Mucubatrachus* (type species: *Hylodes briceni* Boulenger, 1903) and *Paramophrynella* (type species: *Eupsophus ginesi* Rivero, 1964) proposed by La Marca (2007 "2006") are herein considered junior synonyms of *Pristimantis* (as assumed by Hedges *et al.*, 2008a) following Barrio-Amorós *et al.* (2013), who found both to be embedded within a small sample (12 nominal species) of *Pristimantis* in parsimony and maximum likelihood analyses of 12S and 16S rRNA gene sequences.

Pristimantis.—Heinicke *et al.* (2007) resurrected the name *Pristimantis* for most South American species placed in *"Eleutherodactylus"* by Frost *et al.* (2006) and earlier authors. *Pristimantis* is currently the largest amphibian genus in the world, containing more than 470 species. The monophyly of this large and phenotypically diverse taxon has been corroborated by subsequent analyses of molecular data (Pyron & Wiens, 2011, using 107 nominal species, all sampled by us; Canedo & Haddad [2012] using 86 nominal species, three not sampled by us; Pinto-Sánchez *et al.* [2012] using 133 nominal species, 19 not sampled by us; and this study, using 124 nominal species). No morphological synapomorphy has been identified, but Crawford *et al.* (2010b) proposed a potential molecular synapomorphy based on structural similarity of nucleotide sequences: the loss of the D-stem of the $\mathrm{tRNA}_{\mathrm{CYS}}$ gene. Our study confirms the absence of the D-stem in nine species of *Pristimantis* and its presence in 25 species of *Craugastor*, 2 species of *Eleutherodactylus*, and *Oreobates quixensis*.

Hedges *et al.* (2008a) further parsed *Pristimantis* into three subgenera, *Hypodictyon*, *Pristimantis*, and *Yunganastes*. Hedges *et al.* (2008a) allocated the 385 of the subgenus *Pristimantis* to 16 species groups (their polyphyletic *P. unistrigatus* group alone contained 193 species), including all groups previously recognized by Lynch & Duellman (1997). Hedges *et al.* (2008a) found the subgenus *Pristimantis* to be paraphyletic with respect to *Hypodiction* in their analysis 1 (species rich) molecular phylogeny (p. 16), and, although the subgenera were reciprocally monophyletic in their analysis 2 (intermediate; p. 19) and 3 (gene rich) results (p. 20), many species appearing basally in their analysis 1 topology were not included in the latter analyses. As discussed above, maximum likelihood analysis of their combined datasets does not support the monophyly of the subgenus *Pristimantis*. Similarly, TA + PA analysis of our expanded dataset reveals the subgenus *Pristimantis* to be paraphyletic with respect to *Hypodictyon* because *P. caprifer* (of the nominal *P. conspicillatus* group), *P. euphronides* and *P. shrevei* (both in the nominal *P. unistrigatus* group), cluster together as sister of all other species of the genus *Pristimantis*. In our SA + ML analysis (see also Pyron & Wiens, 2012), these three species are embedded in the subgenus *Pristimantis* and form the sister taxon of the *P. conspicillatus* + *P. peruvianus* species groups. Consequently, we recognize a single genus, *Pristimantis*, with no infrageneric units other than a few monophyletic species groups (see below) until a thorough analysis of the morphology coupled with a more taxon-dense phylogenetic analysis allows useful partitioning of this large group.

We did not recover the two species series recognized by Hedges *et al.* (2008a) within their subgenus *Hypodyction* and, therefore, do not retain those species series within *Pristimantis*. Instead, they are merged into a single species group, equivalent in content to *Hypodictyon,* which we term the *P. ridens* group. To this group we add *P. tanyrhynchus*—a species originally placed in the *P. conspicillatus* group by Lehr (2007)—because it is almost identical to *P. lanthanites*, a parapatric species nested within this series in our analyses, and also *P. erythropleura*, *P. paisa* and *P. viejas* based on the results of Pinto-Sánchez *et al.* (2012).

Of the 16 species groups recognized and diagnosed by Hedges *et al.* (2008a) within the former subgenus *Pristimantis*, none was recovered monophyletic in the TA + PA analyses. In SA + ML only the *P. pardalis* group (Wang *et al.*, 2008) was monophyletic, while only the *P. peruvianus* group was monophyletic in SA + PA. Hedges *et al.*'s (2008a: 113) conjectured that the recovered non-monophyly of groups might be related to insufficient taxon sampling; however, the non-monophyly of species groups has increased with the addition of taxa. Thus, in the Pinto-Sánchez *et al.* (2012) analysis of 133 species only the *P. myersi*, and *P. pardalis* groups were monophyletic, but our inclusion of *P. thymelensis* (of the *P. orcesi* group) also rendered the *P. myersi* group paraphyletic.

A few species groups can be rendered monophyletic by making a few changes and/or merging groups. The *Pristimantis conspicillatus* and *P. peruvianus* species groups can be rendered monophyletic by including *P. peruvianus* within the *P. conspicillatus* group (as done by Lynch & Duellman, 1997) because the terminal identified as *P. peruvianus* by Hedges *et al.* (2008a), as well as those used by Pinto-Sánchez *et al.* (2012), are actually *P. reichlei* (Table 1). Also, we confirm that five species tentatively placed in the *P. conspicillatus* group that were not sampled by Hedges *et al.* (2008a) are part of this group (*P. adiastolus*, *P. chiastonotus*, *P. koehleri*, *P. gaigei,* and *P. samaipatae*). Canedo & Haddad (2012) also discovered that three species placed in *Ischnocnema* by Hedges *et al.* (2008a) are part of the *P. conspicillatus* group (*P. paulodutrai*, *P. ramagii*, and *P. vinhai*). In addition, we place *P. dundeei* and *P. ventrigranulosus* in this group following Maciel *et al.* (2012). We exclude *P. caprifer*, *P. carmelitae*, *P. carlossanchezi*, *P. insignitus*, *P. padrecarlosi*, *P. pedimontanus*, and *P. viridicans* from the *P. conspicillatus* group and leave them unassigned to any group because their external morphology does not match the characteristics shared by confirmed species of the clade (dorsal skin shagreen without keratinized tubercles; smooth or granular belly, not aerolate; first finger longer than second; tarsal fold present). We also exclude *P. savagei* from the group following Pinto-Sánchez *et al.* (2012). We remove *P. thectopternus* from the group and place it in the *P. ridens* group. *Pristimantis zeuctotylus* remains in the group despite the results of Hedges *et al.* (2008a) and Pinto-Sánchez *et al.* (2012) because their terminal was misidentified (see Table 1). For a complete list of species recognized in the group see Appendix 2.

With the transfer of *Pristimantis peruvianus* to the *P. conspicillatus* group, the former *P. peruvianus* group requires a new name, which we name as the *P. danae* species group (following the International Code of Zoological Nomenclature, 1999, in its recommendation to use the oldest available species name). We add *P. reichlei* to this group following the results of this study. From the "*P. peruvianus* group" (now *P. danae* group) of earlier authors we remove *P. vilcabambae*, which is left unassigned to group because it presents a distinctive morphology not otherwise observed among species of the *P. danae* group or any other group (Chaparro *et al.*, 2012). *Pristimantis* *crepitans*, another former member of this group, was recently placed in *Oreobates* by Padial *et al.* (2012) on the basis of morphology, and this position was recently corroborated by molecular evidence (Pereyra *et al.*, 2014)

The *Pristimantis devillei* species group also requires minor surgery. This species group was not monophyletic in our analyses or those of other authors. However, Hedges *et al.* (2008a) and subsequent studies recovered a clade that unites species of the *P. curtipes*, *P. devillei*, and *P. surdus* species groups, as well as a species of the *P. unistrigatus* group (*P. thymalopsoides*). Species of this clade share the presence of cranial crests (a putative synapomorphy) and are also distributed sympatrically. We call this clade the *P. devillei* species group, and assign to it all species of the former *P. curtipes*, *P. devillei*, and *P. surdus* species groups, plus *P. thymalopsoides*. We exclude *P. appendiculatus* and *P. cryophilius* because they fall elsewhere on the tree.

The *Pristimantis myersi* group is non-monophyletic. However, by transferring *P. thymelensis* to the *P. myersi* group we delimit a monophyletic *P. myersi* species group (see Appendix 2) including the recently described *P. munozi*, as suggested in the original description (Rojas-Runjaic *et al.*, 2014).

The *Pristimantis lacrimosus* group of Hedges *et al.* (2008a) is not monophyletic. *Pristimantis acuminatus* was placed by Hedges *et al.* (2008a) within the *P. unistrigatus* group, a group we do not recognize because of its rampant non-monophyly (see below). Nevertheless, this species clusters with species of the *P. lacrimosus* group. We therefore transfer *P. acuminatus* to the *P. lacrimosus* group, and we also include several other species that present putatively synapomorphic character-states of the group (acuminate snout, smooth dorsal skin, round and ovate finger and toe discs): *P. geyi* (placed in the *P. unistrigatus* group by Lehr *et al.*, 2013), *P. padiali* (placed in the *P. unistrigatus* group by Moravec *et al.*, 2010), *P. pseudoacuminatus* (placed in the *P. unistrigatus* group by Hedges *et al.*, 2008a), and *P. tantanti* (placed in the *P. unistrigatus* group by Lehr *et al.*, 2007).

All other groups within *Pristimantis* recognized by Hedges *et al.* (2008a) are demonstrably non-monophyletic and, therefore, are of little value as working units in species-level taxonomy. The species groups formerly in *Eleutherodactylus* and now in *Pristimantis*, assembled over the years based on impressions of similarity (*e.g.*, Lynch & Duellman, 1997), were either not, or only modestly, revised by Hedges *et al.* (2008a), who retained most of them as they were, even when their data showed them to be non-monophyletic. Because there was no tradition of using synapomorphy schemes for those groups during their long, unsteady development, infrageneric taxonomic groupings remain based on impressions of similarity, something that has rendered the taxonomic placement of most newly described species arbitrary and, as a result, frequently erroneous. Despite these problems, the number of new *Pristimantis* species continues to increase rapidly, and the lack of morphological synapomorphies for any of its species groups makes the assignment of new species to groups problematic without genetic data, something that leads to considerable confusion in the literature. Recognizing only groups for which evidence supports their monophyly results in a better understanding of where we stand in our knowledge of the overarching group. Leaving a large number of species unassigned to group is unavoidable and something we hope will foster the identification of new phenotypic characters that diagnose monophyletic groups (*e.g.*, Taboada *et al.*, 2013).

Yunganastes.—This genus is endemic to the Andes of Bolivia and southern Peru. Part of this taxon was first recognized as the *Eleutherodactylus fraudator* species group by Köhler (2000), later extended and named as a subgenus by Padial *et al.* (2007) and as genus by Padial *et al.* (2009). The genus is diagnosed by a unique morphological synapomorphy, a derived condition of the path of the mandibular ramus of the trigeminal nerve, discovered by T. Grant *in* Frost *et al.* (2006) in *Y. pluvicanorus* (as *Eleutherodactylus pluvicanorus*) and corroborated by Padial *et al.* (2007) for other species of the group. The initial misidentification of that condition as the "E" condition of Lynch (1986a) suggested a close relationship of this genus with *Craugastor* (De la Riva & Lynch, 1997). Due to sequence misidentification in GenBank, the genus was not recovered by Pyron & Wiens (2011) and Pinto-Sánchez *et al.* (2012). In addition, Pyron & Wiens (2011) overlooked this taxon in their taxonomy and did not include it in their Pristimantinae despite having found *Yunganastes* (misidentified as *Pristimantis*) to be the sister taxon of *Pristimantis*.

Eleutherodactylidae

This taxon corresponds to Eleutherodactylidae of Hedges *et al.* (2008a). It includes the South American genera *Adelophryne* and *Phyzelaphryne*, the Middle American genus *Diasporus*, and the Antillean–Middle American genus *Eleutherodactylus*. This clade was discovered by Heinicke *et al.* (2007) and has been corroborated by Hedges *et al.* (2008a), Pyron & Wiens (2011), and Canedo & Haddad (2012). Hedges *et al.* (2008a) proposed as synapomorphic the absence of nuptial pads in males of this clade.

Hedges *et al.* (2008a) erected two subfamilies within Eleutherodactylidae, Eleutherodactylinae for *Eleutherodactylus* and *Diasporus*, and Phyzelaphryninae for *Adelophryne* and *Phyzelaphryne*. Previously, the only hypothesis suggesting a relationship between Phyzelaphryninae and Eleutherodactylinae was formulated by Frost *et al.* (2006), who noted that the conspicuously pointed tips on the toe discs would ally *Adelophryne* with *Phyzelaphryne* and the *Eleutherodactylus diastema* group (now *Diasporus*).

Eleutherodactylinae

This clade includes the genera *Diasporus* and *Eleutherodactylus* as sister groups and was previously recovered by Hedges *et al.* (2008a), Pyron & Wiens (2011), and Canedo & Haddad (2012). Within *Eleutherodactylus*, Hedges *et al.* (2008a) recognized the subgenera *Eleutherodactylus*, *Euhyas*, *Pelorius*, and *Syrrhophus*, with the subgenus *Schwartzius* as the sister group of them all. We recover these groups as monophyletic and continue to recognize all of these subgenera, although we note that the inclusion of the wildcard *Eleutherodactylus diasporus* in *Euhyas* is assumed and must be tested by adding the DNA sequences that are missing for this taxon. All of these subgenera except the Hispaniolan endemic *Schwartzius* were recognized by Hedges (1989) on the basis of allozymic evidence, and were treated by Frost *et al.* (2006) as genera. Although this arrangement has not been followed by most authors, we expect that in the future all of these will be recognized as genera. Distinct characteristics of liver shape have been proposed as synapomorphic for each of the subgenera, as well as for *Diasporus* (Hedges, 1989; Hedges *et al.*, 2008a).

Among the species series recognized by Hedges *et al.* (2008a) for the subgenera of *Eleutherodactylus*, all but the *Eleutherodactylus martinicensis* series are monophyletic in our preferred topologies. Therefore, we restrict the *E. martinicensis* series to the monophyletic *E. martinicensis* group of Hedges *et al.* (2008a) and, accordingly, remove the *E. antillensis* group from the *E. martinicensis* series and place it in its own species series. Similarly, the *E. antillensis* subgroup is paraphyletic with respect to the *E. gryllus* group, so we combine the species of these two subgroups into a single monophyletic *E. antillensis* subgroup. Also, the *E. bakeri* group of *Euhyas* is paraphyletic because *E. glanduliferoides* is the sister of *E. jugans*. We therefore transfer *E. glanduliferoides* to the *E. jugans* group to restore the monophyly of both the *E. bakeri* and *E. jugans* species groups.

The most problematic taxa are subgroups recognized within the *E. luteolus* species group within *Euhyas*, with all the groups we tested being para- or polyphyletic. Therefore, we reject these subgroups and refer species only to the more inclusive *E. luteolus* species group, which is endemic to Jamaica. Hedges *et al.*'s (2008a) analyses did not resolve the relationships among subgroups within this clade, although the subgroups are partially recovered by protein variation, albumin immunology, and karyology and are all morphologically distinctive according to Hedges *et al.* (2008a).

Within *Euhyas*, Rodríguez *et al.* (2013) inferred new phylogenetic relationships for the *E. limbatus* group that partially conflict with Hedges *et al.* (2008a) and with our TA + PA and SA + PA results, although not with our SA + ML results. Their clade-Bayes tree (see Wheeler and Pickett, 2008) shows *E. etheridgei* as sister of all other species of the *E. limbatus* group and *E. cubanus* as sister of a clade containing *E. orientalis* as the sister group of a clade with two subclades, one with *E. limbatus* and *E. jaumei* as sister taxa, and another with *E. iberia* and an unnamed species as sister taxa. None of these conflicts require taxonomic changes.

Morphological evidence previously supported the monophyly of a mainly Antillean clade of *Eleutherodactylus* (Lynch, 1971), although some of its species were considered to be allied with mainland forms (*e.g.*, *Sminthillus* [now *Eleutherodactylus*] *limbatus* and *Eleutherodactylus auriculatus*; Lynch & Duellman, 1997). Also, Lynch's (1971) alpha division of Eleutherodactylini, based on the fusion of frontoparietals and proötic, grouped *Syrrhophus*, *Tomodactylus* (now in the synonymy of *Syrrhophus*), *Pelorius* (*E. inoptatus*), and the subgenus *Eleutherodactylus* (*E. karlschmidti*), although *Sminthillus* (= *Eleutherodactylus limbatus*) was considered distinct from the alpha and beta divisions. Heyer (1975) and Ardila-Robayo (1979) suggested a monophyletic group composed of *Eleutherodactylus*, *Syrrhophus,* and *Tomodactylus* based on morphological characteristics, although none of these are apparently synapomorphic.

The monophyly of *Diasporus* is corroborated in all our analyses. Hedges *et al.* (2008a) only sampled *D. diastema* and allocated seven other species to the genus based on the presence of a pointed tip of the ungual flap, an oval palmar tubercle, and prominent vomerine teeth. Although the pointed tip of the ungual flap characteristic of *Diasporus* is also found in *Pristimantis chalceus* (Lynch, 2001), that species groups with other species of *Pristimantis*. Our analyses recovered *D. diastema* as the sister taxon of *D. quidditus* and *D. citrinobapheus*. Hertz et al (2012) purported to test the monophyly of *Diasporus* and sampled 535 bp of 16S mtDNA for five nominal species, including a new taxon (*D. citrinobapheus*). However, their outgroup sampling consisted of only one species of *Pristimantis* (*P. ridens*), so the monophyly of *Diasporus* was an assumption of their analysis and not the result of a test. Populations referred to *D. citrinobapheus* were found to form the sister taxon of another clade composed of allopatric populations of *D.* aff. *diastema* from an area relatively near to the type locality (50 km airline distance) of *D. citrinobapheus* and showed divergences of 1.8%. We therefore assign those populations to *D. citrinobapheus* and, accordingly, the sequences from GenBank we analyzed (deposited by Crawford *et al.* 2010a) as *D.* aff. *diastema* should be reidentified as *D. citrinobapheus.* Nevertheless, the taxonomic status of *D. citrinobapheus* is problematic because no morphological character reported by Hertz *et al.* (2012) allows it to be distinguished from *D. tigrillo* (Savage, 1997) and sequence data are currently not available for the latter species. Although populations assigned to these two species are separated by ca. 200 km, they both occur at the same elevations and in the same habitat. Hertz *et al.* (2012) also sampled *D. diastema* (paraphyletic in their analysis), *D. hylaeformis* (paraphyletic in their analysis), *D. quidditus*, and *D. vocator.* Pinto-Sánchez *et al.* (2012) included sequences of two additional species of *Diasporus* (*D. hylaeformis* and *D. vocator*) in their outgroup sample, but they were not available in time to be included in the present study.

Phyzelaphryninae

This taxon includes the South American genera *Adelophryne* and *Phyzelaphryne*, and was found to be monophyletic previously (Hedges *et al.*, 2008a; Pyron & Wiens, 2011; Canedo & Haddad, 2012; Fouquet *et al.* 2012). Hoogmoed & Lescure (1984) erected the genus *Adelophryne* and considered it and *Phyzelaphryne* to be sister taxa based on the shared occurrence of slightly expanded terminal discs with incomplete circumferential grooves and pointed tips. Nevertheless, they considered that their new genus *Adelophryne* was distinguished from the monotypic *Phyzelaphryne* on the basis of its flattened digits, indistinct subarticular tubercles, long and slender tongue, and phalangeal reduction in the fourth finger. Hoogmoed and Lescure (1984) rejected a close relationship of Eleutherodactylini to other brachycephaloids with pointed digital tips, such as *Barycholos*, *Phyllonastes* (now *Noblella*), and *E. nigrovittatus* (now *Hypodactylus*), an observation corroborated by our results. Frost *et al.* (2006) suggested that phalangeal reduction in *Adelophryne* and *Phyzelaphryne* might support a relationship among these genera and genera now placed in Holoadeninae (*Euparkerella* and *Phyllonastes*) or to *Brachycephalus*, but they also considered the alternative hypothesis, mentioned above, that would ally these two genera with *Diasporus*.

Hedges *et al.* (2008a) did not address the monophyly of *Adelophryne*, only including *Adelophryne patamona* (mistakenly identified as *A. adiastola* fide Fouquet *et al.*, 2012). Canedo & Haddad (2012) included two terminals, *A. patamona* (used previously by Hedges *et al.*, 2008a) and *A. baturitensis*, recovering them as sister taxa. Fouquet *et al.* (2012) included sequences of six of the eight nominal species now referred to *Adelophryne* (Frost, 2014) and an ample array of populations plus gene sequences from several populations of *Phyzelaphryne*. They used parsimony, maximum likelihood, and Bayesian methods to analyze a similarity-alignment of 5841 bp from four mitochondrial (12S, 16S, cytb, COI) and three nuclear (POMC, RAG1, TYR) loci. Their analyses corroborated the sister relationship between *Adelophryne* and *Phyzelaphryne* and revealed a number of likely new species.

As noted by Fouquet *et al.* (2012), the morphological distinction between *Adelophryne* and *Phyzelaphryne* was ambiguous from the beginning. In fact, specimens from Vaupes (Colombia) used in the original description of *Phyzelaphryne miriamae* and the advertisement call (Heyer, 1977) correspond to *Adelophryne adiastola* (Hoogmoed & Lescure, 1984), and Lynch (2005) identified as *A. adiastola*, specimens that corresponds to *Phyzelaphryne* (Fouquet *et al.*, 2012). Nevertheless Fouquet *et al.* (2012) did not find *Phyzelaphryne* to be embedded within *Adelophryne*, and we follow them, reluctantly, in retaining it as a monotypic genus. *Phyzelaphryne* is endemic to central Amazonia, and *Adelophryne* only occupies the northern Amazonia, the Guianan region, and eastern Brazil.

Conclusions

With more than 1000 named species (and many others awaiting description) distributed across the New World tropics, Brachycephaloidea is one of the most important extant frog groups. In this paper, we tested previous phylogenetic hypotheses for the group by combining DNA sequences of 22 genes from 431 ingroup and 25 outgroup terminals and performing a tree-alignment analysis under the parsimony optimality criterion in the program POY. On the basis of our results, we recognize three families within Brachycephaloidea (Brachycephalidae, Craugastoridae, and Eleutherodactylidae), all of which are currently diagnosable solely on molecular grounds. We also recognize five subfamilies (Craugastorinae, Eleutherodactylinae, Holoadeninae, Phyzelaphryninae, and Pristimantinae) corresponding in large part to previous families and subfamilies. Our analyses upheld the monophyly of all tested genera, but we found numerous subgeneric taxa to be non-monophyletic and modified the taxonomy accordingly.

Although knowledge of the systematics of terraranas has grown significantly in recent years, our study highlights the many weaknesses and lacunae in our understanding and points to those problems most urgently in need of research. The monophyly of a several eleutherodactylid clades is compromised by the wildcard taxon *Eleutherodactylus dilatus*, making it imperative to increase the coverage of DNA sequences for this species. Fieldwork is required to collect several key taxa, including *Atopophrynus*, *Dischidodactylus*, *Geobatrachus*, and *Niceforonia*, all of which have been excluded from phylogenetic analyses due to lack of tissues for DNA extraction. Similarly, there is a general need to include DNA sequences for a larger proportion of the species of Brachycephaloidea, especially within the massive, highly diverse genus *Pristimantis*.

Nevertheless, increased taxonomic representation of DNA sequences alone seems unlikely to provide entirely satisfactory solutions. For example, greater taxon sampling in *Pristimantis* has increased the degree of non-monophyly of subgeneric groups. Similarly, *Ceuthomantis smaragdinus* is both one of the most completely sequenced and recalcitrant species in our dataset, with vastly different positions in different analyses. As such, we think we might be reaching the limits of the ability of current Sanger sequencing-based approaches to decisively test many competing phylogenetic hypotheses. Next-generation sequencing technologies promise a deluge of new sequences that will surely have an important effect on inferred relationships; however, morphological evidence might provide answers that molecular phylogenetic studies are unable to address, at least at present. For example, examination of the hyale of even a single phyzelaphrynine would provide a crucial test of that group's relationship to *Geobatrachus* (and *Atopophrynus*), and the incongruence between current phylogenetic hypotheses and traditionally recognized species groups might be resolved by including in phylogenetic analyses the morphological characters used to erect those groups.

The most far-reaching conclusion of this study is that methods of analysis matter empirically and, therefore, must be chosen based on understanding of their underlying assumptions and operations and not slogans and social trends. For example, proponents of maximum likelihood methods have consistently claimed to be motivated by the desire to model evolution objectively, yet the most popular maximum likelihood programs model gaps as if they were unknown nucleotides instead of insertion and deletion events, thereby treating evidence of absence as absence of evidence. Our results provide a clear empirical demonstration of the different effects of wildcard taxa caused by missing data in parsimony and maximum likelihood analyses. Specifically, maximum likelihood analyses consistently (81% bootstrap frequency) provided spurious resolution despite a lack of evidence, whereas parsimony correctly depicted the ambiguity due to missing data by collapsing unsupported nodes. As expected, optimality criterion, model assumptions, and gap treatment affected topological results. However, we found that the topological effects of alignment method were just as significant. Further, the optimal tree-alignment indicates that insertions and deletions occurred in twice as many aligned positions as implied by the optimal similarity-alignment, confirming previous findings that sequence turnover through insertion and deletion events plays a greater role in molecular evolution than indicated by similarity-alignments. Given the magnitude of the effect that alignment methods have on inferences, the attention paid in the phylogenetics literature to alignment, both empirically and theoretically, has been disproportionately small.

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APPENDIX 1. GenBank accession numbers for loci and terminals of terraranas (Brachycephaloidea) and outgroups sampled in this study.

	12S Tval Tleu	16S	28S	C-MYC
Acris crepitans	EF566970	EF566970	AY844194	AY819194 AY819268
Adelophryne patamona	EU186679	EU186679	GQ345136	GQ345149 GQ345167
Agalychnis callidryas	DQ283423	DQ283423	-	EF174321
Barycholos pulcher	EU186727	EU186709	-	-
Barycholos ternetzi	-	DQ283094	DQ283496	-
Brachycephalus alipioi	HQ435676	HQ435690	-	-
Brachycephalus brunneus	HQ435677	HQ435691	-	-
Brachycephalus didactylus	HQ435678	HQ435692	-	-
Brachycephalus ephippium	DQ283091	DQ283091	DQ283494	GQ345145 GQ345162
Brachycephalus ferruginus	HQ435681	HQ435695	-	-
Brachycephalus garbeanus	HQ435680	HQ435694	-	-
Brachycephalus hermogenesi	HQ435682	-	-	-
Brachycephalus izecksohni	HQ435683	HQ435696	-	-
Brachycephalus nodoterga	HQ435684	HQ435697	-	-
Brachycephalus pernix	HQ435685	HQ435698	-	-
Brachycephalus pitanga	HQ435686	HQ435699	-	-
Brachycephalus pombali	HQ435687	HQ435700	-	-
Brachycephalus toby	HQ435688	HQ435701	-	-
Brachycephalus vertebralis	HQ435689	HQ435702	-	-
Bryophryne cophites	EF493537	EF493537	-	-
Calyptocephalella gayi	DQ283439	DQ283439	DQ283748	AY819175
Ceuthomantis smaragdinus	GQ345132	GQ345132	GQ345140	GQ345154 GQ345169
Craugastor aff. azueroensis	-	FJ784393	-	-
Craugastor alfredi	DQ283318	DQ283318	DQ283649	-
Craugastor andi	EU186687	EU186687	-	-
Craugastor angelicus	EU186681	EU186681	-	-
Craugastor augusti	AY326011	AY326011	-	-
Craugastor bocourti	EF493713	EF493713	-	AY211301
Craugastor bransfordii	EF493822	FJ784496	-	AY211321
Craugastor cf. augusti	DQ283271	DQ283271	DQ283627	-
Craugastor cf. longirostris	EF562328	FJ784556	-	EF562426
Craugastor chac	-	-	-	-
Craugastor crassidigitus	EU186733	FJ784407	-	AY337269 AY337269
Craugastor sp. MVUP1863	-	-	-	-
Craugastor cuaquero	EF493531	EF493531	-	-
Craugastor daryi	EU186738	EU186720	-	AY211316 AY211316

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APPENDIX 1. (Continued)

	12S Tval Tleu	16S	28S	C-MYC
Craugastor emcelae	AY326001	AY326001	-	-
Craugastor fitzingeri	-	-	-	AY211297 AY211297
Craugastor fleischmanni	-	FJ784492	-	-
Craugastor gollmeri	EU186731	EU186713	-	AY211279 AY211279
Craugastor laticeps	-	-	-	AY337267 AY337267
Craugastor lauraster	EU186732	EU186714	-	-
Craugastor lineatus	EU186685	EU186685	-	-
Craugastor loki	EF493395	EF493395	-	-
Craugastor longirostris	EU186688	EU186688	-	-
Craugastor megacephalus	EU186683	EU186683	-	AY211296 AY211296
Craugastor melanostictus	AY326006	AY326006	-	-
Craugastor mexicanus	-	-	-	AY211312 AY211312
Craugastor mimus	-	-	-	AY211281 AY211281
Craugastor montanus	-	FJ784523	-	AY211308 AY211308
Craugastor noblei	EU186737	-	-	AY211285 AY211285
Craugastor obsesus	-	-	-	-
Craugastor omiltemanus	-	-	-	AY337271 AY337271
Craugastor persimilis	EF493360	EF493360	-	AY211299 AY211299
Craugastor podiciferus	-	-	-	AY211319 GQ345164 AY211319
Craugastor polyptychus	DQ283168	DQ283168	-	AY211322 AY211322
Craugastor punctariolus	EF493711	EF493711	DQ283558	-
Craugastor pygmaeus	-	-	-	AY211314 AY211314
Craugastor raniformis	DQ283105	DQ283106	-	-
Craugastor ranoides	DQ283317	DQ283317	DQ283505	AY211287 AY211287
Craugastor rhodopis	EU186680	EU186680	DQ283648	AY211315 AY211315
Craugastor rugulosus	EU186669	EU186669	-	-
Craugastor rupinius	-	-	-	-
Craugastor saltator	EF493712	EF493712	-	AY211311 AY211311
Craugastor sandersoni	EU186675	EU186675	-	-
Craugastor sp. EU186675	EU186697	EU186697	-	-

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APPENDIX 1. (Continued)

	12S Tval Tleu	16S	28S	C-MYC
Craugastor sp. EU186697	EU186698	EU186698	-	-
Craugastor sp. EU186698	EU186703	EU186703	-	-
Craugastor sp. EU186703	EF562287	EF562353	-	-
Craugastor sp. FMNH257689	-	-	-	EF562446
Craugastor sp. UTAA 55247	-	-	-	-
Craugastor spatulatus	EU186674	-	-	-
Craugastor stejnegerianus	EF562325	EF562360	-	AY211320 AY211320
Craugastor stuarti	EU186684	EU186684	-	-
Craugastor tabasarae	EF562326	FJ784515	-	EF562424
Craugastor talamancae	-	FJ784572	-	AY337270 AY337270
Craugastor tarahumaraensis	EU186702	EU186702	-	-
Craugastor trachydermus	-	-	-	AY211300 AY211300
Craugastor underwoodi	EF562323	EF562362	-	AY211303 AY211303
Craugastor uno	EU186673	-	-	-
Craugastor xucanebi	-	-	-	AY211298 AY211298
Cryptobatrachus boulengeri	-	-	-	-
Cryptobatrachus fuhrmanni	AY326050	AY326050	-	-
Diasporus citrinobapheus	-	FJ784484	-	-
Diasporus diastema	EU186682	EU186682	GQ345135	GQ345148
Diasporus quidditus	-	FJ784405	-	-
Eleutherodactylus abbotti	EF493540	EF493540	-	-
Eleutherodactylus acmonis	EF493787	EF493637	-	-
Eleutherodactylus albipes	EF493386	EF493386	-	-
Eleutherodactylus alcoae	EF493382	EF493382	-	-
Eleutherodactylus alticola	EF493768	EF493620	-	-
Eleutherodactylus amadeus	EF493805	EF493644	-	-
Eleutherodactylus amplinympha	EF493732	EF493560	-	-
Eleutherodactylus andrewsi	EF493544	EF493623	-	-
Eleutherodactylus antillensis	EF493728	EF493556	-	-
Eleutherodactylus apostates	EF493811	EF493650	-	-
Eleutherodactylus armstrongi	EF493778	EF493611	-	-
Eleutherodactylus atkinsi	EF493797	EF493598	-	-
Eleutherodactylus audanti	EU186662	EU186662	-	-
Eleutherodactylus auriculatoides	EF493754	EF493572	-	-
Eleutherodactylus auriculatus	EF493344	EF493344	-	-
Eleutherodactylus bakeri	EF493808	EF493647	-	-
Eleutherodactylus barlagnei	EF493735	EF493563	-	-

......continued on the next page

APPENDIX 1. (Continued)

	12S Tval Tleu	16S	28S	C-MYC
Eleutherodactylus bartonsmithi	FJ527412	EF493576 GQ426529 FJ527381	-	-
Eleutherodactylus blairhedgesi	EF493371	EF493606	-	-
Eleutherodactylus bothroboans	EU186655	EU186655	-	-
Eleutherodactylus bresslerae	EF493785	EF493635	-	-
Eleutherodactylus brevirostris	EF493819	EF493657	-	-
Eleutherodactylus brittoni	EF493727	EF493554	-	-
Eleutherodactylus caribe	EF493385	EF493385	-	-
Eleutherodactylus casparii	EF493788	EF493599	-	-
Eleutherodactylus cavernicola	EF493763	EF493614	-	-
Eleutherodactylus cf. *auriculatus*	FJ527410	FJ527323	-	-
Eleutherodactylus cf. *varleyi*	EF493345	EF493345	-	-
Eleutherodactylus chlorophenax	EF493543	-	-	-
Eleutherodactylus cochranae	EF493725	EF493555	-	-
Eleutherodactylus cooki	EF493539	EF493539	-	GQ345166
Eleutherodactylus coqui	GQ345176	GQ345176	-	-
Eleutherodactylus corona	EF493807	EF493645	-	-
Eleutherodactylus counouspeus	EF493719	EF493719	-	-
Eleutherodactylus cubanus	EF493796	EF493594	-	-
Eleutherodactylus cundalli	EF493761	EF493612	-	-
Eleutherodactylus cuneatus	EF493775	EF493608	-	-
Eleutherodactylus darlingtoni	EF493777	EF493610	-	-
Eleutherodactylus dilatus	-	-	-	AY337268 AY337268
Eleutherodactylus dimidiatus	EF493802	EF493640	-	-
Eleutherodactylus dolomedes	EF493809	EF493648	-	-
Eleutherodactylus eileenae	FJ527416	EF493577 Q426533 FJ527401	-	-
Eleutherodactylus emiliae	EF493368	EF493638	-	-
Eleutherodactylus eneidae	EF493729	EF493557	-	-
Eleutherodactylus etheridgei	EF493794	EF493593	-	-
Eleutherodactylus eunaster	EF493804	EF493646	-	-
Eleutherodactylus flavescens	EF493731	EF493559	-	-
Eleutherodactylus fowleri	EF493752	EF493568	-	-
Eleutherodactylus furcyensis	EF493814	EF493654	-	-
Eleutherodactylus fuscus	EF493769	EF493618	-	-
Eleutherodactylus glamyrus	FJ527413	EF493575 GQ426530 FJ527388	-	-
Eleutherodactylus glandulifer	EF493816	EF493655	-	-
Eleutherodactylus glanduliferoides	EF493546	-	-	-
Eleutherodactylus glaphycompus	EF493383	EF493383	-	-
Eleutherodactylus glaucoreius	EF493762	EF493613	-	-

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APPENDIX 1. (Continued)

	12S Tval Tleu	16S	28S	C-MYC
Eleutherodactylus goini	EF493791	EF493604	-	-
Eleutherodactylus gossei	EF493716	EF493716	-	-
Eleutherodactylus grabhami	EF493772	EF493624	-	-
Eleutherodactylus grahami	EF493781	EF493632	-	-
Eleutherodactylus greyi	EF493801	EF493628	-	-
Eleutherodactylus griphus	EF493381	EF493381	-	-
Eleutherodactylus gryllus	EF493724	EF493552	-	-
Eleutherodactylus guanahacabibes	EF493789	EF493600	-	-
Eleutherodactylus guantanamera	EF493749	EF493565	-	-
Eleutherodactylus gundlachi	EF493798	EF493597	-	-
Eleutherodactylus haitianus	EF493743	EF493583	-	-
Eleutherodactylus hedricki	EF493553 EF493726	EF493553	-	-
Eleutherodactylus heminota	EF493806	EF493649	-	-
Eleutherodactylus hypostenor	EF493757	EF493585	-	-
Eleutherodactylus iberia	EF493374	EF493591	-	-
Eleutherodactylus inoptatus	EF493380	EF493380	-	-
Eleutherodactylus intermedius	EF493799	EF493595	-	-
Eleutherodactylus ionthus	EF493748	EF493564	-	-
Eleutherodactylus jamaicensis	EF493770	EF493621	-	-
Eleutherodactylus jaumei	EU186672	EU186672	-	-
Eleutherodactylus johnstonei	EF493733	EF493561	-	-
Eleutherodactylus juanariveroi	EF493538	-	-	-
Eleutherodactylus jugans	EF493810	EF493652	-	-
Eleutherodactylus junori	EF493764	EF493617	-	-
Eleutherodactylus klinikowskii	EF493547	-	-	-
Eleutherodactylus lamprotes	EF493379	EF493379	-	-
Eleutherodactylus leberi	EF493342	EF493342	-	-
Eleutherodactylus lentus	EF493717	EF493717	-	-
Eleutherodactylus leoncei	EF493715	EF493715	-	-
Eleutherodactylus limbatus	EF493795	EF493590	-	-
Eleutherodactylus locustus	EF493730	EF493558	-	-
Eleutherodactylus luteolus	EF493545	EF493545	-	-
Eleutherodactylus maestrensis	EF493369	EF493639	-	-
Eleutherodactylus mariposa	FJ527414	EF493573 GQ426531 FJ527394	-	-
Eleutherodactylus marnockii	DQ283102	DQ283101	DQ283502	-
Eleutherodactylus martinicensis	EF493343	EF493343	-	-
Eleutherodactylus melacara	EF493751	EF493567	-	-
Eleutherodactylus minutus	EF493741	EF493578	-	-
Eleutherodactylus monensis	EF493783	EF493633	-	-
Eleutherodactylus montanus	EF493756	EF493571	-	-

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APPENDIX 1. (Continued)

	12S Tval Tleu	16S	28S	C-MYC
Eleutherodactylus nitidus	EU186730	DQ283316	DQ283647	-
Eleutherodactylus nortoni	EF493760	EF493588	-	-
Eleutherodactylus nubicola	EF49377	EF493622	-	-
Eleutherodactylus orcutti	EF493750	EF493566	-	-
Eleutherodactylus orientalis	EF493767	EF493619	-	-
Eleutherodactylus oxyrhyncus	EF493373	EF493592	-	-
Eleutherodactylus pantoni	EF493812	EF493651	-	AY211282 AY211282
Eleutherodactylus parabates	EF493766	EF493616	-	-
Eleutherodactylus parapelates	EF493746	EF493581	-	-
Eleutherodactylus patriciae	EF493758	EF493587	-	-
Eleutherodactylus paulsoni	EF493755	EF493570	-	-
Eleutherodactylus pentasyringos	EF493815	EF493659	-	-
Eleutherodactylus pezopetrus	EF493765	EF493615	-	-
Eleutherodactylus pictissimus	EF493793	EF493601	-	-
Eleutherodactylus pinarensis	EF493782	EF493631	-	-
Eleutherodactylus pinchoni	EF493792	EF493607	-	-
Eleutherodactylus pipilans	EF493734	EF493562	-	-
Eleutherodactylus pituinus	EU186729	EU186711	-	-
Eleutherodactylus planirostris	EF493747	EF493582	DQ283629	-
Eleutherodactylus poolei	DQ283107	DQ283107	-	-
Eleutherodactylus portoricensis	EF493742	EF493579	-	-
Eleutherodactylus principalis	EF493720	EF493548	-	-
Eleutherodactylus probolaeus	FJ527411	FJ527377	-	-
Eleutherodactylus rhodesi	EF493784	EF493634	-	-
Eleutherodactylus richmondi	EF493779	EF493629	-	-
Eleutherodactylus ricordii	EF493541	EF493541	-	-
Eleutherodactylus riparius	EF493786	EF493636	-	-
Eleutherodactylus rivularis	Y10944	Y10944	-	-
Eleutherodactylus rogersi	EF493376	EF493626	-	-
Eleutherodactylus ronaldi	EF493372	EF493603	-	-
Eleutherodactylus rufifemoralis	FJ527415	EF493574 GQ426532 FJ527396	-	-
Eleutherodactylus ruthae	EF493813	EF493653	-	-
Eleutherodactylus schmidti	EF493759	EF493586	-	-
Eleutherodactylus schwartzi	EU186653	EU186653	-	-
Eleutherodactylus sciagraphus	EF493723	EF493551	-	-
Eleutherodactylus simulans	EF493817	EF493656	-	-
Eleutherodactylus sisyphodemus	-	-	-	-
Eleutherodactylus sommeri	EF493773	EF493625	-	-
Eleutherodactylus sp. USNM337773	EU186654	EU186654	-	-
Eleutherodactylus symingtoni	EF493745	-	-	-

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APPENDIX 1. (Continued)

	12S Tval Tleu	16S	28S	C-MYC
Eleutherodactylus thomasi	EF493821	EF493643	-	-
Eleutherodactylus thorectes	EF493370	EF493605	-	-
Eleutherodactylus toa	EF493384	EF493384	-	-
Eleutherodactylus tonyi	EF493774	EF493627	-	-
Eleutherodactylus turquinensis	EF493790	EF493602	-	-
Eleutherodactylus unicolor	EF493776	EF493609	-	-
Eleutherodactylus olibrus	EF493542	EF493542	-	-
Eleutherodactylus varleyi	EF493800	EF493596	-	-
Eleutherodactylus ventrilineatus	EF493818	EF493658	-	-
Eleutherodactylus weinlandi	EF493780	EF493630	-	-
Eleutherodactylus wetmorei	EU186652	EU186652	-	-
Eleutherodactylus wightmanae	EU186651	EU186651	-	-
Eleutherodactylus zeus	EF493718	EF493718	-	-
Eleutherodactylus zugi	EF493347	EF493347	-	-
Flectonotus fitzgeraldi	AY819355 DQ679381	AY819355 DQ679381	-	AY819189 AY819265
Fritziana aff. *fissilis*	AY843589	AY843589	AY844215	-
Gastrotheca cornuta	AY843591	AY843591	-	-
Gastrotheca marsupiata	AY819356 DQ679397	AY819356 DQ679397	-	AY819190
Gastrotheca piperata	AY843590	AY843590	-	-
Haddadus binotatus	EF493361	EF493361	DQ283493	GQ345147 GQ345165
Hemiphractus bubalus	DQ679263 DQ679412	DQ679263 DQ679412	GQ345134	-
Hemiphractus helioi	AY843594	AY843594	-	-
Hemiphractus proboscideus	DQ679303 DQ679413	DQ679303 DQ679413	-	AY819192 AY819266
Holoaden bradei	EF493378	EF493366	-	-
Holoaden luederwaldti	EU186728	EU186710	-	-
Hyla arenicolor	EF566960	EF566960	-	AY819197 AY819271
Hyla chinensis	AY458593	AY458593	-	DQ055761
Hyla cinerea	AY680271	AY680271	AY844241	AY819201 AY819275
Hypodactylus brunneus	EF493357	EF493357	GQ345138	GQ345151
Hypodactylus dolops	EF493394	EF493394	-	-
Hypodactylus elassodiscus	EF493358	EF493358	-	-
Hypodactylus peraccai	EF493710	EF493710	-	-
Ischnocnema guentheri	EF493533	EF493533	-	GQ345163
Ischnocnema hoehnei	EF493359	-	-	-
Ischnocnema holti	EU186740	EU186722	-	-
Ischnocnema juipoca	DQ283093	DQ283093	DQ283495	-

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APPENDIX 1. (Continued)

	12S Tval Tleu	16S	28S	C-MYC
Ischnocnema parva	EF493532	EF493532	-	-
Leptodactylus melanonotus	AY943224 FJ882762	AY943224 FJ882762	-	AY337266 AY337266
Leptodactylus ocellatus	AY843688	AY843688	AY844302	-
Litoria caerulea	AY326038 AY819531	AY326038 AY819531	-	AY819234 AY819308
Litoria infrafrenata	AY843694	AY843694	AY844304	-
Lynchius flavomaculatus	EU186667	-	-	-
Lynchius nebulanastes	EU186704	EU186704	-	AY819320
Lynchius parkeri	EU186705	EU186705	-	-
Lynchius simmonsi	JF809940	JF810004	-	-
Lynchius sp1. MHSNM19914	AM039708	AM039640	-	-
Lynchius sp1. MTD45954	AM039707	AM039639	-	-
Noblella lochites	EU186699	EU186699	-	-
Noblella sp. MTD45180	AM039714	AM039646	-	-
Oreobates amarakaeri	JF809934	JF809996	-	-
Oreobates ayacucho	JF809933	JF809970	-	-
Oreobates barituensis	JF809935	JF809999	-	-
Oreobates choristolemma	JF809921 FJ539072	EU368894 FJ539067	-	-
Oreobates cruralis	EU186666	EU186666	-	-
Oreobates discoidalis	JF809925 FJ539073	EU368896 FJ539068	-	-
Oreobates gemcare	JF809930	JF809960	-	-
Oreobates granulosus	JF809929 FJ539074	EU368897	-	-
Oreobates heterodactylus	JF809923 FJ438816	EU192296 FJ438805	-	-
Oreobates ibischi	FJ438817	FJ438794 FJ438806	-	-
Oreobates lehri	JF809927	JF809957	-	-
Oreobates lundbergi	JF809928	JF809958	-	-
Oreobates machiguenga	JF809932	JF809969	-	-
Oreobates madidi	JF809922 FJ539075	EU368900 FJ539070	-	-
Oreobates pereger	JF809926	JF809955	-	-
Oreobates quixensis	EF493828	EF493662	-	-
Oreobates remotus	-	JN688273	-	-
Oreobates sanctaecrucis	JF809924	JF809951	-	-
Oreobates sanderi	-	EU368904	-	-
Oreobates saxatilis	JF809931	JF809962	-	-
Phrynopus auriculatus	EF493708	EF493708	-	-
Phrynopus barthlenae	AM039721	AM039653	-	-
Phrynopus bracki	EF493709	EF493709	GQ345137	GQ345150 GQ345168

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APPENDIX 1. (Continued)

	12S Tval Tleu	16S	28S	C-MYC
Phrynopus bufoides	AM039713	AM039645	-	-
Phrynopus heimorum	AM039704	AM039635	-	-
Phrynopus horstpauli	AM039715	AM039651	-	-
Phrynopus juninensis	AM039725	AM039657	-	-
Phrynopus kauneorum	AM039718	AM039655	-	-
Phrynopus pesantesi	AM039724	AM039656	-	-
Phrynopus tautzorum	AM039720	AM039652	-	-
Phrynopus tribulosus	EU186725	EU186725	-	-
Phyllomedusa hypochondrialis	AY843724	AY843724	-	-
Phyzelaphryne miriamae	EU186689	EU186689	-	-
Pristimantis acerus	EF493678	EF493678	-	-
Pristimantis achatinus	EF493827	EF493660	-	-
Pristimantis achuar	-	EU130626	-	-
Pristimantis actites	EF493696	-	-	-
Pristimantis acuminatus	-	EU130579	-	-
Pristimantis adiastolus	AY964086	-	-	-
Pristimantis adnus	-	-	-	-
Pristimantis aff. cruentus	-	-	-	-
Pristimantis albertus	EU186695	EU186695	-	-
Pristimantis altae	-	-	-	-
Pristimantis altamazonicus	EF493670	EF493670	-	-
Pristimantis altammnis	-	EU130617	-	-
Pristimantis aniptopalmatus	EF493390	EF493390	-	-
Pristimantis appendiculatus	EF493524	EF493524	-	-
Pristimantis ardalonychus	EU186664	EU186664	-	-
Pristimantis bipunctatus	EF493702	EF493702	-	-
Pristimantis bromeliaceus	EF493351	EF493351	-	-
Pristimantis buckleyi	EF493350	EF493350	-	-
Pristimantis cajamarcensis	EF493823	EF493663	-	-
Pristimantis calcarulatus	EF493523	EF493523	-	-
Pristimantis caprifer	EF493391	EF493391	-	-
Pristimantis caryophyllaceus	EU186686	EU186686	-	-
Pristimantis celator	EF493685	EF493685	-	-
Pristimantis cerasinus	-	FJ784391	-	-
Pristimantis ceuthospilus	EF493520	EF493520	-	-
Pristimantis cf. mendax	EU186659	EU186659	-	-
Pristimantis chalceus	EF493675	EF493675	-	-
Pristimantis chiastonotus	-	EU201061	-	-
Pristimantis chloronotus	AY326007	AY326007	-	-
Pristimantis citriogaster	EF493700	EF493700	-	-
Pristimantis colomai	EF493354	EF493354	-	-
Pristimantis condor	EF493701	EF493701	-	-

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APPENDIX 1. (Continued)

	12S Tval Tleu	16S	28S	C-MYC
Pristimantis conspicillatus	EF493529	EF493529	-	-
Pristimantis cremnobates	EF493528	EF493528	-	-
Pristimantis crenunguis	EF493693	EF493693 EF493666	-	-
Pristimantis croceoinguinis	EF493669	-	-	-
Pristimantis crucifer	EU186736	EU186718	-	-
Pristimantis cruciocularis	EU186656	EU186656	-	-
Pristimantis cruentus	EF493697	EF493697 FJ784557	-	-
Pristimantis cryophilius	EF493672	EF493672	-	-
Pristimantis curtipes	EF493513	EF493513	-	AY819177 AY819256
Pristimantis danae	-	EU192270	-	-
Pristimantis dendrobatoides	EU186735	EU186717	-	-
Pristimantis devillei	EF493688	EF493688	-	-
Pristimantis diadematus	EU186668	EU186668	-	-
Pristimantis dissimulatus	EF493522	EF493522	-	-
Pristimantis duellmani	AY326003	AY326003	-	-
Pristimantis eriphus	EU186671	EU186671	-	-
Pristimantis euphronides	EF493527	EF493527	-	-
Pristimantis fenestratus	EF493703	EF493703	-	-
Pristimantis festae	EF493515	EF493515	-	-
Pristimantis gaigeae	-	FJ784490	-	AY211290 AY211290
Pristimantis galdi	EU186670	EU186670	-	-
Pristimantis gentryi	EF493511	EF493511	-	-
Pristimantis glandulosus	EF493676	EF493676	-	-
Pristimantis imitatrix	EF493824	EF493667	-	-
Pristimantis inguinalis	EU186676	EU186676	-	-
Pristimantis inusitatus	EF493677	EF493677	-	-
Pristimantis kichwarum	-	EU130582	-	-
Pristimantis koehleri	FJ438810	FJ438799	-	-
Pristimantis labiosus	EF493694	EF493694	-	-
Pristimantis lanthanites	EF493695	EF493695	-	-
Pristimantis latidiscus	EF493698	EF493698	-	-
Pristimantis leoni	-	EF493684	-	-
Pristimantis lirellus	EF493521	EF493521	-	-
Pristimantis llojsintuta	-	EU712640	-	-
Pristimantis luteolateralis	EF493517	EF493517	-	-
Pristimantis lymani	EF493392	EF493392	-	-
Pristimantis malkini	EU186663	EU186663	-	-
Pristimantis marmoratus	EU186692	EU186692	-	-
Pristimantis melanogaster	EF493826	EF493664	-	-

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APPENDIX 1. (Continued)

	12S Tval Tleu	16S	28S	C-MYC
Pristimantis minutulus	EU186657	EU186657	-	-
Pristimantis museosus	-	FJ784559	-	-
Pristimantis nyctophylax	EF493526	EF493526	-	-
Pristimantis ockendeni	EF493519	EF493519	-	-
Pristimantis ocreatus	EF493682	EF493682	-	-
Pristimantis orcesi	EF493679	EF493679	-	-
Pristimantis orestes	EF493388	EF493388	-	-
Pristimantis ornatus	EU186660	EU186660	-	-
Pristimantis pardalis	-	FJ784590	-	-
Pristimantis parvillus	EF493352	EF493352	-	-
Pristimantis petrobardus	EF493825	EF493367	-	-
Pristimantis pharangobates	AY843586	AY843586	AY844213	-
Pristimantis phoxocephalus	EF493349	EF493349	-	-
Pristimantis pirrensis	-	-	-	-
Pristimantis platydactylus	-	EU712671	-	-
Pristimantis prolatus	EU186701	EU186701	-	-
Pristimantis pulvinatus	EU186741	EU186723	-	-
Pristimantis pycnodermis	EF493680	EF493680	-	-
Pristimantis pyrrhomerus	EF493683	EF493683	-	-
Pristimantis quaquaversus	-	EU130580	-	-
Pristimantis quinquagesimus	EF493690	EF493690	-	-
Pristimantis reichlei	EF493707	EF493707	-	-
Pristimantis rhabdocnemus	EU186724	EU186706	-	-
Pristimantis rhabdolaemus	EF493706	EF493706	-	-
Pristimantis rhodoplichus	EF493674	EF493674	-	-
Pristimantis ridens	EF493355	EF493355	-	AY211306 AY211306
Pristimantis riveti	EF493348	EF493348	-	-
Pristimantis rozei	EF493691	EF493691	-	-
Pristimantis sagittulus	EF493705	EF493705	-	-
Pristimantis saltissimus	EU186693	EU186693	-	-
Pristimantis samaipatae	FJ438814	FJ438803	-	-
Pristimantis schultei	EF493681	EF493681	-	-
Pristimantis shrevei	EF493692	EF493692	-	-
Pristimantis simonbolivari	EF493671	EF493671	-	-
Pristimantis simonsii	EU186665	EU186665	-	AY819321 AY819314
Pristimantis skydmainos	EF493393	EF493393	-	-
Pristimantis sp. (ROM 43978)	EU186678	EU186678	-	-
Pristimantis sp. KU179221	EU186700	EU186700	-	-
Pristimantis sp. KU202623	AY326002	AY326002	-	-
Pristimantis sp. KU218140	EU186661	EU186661	-	-
Pristimantis sp. KU291666	EU186694	EU186694	-	-

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APPENDIX 1. (Continued)

	12S Tval Tleu	16S	28S	C-MYC
Pristimantis sp. LSUMZ16898	EU186690	EU186690	-	-
Pristimantis sp. MTD45201	AM039726	AM039658	-	-
Pristimantis sp. SBH268110	EU186739	EU186721	-	-
Pristimantis spinosus	EF493673	EF493673	-	-
Pristimantis stictogaster	EF493704	EF493704	-	-
Pristimantis subsigillatus	EF493525	EF493525	-	-
Pristimantis supernatis	AY326005	AY326005	-	-
Pristimantis surdus	EF493687	EF493687	-	-
Pristimantis terraebolivaris	EU186650	EU186650	-	-
Pristimantis thymalopsoides	EF493514	EF493514	-	-
Pristimantis thymelensis	EF493516	EF493516	-	-
Pristimantis toftae	EF493353	EF493353	-	-
Pristimantis truebae	EF493512	EF493512	-	-
Pristimantis unistrigatus	EF493387	EF493387	-	-
Pristimantis urichi	EF493699	EF493699	-	-
Pristimantis verecundus	EF493686	EF493686	-	-
Pristimantis versicolor	EF493389	EF493389	-	-
Pristimantis vertebralis	EF493689	EF493689	-	-
Pristimantis w nigrum	AY326004	AY326004	-	-
Pristimantis walkeri	EF493518	EF493518	-	-
Pristimantis wiensi	EF493377	EF493668	-	-
Psychrophrynella guillei	AY843720	AY843720	AY844323	-
Psychrophrynella iatamasi	AM039712	AM039644	-	-
Psychrophrynella saltator	AM039710	AM039642	-	-
Psychrophrynella usurpator	EF493714	EF493714	-	-
Psychrophrynella wettsteini	EU186696	EU186696	GQ345139	GQ345153
Stefania evansi	AY843767	AY843767	AY844353	AY819193 AY819267
Stefania ginesi	DQ679266 DQ679417	DQ679266 DQ679417	-	-
Stefania schuberti	AY843768	AY843768	AY844354	-
Strabomantis anomalus	EF493534	EF493534	-	-
Strabomantis biporcatus	EU186691	EU186691	-	GQ345152
Strabomantis bufoniformis	DQ283165	DQ283165	DQ283555	-
Strabomantis necerus	EF493535	EF493535	-	-
Strabomantis sulcatus	EF493536	EF493536	-	-
Xenopus laevis	NC001573	NC001573	X59734	BC070712
Yunganastes ahskapara	FJ438807	EU192233 FJ438796	-	-
Yunganastes bisignatus	JF809936 FJ438808	EU192235 FJ438797	-	-
Yunganastes fraudator	JF809938	FJ539065	-	-

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APPENDIX 1. (Continued)

	12S Tval Tleu	16S	28S	C-MYC
Yunganastes mercedesae	JF809939 FJ539071	FJ539066	-	-
Yunganastes pluvicanorus	JF809937 FJ438812	EU192247 FJ438801	-	-
	COI	CXCR4	CYTB	HH3
Acris crepitans	-	EF107468	AY843782	DQ284107
Adelophryne patamona	-	GQ345185	GQ345201	GQ345215
Agalychnis callidryas	FJ766570	-	-	DQ284401
Barycholos pulcher	-	-	-	-
Barycholos ternetzi	-	-	-	DQ284144
Brachycephalus alipioi	-	-	HQ435703	-
Brachycephalus brunneus	-	GQ345187	HQ435704	-
Brachycephalus didactylus	-	-	HQ435705	-
Brachycephalus ephippium	-	GQ345180	HQ435706	GQ345212
Brachycephalus ferruginus	-	-	HQ435708	-
Brachycephalus garbeanus	-	-	HQ435707	-
Brachycephalus hermogenesi	-	-	HQ435709	-
Brachycephalus izecksohni	-	-	HQ435710	-
Brachycephalus nodoterga	-	-	HQ435711	-
Brachycephalus pernix	-	-	HQ435712	-
Brachycephalus pitanga	-	-	HQ435713	-
Brachycephalus pombali	-	-	HQ435714	-
Brachycephalus toby	-	-	HQ435715	-
Brachycephalus vertebralis	-	-	HQ435716	-
Bryophryne cophites	-	-	-	-
Calyptocephalella gayi	-	EF107495	-	DQ284415
Ceuthomantis smaragdinus	-	GQ345190	GQ345206	GQ345220
Craugastor aff. azueroensis	FJ766636	-	-	-
Craugastor alfredi	-	-	-	DQ284318
Craugastor andi	-	-	EF629473	-
Craugastor angelicus	-	-	-	-
Craugastor augusti	-	-	-	DQ284291
Craugastor bocourti	-	-	-	-
Craugastor bransfordii	FJ766631	-	-	-
Craugastor cf. augusti	-	-	-	-
Craugastor cf. longirostris	FJ766677 EF629439	-	EF629468	-
Craugastor chac	-	-	-	-
Craugastor crassidigitus	FJ766638 EF629407	-	EF629471	-
Craugastor sp. MVUP1863	EF629425	-	-	-
Craugastor cuaquero	EF629438	-	EF629472	-
Craugastor daryi	-	-	-	-

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APPENDIX 1. (Continued)

	COI	CXCR4	CYTB	HH3
Craugastor emcelae	-	-	-	-
Craugastor fitzingeri	FJ766646 EF629416	-	EF629469	-
Craugastor fleischmanni	EF629424	-	EF629470	-
Craugastor gollmeri	FJ766654	-	-	-
Craugastor laticeps	-	-	-	-
Craugastor lauraster	-	-	-	-
Craugastor lineatus	-	-	-	-
Craugastor loki	-	-	-	-
Craugastor longirostris	DQ350199	-	EF635373	-
Craugastor megacephalus	FJ766657	-	EF635374	-
Craugastor melanostictus	EF629437	-	-	-
Craugastor mexicanus	-	-	-	-
Craugastor mimus	-	-	-	-
Craugastor montanus	-	-	-	-
Craugastor noblei	FJ766666	-	-	-
Craugastor obsesus	-	-	-	-
Craugastor omiltemanus	-	-	-	-
Craugastor persimilis	-	-	-	-
Craugastor podiciferus	-	GQ345182	GQ345197	-
Craugastor polyptychus	-	-	-	-
Craugastor punctariolus	FJ766667	-	-	DQ284206
Craugastor pygmaeus	-	-	-	-
Craugastor raniformis	EF629426	-	EF629461	-
Craugastor ranoides	-	-	DQ350246	DQ284154
Craugastor rhodopis	-	-	-	DQ284317
Craugastor rugulosus	-	-	-	-
Craugastor rupinius	-	-	-	-
Craugastor saltator	-	-	-	-
Craugastor sandersoni	-	-	-	-
Craugastor sp. EU186675	-	-	-	-
Craugastor sp. EU186697	-	-	-	-
Craugastor sp. EU186698	-	-	-	-
Craugastor sp. EU186703	-	-	-	-
Craugastor sp. FMNH257689	EF562391	-	-	-
Craugastor sp. UTAA 55247	-	-	-	-
Craugastor spatulatus	-	-	-	-
Craugastor stejnegerianus	EF562411	-	-	-
Craugastor stuarti	-	-	-	-
Craugastor tabasarae	EF629428	-	EF629467	-
Craugastor talamancae	FJ766693 EF629433	-	EF629457	-
Craugastor tarahumaraensis	-	-	-	-

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APPENDIX 1. (Continued)

	COI	CXCR4	CYTB	HH3
Craugastor trachydermus	-	-	-	-
Craugastor underwoodi	EF562394	-	-	-
Craugastor uno	-	-	-	-
Craugastor xucanebi	-	-	-	-
Cryptobatrachus boulengeri	-	-	-	-
Cryptobatrachus fuhrmanni	-	-	-	-
Diasporus citrinobapheus	FJ766810	-	-	-
Diasporus diastema	-	GQ345184	GQ345200	GQ345214
Diasporus quidditus	-	-	-	-
Eleutherodactylus abbotti	-	-	-	-
Eleutherodactylus acmonis	-	-	-	-
Eleutherodactylus albipes	-	-	-	-
Eleutherodactylus alcoae	-	-	-	-
Eleutherodactylus alticola	-	-	-	-
Eleutherodactylus amadeus	-	-	-	-
Eleutherodactylus amplinympha	-	-	-	-
Eleutherodactylus andrewsi	-	-	-	-
Eleutherodactylus antillensis	-	-	-	-
Eleutherodactylus apostates	-	-	-	-
Eleutherodactylus armstrongi	-	-	-	-
Eleutherodactylus atkinsi	-	-	-	-
Eleutherodactylus audanti	-	-	-	-
Eleutherodactylus auriculatoides	-	-	-	-
Eleutherodactylus auriculatus	-	-	GQ426512	-
Eleutherodactylus bakeri	-	-	-	-
Eleutherodactylus barlagnei	-	-	-	-
Eleutherodactylus bartonsmithi	GQ357661	-	GQ426514	-
Eleutherodactylus blairhedgesi	-	-	-	-
Eleutherodactylus bothroboans	-	-	-	-
Eleutherodactylus bresslerae	-	-	-	-
Eleutherodactylus brevirostris	-	-	-	-
Eleutherodactylus brittoni	-	-	-	-
Eleutherodactylus caribe	-	-	HQ831645	-
Eleutherodactylus casparii	-	-	HQ831543	-
Eleutherodactylus cavernicola	-	-	-	-
Eleutherodactylus cf. auriculatus	GQ357659	-	-	-
Eleutherodactylus cf. varleyi	-	-	-	-
Eleutherodactylus chlorophenax	-	-	-	-
Eleutherodactylus cochranae	-	-	-	-
Eleutherodactylus cooki	-	-	HQ831648	GQ345213
Eleutherodactylus coqui	-	EF107500	EF637038	-
Eleutherodactylus corona	-	-	-	-

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APPENDIX 1. (Continued)

	COI	CXCR4	CYTB	HH3
Eleutherodactylus counouspeus	-	-	-	-
Eleutherodactylus cubanus	-	-	-	-
Eleutherodactylus cundalli	-	-	-	-
Eleutherodactylus cuneatus	-	-	-	-
Eleutherodactylus darlingtoni	-	-	-	-
Eleutherodactylus dilatus	-	-	-	-
Eleutherodactylus dimidiatus	-	-	-	-
Eleutherodactylus dolomedes	-	-	-	-
Eleutherodactylus eileenae	GQ357665	-	GQ426518	-
Eleutherodactylus emiliae	-	-	-	-
Eleutherodactylus eneidae	-	-	-	-
Eleutherodactylus etheridgei	-	-	-	-
Eleutherodactylus eunaster	-	-	-	-
Eleutherodactylus flavescens	-	-	-	-
Eleutherodactylus fowleri	-	-	-	-
Eleutherodactylus furcyensis	-	-	-	-
Eleutherodactylus fuscus	-	-	-	-
Eleutherodactylus glamyrus	GQ357662	-	GQ426515	-
Eleutherodactylus glandulifer	-	-	-	-
Eleutherodactylus glanduliferoides	-	-	-	-
Eleutherodactylus glaphycompus	-	-	-	-
Eleutherodactylus glaucoreius	-	-	-	-
Eleutherodactylus goini	-	-	HQ831546	-
Eleutherodactylus gossei	-	-	HQ831646	-
Eleutherodactylus grabhami	-	-	-	-
Eleutherodactylus grahami	-	-	-	-
Eleutherodactylus greyi	-	-	-	-
Eleutherodactylus griphus	-	-	-	-
Eleutherodactylus gryllus	-	-	-	-
Eleutherodactylus guanahacabibes	-	-	HQ831553	-
Eleutherodactylus guantanamera	-	-	-	-
Eleutherodactylus gundlachi	-	-	-	-
Eleutherodactylus haitianus	-	-	-	-
Eleutherodactylus hedricki	-	-	-	-
Eleutherodactylus heminota	-	-	-	-
Eleutherodactylus hypostenor	-	-	-	-
Eleutherodactylus iberia	-	-	-	-
Eleutherodactylus inoptatus	-	-	HQ831644	-
Eleutherodactylus intermedius	-	-	-	-
Eleutherodactylus ionthus	-	-	-	-
Eleutherodactylus jamaicensis	-	-	-	-
Eleutherodactylus jaumei	-	-	-	-

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APPENDIX 1. (Continued)

	COI	CXCR4	CYTB	HH3
Eleutherodactylus johnstonei	-	-	DQ198159	-
Eleutherodactylus juanariveroi	-	-	-	-
Eleutherodactylus jugans	-	-	-	-
Eleutherodactylus junori	-	-	-	-
Eleutherodactylus klinikowskii	-	-	-	-
Eleutherodactylus lamprotes	-	-	-	-
Eleutherodactylus leberi	-	-	-	-
Eleutherodactylus lentus	-	-	-	-
Eleutherodactylus leoncei	-	-	-	-
Eleutherodactylus limbatus	-	-	-	-
Eleutherodactylus locustus	-	-	-	-
Eleutherodactylus luteolus	-	-	HQ831647	-
Eleutherodactylus maestrensis	-	-	-	-
Eleutherodactylus mariposa	GQ357663	-	GQ426516	-
Eleutherodactylus marnockii	-	EF107463	-	DQ284151
Eleutherodactylus martinicensis	-	-	-	-
Eleutherodactylus melacara	-	-	-	-
Eleutherodactylus minutus	-	-	-	-
Eleutherodactylus monensis	-	-	-	-
Eleutherodactylus montanus	-	-	-	-
Eleutherodactylus nitidus	-	-	-	DQ284316
Eleutherodactylus nortoni	-	-	-	-
Eleutherodactylus nubicola	-	-	-	-
Eleutherodactylus orcutti	-	-	-	-
Eleutherodactylus orientalis	-	-	-	-
Eleutherodactylus oxyrhyncus	-	-	-	-
Eleutherodactylus pantoni	-	-	-	-
Eleutherodactylus parabates	-	-	-	-
Eleutherodactylus parapelates	-	-	-	-
Eleutherodactylus patriciae	-	-	-	-
Eleutherodactylus paulsoni	-	-	-	-
Eleutherodactylus pentasyringos	-	-	-	-
Eleutherodactylus pezopetrus	-	-	-	-
Eleutherodactylus pictissimus	-	-	-	-
Eleutherodactylus pinarensis	-	-	-	-
Eleutherodactylus pinchoni	-	-	-	-
Eleutherodactylus pipilans	-	-	-	-
Eleutherodactylus pituinus	-	-	-	-
Eleutherodactylus planirostris	-	-	HQ831615	DQ284294
Eleutherodactylus poolei	-	-	-	-
Eleutherodactylus portoricensis	-	-	EF636947	-
Eleutherodactylus principalis	GQ357660	-	GQ426513	-

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APPENDIX 1. (Continued)

	COI	CXCR4	CYTB	HH3
Eleutherodactylus probolaeus	-	-	-	-
Eleutherodactylus rhodesi	-	-	-	-
Eleutherodactylus richmondi	-	-	-	-
Eleutherodactylus ricordii	-	-	-	-
Eleutherodactylus riparius	-	-	-	-
Eleutherodactylus rivularis	-	-	-	-
Eleutherodactylus rogersi	-	-	HQ831623	-
Eleutherodactylus ronaldi	GQ357664	-	GQ426517	-
Eleutherodactylus rufifemoralis	-	-	-	-
Eleutherodactylus ruthae	-	-	-	-
Eleutherodactylus schmidti	-	-	-	-
Eleutherodactylus schwartzi	-	-	-	-
Eleutherodactylus sciagraphus	-	-	-	-
Eleutherodactylus simulans	-	-	HQ831629	-
Eleutherodactylus sisyphodemus	-	-	-	-
Eleutherodactylus sommeri	-	-	-	-
Eleutherodactylus sp. USNM337773	-	-	-	-
Eleutherodactylus symingtoni	-	-	-	-
Eleutherodactylus thomasi	-	-	-	-
Eleutherodactylus thorectes	-	-	HQ831649	-
Eleutherodactylus toa	-	-	-	-
Eleutherodactylus tonyi	-	-	HQ831643	-
Eleutherodactylus turquinensis	-	-	-	-
Eleutherodactylus unicolor	-	-	-	-
Eleutherodactylus olibrus	-	-	-	-
Eleutherodactylus varleyi	-	-	-	-
Eleutherodactylus ventrilineatus	-	-	-	-
Eleutherodactylus weinlandi	-	-	-	-
Eleutherodactylus wetmorei	-	-	-	-
Eleutherodactylus wightmanae	-	-	-	-
Eleutherodactylus zeus	-	-	-	-
Eleutherodactylus zugi	-	-	-	-
Flectonotus fitzgeraldi	-	GQ345177	-	-
Fritziana aff. fissilis	-	-	AY843809	-
Gastrotheca cornuta	FJ766706	-	AY843811	-
Gastrotheca marsupiata	-	-	-	-
Gastrotheca piperata	-	-	AY843810	DQ284069
Haddadus binotatus	-	GQ345183	GQ345198	DQ284142
Hemiphractus bubalus	-	GQ345179	-	-
Hemiphractus helioi	-	-	AY843813	DQ284084
Hemiphractus proboscideus	-	-	-	-
Holoaden bradei	-	-	-	-

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APPENDIX 1. (Continued)

	COI	CXCR4	CYTB	HH3
Holoaden luederwaldti	-	-	-	-
Hyla arenicolor	-	AY364190	AY843824	-
Hyla chinensis	AY458593	-	AY458593	-
Hyla cinerea	FJ226785	DQ306493	AY843846	DQ284057
Hypodactylus brunneus	-	GQ345187	GQ345203	GQ345218
Hypodactylus dolops	-	-	-	-
Hypodactylus elassodiscus	-	-	-	-
Hypodactylus peraccai	-	-	-	-
Ischnocnema guentheri	-	GQ345181	GQ345196	-
Ischnocnema hoehnei	-	-	-	-
Ischnocnema holti	-	-	-	-
Ischnocnema juipoca	-	-	-	DQ284143
Ischnocnema parva	-	-	HQ435717	-
Leptodactylus melanonotus	-	AY364194	-	-
Leptodactylus ocellatus	-	DQ306492	AY843934	DQ284104
Litoria caerulea	-	AY948783	AY843938	-
Litoria infrafrenata	FJ952337	GQ365990	AY843940	-
Lynchius flavomaculatus	-	-	-	-
Lynchius nebulanastes	-	-	-	-
Lynchius parkeri	-	-	-	-
Lynchius simmonsi	-	-	-	-
Lynchius sp1. MHSNM19914	-	-	-	-
Lynchius sp1. MTD45954	-	-	-	-
Noblella lochites	-	-	-	-
Noblella sp. MTD45180	-	-	-	-
Oreobates amarakaeri	-	-	-	-
Oreobates ayacucho	-	-	-	-
Oreobates barituensis	-	-	-	-
Oreobates choristolemma	-	-	-	-
Oreobates cruralis	-	-	-	-
Oreobates discoidalis	-	-	-	-
Oreobates gemcare	-	-	-	-
Oreobates granulosus	-	-	-	-
Oreobates heterodactylus	-	-	-	-
Oreobates ibischi	-	-	-	-
Oreobates lehri	-	-	-	-
Oreobates lundbergi	-	-	-	-
Oreobates machiguenga	-	-	-	-
Oreobates madidi	-	-	-	-
Oreobates pereger	-	-	-	-
Oreobates quixensis	-	-	-	-
Oreobates remotus	-	-	-	-

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APPENDIX 1. (Continued)

	COI	CXCR4	CYTB	HH3
Oreobates sanctaecrucis	-	-	-	-
Oreobates sanderi	-	-	-	-
Oreobates saxatilis	-	-	-	DQ284091
Phrynopus auriculatus	-	-	-	-
Phrynopus barthlenae	-	-	-	-
Phrynopus bracki	-	GQ345186	GQ345202	GQ345217
Phrynopus bufoides	-	-	-	-
Phrynopus heimorum	-	-	-	-
Phrynopus horstpauli	-	-	-	-
Phrynopus juninensis	-	-	-	-
Phrynopus kauneorum	-	-	-	-
Phrynopus pesantesi	-	-	-	-
Phrynopus tautzorum	-	-	-	-
Phrynopus tribulosus	-	-	-	-
Phyllomedusa hypochondrialis	-	AY948786	AY843969	GQ345210
Phyzelaphryne miriamae	-	-	-	-
Pristimantis acerus	-	-	-	-
Pristimantis achatinus	-	-	-	-
Pristimantis achuar	-	-	EU130679	-
Pristimantis actites	-	-	-	-
Pristimantis acuminatus	-	-	-	-
Pristimantis adiastolus	-	-	-	-
Pristimantis adnus	-	-	-	-
Pristimantis aff. cruentus	-	-	-	-
Pristimantis albertus	-	-	-	-
Pristimantis altae	-	-	-	-
Pristimantis altamazonicus	-	-	-	-
Pristimantis altammnis	-	-	EU130665	-
Pristimantis aniptopalmatus	-	-	-	-
Pristimantis appendiculatus	-	-	-	-
Pristimantis ardalonychus	-	-	-	-
Pristimantis bipunctatus	-	-	-	-
Pristimantis bromeliaceus	-	-	-	-
Pristimantis buckleyi	-	-	-	-
Pristimantis cajamarcensis	-	-	-	-
Pristimantis calcarulatus	-	-	-	-
Pristimantis caprifer	-	-	-	-
Pristimantis caryophyllaceus	FJ766774	-	-	-
Pristimantis celator	-	-	-	-
Pristimantis cerasinus	FJ766776	-	-	-
Pristimantis ceuthospilus	-	-	-	-
Pristimantis cf. mendax	-	-	-	-

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APPENDIX 1. (Continued)

	COI	CXCR4	CYTB	HH3
Pristimantis chalceus	-	-	-	-
Pristimantis chiastonotus	-	-	-	-
Pristimantis chloronotus	-	-	-	-
Pristimantis citriogaster	-	-	-	-
Pristimantis colomai	-	-	-	-
Pristimantis condor	-	-	-	-
Pristimantis conspicillatus	-	-	-	-
Pristimantis cremnobates	-	-	-	-
Pristimantis crenunguis	-	-	-	-
Pristimantis croceoinguinis	-	-	-	-
Pristimantis crucifer	-	-	-	-
Pristimantis cruciocularis	-	-	-	-
Pristimantis cruentus	FJ766786	AY948792	-	GQ345216
Pristimantis cryophilius	-	-	-	-
Pristimantis curtipes	-	-	-	-
Pristimantis danae	-	-	EF636950	-
Pristimantis dendrobatoides	-	-	-	-
Pristimantis devillei	-	-	-	-
Pristimantis diadematus	-	-	-	-
Pristimantis dissimulatus	-	-	-	-
Pristimantis duellmani	-	-	-	-
Pristimantis eriphus	-	-	-	-
Pristimantis euphronides	-	-	-	-
Pristimantis fenestratus	-	-	EF636949	-
Pristimantis festae	-	-	-	-
Pristimantis gaigeae	FJ766792	-	-	-
Pristimantis galdi	-	-	-	-
Pristimantis gentryi	-	-	-	-
Pristimantis glandulosus	-	-	-	-
Pristimantis imitatrix	-	-	-	-
Pristimantis inguinalis	-	-	-	-
Pristimantis inusitatus	-	-	-	-
Pristimantis kichwarum	-	-	EF581021	-
Pristimantis koehleri	-	-	-	-
Pristimantis labiosus	-	-	-	-
Pristimantis lanthanites	-	-	-	-
Pristimantis latidiscus	-	-	-	-
Pristimantis leoni	-	-	-	-
Pristimantis lirellus	-	-	-	-
Pristimantis llojsintuta	-	-	-	-
Pristimantis luteolateralis	-	-	-	-
Pristimantis lymani	-	-	-	-

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APPENDIX 1. (Continued)

	COI	CXCR4	CYTB	HH3
Pristimantis malkini	-	-	-	-
Pristimantis marmoratus	-	-	-	-
Pristimantis melanogaster	-	-	-	-
Pristimantis minutulus	-	-	-	-
Pristimantis museosus	FJ766799	-	-	-
Pristimantis nyctophylax	-	-	-	-
Pristimantis ockendeni	-	-	-	-
Pristimantis ocreatus	-	-	-	-
Pristimantis orcesi	-	-	-	-
Pristimantis orestes	-	-	-	-
Pristimantis ornatus	-	-	-	-
Pristimantis pardalis	FJ766804	-	-	-
Pristimantis parvillus	-	-	-	-
Pristimantis petrobardus	-	-	-	-
Pristimantis pharangobates	-	-	-	-
Pristimantis phoxocephalus	-	-	-	-
Pristimantis pirrensis	-	-	-	-
Pristimantis platydactylus	-	-	EF636948	-
Pristimantis prolatus	-	-	-	-
Pristimantis pulvinatus	-	-	-	-
Pristimantis pycnodermis	-	-	-	-
Pristimantis pyrrhomerus	-	-	-	-
Pristimantis quaquaversus	-	-	EU130578	-
Pristimantis quinquagesimus	-	-	-	-
Pristimantis reichlei	-	-	-	-
Pristimantis rhabdocnemus	-	-	-	-
Pristimantis rhabdolaemus	-	-	-	-
Pristimantis rhodoplichus	-	-	-	-
Pristimantis ridens	FJ766808	-	-	-
Pristimantis riveti	-	-	-	-
Pristimantis rozei	-	-	-	-
Pristimantis sagittulus	-	-	-	-
Pristimantis saltissimus	-	-	-	-
Pristimantis samaipatae	-	-	EU368890	-
Pristimantis schultei	-	-	-	-
Pristimantis shrevei	-	-	-	-
Pristimantis simonbolivari	-	-	-	-
Pristimantis simonsii	-	-	-	-
Pristimantis skydmainos	-	-	-	-
Pristimantis sp. (ROM 43978)	-	-	-	-
Pristimantis sp. KU179221	-	-	-	-
Pristimantis sp. KU202623	-	-	-	-

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APPENDIX 1. (Continued)

	COI	CXCR4	CYTB	HH3
Pristimantis sp. KU218140	-	-	-	-
Pristimantis sp. KU291666	-	-	-	-
Pristimantis sp. LSUMZ16898	-	-	-	-
Pristimantis sp. MTD45201	-	-	-	-
Pristimantis sp. SBH268110	-	-	-	-
Pristimantis spinosus	-	-	-	-
Pristimantis stictogaster	-	-	-	-
Pristimantis subsigillatus	-	-	-	-
Pristimantis supernatis	-	-	-	-
Pristimantis surdus	-	-	-	-
Pristimantis terraebolivaris	-	-	-	-
Pristimantis thymalopsoides	-	-	-	-
Pristimantis thymelensis	-	-	-	-
Pristimantis toftae	-	-	-	-
Pristimantis truebae	-	-	-	-
Pristimantis unistrigatus	-	-	-	-
Pristimantis urichi	-	-	-	-
Pristimantis verecundus	-	-	-	-
Pristimantis versicolor	-	-	-	-
Pristimantis vertebralis	-	-	-	-
Pristimantis wnigrum	-	-	-	-
Pristimantis walkeri	-	-	-	-
Pristimantis wiensi	-	-	-	-
Psychrophrynella guillei	-	-	-	DQ284371
Psychrophrynella iatamasi	-	-	-	-
Psychrophrynella saltator	-	-	-	-
Psychrophrynella usurpator	-	-	GQ345205	-
Psychrophrynella wettsteini	-	GQ345189	-	GQ345219
Stefania evansi	-	-	-	-
Stefania ginesi	-	GQ345178	-	GQ345211
Stefania schuberti	-	-	AY844013	-
Strabomantis anomalus	-	-	-	-
Strabomantis biporcatus	-	GQ345188	GQ345204	-
Strabomantis bufoniformis	FJ766635	-	-	DQ284203
Strabomantis necerus	-	-	-	-
Strabomantis sulcatus	-	-	-	-
Xenopus laevis	NC001573	NM001087212	NC001573	NM001091579
Yunganastes ahskapara	-	-	-	-
Yunganastes bisignatus	-	-	-	-
Yunganastes fraudator	-	-	-	-
Yunganastes mercedesae	-	-	-	-
Yunganastes pluvicanorus	-	-	-	-

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APPENDIX 1. (Continued)

-	NCX1	ND1 ND2 tRNAcyst	POMC	RAG1
Acris crepitans	EF107244	AY819491	AY819109	EF107304 AY844358
Adelophryne patamona	GQ345233	GQ345247	GQ345262	GQ345280 GQ345296 EU186751
Agalychnis callidryas	-	FJ489334	-	AY323765 EF493362
Barycholos pulcher	-	-	-	EU186744
Barycholos ternetzi	-	-	-	-
Brachycephalus alipioi	-	-	-	HQ435718
Brachycephalus brunneus	-	-	-	HQ435719
Brachycephalus didactylus	-	-	-	HQ435720
Brachycephalus ephippium	GQ345228	GQ345243	GQ345256	GQ345275 GQ345290 EU186761
Brachycephalus ferruginus	-	-	-	HQ435723
Brachycephalus garbeanus	-	-	-	HQ435722
Brachycephalus hermogenesi	-	-	-	HQ435724
Brachycephalus izecksohni	-	-	-	HQ435725
Brachycephalus nodoterga	-	-	-	HQ435726
Brachycephalus pernix	-	-	-	HQ435727
Brachycephalus pitanga	-	-	-	HQ435728
Brachycephalus pombali	-	-	-	HQ435729
Brachycephalus toby	-	-	-	HQ435730
Brachycephalus vertebralis	-	-	-	HQ435731
Bryophryne cophites	-	-	-	EF493423
Calyptocephalella gayi	EF107275	AY819471 FJ882734	AY819090	AY583337
Ceuthomantis smaragdinus	GQ345238	GQ345251	GQ345267	GQ345285
Craugastor aff. azueroensis	-	-	-	-
Craugastor alfredi	-	-	-	-
Craugastor andi	-	-	-	-
Craugastor angelicus	-	-	-	-
Craugastor augusti	-	AY273108	-	-
Craugastor bocourti	-	AY273110	-	-
Craugastor bransfordii	-	AY273140	-	-
Craugastor cf. augusti	-	-	-	-
Craugastor cf. longirostris	-	-	-	-
Craugastor chac	-	AY273130	-	-
Craugastor crassidigitus	-	AY273114	-	-
Craugastor sp. MVUP1863	-	-	-	-
Craugastor cuaquero	-	-	-	-

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APPENDIX 1. (Continued)

	NCX1	ND1 ND2 tRNAcyst	POMC	RAG1
Craugastor daryi	-	AY273107	-	EF493452
Craugastor emcelae	-	-	-	-
Craugastor fitzingeri	-	GQ345245 AY273117	-	-
Craugastor fleischmanni	-	-	-	-
Craugastor gollmeri	-	AY273123	-	-
Craugastor laticeps	-	AY273129	-	-
Craugastor lauraster	-	AY273138	-	-
Craugastor lineatus	-	AY273126	-	-
Craugastor loki	-	AY273134	-	-
Craugastor longirostris	-	AY273116	-	EF493454
Craugastor megacephalus	-	AY273111	-	-
Craugastor melanostictus	-	-	-	-
Craugastor mexicanus	-	AY273118	-	-
Craugastor mimus	-	AY273125	-	-
Craugastor montanus	-	AY273121	-	EF493453
Craugastor noblei	-	EU443195	-	-
Craugastor obsesus	-	-	-	-
Craugastor omiltemanus	-	-	-	-
Craugastor persimilis	-	AY273141	-	-
Craugastor podiciferus	GQ345230	AY273135	GQ345258	GQ345277 GQ345292 EF493450
Craugastor polyptychus	-	AY273139	-	-
Craugastor punctariolus	-	-	-	-
Craugastor pygmaeus	-	AY273119	-	EF493451
Craugastor raniformis	-	-	-	-
Craugastor ranoides	-	AY273112	-	-
Craugastor rhodopis	-	AY273133	-	-
Craugastor rugulosus	-	-	-	-
Craugastor rupinius	-	-	-	-
Craugastor saltator	-	AY273122	-	-
Craugastor sandersoni	-	-	-	-
Craugastor sp. EU186675	-	-	-	-
Craugastor sp. EU186697	-	-	-	-
Craugastor sp. EU186698	-	-	-	-
Craugastor sp. EU186703	-	-	-	-
Craugastor sp. FMNH257689	-	-	-	-
Craugastor sp. UTAA 55247	-	AY273120	-	-
Craugastor spatulatus	-	-	-	EU186749
Craugastor stejnegerianus	-	AY273137	-	-
Craugastor stuarti	-	-	-	-

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APPENDIX 1. (Continued)

	NCX1	ND1 ND2 tRNAcyst	POMC	RAG1
Craugastor tabasarae	-	AY273115	-	-
Craugastor talamancae	-	-	-	-
Craugastor tarahumaraensis	-	-	-	-
Craugastor trachydermus	-	AY273106	-	-
Craugastor underwoodi	-	AY273136	-	-
Craugastor uno	-	-	-	EU186748
Craugastor xucanebi	-	-	-	-
Cryptobatrachus boulengeri	-	AY819485	-	-
Cryptobatrachus fuhrmanni	-	-	-	-
Diasporus citrinobapheus	-	-	-	-
Diasporus diastema	GQ345232	-	GQ345261	GQ345279 GQ345295 EU186752
Diasporus quidditus	-	-	-	-
Eleutherodactylus abbotti	-	-	-	EF493412
Eleutherodactylus acmonis	-	-	-	-
Eleutherodactylus albipes	-	-	-	EF493409
Eleutherodactylus alcoae	-	-	-	EF493406
Eleutherodactylus alticola	-	-	-	-
Eleutherodactylus amadeus	-	-	-	-
Eleutherodactylus amplinympha	-	-	-	-
Eleutherodactylus andrewsi	-	-	-	-
Eleutherodactylus antillensis	-	-	-	-
Eleutherodactylus apostates	-	-	-	-
Eleutherodactylus armstrongi	-	-	-	-
Eleutherodactylus atkinsi	-	-	-	-
Eleutherodactylus audanti	-	-	-	-
Eleutherodactylus auriculatoides	-	-	-	-
Eleutherodactylus auriculatus	-	-	-	EF493417
Eleutherodactylus bakeri	-	-	-	-
Eleutherodactylus barlagnei	-	-	-	-
Eleutherodactylus bartonsmithi	-	-	-	GQ426499
Eleutherodactylus blairhedgesi	-	-	-	-
Eleutherodactylus bothroboans	-	-	-	-
Eleutherodactylus bresslerae	-	-	-	-
Eleutherodactylus brevirostris	-	-	-	-
Eleutherodactylus brittoni	-	-	-	-
Eleutherodactylus caribe	-	-	HQ831996	HQ831827 EF493411
Eleutherodactylus casparii	-	-	HQ831915	HQ831746
Eleutherodactylus cavernicola	-	-	-	-
Eleutherodactylus cf. *auriculatus*	-	-	-	GQ426493

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APPENDIX 1. (Continued)

	NCX1	ND1 ND2 tRNAcyst	POMC	RAG1
Eleutherodactylus cf. *varleyi*	-	-	-	EF493408
Eleutherodactylus chlorophenax	-	-	-	-
Eleutherodactylus cochranae	-	-	-	-
Eleutherodactylus cooki	-	-	HQ831999	HQ831830 GQ345294 EF493413
Eleutherodactylus coqui	EF107282	FJ882750	-	EF107341
Eleutherodactylus corona	-	-	-	-
Eleutherodactylus counouspeus	-	-	-	EU186760
Eleutherodactylus cubanus	-	-	-	-
Eleutherodactylus cundalli	-	-	-	-
Eleutherodactylus cuneatus	-	-	-	-
Eleutherodactylus darlingtoni	-	-	-	-
Eleutherodactylus dilatus	-	-	-	-
Eleutherodactylus dimidiatus	-	-	-	-
Eleutherodactylus dolomedes	-	-	-	-
Eleutherodactylus eileenae	-	-	-	GQ426503
Eleutherodactylus emiliae	-	-	-	-
Eleutherodactylus eneidae	-	-	-	-
Eleutherodactylus etheridgei	-	-	-	-
Eleutherodactylus eunaster	-	-	-	-
Eleutherodactylus flavescens	-	-	-	-
Eleutherodactylus fowleri	-	-	-	-
Eleutherodactylus furcyensis	-	-	-	-
Eleutherodactylus fuscus	-	-	-	-
Eleutherodactylus glamyrus	-	-	-	GQ426500
Eleutherodactylus glandulifer	-	-	-	-
Eleutherodactylus glanduliferoides	-	-	-	-
Eleutherodactylus glaphycompus	-	-	-	-
Eleutherodactylus glaucoreius	-	-	-	-
Eleutherodactylus goini	-	-	HQ831918	HQ831749
Eleutherodactylus gossei	-	-	HQ831997	HQ831828 EF493410
Eleutherodactylus grabhami	-	-	-	-
Eleutherodactylus grahami	-	-	-	-
Eleutherodactylus greyi	-	-	-	-
Eleutherodactylus griphus	-	-	-	EF493415
Eleutherodactylus gryllus	-	-	-	-
Eleutherodactylus guanahacabibes	-	-	HQ831925	HQ831752
Eleutherodactylus guantanamera	-	-	-	-
Eleutherodactylus gundlachi	-	-	-	-
Eleutherodactylus haitianus	-	-	-	-

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APPENDIX 1. (Continued)

	NCX1	ND1 ND2 tRNAcyst	POMC	RAG1
Eleutherodactylus hedricki	-	-	-	-
Eleutherodactylus heminota	-	-	-	-
Eleutherodactylus hypostenor	-	-	-	-
Eleutherodactylus iberia	-	-	-	-
Eleutherodactylus inoptatus	-	-	HQ831995	HQ831826 EF493405
Eleutherodactylus intermedius	-	-	-	-
Eleutherodactylus ionthus	-	-	-	-
Eleutherodactylus jamaicensis	-	-	-	-
Eleutherodactylus jaumei	-	-	-	-
Eleutherodactylus johnstonei	-	-	-	-
Eleutherodactylus juanariveroi	-	-	-	-
Eleutherodactylus jugans	-	-	-	-
Eleutherodactylus junori	-	-	-	-
Eleutherodactylus klinikowskii	-	-	-	-
Eleutherodactylus lamprotes	-	-	-	EU186759
Eleutherodactylus leberi	-	-	-	EF493403
Eleutherodactylus lentus	-	-	-	EF493418
Eleutherodactylus leoncei	-	-	-	EF493404
Eleutherodactylus limbatus	-	-	-	-
Eleutherodactylus locustus	-	-	-	-
Eleutherodactylus luteolus	-	-	HQ831998	HQ831829 EU186757
Eleutherodactylus maestrensis	-	-	-	-
Eleutherodactylus mariposa	-	-	-	GQ426501
Eleutherodactylus marnockii	EF107238	FJ882745	-	EF107300 EF493399
Eleutherodactylus martinicensis	-	-	-	EF493419
Eleutherodactylus melacara	-	-	-	-
Eleutherodactylus minutus	-	-	-	-
Eleutherodactylus monensis	-	-	-	-
Eleutherodactylus montanus	-	-	-	-
Eleutherodactylus nitidus	-	-	-	-
Eleutherodactylus nortoni	-	-	-	-
Eleutherodactylus nubicola	-	-	-	-
Eleutherodactylus orcutti	-	-	-	-
Eleutherodactylus orientalis	-	-	-	-
Eleutherodactylus oxyrhyncus	-	-	-	-
Eleutherodactylus pantoni	-	AY273104	-	-
Eleutherodactylus parabates	-	-	-	-
Eleutherodactylus parapelates	-	-	-	-
Eleutherodactylus patriciae	-	-	-	-

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APPENDIX 1. (Continued)

	NCX1	ND1 ND2 tRNAcyst	POMC	RAG1
Eleutherodactylus paulsoni	-	-	-	-
Eleutherodactylus pentasyringos	-	-	-	-
Eleutherodactylus pezopetrus	-	-	-	-
Eleutherodactylus pictissimus	-	-	-	-
Eleutherodactylus pinarensis	-	-	-	-
Eleutherodactylus pinchoni	-	-	-	-
Eleutherodactylus pipilans	-	AY273105	-	-
Eleutherodactylus pituinus	-	-	-	-
Eleutherodactylus planirostris	-	GQ345246	HQ831975	HQ831774 EF493396
Eleutherodactylus poolei	-	-	-	-
Eleutherodactylus portoricensis	-	-	-	-
Eleutherodactylus principalis	-	-	-	GQ426498
Eleutherodactylus probolaeus	-	-	-	-
Eleutherodactylus rhodesi	-	-	-	-
Eleutherodactylus richmondi	-	-	-	EU186758
Eleutherodactylus ricordii	-	-	-	-
Eleutherodactylus riparius	-	-	-	-
Eleutherodactylus rivularis	-	-	-	-
Eleutherodactylus rogersi	-	-	HQ831981	HQ831808
Eleutherodactylus ronaldi	-	-	-	GQ426502
Eleutherodactylus rufifemoralis	-	-	-	-
Eleutherodactylus ruthae	-	-	-	-
Eleutherodactylus schmidti	-	-	-	-
Eleutherodactylus schwartzi	-	-	-	-
Eleutherodactylus sciagraphus	-	-	-	-
Eleutherodactylus simulans	-	-	HQ831986	HQ831813
Eleutherodactylus sisyphodemus	-	-	-	-
Eleutherodactylus sommeri	-	-	-	-
Eleutherodactylus sp. USNM337773	-	-	-	-
Eleutherodactylus symingtoni	-	-	-	-
Eleutherodactylus thomasi	-	-	-	-
Eleutherodactylus thorectes	-	-	HQ832000	HQ831831 EF493416
Eleutherodactylus toa	-	-	-	-
Eleutherodactylus tonyi	-	-	HQ831994	HQ831824
Eleutherodactylus turquinensis	-	-	-	-
Eleutherodactylus unicolor	-	-	-	EF493398
Eleutherodactylus olibrus	-	-	-	-
Eleutherodactylus varleyi	-	-	-	-
Eleutherodactylus ventrilineatus	-	-	-	-
Eleutherodactylus weinlandi	-	-	-	-

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APPENDIX 1. (Continued)

	NCX1	ND1 ND2 tRNAcyst	POMC	RAG1
Eleutherodactylus wetmorei	-	-	-	-
Eleutherodactylus wightmanae	-	-	-	-
Eleutherodactylus zeus	-	-	-	EF493402
Eleutherodactylus zugi	-	-	-	EF493401
Flectonotus fitzgeraldi	GQ345224	AY819486	AY819104	DQ679274
Fritziana aff. fissilis	-	-	-	AY844379
Gastrotheca cornuta	-	DQ679347	DQ679314	DQ679280
Gastrotheca marsupiata	-	AY819487	AY819105	DQ679289
Gastrotheca piperata	-	-	-	AY844380
Haddadus binotatus	GQ345231	-	GQ345259	GQ345278 GQ345293 EF493397
Hemiphractus bubalus	GQ345226	DQ679370	DQ679335	DQ679303
Hemiphractus helioi	-	-	-	AY844382
Hemiphractus proboscideus	-	AY819489	AY819107	DQ679304
Holoaden bradei	-	-	-	EF493449
Holoaden luederwaldti	-	-	-	EU186747
Hyla arenicolor	EF107241	AY819494	AY819112	AY364220 AY844391
Hyla chinensis	-	AY458593 AY458593	DQ055789	-
Hyla cinerea	-	AY819498	AY819116	AY323766
Hypodactylus brunneus	GQ345235	GQ345248	GQ345264	GQ345282 GQ345298 EF493422
Hypodactylus dolops	-	-	-	EF493414
Hypodactylus elassodiscus	-	-	-	-
Hypodactylus peraccai	-	-	-	EF493420
Ischnocnema guentheri	GQ345229	-	GQ345257	GQ345276 GQ345291 EF493407
Ischnocnema hoehnei	-	-	-	-
Ischnocnema holti	-	-	-	-
Ischnocnema juipoca	-	-	-	-
Ischnocnema parva	-	-	-	EF493400
Leptodactylus melanonotus	AY948838	AY948760 AY273099	-	AY364224
Leptodactylus ocellatus	-	-	DQ158259	DQ158343 AY844470
Litoria caerulea	AY948821	AY819531	AY819149	AY323767 EF493446
Litoria infrafrenata	-	GQ366302	-	AY844474
Lynchius flavomaculatus	-	-	-	EU186745

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APPENDIX 1. (Continued)

	NCX1	ND1 ND2 tRNAcyst	POMC	RAG1
Lynchius nebulanastes	-	-	AY819154	-
Lynchius parkeri	-	-	-	-
Lynchius simmonsi	-	-	-	JF809915
Lynchius sp1. MHSNM19914	-	-	-	-
Lynchius sp1. MTD45954	-	-	-	-
Noblella lochites	-	-	-	EU186756
Noblella sp. MTD45180	-	-	-	-
Oreobates amarakaeri	-	-	-	JF809913
Oreobates ayacucho	-	-	-	JF809912
Oreobates barituensis	-	-	-	JF809914
Oreobates choristolemma	-	-	-	JF809881
Oreobates cruralis	-	-	-	EU186743
Oreobates discoidalis	-	-	-	JF809904
Oreobates gemcare	-	-	-	JF809909
Oreobates granulosus	-	-	-	JF809908
Oreobates heterodactylus	-	-	-	JF809902
Oreobates ibischi	-	-	-	-
Oreobates lehri	-	-	-	JF809906
Oreobates lundbergi	-	-	-	JF809907
Oreobates machiguenga	-	-	-	JF809911
Oreobates madidi	-	-	-	JF809901
Oreobates pereger	-	-	-	JF809885
Oreobates quixensis	-	GU168783	-	-
Oreobates remotus	-	-	-	-
Oreobates sanctaecrucis	-	-	-	JF809903
Oreobates sanderi	-	-	-	-
Oreobates saxatilis	-	-	-	JF809910
Phrynopus auriculatus	-	-	-	-
Phrynopus barthlenae	-	-	-	-
Phrynopus bracki	GQ345234	-	GQ345263	GQ345281 GQ345297 EF493421
Phrynopus bufoides	-	-	-	-
Phrynopus heimorum	-	-	-	-
Phrynopus horstpauli	-	-	-	-
Phrynopus juninensis	-	-	-	-
Phrynopus kauneorum	-	-	-	-
Phrynopus pesantesi	-	-	-	-
Phrynopus tautzorum	-	-	-	-
Phrynopus tribulosus	-	-	-	-
Phyllomedusa hypochondrialis	AY948826	AY948748 AY819535	-	AY948929 AY844496

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APPENDIX 1. (Continued)

	NCX1	ND1 ND2 tRNAcyst	POMC	RAG1
Phyzelaphryne miriamae	-	-	-	EU186753
Pristimantis acerus	-	-	-	-
Pristimantis achatinus	-	-	-	-
Pristimantis achuar	-	-	-	-
Pristimantis actites	-	-	-	EF493432
Pristimantis acuminatus	-	-	-	-
Pristimantis adiastolus	-	-	-	-
Pristimantis adnus	-	EU443191	-	-
Pristimantis aff. cruentus	-	EU443193	-	-
Pristimantis albertus	-	-	-	-
Pristimantis altae	-	EU443185	-	-
Pristimantis altamazonicus	-	GU168782	-	EF493441
Pristimantis altammnis	-	-	-	-
Pristimantis aniptopalmatus	-	-	-	-
Pristimantis appendiculatus	-	-	-	-
Pristimantis ardalonychus	-	-	-	-
Pristimantis bipunctatus	-	-	-	EF493430
Pristimantis bromeliaceus	-	-	-	-
Pristimantis buckleyi	-	-	-	-
Pristimantis cajamarcensis	-	-	-	-
Pristimantis calcarulatus	-	-	-	-
Pristimantis caprifer	-	-	-	-
Pristimantis caryophyllaceus	-	-	-	-
Pristimantis celator	-	-	-	-
Pristimantis cerasinus	-	EU443194	-	-
Pristimantis ceuthospilus	-	-	-	-
Pristimantis cf. *mendax*	-	-	-	-
Pristimantis chalceus	-	-	-	-
Pristimantis chiastonotus	-	-	-	-
Pristimantis chloronotus	-	-	-	-
Pristimantis citriogaster	-	-	-	-
Pristimantis colomai	-	-	-	EF493440
Pristimantis condor	-	-	-	EF493443
Pristimantis conspicillatus	-	-	-	EF493437
Pristimantis cremnobates	-	-	-	EF493424
Pristimantis crenunguis	-	-	-	-
Pristimantis croceoinguinis	-	-	-	-
Pristimantis crucifer	-	-	-	-
Pristimantis cruciocularis	-	-	-	-
Pristimantis cruentus	AY948836	FJ882747 EU443186	-	AY948935
Pristimantis cryophilius	-	-	-	-

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APPENDIX 1. (Continued)

	NCX1	ND1 ND2 tRNAcyst	POMC	RAG1
Pristimantis curtipes	-	AY819473	AY819092	DQ679272 EF493435
Pristimantis danae	-	-	-	-
Pristimantis dendrobatoides	-	-	-	-
Pristimantis devillei	-	-	-	-
Pristimantis diadematus	-	-	-	-
Pristimantis dissimulatus	-	-	-	-
Pristimantis duellmani	-	-	-	EF493438
Pristimantis eriphus	-	-	-	-
Pristimantis euphronides	-	-	-	EF493427
Pristimantis fenestratus	-	-	-	-
Pristimantis festae	-	-	-	-
Pristimantis gaigeae	-	-	-	-
Pristimantis galdi	-	-	-	EU186746
Pristimantis gentryi	-	-	-	-
Pristimantis glandulosus	-	-	-	-
Pristimantis imitatrix	-	-	-	-
Pristimantis inguinalis	-	-	-	-
Pristimantis inusitatus	-	-	-	-
Pristimantis kichwarum	-	-	-	-
Pristimantis koehleri	-	-	-	-
Pristimantis labiosus	-	-	-	-
Pristimantis lanthanites	-	-	-	-
Pristimantis latidiscus	-	-	-	-
Pristimantis leoni	-	-	-	EF493433
Pristimantis lirellus	-	-	-	-
Pristimantis llojsintuta	-	-	-	-
Pristimantis luteolateralis	-	-	-	-
Pristimantis lymani	-	-	-	-
Pristimantis malkini	-	-	-	-
Pristimantis marmoratus	-	-	-	-
Pristimantis melanogaster	-	-	-	-
Pristimantis minutulus	-	-	-	-
Pristimantis museosus	-	AY273103	-	-
Pristimantis nyctophylax	-	-	-	EF493425
Pristimantis ockendeni	-	-	-	EF493434
Pristimantis ocreatus	-	-	-	-
Pristimantis orcesi	-	-	-	-
Pristimantis orestes	-	-	-	-
Pristimantis ornatus	-	-	-	-
Pristimantis pardalis	-	AY273102	-	-
Pristimantis parvillus	-	-	-	-

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APPENDIX 1. (Continued)

	NCX1	ND1 ND2 tRNAcyst	POMC	RAG1
Pristimantis petrobardus	-	-	-	-
Pristimantis pharangobates	-	-	-	-
Pristimantis phoxocephalus	-	-	-	-
Pristimantis pirrensis	-	EU443190	-	-
Pristimantis platydactylus	-	-	-	-
Pristimantis prolatus	-	-	-	-
Pristimantis pulvinatus	-	-	-	-
Pristimantis pycnodermis	-	-	-	-
Pristimantis pyrrhomerus	-	-	-	-
Pristimantis quaquaversus	-	-	-	-
Pristimantis quinquagesimus	-	-	-	-
Pristimantis reichlei	-	-	-	EF493436
Pristimantis rhabdocnemus	-	-	-	-
Pristimantis rhabdolaemus	-	-	-	-
Pristimantis rhodoplichus	-	-	-	-
Pristimantis ridens	-	EU443162	-	-
Pristimantis riveti	-	-	-	-
Pristimantis rozei	-	-	-	EF493429
Pristimantis sagittulus	-	-	-	EF493439
Pristimantis saltissimus	-	-	-	-
Pristimantis samaipatae	-	-	-	-
Pristimantis schultei	-	-	-	-
Pristimantis shrevei	-	-	-	-
Pristimantis simonbolivari	-	-	-	-
Pristimantis simonsii	-	-	AY819155	-
Pristimantis skydmainos	-	-	-	-
Pristimantis sp. (ROM 43978)	-	-	-	-
Pristimantis sp. KU179221	-	-	-	-
Pristimantis sp. KU202623	-	-	-	-
Pristimantis sp. KU218140	-	-	-	-
Pristimantis sp. KU291666	-	-	-	-
Pristimantis sp. LSUMZ16898	-	-	-	-
Pristimantis sp. MTD45201	-	-	-	-
Pristimantis sp. SBH268110	-	-	-	-
Pristimantis spinosus	-	-	-	-
Pristimantis stictogaster	-	-	-	EF493445
Pristimantis subsigillatus	-	-	-	-
Pristimantis supernatis	-	-	-	-
Pristimantis surdus	-	-	-	-
Pristimantis terraebolivaris	-	-	-	-
Pristimantis thymalopsoides	-	-	-	-

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APPENDIX 1. (Continued)

	NCX1	ND1 ND2 tRNAcyst	POMC	RAG1
Pristimantis thymelensis	-	-	-	EF493442
Pristimantis toftae	-	-	-	-
Pristimantis truebae	-	-	-	-
Pristimantis unistrigatus	-	-	-	EF493444
Pristimantis urichi	-	-	-	EF493426
Pristimantis verecundus	-	-	-	-
Pristimantis versicolor	-	-	-	EF493431
Pristimantis vertebralis	-	-	-	-
Pristimantis w nigrum	-	-	DQ158260	DQ158344
Pristimantis walkeri	-	-	-	EF493428
Pristimantis wiensi	-	-	-	-
Psychrophrynella guillei	-	-	-	-
Psychrophrynella iatamasi	-	-	-	-
Psychrophrynella saltator	-	-	-	-
Psychrophrynella usurpator	-	-	-	EU186762
Psychrophrynella wettsteini	GQ345237	GQ345250	GQ345266	GQ345284 GQ345300 EU186755
Stefania evansi	-	AY819490	AY819108	DQ679307
Stefania ginesi	GQ345225	DQ679373	DQ679338	DQ679308
Stefania schuberti	-	-	-	DQ679308
Strabomantis anomalus	-	-	-	EF493447
Strabomantis biporcatus	GQ345236	GQ345249	GQ345265	GQ345283 EU186754
Strabomantis bufoniformis	-	-	-	-
Strabomantis necerus	-	-	-	GQ345299
Strabomantis sulcatus	-	-	-	-
Xenopus laevis	X90839	NC001573	M11346	NM001172083
Yunganastes ahskapara	-	-	-	JF809919
Yunganastes bisignatus	-	-	-	JF809918
Yunganastes fraudator	-	-	-	JF809916
Yunganastes mercedesae	-	-	-	JF809920
Yunganastes pluvicanorus	-	-	-	JF809917
	RHOD	SIA	SLC8A3	TYR
Acris crepitans	AY844533	AY844762	EF107403	AY844019
Adelophryne patamona	GQ345302	GQ345312	GQ345331	EU186772
Agalychnis callidryas	AY844537	AY844765	-	DQ283018
Barycholos pulcher	-	-	-	EU186765
Barycholos ternetzi	DQ283810	-	-	DQ282921
Brachycephalus alipioi	-	-	-	HQ435732
Brachycephalus brunneus	-	-	-	HQ435733
Brachycephalus didactylus	-	-	-	HQ435734

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APPENDIX 1. (Continued)

	RHOD	SIA	SLC8A3	TYR
Brachycephalus ephippium	DQ283808	DQ282673	GQ345326	DQ282919
Brachycephalus ferruginus	-	-	-	HQ435737
Brachycephalus garbeanus	-	-	-	HQ435736
Brachycephalus hermogenesi	-	-	-	HQ435738
Brachycephalus izecksohni	-	-	-	HQ435739
Brachycephalus nodoterga	-	-	-	HQ435740
Brachycephalus pernix	-	-	-	HQ435741
Brachycephalus pitanga	-	-	-	HQ435742
Brachycephalus pombali	-	-	-	HQ435743
Brachycephalus toby	-	-	-	HQ435744
Brachycephalus vertebralis	-	-	-	HQ435745
Bryophryne cophites	-	-	-	EF493508
Calyptocephalella gayi	DQ284036	DQ282893	EF107440	-
Ceuthomantis smaragdinus	GQ345305	GQ345317	GQ345336	-
Craugastor aff. azueroensis	-	-	-	-
Craugastor alfredi	-	-	-	-
Craugastor andi	-	-	-	-
Craugastor angelicus	-	-	-	-
Craugastor augusti	DQ283935	DQ282786	-	DQ282963
Craugastor bocourti	-	-	-	-
Craugastor bransfordii	-	-	-	-
Craugastor cf. *augusti*	-	-	-	-
Craugastor cf. *longirostris*	-	-	-	-
Craugastor chac	-	-	-	-
Craugastor crassidigitus	-	-	-	-
Craugastor sp. MVUP1863	-	-	-	-
Craugastor cuaquero	-	-	-	-
Craugastor daryi	-	-	-	EF493480
Craugastor emcelae	-	-	-	-
Craugastor fitzingeri	-	-	-	-
Craugastor fleischmanni	-	-	-	-
Craugastor gollmeri	-	-	-	-
Craugastor laticeps	-	-	-	-
Craugastor lauraster	-	-	-	-
Craugastor lineatus	-	-	-	-
Craugastor loki	-	-	-	-
Craugastor longirostris	-	-	-	EF493482
Craugastor megacephalus	-	-	-	-
Craugastor melanostictus	-	-	-	-
Craugastor mexicanus	-	-	-	-
Craugastor mimus	-	-	-	-
Craugastor montanus	-	-	-	EF493478

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APPENDIX 1. (Continued)

	RHOD	SIA	SLC8A3	TYR
Craugastor noblei	-	-	-	-
Craugastor obsesus	-	-	-	-
Craugastor omiltemanus	-	-	-	-
Craugastor persimilis	-	-	-	-
Craugastor podiciferus	-	-	GQ345328	EF493481
Craugastor polyptychus	-	-	-	-
Craugastor punctariolus	DQ283862	-	-	-
Craugastor pygmaeus	-	-	-	EF493479
Craugastor raniformis	-	-	-	-
Craugastor ranoides	DQ283820	-	-	DQ282928
Craugastor rhodopis	DQ283960	DQ282808	-	DQ282968
Craugastor rugulosus	-	-	-	-
Craugastor rupinius	-	-	-	-
Craugastor saltator	-	-	-	-
Craugastor sandersoni	-	-	-	-
Craugastor sp. EU186675	-	-	-	-
Craugastor sp. EU186697	-	-	-	-
Craugastor sp. EU186698	-	-	-	-
Craugastor sp. EU186703	-	-	-	-
Craugastor sp. FMNH257689	-	-	-	-
Craugastor sp. UTAA 55247	-	-	-	-
Craugastor spatulatus	-	-	-	EU186770
Craugastor stejnegerianus	-	-	-	-
Craugastor stuarti	-	-	-	-
Craugastor tabasarae	-	-	-	-
Craugastor talamancae	-	-	-	-
Craugastor tarahumaraensis	-	-	-	-
Craugastor trachydermus	-	-	-	-
Craugastor underwoodi	-	-	-	-
Craugastor uno	-	-	-	EU186769
Craugastor xucanebi	-	-	-	-
Cryptobatrachus boulengeri	-	-	-	-
Cryptobatrachus fuhrmanni	-	-	-	-
Diasporus citrinobapheus	-	-	-	-
Diasporus diastema	-	GQ34531	GQ345330	EU186773
Diasporus quidditus	-	-	-	-
Eleutherodactylus abbotti	-	-	-	EF493457
Eleutherodactylus acmonis	-	-	-	-
Eleutherodactylus albipes	-	-	-	EF493475
Eleutherodactylus alcoae	-	-	-	EF493469
Eleutherodactylus alticola	-	-	-	-
Eleutherodactylus amadeus	-	-	-	-

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APPENDIX 1. (Continued)

	RHOD	SIA	SLC8A3	TYR
Eleutherodactylus amplinympha	-	-	-	-
Eleutherodactylus andrewsi	-	-	-	-
Eleutherodactylus antillensis	-	-	-	-
Eleutherodactylus apostates	-	-	-	-
Eleutherodactylus armstrongi	-	-	-	-
Eleutherodactylus atkinsi	-	-	-	-
Eleutherodactylus audanti	-	-	-	-
Eleutherodactylus auriculatoides	-	-	-	EF493458
Eleutherodactylus auriculatus	-	-	-	-
Eleutherodactylus bakeri	-	-	-	-
Eleutherodactylus barlagnei	-	-	-	-
Eleutherodactylus bartonsmithi	-	-	-	-
Eleutherodactylus blairhedgesi	-	-	-	-
Eleutherodactylus bothroboans	-	-	-	-
Eleutherodactylus bresslerae	-	-	-	-
Eleutherodactylus brevirostris	-	-	-	-
Eleutherodactylus brittoni	-	-	-	-
Eleutherodactylus caribe	-	-	-	EF493472
Eleutherodactylus casparii	-	-	-	-
Eleutherodactylus cavernicola	-	-	-	-
Eleutherodactylus cf. *auriculatus*	-	-	-	-
Eleutherodactylus cf. *varleyi*	-	-	-	-
Eleutherodactylus chlorophenax	-	-	-	-
Eleutherodactylus cochranae	-	-	-	-
Eleutherodactylus cooki	-	GQ345310	-	EF493455
Eleutherodactylus coqui	-	-	EF107445	-
Eleutherodactylus corona	-	-	-	-
Eleutherodactylus counouspeus	-	-	-	-
Eleutherodactylus cubanus	-	-	-	-
Eleutherodactylus cundalli	-	-	-	-
Eleutherodactylus cuneatus	-	-	-	-
Eleutherodactylus darlingtoni	-	-	-	-
Eleutherodactylus dilatus	-	-	-	-
Eleutherodactylus dimidiatus	-	-	-	-
Eleutherodactylus dolomedes	-	-	-	-
Eleutherodactylus eileenae	-	-	-	-
Eleutherodactylus emiliae	-	-	-	-
Eleutherodactylus eneidae	-	-	-	-
Eleutherodactylus etheridgei	-	-	-	-
Eleutherodactylus eunaster	-	-	-	-
Eleutherodactylus flavescens	-	-	-	-
Eleutherodactylus fowleri	-	-	-	-

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APPENDIX 1. (Continued)

	RHOD	SIA	SLC8A3	TYR
Eleutherodactylus furcyensis	-	-	-	-
Eleutherodactylus fuscus	-	-	-	-
Eleutherodactylus glamyrus	-	-	-	-
Eleutherodactylus glandulifer	-	-	-	-
Eleutherodactylus glanduliferoides	-	-	-	-
Eleutherodactylus glaphycompus	-	-	-	-
Eleutherodactylus glaucoreius	-	-	-	-
Eleutherodactylus goini	-	-	-	-
Eleutherodactylus gossei	-	-	-	EF493466
Eleutherodactylus grabhami	-	-	-	-
Eleutherodactylus grahami	-	-	-	-
Eleutherodactylus greyi	-	-	-	-
Eleutherodactylus griphus	-	-	-	EF493465
Eleutherodactylus gryllus	-	-	-	-
Eleutherodactylus guanahacabibes	-	-	-	-
Eleutherodactylus guantanamera	-	-	-	-
Eleutherodactylus gundlachi	-	-	-	-
Eleutherodactylus haitianus	-	-	-	-
Eleutherodactylus hedricki	-	-	-	-
Eleutherodactylus heminota	-	-	-	-
Eleutherodactylus hypostenor	-	-	-	-
Eleutherodactylus iberia	-	-	-	-
Eleutherodactylus inoptatus	-	-	-	EF493463
Eleutherodactylus intermedius	-	-	-	-
Eleutherodactylus ionthus	-	-	-	-
Eleutherodactylus jamaicensis	-	-	-	-
Eleutherodactylus jaumei	-	-	-	-
Eleutherodactylus johnstonei	-	-	-	-
Eleutherodactylus juanariveroi	-	-	-	-
Eleutherodactylus jugans	-	-	-	-
Eleutherodactylus junori	-	-	-	-
Eleutherodactylus klinikowskii	-	-	-	-
Eleutherodactylus lamprotes	-	-	-	EF493460
Eleutherodactylus leberi	-	-	-	EF493459
Eleutherodactylus lentus	-	-	-	EF493471
Eleutherodactylus leoncei	-	-	-	EF493468
Eleutherodactylus limbatus	-	-	-	-
Eleutherodactylus locustus	-	-	-	-
Eleutherodactylus luteolus	-	-	-	EF493464
Eleutherodactylus maestrensis	-	-	-	-
Eleutherodactylus mariposa	-	-	-	-
Eleutherodactylus marnockii	DQ283817	DQ282677	EF107388	EF493476

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APPENDIX 1. (Continued)

	RHOD	SIA	SLC8A3	TYR
Eleutherodactylus martinicensis	-	-	-	EF493456
Eleutherodactylus melacara	-	-	-	-
Eleutherodactylus minutus	-	-	-	-
Eleutherodactylus monensis	-	-	-	-
Eleutherodactylus montanus	-	-	-	-
Eleutherodactylus nitidus	DQ283959	DQ282807	-	-
Eleutherodactylus nortoni	-	-	-	-
Eleutherodactylus nubicola	-	-	-	-
Eleutherodactylus orcutti	-	-	-	-
Eleutherodactylus orientalis	-	-	-	-
Eleutherodactylus oxyrhyncus	-	-	-	-
Eleutherodactylus pantoni	-	-	-	-
Eleutherodactylus parabates	-	-	-	-
Eleutherodactylus parapelates	-	-	-	-
Eleutherodactylus patriciae	-	-	-	-
Eleutherodactylus paulsoni	-	-	-	-
Eleutherodactylus pentasyringos	-	-	-	-
Eleutherodactylus pezopetrus	-	-	-	-
Eleutherodactylus pictissimus	-	-	-	-
Eleutherodactylus pinarensis	-	-	-	-
Eleutherodactylus pinchoni	-	-	-	-
Eleutherodactylus pipilans	-	-	-	-
Eleutherodactylus pituinus	-	-	-	-
Eleutherodactylus planirostris	DQ283937	DQ282788	-	DQ282964
Eleutherodactylus poolei	-	-	-	-
Eleutherodactylus portoricensis	-	-	-	-
Eleutherodactylus principalis	-	-	-	-
Eleutherodactylus probolaeus	-	-	-	-
Eleutherodactylus rhodesi	-	-	-	-
Eleutherodactylus richmondi	-	-	-	EF493461
Eleutherodactylus ricordii	-	-	-	-
Eleutherodactylus riparius	-	-	-	-
Eleutherodactylus rivularis	-	-	-	-
Eleutherodactylus rogersi	-	-	-	-
Eleutherodactylus ronaldi	-	-	-	-
Eleutherodactylus rufifemoralis	-	-	-	-
Eleutherodactylus ruthae	-	-	-	-
Eleutherodactylus schmidti	-	-	-	-
Eleutherodactylus schwartzi	-	-	-	-
Eleutherodactylus sciagraphus	-	-	-	-
Eleutherodactylus simulans	-	-	-	-
Eleutherodactylus sisyphodemus	-	-	-	-

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APPENDIX 1. (Continued)

	RHOD	SIA	SLC8A3	TYR
Eleutherodactylus sommeri	-	-	-	-
Eleutherodactylus sp. USNM337773	-	-	-	-
Eleutherodactylus symingtoni	-	-	-	-
Eleutherodactylus thomasi	-	-	-	-
Eleutherodactylus thorectes	-	-	-	EF493473
Eleutherodactylus toa	-	-	-	-
Eleutherodactylus tonyi	-	-	-	-
Eleutherodactylus turquinensis	-	-	-	-
Eleutherodactylus unicolor	-	-	-	EF493462
Eleutherodactylus olibrus	-	-	-	-
Eleutherodactylus varleyi	-	-	-	EF493467
Eleutherodactylus ventrilineatus	-	-	-	-
Eleutherodactylus weinlandi	-	-	-	-
Eleutherodactylus wetmorei	-	-	-	-
Eleutherodactylus wightmanae	-	-	-	-
Eleutherodactylus zeus	-	-	-	EF493477
Eleutherodactylus zugi	-	-	-	EF493474
Flectonotus fitzgeraldi	-	-	GQ345322	-
Fritziana aff. *fissilis*	AY844562	AY844788	-	AY844038
Gastrotheca cornuta	-	-	-	AY844040
Gastrotheca marsupiata	-	-	-	AY844039
Gastrotheca piperata	AY844563	AY844789	-	-
Haddadus binotatus	DQ283807	GQ345309	GQ345329	DQ282918
Hemiphractus bubalus	-	-	GQ345324	-
Hemiphractus helioi	AY844566	AY844792	-	-
Hemiphractus proboscideus	-	-	-	-
Holoaden bradei	-	-	-	EU186779
Holoaden luederwaldti	-	-	-	EU186768
Hyla arenicolor	AY844577	AY844802	EF107393	AY844048
Hyla chinensis	-	-	-	-
Hyla cinerea	AY844597	AY844816	-	AY844063
Hypodactylus brunneus	-	GQ345315	GQ345333	EF493484
Hypodactylus dolops	GQ345304	-	-	EF493483
Hypodactylus elassodiscus	-	-	-	-
Hypodactylus peraccai	-	-	-	EF493485
Ischnocnema guentheri	-	GQ345308	GQ345327	EF493510
Ischnocnema hoehnei	-	-	-	-
Ischnocnema holti	-	-	-	-
Ischnocnema juipoca	DQ283809	-	-	DQ282920
Ischnocnema parva	-	-	-	EF493509
Leptodactylus melanonotus	AY364405	-	AY948900	DQ347193
Leptodactylus ocellatus	AY844681	AY844890	-	-

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APPENDIX 1. (Continued)

	RHOD	SIA	SLC8A3	TYR
Litoria caerulea	AY844685	AY844893	AY948877	AY844131
Litoria infrafrenata	AY844687	-	-	-
Lynchius flavomaculatus	-	-	-	EU186766
Lynchius nebulanastes	-	-	-	-
Lynchius parkeri	-	-	-	-
Lynchius simmonsi	-	-	-	JF809894
Lynchius sp1. MHSNM19914	-	-	-	-
Lynchius sp1. MTD45954	-	-	-	-
Noblella lochites	-	-	-	EU186777
Noblella sp. MTD45180	-	-	-	-
Oreobates amarakaeri	-	-	-	JF809891
Oreobates ayacucho	-	-	-	JF809890
Oreobates barituensis	-	-	-	JF809892
Oreobates choristolemma	-	-	-	JF809881
Oreobates cruralis	-	-	-	EU186764
Oreobates discoidalis	-	-	-	JF809884
Oreobates gemcare	-	-	-	-
Oreobates granulosus	-	-	-	JF809887
Oreobates heterodactylus	-	-	-	JF809882
Oreobates ibischi	-	-	-	-
Oreobates lehri	-	-	-	-
Oreobates lundbergi	-	-	-	JF809886
Oreobates machiguenga	JF809911	-	-	JF809889
Oreobates madidi	-	-	-	-
Oreobates pereger	-	-	-	JF809885
Oreobates quixensis	-	-	-	QZ31186
Oreobates remotus	-	-	-	-
Oreobates sanctaecrucis	-	-	-	JF809883
Oreobates sanderi	-	-	-	-
Oreobates saxatilis	DQ283788	DQ282661	-	JF809888
Phrynopus auriculatus	-	-	-	-
Phrynopus barthlenae	-	-	-	-
Phrynopus bracki	GQ345303	GQ345314	GQ345332	EF493507
Phrynopus bufoides	-	-	-	-
Phrynopus heimorum	-	-	-	-
Phrynopus horstpauli	-	-	-	-
Phrynopus juninensis	-	-	-	-
Phrynopus kauneorum	-	-	-	-
Phrynopus pesantesi	-	-	-	-
Phrynopus tautzorum	-	-	-	-
Phrynopus tribulosus	-	-	-	-
Phyllomedusa hypochondrialis	AY844711	AY844916	AY948882	AY844153

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APPENDIX 1. (Continued)

	RHOD	SIA	SLC8A3	TYR
Phyzelaphryne miriamae	-	-	-	EU186774
Pristimantis acerus	-	-	-	-
Pristimantis achatinus	-	-	-	-
Pristimantis achuar	-	-	-	-
Pristimantis actites	-	-	-	EF493494
Pristimantis acuminatus	-	-	-	-
Pristimantis adiastolus	-	-	-	-
Pristimantis adnus	-	-	-	-
Pristimantis aff. cruentus	-	-	-	-
Pristimantis albertus	-	-	-	-
Pristimantis altae	-	-	-	-
Pristimantis altamazonicus	-	-	-	EU186778
Pristimantis altammnis	-	-	-	-
Pristimantis aniptopalmatus	-	-	-	-
Pristimantis appendiculatus	-	-	-	-
Pristimantis ardalonychus	-	-	-	-
Pristimantis bipunctatus	-	-	-	EF493492
Pristimantis bromeliaceus	-	-	-	-
Pristimantis buckleyi	-	-	-	-
Pristimantis cajamarcensis	-	-	-	-
Pristimantis calcarulatus	-	-	-	-
Pristimantis caprifer	-	-	-	-
Pristimantis caryophyllaceus	-	-	-	-
Pristimantis celator	-	-	-	-
Pristimantis cerasinus	-	-	-	-
Pristimantis ceuthospilus	-	-	-	-
Pristimantis cf. mendax	-	-	-	-
Pristimantis chalceus	-	-	-	-
Pristimantis chiastonotus	-	-	-	-
Pristimantis chloronotus	-	-	-	-
Pristimantis citriogaster	-	-	-	-
Pristimantis colomai	-	-	-	EF493502
Pristimantis condor	-	-	-	EF493504
Pristimantis conspicillatus	-	-	-	EF493499
Pristimantis cremnobates	-	-	-	EF493486
Pristimantis crenunguis	-	-	-	-
Pristimantis croceoinguinis	-	-	-	-
Pristimantis crucifer	-	-	-	-
Pristimantis cruciocularis	-	-	-	-
Pristimantis cruentus	-	GQ345313	AY948898	-
Pristimantis cryophilius	-	-	-	-
Pristimantis curtipes	-	-	-	EF493497

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APPENDIX 1. (Continued)

	RHOD	SIA	SLC8A3	TYR
Pristimantis danae	-	-	-	-
Pristimantis dendrobatoides	-	-	-	-
Pristimantis devillei	-	-	-	-
Pristimantis diadematus	-	-	-	-
Pristimantis dissimulatus	-	-	-	-
Pristimantis duellmani	-	-	-	EF493500
Pristimantis eriphus	-	-	-	-
Pristimantis euphronides	-	-	-	EF493489
Pristimantis fenestratus	-	-	-	-
Pristimantis festae	-	-	-	-
Pristimantis gaigeae	-	-	-	-
Pristimantis galdi	-	-	-	EU186767
Pristimantis gentryi	-	-	-	-
Pristimantis glandulosus	-	-	-	-
Pristimantis imitatrix	-	-	-	-
Pristimantis inguinalis	-	-	-	-
Pristimantis inusitatus	-	-	-	-
Pristimantis kichwarum	-	-	-	-
Pristimantis koehleri	-	-	-	-
Pristimantis labiosus	-	-	-	-
Pristimantis lanthanites	-	-	-	-
Pristimantis latidiscus	-	-	-	-
Pristimantis leoni	-	-	-	EF493495
Pristimantis lirellus	-	-	-	-
Pristimantis llojsintuta	-	-	-	-
Pristimantis luteolateralis	-	-	-	-
Pristimantis lymani	-	-	-	-
Pristimantis malkini	-	-	-	-
Pristimantis marmoratus	-	-	-	-
Pristimantis melanogaster	-	-	-	-
Pristimantis minutulus	-	-	-	-
Pristimantis museosus	-	-	-	-
Pristimantis nyctophylax	-	-	-	EF493487
Pristimantis ockendeni	-	-	-	EF493496
Pristimantis ocreatus	-	-	-	-
Pristimantis orcesi	-	-	-	-
Pristimantis orestes	-	-	-	-
Pristimantis ornatus	-	-	-	-
Pristimantis pardalis	-	-	-	-
Pristimantis parvillus	-	-	-	-
Pristimantis petrobardus	-	-	-	-
Pristimantis pharangobates	AY844559	-	-	AY844035

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APPENDIX 1. (Continued)

	RHOD	SIA	SLC8A3	TYR
Pristimantis phoxocephalus	-	-	-	-
Pristimantis pirrensis	-	-	-	-
Pristimantis platydactylus	-	-	-	-
Pristimantis prolatus	-	-	-	-
Pristimantis pulvinatus	-	-	-	-
Pristimantis pycnodermis	-	-	-	-
Pristimantis pyrrhomerus	-	-	-	-
Pristimantis quaquaversus	-	-	-	-
Pristimantis quinquagesimus	-	-	-	-
Pristimantis reichlei	-	-	-	EF493498
Pristimantis rhabdocnemus	-	-	-	-
Pristimantis rhabdolaemus	-	-	-	-
Pristimantis rhodoplichus	-	-	-	-
Pristimantis ridens	-	-	-	-
Pristimantis riveti	-	-	-	-
Pristimantis rozei	-	-	-	EF493491
Pristimantis sagittulus	-	-	-	EF493501
Pristimantis saltissimus	-	-	-	-
Pristimantis samaipatae	-	-	-	-
Pristimantis schultei	-	-	-	-
Pristimantis shrevei	-	-	-	-
Pristimantis simonbolivari	-	-	-	-
Pristimantis simonsii	-	-	-	-
Pristimantis skydmainos	-	-	-	-
Pristimantis sp. (ROM 43978)	-	-	-	EF376158
Pristimantis sp. KU179221	-	-	-	-
Pristimantis sp. KU202623	-	-	-	-
Pristimantis sp. KU218140	-	-	-	-
Pristimantis sp. KU291666	-	-	-	-
Pristimantis sp. LSUMZ16898	-	-	-	-
Pristimantis sp. MTD45201	-	-	-	-
Pristimantis sp. SBH268110	-	-	-	-
Pristimantis spinosus	-	-	-	-
Pristimantis stictogaster	-	-	-	EF493506
Pristimantis subsigillatus	-	-	-	-
Pristimantis supernatis	-	-	-	-
Pristimantis surdus	-	-	-	-
Pristimantis terraebolivaris	-	-	-	-
Pristimantis thymalopsoides	-	-	-	-
Pristimantis thymelensis	-	-	-	EF493503
Pristimantis toftae	-	-	-	-
Pristimantis truebae	-	-	-	-

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APPENDIX 1. (Continued)

	RHOD	SIA	SLC8A3	TYR
Pristimantis unistrigatus	-	-	-	EF493505
Pristimantis urichi	-	-	-	EF493488
Pristimantis verecundus	-	-	-	-
Pristimantis versicolor	-	-	-	EF493493
Pristimantis vertebralis	-	-	-	-
Pristimantis w nigrum	-	-	-	-
Pristimantis walkeri	-	-	-	EF493490
Pristimantis wiensi	-	-	-	-
Psychrophrynella guillei	-	-	-	DQ282995
Psychrophrynella iatamasi	-	-	-	-
Psychrophrynella saltator	-	-	-	-
Psychrophrynella usurpator	-	-	-	EU186780
Psychrophrynella wettsteini	-	GQ345316	GQ345335	EU186776
Stefania evansi	AY844755	AY844950	AY844189	AY844189
Stefania ginesi	-	-	GQ345323	-
Stefania schuberti	AY844756	AY844951	-	-
Strabomantis anomalus	-	-	-	-
Strabomantis biporcatus	-	-	GQ345334	-
Strabomantis bufoniformis	-	DQ282718	-	DQ282942
Strabomantis necerus	-	-	-	-
Strabomantis sulcatus	-	-	-	-
Xenopus laevis	NM001087048	NM001091969	NM001093062	AY341764
Yunganastes ahskapara	-	-	-	JF809898
Yunganastes bisignatus	-	-	-	JF809897
Yunganastes fraudator	-	-	-	JF809895
Yunganastes mercedesae	-	-	-	JF809899
Yunganastes pluvicanorus	-	-	-	JF809896

APPENDIX 2. Taxonomy of Brachycephaloidea (Amphibia: Anura).

SUPERFAMILY: Brachycephaloidea Günther, 1858. Content: 3 families, 1002 species.

Incertae sedis:

Genus: *Atopophrynus* Lynch & Ruiz-Carranza, 1982. Content: 1 species: *A. syntomopus* Lynch & Ruiz-Carranza, 1982.

Genus: *Geobatrachus* Ruthven, 1915. Content: 1 species: *G. walkeri* Ruthven, 1915.

FAMILY: Brachycephalidae Günther, 1858. Content: 2 genera, 54 species.

Genus: *Brachycephalus* Fitzinger, 1826. Content: 21 species: *B. alipioi* Pombal & Gasparini, 2006; *B. atelopoide* Miranda-Ribeiro, 1920; *B. brunneus* Ribeiro, Alves, Haddad & Reis, 2005; *B. bufonoides* Miranda-Ribeiro, 1920; *B. crispus* Condez, Clemente-Carvalho, Haddad & Dos Reis, 2014; *B. didactylus* (Izecksohn, 1971); *B. ephippium* (Spix, 1824); *B. ferruginus* Alves, Ribeiro, Haddad & Reis, 2006; *B. garbeanus* Miranda-Ribeiro, 1920; *B. guarani* Clemente-Carvalho, Giaretta, Condez, Haddad & Reis, 2012; *B. hermogenesi* (Giaretta & Sawaya, 1998); *B. izecksohni* Ribeiro, Alves, Haddad & Reis, 2005; *B. margarititatus* Pombal & Izecksohn, 2011; *B. nodoterga* Miranda-Ribeiro, 1920; *B. pernix* Pombal, Wistuba & Bornschein, 1998; *B. pitanga* Alves, Sawaya, Reis & Haddad, 2009; *B. pombali* Alves, Ribeiro, Haddad & Reis, 2006; *B. pulex* Napoli, Caramaschi, Cruz & Dias, 2011; *B. toby* Haddad, Alves, Clemente-Carvalho & Reis, 2010; *B. tridactylus* Garey, Lima, Hartmann & Haddad, 2012; *B. vertebralis* Pombal, 2001.

Genus: *Ischnocnema* Reinhardt & Lütken, 1862 "1861". Content: 33 species: 4 species series & 2 species unassigned to species series: *I. manezinho* (Garcia, 1996); *I. sambaqui* (Castanho & Haddad, 2000).

***Ischnocnema guentheri* species series.** Content: 10 species: *I. epipeda* (Heyer, 1984); *I. erythromera* (Heyer, 1984); *I. gualteri* (Lutz, 1974); *I. guentheri* (Steindachner, 1864); *I. henselii* (Peters, 1870); *I. hoehnei* (Lutz, 1958); *I. izecksohni* (Caramaschi & Kisteumacher, 1989 "1988"); *I. nasuta* (Lutz, 1925); *I. oea* (Heyer, 1984); *I. venancioi* (Lutz, 1958).

***Ischnocnema lactea* species series.** Content: 10 species: *I. concolor* Targino, Costa & Carvalho-e-Silva, 2009; *I. gehrtii* (Miranda-Ribeiro, 1926); *I. holti* (Cochran, 1948); *I. lactea* (Miranda-Ribeiro, 1923); *I. melanopygia* Targino, Costa & Carvalho-e-Silva, 2009; *I. nigriventris* (Lutz, 1925); *I. paranaensis* (Langone & Segalla, 1996); *I. randorum* (Heyer, 1985); *I. spanios* (Heyer, 1985); *I. vizottoi* Martins & Haddad, 2010.

***Ischnocnema parva* species series.** Content: 3 species: *I. nanahallux* Brusquetti, Thomé, Canedo, Condez & Haddad, 2013; *I. parva* (Girard, 1853); *I. pusilla* (Bokermann, 1967).

***Ischnocnema verrucosa* species series.** Content: 8 species: *I. abdita* Canedo & Pimenta, 2010; *I. bolbodactyla* (Lutz, 1925); *I. juipoca* (Sazima & Cardoso, 1978); *I. karst* Canedo, Targino, Leite & Haddad, 2012; *I. octavioi* (Bokermann, 1965); *I. penaxavantinho* Giaretta, Toffoli & Oliveira, 2007; *I. surda* Canedo, Pimenta, Leite & Caramaschi, 2010; *I. verrucosa* (Reinhardt & Lütken, 1862 "1861").

FAMILY: Craugastoridae Hedges, Duellman & Heinicke, 2008. Content: 3 subfamilies, 18 genera, 742 species.

SUBFAMILY: Craugastorinae Hedges, Duellman & Heinicke, 2008. Content: 3 genera, 132 species.

Genus: *Craugastor* Cope, 1862. Content: 3 subgenera, 113 species.

Subgenus: *Campbellius* Hedges, Duellman & Heinicke, 2008. Content: 13 species: *C. adamastus* (Campbell, 1994); *C. chrysozetetes* (McCranie, Savage & Wilson, 1989); *C. cruzi* (McCranie, Savage & Wilson, 1989); *C. daryi* (Ford & Savage, 1984); *C. epochthidius* (McCranie & Wilson, 1997); *C. fecundus* (McCranie & Wilson, 1997); *C. matudai* (Taylor, 1941); *C. milesi* (Schmidt, 1933); *C. myllomyllon* (Savage, 2000); *C. omoaensis* (McCranie & Wilson, 1997); *C. saltuarius* (McCranie & Wilson, 1997); *C. stadelmani* (Schmidt, 1936); *C. trachydermus* (Campbell, 1994).

Subgenus: *Craugastor* Cope, 1862. Content: 8 species series, 79 species.

***Craugastor (Craugastor) fitzingeri* species series.** Content: 2 species groups, 15 species.

Craugastor (Craugastor) fitzingeri species group: Content: 8 species: *C. chingopetaca* Köhler & Sunyer, 2006; *C. crassidigitus* (Taylor, 1952); *C. fitzingeri* (Schmidt, 1857); *C. longirostris* (Boulenger, 1898); *C. raniformis* (Boulenger, 1896); *C. tabasarae* (Savage, Hollingsworth, Lips & Jaslow, 2004); *C. talamancae* (Dunn, 1931); *C. taurus* (Taylor, 1958).

Craugastor (Craugastor) melanostictus species group: Content: 7 species: *C. andi* (Savage, 1974); *C. cuaquero* (Savage, 1980); *C. emcelae* (Lynch, 1985); *C. melanostictus* (Cope, 1875 "1876"); *C. monnichorum* (Dunn, 1940); *C. phasma* (Lips & Savage, 1996); *C. rayo* (Savage & DeWeese, 1979).

***Craugastor (Craugastor) mexicanus* species series.** Content: 7 species: *C. hobartsmithi* (Taylor, 1937 "1936"); *C. mexicanus* (Brocchi, 1877); *C. montanus* (Taylor, 1942); *C. occidentalis* (Taylor, 1941); *C. omiltemanus* (Günther, 1900); *C. pygmaeus* (Taylor, 1937 "1936"); *C. saltator* (Taylor, 1941).

***Craugastor (Craugastor) rhodopis* species series.** Content: 2 species groups, 10 species.

Craugastor (Craugastor) podiciferus species group: Content: 8 species: *C. bransfordii* (Cope, 1886); *C. jota* (Lynch, 1980); *C. lauraster* (Savage, McCranie & Espinal, 1996); *C. persimilis* (Barbour, 1926); *C. podiciferus* (Cope, 1875 "1876"); *C. polyptychus* (Cope, 1886); *C. stejnegerianus* (Cope, 1893); *C. underwoodi* (Boulenger, 1896).

Craugastor (Craugastor) rhodopis species group: Content: 2 species: *C. loki* (Shannon & Werler, 1955); *C. rhodopis* (Cope, 1867 "1866").

***Craugastor (Craugastor) punctariolus* species series.** Content: 38 species: *C. aphanus* (Campbell, 1994); *C. amniscola* (Campbell & Savage, 2000); *C. anciano* (Savage, McCranie & Wilson, 1988); *C. angelicus* (Savage, 1975); *C. aurilegulus* (Savage, McCranie & Wilson, 1988); *C. azueroensis* (Savage, 1975); *C. berkenbuschii* (Peters, 1870 "1869"); *C. brocchi* (Boulenger, 1882); *C. catalinae* (Campbell & Savage, 2000); *C. charadra* (Campbell & Savage, 2000); *C. emleni* (Dunn, 1932); *C. escoces* (Savage, 1975); *C. evanesco* Ryan, Savage, Lips & Giermakowski, 2010; *C. fleischmanni* (Boettger, 1892); *C. inachus* (Campbell & Savage, 2000); *C. gulosus* (Cope, 1875 "1876"); *C. laevissimus* (Werner, 1896); *C. megacephalus* (Cope, 1875 "1876")[9]; *C. merendonensis* (Schmidt, 1933); *C. obesus* (Barbour, 1928); *C. olanchano* (McCranie & Wilson, 1999); *C. opimus* (Savage & Myers, 2002); *C. palenque* (Campbell & Savage, 2000); *C. pechorum* (McCranie & Wilson, 1999); *C. pelorus* (Campbell & Savage, 2000); *C. pozo* (Johnson & Savage, 1995); *C. psephosypharus* (Campbell, Savage & Meyer, 1994); *C. punctariolus* (Peters, 1863); *C. ranoides* (Cope, 1886); *C. rhyacobatrachus* (Campbell & Savage, 2000); *C. rivulus* (Campbell & Savage, 2000); *C. rugosus* (Peters, 1873); *C. rugulosus* (Cope, 1870 "1869"); *C. rupinius* (Campbell & Savage, 2000); *C. sabrinus* (Campbell & Savage, 2000; *C. sandersoni* (Schmidt, 1941); *C. vocalis* (Taylor, 1940); *C. vulcani* (Shannon & Werler, 1955).

In the subgenus *Craugastor* but unassigned to species series[10]. Content: 9 species: *C. chac* (Savage, 1987); *C. coffeus* (McCranie & Köhler, 1999); *C. gollmeri* (Peters, 1863); *C. greggi* (Bumzahem, 1955); *C. laticeps* (Duméril, 1853); *C. lineatus* (Brocchi, 1879); *C. mimus* (Taylor, 1955); *C. noblei* (Barbour & Dunn, 1921); *C. rostralis* (Werner, 1896).

Subgenus: *Hylactophryne* Lynch, 1968[11]. Content: 21 species: *C. alfredi* (Boulenger, 1898); *C. augusti* (Dugés, 1879); *C. batrachylus* (Taylor, 1940); *C. bocourti* (Brocchi, 1877); *C. campbelli* (Smith, 2005); *C. cyanochthebius* (McCranie & Smith, 2006); *C. decoratus* (Taylor, 1942); *C. galacticorhinus* (Canseco-Márquez & Smith, 2004); *C. glaucus* (Lynch, 1967); *C. guerreroensis* (Lynch, 1967); *C. megalotympanum* (Shannon & Werler, 1955); *C. nefrens* (Smith, 2005); *C. polymniae* (Campbell, Lamar & Hillis, 1989); *C. silvicola* (Lynch, 1967); *C. spatulatus* (Smith, 1939); *C. stuarti* (Lynch, 1967); *C. tarahumaraensis* (Taylor, 1940); *C. taylori* (Lynch, 1966); *C. uno* (Savage, 1985 "1984"); *C. xucanebi* (Stuart, 1941) *C. yucatanensis* (Lynch, 1965).

Genus: *Haddadus* Hedges, Duellman & Heinicke, 2008. Content: 3 species: *H. aramunha* (Cassimiro, Verdade & Rodrigues, 2008); *H. binotatus* (Spix, 1824); *H. plicifer* (Boulenger, 1888).

Genus: *Strabomantis* Peters, 1863. Content: 2 species series, 16 species.

***Strabomantis biporcatus* species series.** Content: 2 species groups, 10 species.

Strabomantis biporcatus species group. Content: 1 species: *S. biporcatus* Peters, 1863.

Strabomantis cornutus species group. Content: 9 species: *S. cadenai* (Lynch, 1986); *S. cerastes* (Lynch, 1975); *S. cornutus* (Jiménez de la Espada, 1870); *S. helonotus* (Lynch, 1975); *S. ingeri* (Cochran & Goin, 1961); *S. laticorpus* (Myers & Lynch, 1997); *S. necopinus* (Lynch, 1997); *S. ruizi* (Lynch, 1981); *S. sulcatus* (Cope, 1874).

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[9] Transferred from the *Craugastor gulosus* series to the *C. punctariolus* series.

[10] These are all species of the *Craugastor laticeps* series of Hedges *et al.* (2008a), not recognized herein because all its parts were found in a polytomy with the *C. fitzingeri* and *C. punctariolus* series.

[11] The *Craugastor augusti* and *C. bocourti* series of Hedges *et al.* (2008a) are not recognized due to their non-monophyly.

Strabomantis bufoniformis **species series.** Content: 6 species: *S. anatipes* (Lynch & Myers, 1983); *S. anomalus* (Boulenger, 1898); *S. bufoniformis* (Boulenger, 1896); *S. cheiroplethus* (Lynch, 1990); *S. necerus* (Lynch, 1975); *S. zygodactylus* (Lynch & Myers, 1983).

SUBFAMILY: Holoadeninae Hedges, Duellman & Heinicke, 2008[12]. Content: 10 genera, 117 species.

Incertae sedis**:** *"Eleutherodactylus" bilineatus* (Bokermann, 1975 "1974").

Genus: *Barycholos* Heyer, 1969. Content: 2 species: *B. pulcher* (Boulenger, 1898); *B. ternetzi* (Miranda-Ribeiro, 1937).

Genus: *Bryophryne* Hedges, Duellman & Heinicke, 2008. Content: 8 species: *B. abramalagae* Lehr & Catenazzi, 2010; *B. bustamantei* (Chaparro, De la Riva, Padial, Ochoa & Lehr, 2007); *B. cophites* (Lynch, 1975); *B. flammiventris* Lehr & Catenazzi, 2010; *B. gymnotis* Lehr & Catenazzi, 2009; *B. hanssaueri* Lehr & Catenazzi, 2009; *B. nubilosus* Lehr & Catenazzi, 2008; *B. zonalis* Lehr & Catenazzi, 2009.

Genus: *Euparkerella* Griffiths, 1959. Content: 4 species: *E. brasiliensis* (Parker, 1926)**;** *E. cochranae* Izecksohn, 1988; *E. robusta* Izecksohn, 1988; *E. tridactyla* Izecksohn, 1988.

Genus: *Holoaden* Miranda-Ribeiro, 1920. Content: 4 species: *H. bradei* Lutz, 1958; *H. luederwaldti* Miranda-Ribeiro, 1920; *H. pholeter* Pombal, Siqueira, Dorigo, Vrcibradic & Rocha, 2008; *H. suarezi* Martins & Zaher, 2012.

Genus: *Hypodactylus* Hedges, Duellman & Heinicke, 2008. Content: 12 species. *H. adercus* (Lynch, 2003); *H. araiodactylus* (Duellman & Pramuk, 1999); *H. babax* (Lynch, 1989); *H. brunneus* (Lynch, 1975); *H. dolops* (Lynch & Duellman, 1980); *H. elassodiscus* (Lynch, 1973); *H. fallaciosus* (Duellman, 2000); *H. latens* (Lynch, 1989); *H. lucida* (Cannatella, 1984); *H. mantipus* (Boulenger, 1908); *H. nigrovittatus* (Andersson, 1945); *H. peraccai* (Lynch, 1975).

Genus: ***Lynchius* Hedges, Duellman & Heinicke, 2008.** Content: 4 species: *L. flavomaculatus* (Parker, 1938; *L. nebulanastes* (Cannatella, 1984; *L. parkeri* (Lynch, 1975); *L. simmonsi* (Lynch, 1974).

Genus: *Niceforonia* Goin & Cochran, 1963. Content: 3 species: *N. adenobrachia* (Ardila-Robayo, Ruiz-Carranza & Barrera-Rodriguez, 1996); *N. columbiana* (Werner, 1899); *N. nana* Goin & Cochran, 1963.

Genus: *Noblella* Barbour, 1930. Content: 11 species. *N. carrascoicola* (De la Riva & Köhler, 1998); *N. coloma* Guayasamin & Terán-Valdez, 2009; *N. duellmani* (Lehr, Aguilar & Lundberg, 2004); *N. heyeri* (Lynch, 1986); *N. lochites* (Lynch, 1976); *N. lynchi* (Duellman, 1991); *N. myrmecoides* (Lynch, 1976); *N. personina* Harvey, Almendáriz, Brito & Batallas, 2013; *N. peruviana* (Noble, 1921); *N. pygmaea* Lehr & Catenazzi, 2009; *N. ritarasquinae* (Köhler, 2000).

Genus: *Oreobates* Jiménez de la Espada, 1872. Content: 23 species: *O. amarakaeri* Padial, Chaparro, Castroviejo-Fisher, Guayasamin, Lehr, Delgado,Vaira, Teixeira, Aguayo-Vedia & De la Riva, 2012; *O. ayacucho* Lehr, 2007; *O. barituensis* Vaira & Ferrari, 2008; *O. berdemenos* Pereyra, Cardozo, Baldo & Baldo, 2014; *O. choristolemma* (Harvey & Sheehy, 2005); *O. crepitans* (Bokermann, 1965); *O. cruralis* (Boulenger, 1902); *O. discoidalis* (Peracca, 1895); *O. gemcare* Padial, Chaparro, Castroviejo-Fisher, Guayasamin, Lehr, Delgado,Vaira, Teixeira, Aguayo-Vedia & De la Riva, 2012; *O. granulosus* (Boulenger, 1903); *O. heterodactylus* (Miranda-Ribeiro, 1937); *O. ibischi* (Reichle, Lötters & De la Riva, 2001); *O. lehri* (Padial, Chaparro & De la Riva, 2007); *O. lundbergi* (Lehr, 2005); *O. machiguenga* Padial, Chaparro, Castroviejo-Fisher, Guayasamin, Lehr, Delgado,Vaira, Teixeira, Aguayo-Vedia & De la Riva, 2012; *O. madidi* (Padial, Gonzales-Álvarez & De la Riva, 2005); *O. pereger* (Lynch, 1975); *O. quixensis* Jiménez de la Espada, 1872; *O. remotus* Teixeira, Amaro, Recoder, Sena & Rodrigues, 2012; *O. sanctaecrucis* (Harvey & Keck, 1995); *O. sanderi* (Padial, Reichle & De la Riva, 2005); *O. saxatilis* (Duellman, 1990); *O. zongoensis* (Reichle & Köhler, 1997).

Genus: *Phrynopus* Peters, 1873. Content: 25 species: *P. auriculatus* Duellman & Hedges, 2008; *P. badius* Lehr, Moravec, Cusi, 2012*;* *P. barthlenae* Lehr & Aguilar, 2002; *P. bracki* Hedges, 1990; *P. bufoides* Lehr, Lundberg & Aguilar, 2005; *P. curator* Lehr, Moravec, Cusi, 2012; *P. dagmarae* Lehr, Aguilar & Köhler, 2002; *P. heimorum* Lehr, 2001; *P. horstpauli* Lehr, Köhler & Ponce, 2000; *P. interstinctus* Lehr & Oróz, 2012; *P. juninensis* (Shreve, 1938); *P. kauneorum* Lehr, Aguilar & Köhler, 2002; *P. kotosh* Lehr, 2007; *P. lechriorhynchus* Trueb & Lehr, 2008; *P. miroslawae* Chaparro, Padial & De la Riva, 2008; *P. montium* (Shreve, 1938); *P. nicoleae* Chaparro, Padial & De la Riva, 2008; *P. oblivius* Lehr, 2007; *P.*

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[12] This taxon includes all genera placed in Holoadeninae by Hedges *et al.* (2008a) (*Barycholos*, *Bryophryne*, *Euparkerella*, *Holoaden*, *Noblella*, and *Psychrophrynella*), plus *Hypodactylus* and a clade (*Lynchius*, *Oreobates*, *Phrynopus*, and, presumably, *Niceforonia*) that was placed in Strabomantinae by Hedges *et al.* (2008a) and Pristimantinae by Pyron & Wiens (2011).

paucari Lehr, Lundberg & Aguilar, 2005; *P. peruanus* Peters, 1873; *P. pesantesi* Lehr, Lundberg & Aguilar, 2005; *P. tautzorum* Lehr & Aguilar, 2003; *P. thompsoni* Duellman, 2000; *P. tribulosus* Duellman & Hedges, 2008; *P. vestigiatus* Lehr & Oróz, 2012.

Genus: *Psychrophrynella* Hedges, Duellman & Heinicke, 2008. Content: 20 species: *P. adenopleura* (Aguayo-Vedia & Harvey, 2001); *P. ankohuma* (Padial & De la Riva, 2007); *P. bagrecito* (Lynch, 1986); *P. boettgeri* (Lehr, 2006); *P. chacaltaya* (De la Riva, Padial & Cortéz, 2007); *P. condoriri* (De la Riva, Aguayo & Padial, 2007); *P. guillei* (De la Riva, 2007); *P. harveyi* (Muñoz, Aguayo & De la Riva, 2007); *P. iani* (De la Riva, Reichle & Cortéz, 2007); *P. iatamasi* (Aguayo-Vedia & Harvey, 2001); *P. illampu* (De la Riva, Reichle & Padial, 2007); *P. illimani* (De la Riva & Padial, 2007); *P. kallawaya* (De la Riva & Martínez-Solano, 2007); *P. katantika* (De la Riva & Martínez-Solano, 2007); *P. kempffi* (De la Riva, 1992); *P. pinguis* (Harvey & Ergueta-Sandoval, 1998); *P. quimsacruzis* (De la Riva, Reichle & Bosch, 2007); *P. saltator* (De la Riva, Reichle & Bosch, 2007); *P. usurpator* De la Riva, Chaparro & Padial, 2008; *P. wettsteini* (Parker, 1932).

SUBFAMILY: Pristimantinae Ohler & Dubois, 2012[13]. Content: 4 genera, 484 species.

Genus: *Dischidodactylus* Lynch, 1979. Content: 2 species: *D. colonnelloi* Ayarzagüena, 1985 "1983"; *D. duidensis* (Rivero, 1968).

Genus: *Ceuthomantis* Heinicke, Duellman, Trueb, Means, MacCulloch & Hedges, 2009. Content: 4 species: *C. aracamuni* (Barrio-Amorós & Molina, 2006); *C. cavernibardus* (Myers & Donnelly, 1997); *C. duellmani* Barrio-Amorós, 2010; *C. smaragdinus* Heinicke, Duellman, Trueb, Means, MacCulloch & Hedges, 2009.

Genus: *Pristimantis* Jiménez de la Espada, 1870[14]. Content: 11 species groups, 473 species.

Pristimantis bellona species group. Content: 3 species: *P. bellona* (Lynch, 1992); *P. mars* (Lynch & Ruiz-Carranza, 1996); *P. polemistes* (Lynch & Ardila-Robayo, 2004).

Pristimantis chalceus species group. Content: 2 species: *P. chalceus* (Peters, 1873); *P. scolodiscus* (Lynch & Burrowes, 1990).

Pristimantis conspicillatus species group. Content[15]: 33 species: *P. achatinus* (Boulenger, 1898); *P. adiastolus* Duellman & Hedges, 2007; *P. avicuporum* (Duellman & Pramuk, 1999); *P. bipunctatus* (Duellman & Hedges, 2005); *P. buccinator* (Rodriguez, 1994); *P. carranguerorum* (Lynch, 1994); *P. charlottevillensis* (Kaiser, Dwyer, Feichtinger & Schmid, 1995); *P. chiastonotus* (Lynch & Hoogmoed, 1977); *P. citriogaster* (Duellman, 1992); *P. condor* (Lynch & Duellman, 1980); *P. conspicillatus* (Günther, 1858); *P. dundeei* (Heyer & Muñoz, 1999); *P. fenestratus* (Steindachner, 1864); *P. gaigei* (Dunn, 1931); *P. gutturalis* (Hoogmoed, Lynch & Lescure, 1977); *P. johannesdei* (Rivero & Serna, 1988 "1987"); *P. koehleri* Padial & De la Riva, 2009; *P. lymani* (Barbour & Noble, 1920); *P. malkini* (Lynch, 1980); *P. medemi* (Lynch, 1994); *P. meridionalis* (Lehr & Duellman, 2007); *P. metabates* (Duellman & Pramuk, 1999); *P. paulodutrai* (Bokermann, 1975 "1974"); *P. peruvianus* (Melin, 1941)[16]; *P. phalaroinguinis* (Duellman & Lehr, 2007); *P. ramagii* (Boulenger, 1888); *P. samaipatae* (Köhler & Jungfer, 1995); *P. skydmainos* (Flores & Rodriguez, 1997); *P. terraebolivaris* (Rivero, 1961); *P. ventrigranulosus* Maciel, Vaz-Silva, Oliveira & Padial, 2012; *P. vilarsi* (Melin, 1941)[17]; *P. vinhai* (Bokermann, 1975 "1974"); *P. zeuctotylus* (Lynch & Hoogmoed, 1977).

Pristimantis danae species group. Content: 11 species: *P. albertus* Duellman & Hedges, 2007; *P. aniptopalmatus* (Duellman & Hedges, 2005); *P. cuneirostris* (Duellman & Pramuk, 1999); *P. danae* (Duellman, 1978); *P. ornatus* (Lehr, Lundberg, Aguilar & von May, 2006); *P. pharangobates* (Duellman, 1978); *P. reichlei* Padial & De la Riva (2009); *P. rhabdolaemus* (Duellman, 1978); *P. sagittulus* (Lehr, Aguilar & Duellman, 2004); *P. stictogaster* (Duellman & Hedges, 2005); *P. toftae* (Duellman, 1978).

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[13] Originally proposed by Pyron & Wiens (2011) as a *nomen nudum*.

[14] We place *Hypodictyon* in the synonymy of *Pristimantis* and recognize *Pristimantis* as a genus with no subgenera. The two species series of *Hypodictyon* are merged into a single species group within *Pristimantis*, the *Pristimantis ridens* species group. *Hypodictyon* will likely be resurrected in the future, when greater taxon sampling allows an adequate partitioning of *Pristimantis* into multiple genera.

[15] We remove the following species from *P. conspicillatus* species group and consider them unassigned to group: *P. carmelitae* (Ruthven, 1922), *P. carlossanchezi* (Arroyo, 2007), *P. insignitus* (Ruthven, 1917), *P. padrecarlosi* (Mueses-Cisneros, 2006), *P. pedimontanus* (La Marca, 2004), and *P. viridicans* (Lynch, 1977).

[16] Transferred into this group from the *P. peruvianus* group of Hedges *et al.* (2008a), which we consider invalid and reformulate as the *P. danae* group.

[17] Includes *P. stegolepis* (Schlüter & Rödder, 2007) as a junior synonym according to Kok & Barrio-Amorós (2013).

Pristimantis devillei species group[18]. Content: 23 species: *P. acatallelus* (Lynch & Ruiz-Carranza, 1983); *P. buckleyi* (Boulenger, 1882); *P. cacao* (Lynch, 1992); *P. chrysops* (Lynch & Ruiz-Carranza, 1996); *P. curtipes* (Boulenger, 1882); *P. devillei* (Boulenger, 1880); *P. duellmani* (Lynch, 1980); *P. gentryi* (Lynch & Duellman, 1997); *P. hamiotae* (Flores, 1994 "1993"); *P. quinquagesimus* (Lynch & Trueb, 1980); *P. romanorum* Yánez-Muñoz, Meza-Ramos, Cisneros-Heredia & Reyes-Puig, 2011 "2010"; *P. satagius* (Lynch, 1995); *P. silverstonei* (Lynch & Ruiz-Carranza, 1996); *P. siopelus* (Lynch & Burrowes, 1990); *P. sobetes* (Lynch, 1980); *P. sulculus* (Lynch & Burrowes, 1990); *P. surdus* (Boulenger, 1882); *P. susaguae* (Rueda-Almonacid, Lynch & Galvis, 2003); *P. thymalopsoides* (Lynch, 1976); *P. truebae* (Lynch & Duellman, 1997); *P. vertebralis* (Boulenger, 1886); *P. xestus* (Lynch, 1995); *P. xylochobates* (Lynch & Ruiz-Carranza, 1996).

Pristimantis galdi species group[19]. Content: 4 species. *P. delicatus* (Ruthven, 1917); *P. douglasi* (Lynch, 1996); *P. galdi* Jiménez de la Espada, 1870; *P. tribulosus* (Lynch & Rueda-Almonacid, 1997).

Pristimantis lacrimosus species group[20]. Content: 25 species: *P. acuminatus* (Shreve, 1935); *P. apiculatus* (Lynch & Burrowes, 1990); *P. aureolineatus* (Guayasamin, Ron, Cisneros-Heredia, Lamar & McCracken, 2006); *P. boulengeri* (Lynch, 1981); *P. brevifrons* (Lynch, 1981 "1980"); *P. bromeliaceus* (Lynch, 1979); *P. dorsopictus* (Rivero & Serna, 1988 "1987"); *P. eremitus* (Lynch, 1980); *P. geyi* Lehr, Gregory & Catenazzi, 2013; *P. lacrimosus* (Jiménez de la Espada, 1875); *P. latericius* Batallas & Brito, 2014; *P. mendax* (Duellman, 1978); *P. mindo* Arteaga, Yanez-Munoz & Guayasamin, 2013; *P. olivaceus* (Köhler, Morales, Lötters, Reichle & Aparicio, 1998); *P. padiali* Moravec, Lehr, Pérez-Peña, López, Gagliardi-Urrutia & Arista-Tuanama, 2011; *P. pardalinus* (Lehr, Lundberg, Aguilar & von May, 2006); *P. petersi* (Lynch, 1980); *P. prolixodiscus* (Lynch, 1978); *P. royi* (Morales, 2007); *P. pseudoacuminatus* (Shreve, 1935); *P. schultei* (Duellman, 1990); *P. tantanti* (Lehr, Torres-Gastello & Suárez-Segovia, 2007); *P. tayrona* (Lynch & Ruiz-Carranza, 1985); *P. waoranii* (McCracken, Forstner & Dixon, 2007); *P. zimmermanae* (Heyer & Hardy, 1991).

Pristimantis leptolophus species group. Content: 7 species: *P. lasalleorum* (Lynch, 1995); *P. leptolophus* (Lynch, 1980); *P. maculosus* (Lynch, 1991); *P. parectatus* (Lynch & Rueda-Almonacid, 1998); *P. peraticus* (Lynch, 1980); *P. scoloblepharus* (Lynch, 1991); *P. uranobates* (Lynch, 1991).

Pristimantis loustes species group. Content: 3 species: *P. hybotragus* (Lynch, 1992); *P. jaimei* (Lynch, 1992); *P. loustes* (Lynch, 1979).

Pristimantis myersi species group. Content: 17 species: *P. bicantus* Guayasamin & Funk, 2009; *P. festae* (Peracca, 1904); *P. floridus* (Lynch & Duellman, 1997); *P. gladiator* (Lynch, 1976); *P. hectus* (Lynch & Burrowes, 1990); *P. leoni* (Lynch, 1976); *P. lucidosignatus* Rödder & Schmitz, 2009; *P. munozi* Rojas-Runjaic, Delgado & Guayasamin, 2014; *P. myersi* (Goin & Cochran, 1963); *P. ocreatus* (Lynch, 1981); *P. onorei* Rödder & Schmitz, 2009; *P. pyrrhomerus* (Lynch, 1976); *P. repens* (Lynch, 1984); *P. scopaeus* (Lynch, Ruiz-Carranza & Ardila-Robayo, 1996); *P. sirnigeli* Yánez-Muñoz, Meza-Ramos, Cisneros-Heredia & Reyes-Puig, 2011 "2010"; *P. thymelensis* (Lynch, 1972)[21]; *P. xeniolum* (Lynch, 2001).

Pristimantis ridens species group. Content: 33 species: *P. actites* (Lynch, 1979); *P. adnus* Crawford, Ryan & Jaramillo, 2010; *P. almendariz* Brito & Pozo-Zamora, 2013; *P. bicolor* (Rueda-Almonacid & Lynch, 1983); *P. caryophyllaceus* (Barbour, 1928); *P. cerasinus* (Cope, 1875 "1876"); *P. colomai* (Lynch & Duellman, 1997); *P. cremnobates* (Lynch & Duellman, 1980); *P. crenunguis* (Lynch, 1976); *P. cruentus* (Peters, 1873); *P. educatoris* Ryan, Lips & Giermakowski, 2010; *P. epacrus* (Lynch & Suárez-Mayorga, 2000); *P. erythropleura* (Boulenger, 1896); *P. ixalus* (Lynch, 2003); *P. jorgevelosai* (Lynch, 1994); *P. labiosus* (Lynch, Ruiz-Carranza & Ardila-Robayo, 1994); *P. lanthanites* (Lynch, 1975); *P. laticlavius* (Lynch & Burrowes, 1990); *P. latidiscus* (Boulenger, 1898); *P. moro* (Savage, 1965); *P. museosus* (Ibáñez, Jaramillo & Arosemena, 1994); *P. ocellatus* (Lynch & Burrowes, 1990); *P. orpacobates* (Lynch, Ruiz-Carranza & Ardila-Robayo, 1994); *P. paisa* (Lynch & Ardila-Robayo, 1999); *P. ridens* (Cope, 1866); *P. rosadoi* (Flores, 1988); *P. rubicundus* (Jiménez de la Espada, 1875); *P. sanguineus* (Lynch, 1998); *P. tanyrhynchus* Lehr, 2007; *P. thectopternus* (Lynch, 1975)[22]; *P. tenebrionis* (Lynch & Miyata, 1980); *P. viejas* (Lynch & Rueda-Almonacid, 1999); *P. w-nigrum* (Boettger, 1892).

In the genus *Pristimantis* but unassigned to species group[23]**:** 312 species: *P. aaptus* (Lynch & Lescure, 1980); *P. abakapa* Rojas-Runjaic, Salermo, Señaris & Pauly, 2013; *P. academicus* Lehr, Moravec & Gagliardi-Urrutia, 2010; *P. acerus*

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[18] Into this group we transferred all species of the former *P. curtipes, P. devillei,* and *P. surdus* species groups, as well as *P. thymalopsoides.*

[19] The monopyly of this group was not tested by us.

[20] We transfer *Pristimantis acuminatus, P. padiali, P. tantanti,* and *P. pseudoacuminatus* to the *P. lacrimosus* group from the non-monophyletic *P. unistrigatus* group.

[21] Transferred to this species group from the *P. orcesi* species group.

[22] Transferred from the *Pristimantis conspicillatus* species group.

[23] The former, trenchantly non-monophyletic *Pristimantis unistrigatus* species group is the major donor to this category, but also includes species never assigned to groups and groups rejected by us.

(Lynch & Duellman, 1980); *P. achuar* Elmer & Cannatella, 2008; *P. actinolaimus* (Lynch & Rueda-Almonacid, 1998); *P. acutirostris* (Lynch, 1984); *P. aemulatus* (Ruiz-Carranza, Lynch & Ardila-Robayo, 1997); *P. affinis* (Werner, 1899); *P. alalocophus* (Roa-Trujillo & Ruiz-Carranza, 1991); *P. albericoi* (Lynch & Ruiz-Carranza, 1996); *P. altae* (Dunn, 1942); *P. altamazonicus* (Barbour & Dunn, 1921); *P. altamnis* Elmer & Cannatella, 2008; *P. ameliae* Barrio-Amorós, 2012; *P. amydrotus* (Duellman & Lehr, 2007); *P. andinognomus* Lehr & Coloma, 2008; *P. anemerus* (Duellman & Pramuk, 1999); *P. angustilineatus* (Lynch, 1998); *P. anolirex* (Lynch, 1983); *P. anotis* (Walker & Test, 1955); *P. appendiculatus* (Werner, 1894)[24]; *P. aquilonaris* Lehr, Aguilar, Siu-Ting & Jordán, 2007; *P. ardalonychus* (Duellman & Pramuk, 1999); *P. ardyae* Reyes-Puig, Reyes-Puig & Yánez-Muñoz, 2013; *P. atrabracus* (Duellman & Pramuk, 1999); *P. atratus* (Lynch, 1979); *P. aurantiguttatus* (Ruiz-Carranza, Lynch & Ardila-Robayo, 1997); *P. aureoventris* Kok, Means & Bossuyt, 2011; *P. auricarens* (Myers & Donnelly, 2008); *P. avius* (Myers & Donnelly, 1997); *P. bacchus* (Lynch, 1984); *P. baiotis* (Lynch, 1998); *P. balionotus* (Lynch, 1979); *P. bambu* Arteaga-Navarro & Guayasamin, 2011; *P. baryecuus* (Lynch, 1979); *P. batrachites* (Lynch, 2003); *P. bearsei* (Duellman, 1992); *P. bellae* Reyes-Puig & Yánez-Muñoz, 2012; *P. bellator* Lehr, Aguilar, Siu-Ting & Jordán, 2007; *P. bernali* (Lynch, 1986); *P. bicumulus* (Peters, 1863); *P. boconoensis* (Rivero & Mayorga, 1973); *P. bogotensis* (Peters, 1863); *P. braverae* Barrio-Amorós, Heinicke & Hedges, 2013; *P. briceni* (Boulenger, 1903); *P. bustamante* Chaparro, Motta, Gutiérrez & Padial, 2012; *P. cabrerai* (Cochran & Goin, 1970); *P. caeruleonotus* Lehr, Aguilar, Siu-Ting & Jordán, 2007; *P. cajamarcensis* (Barbour & Noble, 1920); *P. calcaratus* (Boulenger, 1908); *P. calcarulatus* (Lynch, 1976); *P. caliginosus* (Lynch, 1996); *P. cantitans* (Myers & Donnelly, 1996); *P. capitonis* (Lynch, 1998); *P. caprifer* (Lynch, 1977)[25]; *P. carlosceroni* Valencia, Bejarano-Munnoz, Yañez-Muñoz, 2013; *P. carlossanchezi* (Arroyo, 2007); *P. carmelitae* (Ruthven, 1922); *P. carvalhoi* (Lutz, 1952); *P. celator* (Lynch, 1976); *P. ceuthospilus* (Duellman & Wild, 1993); *P. chimu* Lehr, 2007; *P. chloronotus* (Lynch, 1969); *P. colodactylus* (Lynch, 1979); *P. colonensis* (Mueses-Cisneros, 2007); *P. colostichos* (La Marca & Smith, 1982); *P. conservatio* Barrio-Amorós, Heinicke & Hedges, 2013; *P. cordovae* (Lehr & Duellman, 2007); *P. corniger* (Lynch & Suárez-Mayorga, 2003); *P. coronatus* Lehr & Duellman, 2007; *P. corrugatus* (Duellman, Lehr & Venegas, 2006); *P. cosnipatae* (Duellman, 1978); *P. cristinae* (Lynch & Ruiz-Carranza, 1985); *P. croceoinguinis* (Lynch, 1968); *P. crucifer* (Boulenger, 1899); *P. cruciocularis* (Lehr, Lundberg, Aguilar & von May, 2006); *P. cryophilius* (Lynch, 1979)[26]; *P. cryptomelas* (Lynch, 1979); *P. cuentasi* (Lynch, 2003); *P. culatensis* (La Marca, 2007); *P. degener* (Lynch & Duellman, 1997); *P. deinops* (Lynch, 1996); *P. delius* (Duellman & Mendelson, 1995); *P. dendrobatoides* Means & Savage, 2007; *P. deyi* Lehr & Catenazzi, 2013; *P. diadematus* (Jiménez de la Espada, 1875); *P. diaphonus* (Lynch, 1986); *P. diogenes* (Lynch & Ruiz-Carranza, 1996); *P. dissimulatus* (Lynch & Duellman, 1997); *P. divnae* Lehr & von May, 2009; *P. duende* (Lynch, 2001); *P. elegans* (Peters, 1863); *P. eriphus* (Lynch & Duellman, 1980); *P. ernesti* (Flores, 1987); *P. esmeraldas* (Guayasamin, 2004); *P. espedeus* Fouquet, Martinez, Courtois, Dewhynter, Pineau, Gaucher, Blanc, Marty & Kok, 2013; *P. eugeniae* (Lynch & Duellman, 1997); *P. euphronides* (Schwartz, 1967); *P. eurydactylus* (Hedges & Schlüter, 1992); *P. exoristus* (Duellman & Pramuk, 1999); *P. factiosus* (Lynch & Rueda-Almonacid, 1998); *P. fallax* (Lynch & Rueda-Almonacid, 1999); *P. farisorum* Mueses-Cisneros, Perdomo-Castillo & Cepeda-Quilindo, 2013; *P. fasciatus* Barrio-Amorós, Rojas-Runjaic & Infante-Rivero, 2008; *P. fetosus* (Lynch & Rueda-Almonacid, 1998); *P. flabellidiscus* (La Marca, 2007); *P. flavobracatus* (Lehr, Lundberg, Aguilar & von May, 2006); *P. frater* (Werner, 1899); *P. gagliardoi* Bustamante & Mendelson, 2008; *P. ganonotus* (Duellman & Lynch, 1988); *P. ginesi* (Rivero, 1964); *P. glandulosus* (Boulenger, 1880); *P. gracilis* (Lynch, 1986); *P. grandiceps* (Lynch, 1984); *P. gryllus* Barrio-Amorós, Guayasamin & Hedges, 2013; *P. guaiquinimensis* (Schlüter & Rödder, 2007)[27]; *P. helvolus* (Lynch & Rueda-Almonacid, 1998); *P. hernandezi* (Lynch & Ruiz-Carranza, 1983); *P. huicundo* (Guayasamin, Almeida-Reinoso & Nogales-Sornosa, 2004); *P. ignicolor* (Lynch & Duellman, 1980); *P. illotus* (Lynch & Duellman, 1997); *P. imitatrix* (Duellman, 1978); *P. incanus* (Lynch & Duellman, 1980); *P. incertus* (Lutz, 1927); *P. incomptus* (Lynch & Duellman, 1980); *P. infraguttatus* (Duellman & Pramuk, 1999); *P. inguinalis* (Parker, 1940); *P. insignitus* (Ruthven, 1917); *P. imthurni* Kok, 2013; *P. inusitatus* (Lynch & Duellman, 1980); *P. jabonensis* (La Marca, 2007); *P. jamescameroni* Kok, 2013; *P. jester* Means & Savage, 2007; *P. juanchoi* (Lynch, 1996); *P. jubatus* (García & Lynch, 2006); *P. kareliae* (La Marca, 2005); *P. katoptroides* (Flores, 1988); *P. kelephus* (Lynch, 1998); *P. kichwarum* Elmer & Cannatella, 2008; *P. kirklandi* (Flores, 1985); *P. lancinii* (Donoso-Barros, 1965 "1964"); *P. lassoalcalai* Barrio-Amorós, Rojas-Runjaic & Barros, 2010; *P. lemur* (Lynch & Rueda-Almonacid, 1998); *P. lentiginosus* (Rivero, 1984 "1982"); *P. leucopus* (Lynch, 1976); *P. leucorrhinus* Boano, Mazzotti & Sindaco, 2008; *P. librarius* (Flores & Vigle, 1994); *P. lichenoides* (Lynch & Rueda-Almonacid, 1997); *P. lindae* (Duellman, 1978); *P. lirellus* (Dwyer, 1995); *P. lividus* (Lynch & Duellman, 1980); *P. llojsintuta* (Köhler & Lötters, 1999); *P. loujosti* Yánez-Muñoz, Cisneros-Heredia & Reyes-Puig, 2011 "2010"; *P. lucasi* Duellman & Chaparro, 2008; *P. luscombei* (Duellman & Mendelson, 1995); *P. luteolateralis* (Lynch, 1976); *P. lutitus* (Lynch, 1984); *P. lynchi* (Duellman & Simmons, 1977); *P. lythrodes* (Lynch & Lescure, 1980); *P. marahuaka* (Fuentes-Ramos & Barrio-Amorós, 2004); *P. mariaelenae* Venegas & Duellman, 2012; *P. marmoratus* (Boulenger, 1900); *P. martiae* (Lynch, 1974); *P. matidiktyo* Ortega-Andrade & Valencia 2012; *P. megalops* (Ruthven, 1917); *P. mazar* Guayasamin, Arteaga-Navarro & Bustamante, 2013; *P. melanogaster* (Duellman & Pramuk, 1999); *P. melanoproctus* (Rivero, 1984 "1982"); *P. memorans* (Myers & Donnelly, 1997); *P. merostictus* (Lynch, 1984); *P. minimus*

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24. Excluded from the *Pristimantis devillei* species group.
25. Removed from the *Pristimantis conspicillatus* group and left unnassigned to species group.
26. Removed from the *Pristimantis devillei* group and left unnassigned to species group.
27. Includes *P. tepuiensis* (Schlüter and Rödder, 2007) as a junior synonym according to Kok and Barrio-Amorós (2013).

Terán-Valdez & Guayasamin, 2010; *P. minutulus* Duellman & Hedges, 2007; *P. miyatai* (Lynch, 1984); *P. mnionaetes* (Lynch, 1998); *P. modipeplus* (Lynch, 1981); *P. molybrignus* (Lynch, 1986); *P. mondolfii* (Rivero, 1984 "1982"); *P. muchimuk* Barrio-Amorós, Mesa, Brewer-Carías & McDiarmid, 2010; *P. muricatus* (Lynch & Miyata, 1980); *P. muscosus* (Duellman & Pramuk, 1999); *P. myops* (Lynch, 1998); *P. nephophilus* (Duellman & Pramuk, 1999); *P. nervicus* (Lynch, 1994); *P. nicefori* (Cochran & Goin, 1970); *P. nigrogriseus* (Andersson, 1945); *P. nyctophylax* (Lynch, 1976); *P. obmutescens* (Lynch, 1980); *P. ockendeni* (Boulenger, 1912); *P. orcesi* (Lynch, 1972); *P. orcus* Lehr, Catenazzi & Rodríguez, 2009; *P. orestes* (Lynch, 1979); *P. ornatissimus* (Despax, 1911); *P. orphnolaimus* (Lynch, 1970); *P. ortizi* (Guayasamin, Almeida-Reinoso & Nogales-Sornosa, 2004); *P. padrecarlosi* (Mueses-Cisneros, 2006); *P. palmeri* (Boulenger, 1912); *P. pardalis* (Barbour, 1928); *P. paramerus* (Rivero, 1984 "1982"); *P. parvillus* (Lynch, 1976); *P. pastazensis* (Andersson, 1945); *P. pataikos* (Duellman & Pramuk, 1999); *P. paululus* (Lynch, 1974); *P. pecki* (Duellman & Lynch, 1988); *P. pedimontanus* (La Marca, 2004); *P. penelopus* (Lynch & Rueda-Almonacid, 1999); *P. percnopterus* (Duellman & Pramuk, 1999); *P. percultus* (Lynch, 1979); *P. permixtus* (Lynch, Ruiz-Carranza & Ardila-Robayo, 1994); *P. petrobardus* (Duellman, 1991); *P. phalarus* (Lynch, 1998); *P. philipi* (Lynch & Duellman, 1995); *P. phoxocephalus* (Lynch, 1979); *P. phragmipleuron* (Rivero & Serna, 1988 "1987"); *P. piceus* (Lynch, Ruiz-Carranza & Ardila-Robayo, 1996); *P. pinguis* (Duellman & Pramuk, 1999); *P. pirrensis* (Ibáñez & Crawford, 2004); *P. platychilus* (Lynch, 1996); *P. platydactylus* (Boulenger, 1903); *P. pleurostriatus* (Rivero, 1984 "1982"); *P. polychrus* (Ruiz-Carranza, Lynch & Ardila-Robayo, 1997); *P. prolatus* (Lynch & Duellman, 1980); *P. proserpens* (Lynch, 1979); *P. pruinatus* (Myers & Donnelly, 1996); *P. pteridophilus* (Lynch & Duellman, 1997); *P. ptochus* (Lynch, 1998); *P. pugnax* (Lynch, 1973); *P. pulvinatus* (Rivero, 1968); *P. pycnodermis* (Lynch, 1979); *P. quantus* (Lynch, 1998); *P. quaquaversus* (Lynch, 1974); *P. quicato* Ospina-Sarria, Méndez-Narváez, Burbano-Yandi & Bolívar-García, 2011; *P. racemus* (Lynch, 1980); *P. reclusas* (Lynch, 2003); *P. renjiforum* (Lynch, 2000); *P. restrepoi* (Lynch, 1996); *P. reticulatus* (Walker & Test, 1955); *P. rhabdocnemus* (Duellman & Hedges, 2005); *P. rhigophilus* (La Marca, 2007); *P. rhodoplichus* (Duellman & Wild, 1993); *P. rhodostichus* (Duellman & Pramuk, 1999); *P. rivasi* Barrio-Amorós, Rojas-Runjaic & Barros, 2010; *P. riveroi* (Lynch & La Marca, 1993); *P. riveti* (Despax, 1911); *P. roseus* (Boulenger, 1918); *P. rozei* (Rivero, 1961); *P. ruedai* (Ruiz-Carranza, Lynch & Ardila-Robayo, 1997); *P. rufioculis* (Duellman & Pramuk, 1999); *P. rufoviridis* Valencia, Yánez-Muñoz, Betancourt-Yépez, Terán-Valdez & Guayasami; *P. ruidus* (Lynch, 1979); *P. ruthveni* (Lynch & Ruiz-Carranza, 1985); *P. salaputium* (Duellman, 1978); *P. saltissimus* Means & Savage, 2007; *P. sanctaemartae* (Ruthven, 1917); *P. sarisarinama* Barrio-Amorós & Brewer-Carias, 2008; *P. savagei* (Pyburn & Lynch, 1981); *P. scitulus* (Duellman, 1978); *P. seorsus* Lehr, 2007; *P. serendipitus* (Duellman & Pramuk, 1999); *P. shrevei* (Schwartz, 1967); *P. signifer* (Ruiz-Carranza, Lynch & Ardila-Robayo, 1997); *P. simonbolivari* (Wiens & Coloma, 1992); *P. simonsii* (Boulenger, 1900); *P. simoteriscus* (Lynch, Ruiz-Carranza & Ardila-Robayo, 1997); *P. simoterus* (Lynch, 1980); *P. spectabilis* Duellman & Chaparro, 2008; *P. spilogaster* (Lynch, 1984); *P. spinosus* (Lynch, 1979); *P. stenodiscus* (Walker & Test, 1955); *P. sternothylax* (Duellman & Wild, 1993); *P. stictoboubonus* (Duellman, Lehr & Venegas, 2006); *P. stipa* Venegas & Duellman, 2012; *P. subsigillatus* (Boulenger, 1902); *P. suetus* (Lynch & Rueda-Almonacid, 1998); *P. supernatis* (Lynch, 1979); *P. taciturnus* (Lynch & Suárez-Mayorga, 2003); *P. taeniatus* (Boulenger, 1912); *P. tamsitti* (Cochran & Goin, 1970); *P. telefericus* (La Marca, 2005); *P. thyellus* (La Marca, 2007); *P. torrenticola* (Lynch & Rueda-Almonacid, 1998); *P. trachyblepharis* (Boulenger, 1918); *P. tubernasus* (Rivero, 1984 "1982"); *P. tungurahua* Reyes-Puig, Yánez-Muñoz, Cisneros-Heredia & Ramírez, 2011 "2010"; *P. turik* Barrio-Amorós, Rojas-Runjaic & Infante-Rivero, 2008; *P. turpinorum* (Hardy, 2001); *P. turumiquirensis* (Rivero, 1961); *P. uisae* (Lynch, 2003); *P. unistrigatus* (Günther, 1859); *P. urichi* (Boettger, 1894); *P. vanadise* (La Marca, 1984); *P. variabilis* (Lynch, 1968); *P. veletis* (Lynch & Rueda-Almonacid, 1997); *P. ventriguttatus* Lehr & Köhler, 2007; *P. ventrimarmoratus* (Boulenger, 1912); *P. verecundus* (Lynch & Burrowes, 1990); *P. versicolor* (Lynch, 1979); *P. vicarius* (Lynch & Ruiz-Carranza, 1983); *P. vidua* (Lynch, 1979); *P. vilcabambae* Lehr, 2007; *P. viridicans* (Lynch, 1977); *P. viridis* (Ruiz-Carranza, Lynch & Ardila-Robayo, 1997)[28]; *P. wagteri* (Venegas, 2007); *P. walkeri* (Lynch, 1974)n, 2011; *P. wiensi* (Duellman & Wild, 1993); *P. yaviensis* (Myers & Donnelly, 1996); *P. yukpa* Barrio-Amorós, Rojas-Runjaic & Infante-Rivero, 2008; *P. yumbo* Yánez-Muñoz, Meza-Ramos, Cisneros-Heredia & Reyes-Puig, 2011 "2010"; *P. yuruaniensis* Rödder & Jungfer, 2008; *P. yustizi* (Barrio-Amorós & Chacón-Ortiz, 2004; *P. zoilae* (Mueses-Cisneros, 2007); *P. zophus* (Lynch & Ardila-Robayo, 1999).

Genus: *Yunganastes* Padial, Castroviejo-Fisher, Köhler, Domic & De la Riva, 2007. Content: 5 species: *Y. ashkapara* (Köhler, 2000); *Y. bisignatus* (Werner, 1899); *Y. fraudator* (Lynch & McDiarmid, 1987); *Y. mercedesae* (Lynch & McDiarmid, 1987); *Y. pluvicanorus* (De la Riva & Lynch, 1997).

FAMILY: Eleutherodactylidae Lutz, 1954. Content: 2 subfamilies, 4 genera, 205 species.

SUBFAMILY: Eleutherodactylinae Lutz, 1954. Content: 2 genera, 196 species.

Genus: *Diasporus* Hedges, Duellman & Heinicke, 2008. Content: 10 species: *D. anthrax* (Lynch, 2001); *D. citrinobapheus* Hertz, Hauenschild, Lotzkat & Köhler, 2012; *D. diastema* (Cope, 1875 "1876); *D. gularis* (Boulenger, 1898); *D.*

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[28] Transferred out of the "*Pristimantis peruvianus* group" (now in the *Pristimantis danae* group).

hylaeformis (Cope, 1875 "1876); *D. igneus* Batista, Ponce & Hertz, 2012; *D. quidditus* (Lynch, 2001); *D. tigrillo* (Savage, 1997); *Diasporus tinker* (Lynch, 2001); *D. ventrimaculatus* Chaves, García-Rodríguez, Mora & Leal, 2009; *D. vocator* (Taylor, 1955).

Genus: *Eleutherodactylus* Duméril & Bibron, 1841. Content: 5 subgenera, 186 species.

Subgenus: *Eleutherodactylus* Duméril & Bibron, 1841. Content: 5 species series, 54 species.

***Eleutherodactylus (Eleutherodactylus) auriculatus* species series.** Content: 3 species groups, 16 species.

Eleutherodactylus (Eleutherodactylus) abbotti species group. Content: 7 species: *E. abbotti* Cochran, 1923; *E. audanti* Cochran, 1934); *E. haitianus* Barbour, 1942; *E. melatrigonum* Schwartz, 1966; *E. notidodes* Schwartz, 1966; *E. parabates* Schwartz, 1964); *E. pituinus* Schwartz, 1965 "1964".

Eleutherodactylus (Eleutherodactylus) auriculatus species group. Content: 7 species: *E. auriculatus* (Cope, 1862); *E. bartonsmithi* Schwartz, 1960; *E. eileenae* Dunn, 1926; *E. glamyrus* Estrada & Hedges, 1997; *E. mariposa* Hedges, Estrada & Thomas, 1992; *E. principalis* Estrada & Hedges, 1997; *E. ronaldi* Schwartz, 1960.

Eleutherodactylus (Eleutherodactylus) minutus species group. Content: 2 species: *E. minutus* Noble, 1923; *E. poolei* Cochran, 1938.

***Eleutherodactylus (Eleutherodactylus) antillensis* species series[29].** Content: 4 species groups, 15 species.

Eleutherodactylus (Eleutherodactylus) antillensis species group[30]. Content: 7 species: *E. antillensis* (Reinhardt & Lütken, 1863 "1862"); *E. brittoni* Schmidt, 1920; *E. cochranae* Grant, 1932; *E. gryllus* Schmidt, 1920; *E. hedricki* Rivero, 1963; *E. jasperi* Drewry & Jones, 1976; *E. juanariveroi* Rios-López & Thomas, 2007.

Eleutherodactylus (Eleutherodactylus) locustus species group. Content: 3 species: *E. cooki* Grant, 1932; *E. eneidae* Rivero, 1959; *E. locustus* Schmidt, 1920.

Eleutherodactylus (Eleutherodactylus) wightmanae species group. Content: 4 species: *E. coqui* Thomas, 1966; *E. portoricensis* Schmidt, 1927; *E. schwartzi* Thomas, 1966; *E. wightmanae* Schmidt, 1920.

Eleutherodactylus (Eleutherodactylus) flavescens species group. Content: 1 species: *E. flavescens* Noble, 1923.

***Eleutherodactylus (Eleutherodactylus) martinicensis* species series[31].** Content: 5 species: *E. amplinympha* Kaiser, Green & Schmid, 1994; *E. barlagnei* Lynch, 1965; *E. johnstonei* Barbour, 1914; *E. martinicensis* (Tschudi, 1838); *E. pinchoni* Schwartz, 1967.

***Eleutherodactylus (Eleutherodactylus) richmondi* species series.** Content: 3 species: *E. karlschmidti* Grant, 1931; *E. richmondi* Stejneger, 1904; *E. unicolor* Stejneger, 1904.

***Eleutherodactylus (Eleutherodactylus) varians* species series.** Content: 4 species groups, 15 species.

Eleutherodactylus (Eleutherodactylus) lamprotes species group. Content: 2 species: *E. fowleri* Schwartz, 1973; *E. lamprotes* Schwartz, 1973.

Eleutherodactylus (Eleutherodactylus) montanus species group. Content: 3 species: *E. auriculatoides* Noble, 1923; *E. montanus* Schmidt, 1919; *E. patriciae* Schwartz, 1965 "1964".

Eleutherodactylus (Eleutherodactylus) varians species group. Content: 2 species subgroups, 7 species.

Eleutherodactylus (Eleutherodactylus) leberi species subgroup. Content: 2 species: *E. leberi* Schwartz, 1965; *E. melacara* Hedges, Estrada & Thomas, 1992.

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[29] We have recast this as a species series with several groups (former subgroups)

[30] This is composed of the former, smaller, *E. antillensis* and *E. gryllus* subgroups.

[31] This is reformulated and is equivalent to the old *Eleutherodactylus martinicensis* species group. The *E. martinicensis* species series of Hedges *et al.* (2008a), which also included the *E. antillensis* and *E. flavescens* groups, we rejected because of its paraphyly.

Eleutherodactylus (Eleutherodactylus) varians species subgroup. Content: 5 species: *E. guantanamera* Hedges, Estrada & Thomas, 1992; *E. ionthus* Schwartz, 1960; *E. olibrus* Schwartz, 1958; *E. staurometopon* Schwartz, 1960; *E. varians* (Gundlach & Peters, 1864).

Eleutherodactylus (Eleutherodactylus) wetmorei species group. Content: 3 species: *E. diplasius* Schwartz, 1973; *E. sommeri* Schwartz, 1977; *E. wetmorei* Cochran, 1932.

Subgenus: *Euhyas* Fitzinger, 1843. Content: 8 species series, 96 species.

***Eleutherodactylus (Euhyas) armstrongi* species series**. Content: 4 species. *E. alcoae* Schwartz, 1971; *E. armstrongi* Noble & Hassler, 1933; *E. darlingtoni* Cochran, 1935; *E. leoncei* Shreve & Williams, 1963.

***Eleutherodacty (Euhyas) dimidiatus* species series**: 2 species groups, 7 species.

Eleutherodactylus (Euhyas) dimidiatus species group. Content: 4 species: *E. albipes* Barbour & Shreve, 1937; *E. dimidiatus* (Cope, 1862); *E. emiliae* Dunn, 1926; *E. maestrensis* Díaz, Cádiz & Navarro, 2005.

Eleutherodactylus (Euhyas) schmidti species group. Content: 3 species: *E. limbensis* Lynn, 1958; *E. rucillensis* Cochran, 1939; *E. schmidti* Noble, 1923.

***Eleutherodactylus (Euhyas) greyi* species series.** Content: 1 species: *E. greyi* Dunn, 1926.

***Eleutherodactylus (Euhyas) luteolus* species series**. Content: 4 species groups, 22 species.

Eleutherodactylus (Euhyas) cuneatus species group. Content: 2 species: *E. cuneatus* (Cope, 1862); *E. turquinensis* Barbour & Shreve, 1937.

Eleutherodactylus (Euhyas) luteolus species group[32]. Content: 17 species: *E. alticola* Lynn, 1937; *E. andrewsi* Lynn, 1937; *E. cavernicola* Lynn, 1954; *E. cundalli* Dunn, 1926; *E. fuscus* Lynn & Dent, 1943; *E. glaucoreius* Schwartz & Fowler, 1973; *E. gossei* Dunn, 1926; *E. grabhami* Dunn, 1926; *E. griphus* Crombie, 1986; *E. jamaicensis* Barbour, 1910; *E. junori* Dunn, 1926; *E. luteolus* (Gosse, 1851); *E. nubicola* Dunn, 1926; *E. orcutti* Dunn, 1928; *E. pantoni* Dunn, 1926; *E. pentasyringos* Schwartz & Fowler, 1973; *E. sisyphodemus* Crombie, 1977.

Eleutherodactylus (Euhyas) riparius species group. Content: 2 species: *E. riparius* Estrada & Hedges, 1998; *E. rivularis* Díaz, Estrada & Hedges, 2001.

Eleutherodactylus (Euhyas) toa species group. Content: 1 species: *E. toa* Estrada & Hedges, 1991.

***Eleutherodactylus (Euhyas) oxyrhyncus* species series.** Content: 6 species groups, 21 species.

Eleutherodactylus (Euhyas) bakeri species group. Content: 10 species: *E. amadeus* Hedges, Thomas & Franz, 1987; *E. bakeri* Cochran, 1935; *E. caribe* Hedges & Thomas, 1992; *E. corona* Hedges & Thomas, 1992; *E. dolomedes* Hedges & Thomas, 1992; *E. eunaster* Schwartz, 1973; *E. glaphycompus* Schwartz, 1973; *E. heminota* Shreve & Williams, 1963; *E. semipalmatus* Shreve, 1936; *E. thorectes* Hedges, 1988.

Eleutherodactylus (Euhyas) glandulifer species group. Content: 4 species: *E. brevirostris* Shreve, 1936; *E. glandulifer* Cochran, 1935; *E. sciagraphus* Schwartz, 1973; *E. ventrilineatus* (Shreve, 1936).

Eleutherodactylus (Euhyas) jugans species group. Content: 2 species: *E. glanduliferoides* Shreve, 1936[33]; *E. jugans* Cochran, 1937.

Eleutherodactylus (Euhyas) oxyrhyncus species group. Content: 2 species: *E. apostates* Schwartz, 1973; *E. oxyrhyncus* (Duméril & Bibron, 1841).

Eleutherodactylus (Euhyas) paulsoni species group. Content: 1 species: *E. paulsoni* Schwartz, 1964.

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[32] This group is composed of species of the former *E. cundalli* species subgroup, *E. gossei* species subgroup, *E. jamaicensis* species subgroup, *E. luteolus* species subgroup, and *E. nubicola* species subgroup of Hedges *et al.* (2008a).

[33] Transferred to this group from the *E. bakeri* group to remedy the paraphyly of the *E. bakeri* group.

Eleutherodactylus (Euhyas) rufifemoralis species group. Content: 2 species: *E. furcyensis* Shreve & Williams, 1963; *E. rufifemoralis* Noble & Hassler, 1933.

***Eleutherodactylus (Euhyas) planirostris* species series.** Content: 6 species groups, 24 species.

Eleutherodactylus (Euhyas) atkinsi species group. Content: 1 species: *E. atkinsi* Dunn, 1925.

Eleutherodactylus (Euhyas) gundlachi species group. Content: 6 species: *E. adelus* Díaz, Cadiz & Hedges, 2003; *E. feichtingeri* Díaz, Hedges & Schmid, 2012; *E. gundlachi* Schmidt, 1920; *E. intermedius* Barbour & Shreve, 1937; *E. tetajulia* Estrada & Hedges, 1996; *E. varleyi* Dunn, 1925.

Eleutherodactylus (Euhyas) limbatus species group. Content: 6 species: *E. cubanus* Barbour, 1942; *E. etheridgei* Schwartz, 1958; *E. iberia* Estrada & Hedges, 1996; *E. jaumei* Estrada & Alonso, 1997; *E. limbatus* (Cope, 1862); *E. orientalis* (Barbour & Shreve, 1937).

Eleutherodactylus (Euhyas) pezopetrus species group. Content: 1 species: *E. pezopetrus* Schwartz, 1960.

Eleutherodactylus (Euhyas) pinarensis species group. Content: 3 species: *E. blairhedgesi* Estrada, Díaz & Rodriguez, 1998 "1997"; *E. pinarensis* Dunn, 1926; *E. thomasi* Schwartz, 1959.

Eleutherodactylus (Euhyas) planirostris species group. Content: 7 species: *E. casparii* Dunn, 1926; *E. goini* Schwartz, 1960; *E. guanahacabibes* Estrada & Rodriguez, 1985; *E. planirostris* (Cope, 1862); *E. rogersi* Goin, 1955; *E. simulans* Díaz & Fong, 2001; *E. tonyi* Estrada & Hedges, 1997.

***Eleutherodactylus (Euhyas) ricordii* species series.** Content: 2 species groups, 14 species.

Eleutherodactylus (Euhyas) lentus species group. Content: 10 species: *E. grahami* Schwartz, 1979; *E. lentus* (Cope, 1862); *E. lucioi* Schwartz, 1980; *E. monensis* (Meerwarth, 1901); *E. paralius* Schwartz, 1976; *E. pictissimus* Cochran, 1935; *E. probolaeus* Schwartz, 1965; *E. rhodesi* Schwartz, 1980; *E. warreni* Schwartz, 1976; *E. weinlandi* Barbour, 1914.

Eleutherodactylus (Euhyas) ricordii species group. Content: 4 species: *E. acmonis* Schwartz, 1960; *E. bresslerae* Schwartz, 1960; *E. michaelschmidi* Díaz, Cádiz & Navarro, 2007; *E. ricordii* (Duméril & Bibron, 1841).

***Eleutherodactylus (Euhyas) zugi* species series**. Content: 3 species : *E. erythroproctus* Schwartz, 1960; *E. klinikowskii* Schwartz, 1959; *E. zugi* Schwartz, 1958.

Subgenus *Pelorius* Hedges, 1989. Content: 2 species series, 9 species.

***Eleutherodactylus (Pelorius) inoptatus* species series.** Content: 3 species: *E. chlorophenax* Schwartz, 1976; *E. inoptatus* (Barbour, 1914); *E. nortoni* Schwartz, 1976.

***Eleutherodactylus (Pelorius) ruthae* species series**. Content: 6 species: *E. aporostegus* Schwartz, 1965; *E. bothroboans* Schwartz, 1965; *E. hypostenor* Schwartz, 1965; *E. parapelates* Hedges & Thomas, 1987; *E. ruthae* Noble, 1923; *E. tychathrous* Schwartz, 1965.

Subgenus *Schwartzius* Hedges, Duellman & Heinicke, 2008. Content: 1 species: *E. counouspeus* Schwartz, 1964.

Subgenus *Syrrhophus* Cope, 1878. Content: 2 species series, 26 species.

***Eleutherodactylus (Syrrhophus) longipes* species series.** Content: 6 species groups, 24 species.

Eleutherodactylus (Syrrhophus) leprus species group. Content: 3 species: *E. cystignathoides* (Cope, 1877); *E. leprus* (Cope, 1879); *E. rubrimaculatus* (Taylor & Smith, 1945).

Eleutherodactylus (Syrrhophus) longipes species group. Content: 2 species: *E. dennisi* (Lynch, 1970); *E. longipes* (Baird, 1859).

Eleutherodactylus (Syrrhophus) marnockii species group. Content: 4 species: *E. guttilatus* (Cope, 1879; *E. marnockii* (Cope, 1878); *E. verrucipes* (Cope, 1885 "1884"); *E. verruculatus* (Peters, 1870).

Eleutherodactylus (Syrrhophus) modestus species group. Content: 5 species: *E. interorbitalis* (Langebartel & Shannon, 1956); *E. modestus* (Taylor, 1942); *E. nivicolimae* (Dixon & Webb, 1966); *E. pallidus* (Duellman, 1958); *E. teretistes* (Duellman, 1958).

Eleutherodactylus (Syrrhophus) nitidus species group. Content: 9 species: *E. albolabris* (Taylor, 1943); *E. angustidigitorum* (Taylor, 1940 "1939"); *E. dilatus* (Davis & Dixon, 1955)[34]; *E. grandis* (Dixon, 1957); *E. maurus* Hedges, 1989; *E. nitidus* (Peters, 1870 "1869"); *E. rufescens* (Duellman & Dixon, 1959); *E. saxatilis* (Webb, 1962); *E. syristes* (Hoyt, 1965).

Eleutherodactylus (Syrrhophus) pipilans species group. Content: 1 species: *E. pipilans* (Taylor, 1940).

***Eleutherodactylus (Syrrhophus) symingtoni* species series.** Content: 2 species: *E. symingtoni* Schwartz, 1957; *E. zeus* Schwartz, 1958.

SUBFAMILY: Phyzelaphryninae Hedges, Duellman & Heinicke, 2008. Content: 2 genera, 9 species.

Genus: *Adelophryne* Hoogmoed & Lescure, 1984. Content: 8 species. *A. adiastola* Hoogmoed & Lescure, 1984; *A. baturitensis* Hoogmoed, Borges & Cascon, 1994; *A. gutturosa* Hoogmoed & Lescure, 1984; *A. maranguapensis* Hoogmoed, Borges & Cascon, 1994; *A. meridionalis* Santana, Fonseca, Neves & Carvalho, 2012; *A. mucronatus* Lourenço de Moraes, Solé & Toledo, 2012; *A. pachydactyla* Hoogmoed, Borges & Cascon, 1994; *A. patamona* MacCulloch, Lathrop, Kok, Minter, Khan & Barrio-Amoros, 2008.

Genus: *Phyzelaphryne* Heyer, 1977. Content: 1 species: *Phyzelaphryne miriamae* Heyer, 1977.

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[34] The inclusion of *E. dilatus* in *Syrrhophus* is assumed and must be tested by inclusion of DNA sequences that are missing for this taxon.