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**New World direct-developing frogs (Anura: Terrarana):
Molecular phylogeny, classification, biogeography, and conservation**

S. BLAIR HEDGES, WILLIAM E. DUELLMAN, & MATTHEW P. HEINICKE



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Table of Contents

Abstract	6
Introduction	6
Materials and Methods	9
Results	12
Systematic Accounts	21
Terrarana, New Taxon	21
Family Brachycephalidae Günther, 1858	22
Genus <i>Brachycephalus</i> Fitzinger, 1826	23
Genus <i>Ischnocnema</i> Reinhardt & Lütken, 1862	25
<i>Ischnocnema guentheri</i> Species Series	27
<i>Ischnocnema lactea</i> Species Series	27
<i>Ischnocnema parva</i> Species Series	28
<i>Ischnocnema ramagii</i> Species Series	28
<i>Ischnocnema verrucosa</i> Species Series	29
Family Craugastoridae, New Family	29
Genus <i>Craugastor</i> Cope, 1862	31
Subgenus <i>Campbellius</i> , New Subgenus	33
Subgenus <i>Craugastor</i> Cope, 1862	35
<i>Craugastor (Craugastor) fitzingeri</i> Species Group	37
<i>Craugastor (Craugastor) melanostictus</i> Species Group	37
<i>Craugastor (Craugastor) gulosus</i> Species Series	38
<i>Craugastor (Craugastor) mexicanus</i> Species Series	39
<i>Craugastor (Craugastor) rhodopis</i> Species Series	40
<i>Craugastor (Craugastor) podiciferus</i> Species Group	41
<i>Craugastor (Craugastor) rhodopis</i> Species Group	41
<i>Craugastor (Craugastor) punctariolus</i> Species Series	42
Subgenus <i>Hylactophryne</i> Lynch, 1968	42
<i>Craugastor (Hylactophryne) augusti</i> Species Series	44
<i>Craugastor (Hylactophryne) bocourti</i> Species Series	45
Genus <i>Haddadus</i> , New Genus	45

Family Eleutherodactylidae Lutz, 1954	47
Subfamily Eleutherodactylinae Lutz 1954	49
Genus <i>Diasporus</i> , New Genus	49
Genus <i>Eleutherodactylus</i> Duméril & Bibron, 1838	50
Subgenus <i>Eleutherodactylus</i> Duméril & Bibron, 1838	52
<i>Eleutherodactylus</i> (<i>Eleutherodactylus</i>) <i>auriculatus</i> Species Series	53
<i>Eleutherodactylus</i> (<i>Eleutherodactylus</i>) <i>abbotti</i> Species Group	54
<i>Eleutherodactylus</i> (<i>Eleutherodactylus</i>) <i>auriculatus</i> Species Group	55
<i>Eleutherodactylus</i> (<i>Eleutherodactylus</i>) <i>minutus</i> Species Group	56
<i>Eleutherodactylus</i> (<i>Eleutherodactylus</i>) <i>martinicensis</i> Species Series	56
<i>Eleutherodactylus</i> (<i>Eleutherodactylus</i>) <i>antillensis</i> Species Group	57
<i>Eleutherodactylus</i> (<i>Eleutherodactylus</i>) <i>antillensis</i> Species Subgroup	57
<i>Eleutherodactylus</i> (<i>Eleutherodactylus</i>) <i>gryllus</i> Species Subgroup	58
<i>Eleutherodactylus</i> (<i>Eleutherodactylus</i>) <i>locustus</i> Species Subgroup	59
<i>Eleutherodactylus</i> (<i>Eleutherodactylus</i>) <i>wightmanae</i> Species Subgroup	59
<i>Eleutherodactylus</i> (<i>Eleutherodactylus</i>) <i>flavescens</i> Species Group	59
<i>Eleutherodactylus</i> (<i>Eleutherodactylus</i>) <i>martinicensis</i> Species Group	59
<i>Eleutherodactylus</i> (<i>Eleutherodactylus</i>) <i>richmondi</i> Species Series	61
<i>Eleutherodactylus</i> (<i>Eleutherodactylus</i>) <i>varians</i> Species Series	61
<i>Eleutherodactylus</i> (<i>Eleutherodactylus</i>) <i>lamprotes</i> Species Group	61
<i>Eleutherodactylus</i> (<i>Eleutherodactylus</i>) <i>montanus</i> Species Group	62
<i>Eleutherodactylus</i> (<i>Eleutherodactylus</i>) <i>varians</i> Species Group	62
<i>Eleutherodactylus</i> (<i>Eleutherodactylus</i>) <i>leberi</i> Species Subgroup	63
<i>Eleutherodactylus</i> (<i>Eleutherodactylus</i>) <i>varians</i> Species Subgroup	64
<i>Eleutherodactylus</i> (<i>Eleutherodactylus</i>) <i>wetmorei</i> Species Group	64
<i>Eleutherodactylus</i> (<i>Euhyas</i>) <i>armstrongi</i> Species Series	66
<i>Eleutherodactylus</i> (<i>Euhyas</i>) <i>dimidiatus</i> Species Series	66
<i>Eleutherodactylus</i> (<i>Euhyas</i>) <i>dimidiatus</i> Species Group	67
<i>Eleutherodactylus</i> (<i>Euhyas</i>) <i>schmidti</i> Species Group	68
<i>Eleutherodactylus</i> (<i>Euhyas</i>) <i>greyi</i> Species Series	68
<i>Eleutherodactylus</i> (<i>Euhyas</i>) <i>luteolus</i> Species Series	69
<i>Eleutherodactylus</i> (<i>Euhyas</i>) <i>cuneatus</i> Species Group	69
<i>Eleutherodactylus</i> (<i>Euhyas</i>) <i>luteolus</i> Species Group	71
<i>Eleutherodactylus</i> (<i>Euhyas</i>) <i>cundalli</i> Species Subgroup	71
<i>Eleutherodactylus</i> (<i>Euhyas</i>) <i>gossei</i> Species Subgroup	71
<i>Eleutherodactylus</i> (<i>Euhyas</i>) <i>jamaicensis</i> Species Subgroup	72
<i>Eleutherodactylus</i> (<i>Euhyas</i>) <i>luteolus</i> Species Subgroup	72
<i>Eleutherodactylus</i> (<i>Euhyas</i>) <i>nubicola</i> Species Subgroup	72
<i>Eleutherodactylus</i> (<i>Euhyas</i>) <i>riparius</i> Species Group	73
<i>Eleutherodactylus</i> (<i>Euhyas</i>) <i>toa</i> Species Group	73
<i>Eleutherodactylus</i> (<i>Euhyas</i>) <i>oxyrhincus</i> Species Series	74
<i>Eleutherodactylus</i> (<i>Euhyas</i>) <i>bakeri</i> Species Group	74
<i>Eleutherodactylus</i> (<i>Euhyas</i>) <i>glandulifer</i> Species Group	76
<i>Eleutherodactylus</i> (<i>Euhyas</i>) <i>jugans</i> Species Group	76
<i>Eleutherodactylus</i> (<i>Euhyas</i>) <i>oxyrhincus</i> Species Group	77
<i>Eleutherodactylus</i> (<i>Euhyas</i>) <i>paulsoni</i> Species Group	77
<i>Eleutherodactylus</i> (<i>Euhyas</i>) <i>ruffifemoralis</i> Species Group	77
<i>Eleutherodactylus</i> (<i>Euhyas</i>) <i>planirostris</i> Species Series	78
<i>Eleutherodactylus</i> (<i>Euhyas</i>) <i>atkinsi</i> Species Group	78
<i>Eleutherodactylus</i> (<i>Euhyas</i>) <i>gundlachi</i> Species Group	78
<i>Eleutherodactylus</i> (<i>Euhyas</i>) <i>limbatus</i> Species Group	80
<i>Eleutherodactylus</i> (<i>Euhyas</i>) <i>pezopetrus</i> Species Group	80
<i>Eleutherodactylus</i> (<i>Euhyas</i>) <i>pinarensis</i> Species Group	81

<i>Eleutherodactylus (Euhyas) planirostris</i> Species Group	81
<i>Eleutherodactylus (Euhyas) ricordii</i> Species Series	81
<i>Eleutherodactylus (Euhyas) lentus</i> Species Group	82
<i>Eleutherodactylus (Euhyas) ricordii</i> Species Group	82
<i>Eleutherodactylus (Euhyas) zugi</i> Species Series	84
Subgenus <i>Pelorius</i> Hedges, 1989	84
<i>Eleutherodactylus (Pelorius) inoptatus</i> Species Series	85
<i>Eleutherodactylus (Pelorius) ruthae</i> Species Series	86
Subgenus <i>Schwartzius</i> , New Subgenus	87
Subgenus <i>Syrrhophus</i> Cope, 1878	88
<i>Eleutherodactylus (Syrrhophus) longipes</i> Species Series	89
<i>Eleutherodactylus (Syrrhophus) leprus</i> Species Group	89
<i>Eleutherodactylus (Syrrhophus) longipes</i> Species Group	90
<i>Eleutherodactylus (Syrrhophus) marnockii</i> Species Group	91
<i>Eleutherodactylus (Syrrhophus) modestus</i> Species Group	91
<i>Eleutherodactylus (Syrrhophus) nitidus</i> Species Group	91
<i>Eleutherodactylus (Syrrhophus) pipilans</i> Species Group	93
<i>Eleutherodactylus (Syrrhophus) symingtoni</i> Species Series	93
Subfamily <i>Phyzelaphryninae</i> , New Subfamily	93
Genus <i>Adelophryne</i> Hoogmoed and Lescure, 1984	94
Genus <i>Phyzelaphryne</i> Heyer, 1977	94
Family <i>Strabomantidae</i> , New Family	95
Subfamily <i>Holoadeninae</i> , New Subfamily	97
Genus <i>Barycholos</i> Heyer, 1969	97
Genus <i>Bryophryne</i> , New Genus	99
Genus <i>Euparkerella</i> Griffiths, 1959	99
Genus <i>Holoaden</i> Miranda-Ribeiro, 1920	100
Genus <i>Noblella</i> Barbour, 1930	102
Genus <i>Psychrophrynella</i> , New Genus	102
Subfamily <i>Strabomantinae</i> , New Subfamily	103
Genus <i>Atopophrynus</i> Lynch & Ruiz-Carranza, 1982	105
Genus <i>Dischidodactylus</i> Lynch, 1979	107
Genus <i>Geobatrachus</i> Ruthven, 1915 1	108
Genus <i>Isodactylus</i> , New Genus	108
Genus <i>Lynchius</i> , New Genus	109
Genus <i>Niceforonia</i> Goin & Cochran, 1963	109
Genus <i>Oreobates</i> Jiménez de la Espada, 1872	111
Genus <i>Phrynopus</i> Peters, 1873	111
Genus <i>Pristimantis</i> Jiménez de la Espada, 1871	112
Subgenus <i>Hypodictyon</i> Cope (1885)	114
<i>Pristimantis (Hypodictyon) ridens</i> Species Series	114
<i>Pristimantis (Hypodictyon) rubicundus</i> Species Series	115
Subgenus <i>Pristimantis</i> Jiménez de la Espada, 1871	116
<i>Pristimantis (Pristimantis) bellona</i> Species Group	118
<i>Pristimantis (Pristimantis) chalceus</i> Species Group	119
<i>Pristimantis (Pristimantis) conspicillatus</i> Species Group	120
<i>Pristimantis (Pristimantis) curtipes</i> Species Group	120
<i>Pristimantis (Pristimantis) devillei</i> Species Group	121
<i>Pristimantis (Pristimantis) frater</i> Species Group	121
<i>Pristimantis (Pristimantis) galdi</i> Species Group	122
<i>Pristimantis (Pristimantis) lacrimosus</i> Species Group	123
<i>Pristimantis (Pristimantis) leptolophus</i> Species Group	123
<i>Pristimantis (Pristimantis) loustes</i> Species Group	124

<i>Pristimantis (Pristimantis) myersi</i> Species Group	125
<i>Pristimantis (Pristimantis) orcesi</i> Species Group	125
<i>Pristimantis (Pristimantis) orestes</i> Species Group	125
<i>Pristimantis (Pristimantis) peruvianus</i> Species Group	126
<i>Pristimantis (Pristimantis) surdus</i> Species Group	126
<i>Pristimantis (Pristimantis) unistrigatus</i> Species Group	127
Subgenus <i>Yunganastes</i> Padial, Castroviejo-Fisher, Köhler, Domic & De la Riva 2007	128
Genus <i>Strabomantis</i> Peters, 1863	129
<i>Strabomantis biporcatus</i> Species Series	130
<i>Strabomantis biporcatus</i> Species Group	131
<i>Strabomantis cornutus</i> Species Group	131
<i>Strabomantis bufoniformis</i> Species Series	132
Discussion	133
Acknowledgments	140
References	141
Appendix I	151
Appendix II	172
Appendix III	181

Abstract

New World frogs recently placed in a single, enormous family (Brachycephalidae) have direct development and reproduce on land, often far away from water. DNA sequences from mitochondrial and nuclear genes of 344 species were analyzed to estimate their relationships. The molecular phylogeny in turn was used as the basis for a revised classification of the group. The 882 described species are placed in a new taxon, Terrarana, and allocated to four families, four subfamilies, 24 genera, 11 subgenera, 33 species series, 56 species groups, and 11 species subgroups. Systematic accounts are provided for all taxa above the species level. Two families (Craugastoridae and Strabomantidae), three subfamilies (Holoadeninae, Phyzelaphryninae, and Strabomantinae), six genera (*Bryophryne*, *Diasporus*, *Haddadus*, *Isodactylus*, *Lynchius*, and *Psychrophrynella*), and two subgenera (*Campbellius* and *Schwartzzius*) are proposed and named as new taxa, 13 subspecies are considered to be distinct species, and 613 new combinations are formed. Most of the 100 informal groups (species series, species groups, and species subgroups) are new or newly defined. *Brachycephalus* and *Ischnocnema* are placed in Brachycephalidae, a relatively small clade restricted primarily to southeastern Brazil. Eleutherodactylidae includes two subfamilies, four genera, and five subgenera and is centered in the Caribbean region. Craugastoridae contains two genera and three subgenera and is distributed mainly in Middle America. Strabomantidae is distributed primarily in the Andes of northwestern South America and includes two subfamilies, 16 genera, and three subgenera. Images and distribution maps are presented for taxa above the species level and a complete list of species is provided. Aspects of the evolution, biogeography, and conservation of Terrarana are discussed.

Key words: Amphibia, Brachycephalidae, Craugastoridae, DNA sequence, Eleutherodactylidae, evolution, Strabomantidae, systematics, taxonomy

Introduction

The twenty-first Century has witnessed a renaissance in systematic biology with respect to theory, methodology, and taxonomy, and perhaps most significantly the application of systematics to such diverse fields as ecology, behavior, and conservation, among others. This resurgence has occurred principally with the sequencing of DNA and use of newly developed methods of analysis. Thus, systematists have discovered a new array of tools and characters for the inference of phylogenetic relationships. These innovative approaches are being used from the levels of local phylogeography to ascertaining the relationships among prokaryotes and eukaryotes. The only work that has attempted to determine the phylogenetic relationships among all liv-

ing taxa of amphibians is that by Frost *et al.* (2006), in which DNA sequences of 522 species were used to create a phylogenetic tree representing nearly 6000 species. One small twig in their molecular tree was a newly classified “Brachycephalidae” represented by 16 species. The phylogeny and classification presented here for that same group are based on DNA sequences from 344 species. Thus, that small twig has grown into a major branch of the amphibian evolutionary tree.

This monograph concerns a large evolutionary radiation (882 species) of New World frogs that breed on land and have direct development. Except for one species known to be ovoviviparous (Drewry & Jones 1976), all of these species are known (or presumed) to lay eggs in terrestrial situations where they hatch into froglets, thereby bypassing the tadpole stage. These frogs range from the southern United States to northern Argentina, although they are most diverse in mountains of Central America, the West Indies, and South America. They represent about 13% of all known amphibian species and 28% of the amphibian taxa in the New World tropics (AmphibiaWeb 2007; Frost 2007; IUCN 2007). Almost all of the included species have been called “eleutherodactylines” at some point in time. A notable exception is the small genus *Brachycephalus* (11 species) which in recent years has become affiliated with this clade in molecular phylogenies.

The “eleutherodactylines” have been considered to be a subunit (Subfamily Eleutherodactylinae or Tribe Eleutherodactylini of Telmatobiinae) of Leptodactylidae (Lynch 1971) whereas *Brachycephalus* has been placed in its own family, Brachycephalidae (e.g., Noble 1931) or in Atelopodidae (Griffiths 1959). Based on life-history data, Duellman and Lynch (1969) suggested that *Brachycephalus* was not an atelopodid. Analyses of molecular data over the last decade (Ruvinsky & Maxson 1996; Darst & Cannatella 2004; Frost *et al.* 2006; Roelants *et al.* 2007) have indicated that Leptodactylidae is not monophyletic and that the “eleutherodactylines” and *Brachycephalus* belong to a separate lineage of neobatrachian anurans. However, the paraphyly of “eleutherodactylines,” with respect to *Brachycephalus*, implied by some of these analyses, cannot be taken as strong evidence given the small representation (1–5%) of “eleutherodactylines” in those studies. Even in our recent study with expanded coverage (Heinicke *et al.* 2007), and in this study (see below), the position of *Brachycephalus* with respect to “eleutherodactylines” has been difficult to resolve. While other lineages have been difficult to resolve as well, the importance of *Brachycephalus* concerns its taxonomic priority in determining the family name.

From an evolutionary and taxonomic standpoint, this clade of frogs is one of the most poorly known major groups of vertebrates. Although new species are readily recognized and described, taxonomists have been unable to agree, for the most part, on how to organize those species into genera, subgenera, and species groups to make this complex more manageable (e.g., Lynch 1976a; Savage 1987; Hedges 1989a; Lynch & Duellman 1997; Frost *et al.* 2006). As a result, most species have been placed in *Eleutherodactylus*, which for years has remained the largest vertebrate genus. Species continue to be described at an increasing rate (Fig. 1). This rate of species discovery was approximately 1–2 species per year during the 19th Century, but then rose sharply during the latter half of the 20th Century to 15 species per year, and continues to increase (Fig. 1).

The taxonomic confusion in part reflects the paucity of characters available for study and the plasticity of the few “useful” characters. Characters such as skin texture, relative length of digits, and size of digital discs have been used extensively, but such characters are of functional importance and subject to evolutionary convergence. For example, almost all arboreal species have large digital tips, and most ground-dwelling species have small digital tips. The larger digital tips of the arboreal species, of course, aid them in climbing. Most major clades of “eleutherodactylines,” such as the Middle American Clade and Caribbean Clade, have arboreal species with large digital tips. Even the states of the single morphological character believed to be the most reliable, the orientation of the trigeminal nerve relative to jaw musculature (Lynch 1986a), have been shown to have evolved independently in different lineages in molecular phylogenies (Frost *et al.* 2006; Heinicke *et al.* 2007). Despite their plasticity, these characters are often useful in defining some clades, as evidenced by agreement with other data sets such as DNA sequences, and they remain major aspects of the organism and cannot be overlooked.

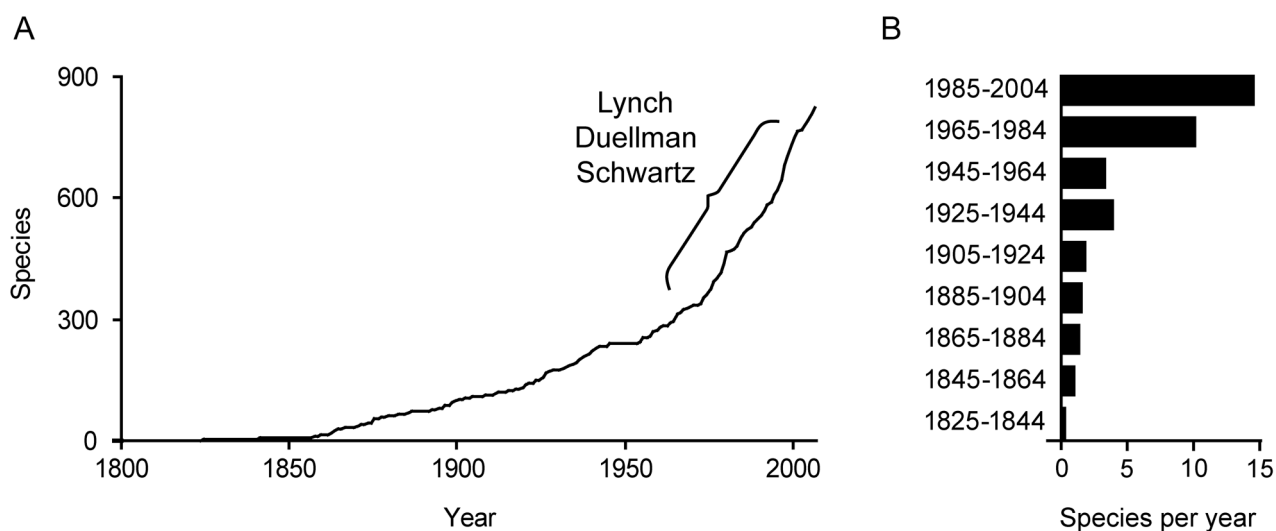


FIGURE 1. The history of discovery of terraranan frogs. (A) Discovery curve showing cumulative number of valid species through time, illustrating an increase in rate in recent decades. The names of the three herpetologists mostly responsible for the rate increase are noted. (B) Average number of valid species described each year, calculated over intervals of 20 years.

Chromosome analyses of “eleutherodactylines” have revealed a surprisingly rapid rate of change for amphibians (including closely related families Hylidae and Bufonidae), comparable to that in mammals (Bogart 1981; Bogart & Hedges 1995). However, chromosome variation, by itself, generally has not proven useful in the classification of “eleutherodactylines” frogs (e.g., Savage 1987; Bogart & Hedges 1995). As data from more species become available, chromosome data will likely be more phylogenetically informative.

Initial molecular studies of *Eleutherodactylus* and relatives using allozymes and albumin immunology (Miyamoto 1983, 1984, 1986; Hedges 1989a, 1989b; Hass & Hedges 1991; Kaiser *et al.* 1994) showed promise for resolving relationships, but those studies were hampered by limited taxonomic sampling and limitations of the methods themselves. Until recently, only a few comparative studies using DNA sequences have been undertaken with these frogs, and they too have had limited taxon sampling, including less than 5% of “eleutherodactylines.” One study included 12 species (Darst & Cannatella 2004), another 39 species (Crawford & Smith 2005) a third used 16 species (Frost *et al.* 2006), a fourth 21 taxa, and a fifth 24 taxa (Padial *et al.* 2007a) (Padial *et al.* 2007b).

Recently, we completed a DNA sequence analysis of 277 species of “eleutherodactylines” and *Brachycephalus* using mitochondrial and nuclear genes (Heinicke *et al.* 2007). The resulting tree resolved three major groups: a Caribbean Clade of 140 species (representing 185 species), a Middle American Clade of 14 species (representing 111 species) and a South American Clade of 87 species (representing 397 species). A smaller Southeast Brazil Clade was also defined that we recognized as *Ischnocnema*. The Middle American Clade had been recognized previously as the subgenus or genus *Craugastor* (Lynch 1986a; Crawford & Smith 2005; Frost *et al.* 2006), although the analysis by Heinicke *et al.* (2007) redefined the group by showing that members of two South American species groups were not part of the clade. The Caribbean and South American clades were both new and unpredicted, because previous analyses had assumed a close relationship between a South American group (the “*Eleutherodactylus*” *unistrigatus* Species Group) and a large assemblage of species in the West Indies of the subgenus *Eleutherodactylus*.

Although our study included approximately one-third of the species in this large clade, the taxonomic coverage was best in the West Indies and comparatively weak in South America. A small sample of *Phrynos*, a genus of terrestrial species lacking T-shaped terminal phalanges and digit discs, suggested that the genus is polyphyletic, as had been noted previously (Duellman & Hedges 2005; Lehr *et al.* 2005). The South-

east Brazil Clade included representatives of several species groups not thought to be closely related, suggesting that many or most species from that region also belong to that clade. Not unexpectedly, we found that the deepest branches in the tree were of lineages in South America, including *Brachycephalus*, and these nodes were, for the most part, unresolved.

Herein, we have added new sequences to that data set and use the results to reorganize the classification of this large clade of frogs. In general, we have taken a conservative approach, and have minimized changes at the generic level so as to cause the least disruption for users of the taxonomy while still reflecting the new evolutionary information. Where appropriate, we use the subgenus category to organize major groups within large genera. This approach provides systematists and evolutionary biologists with information they need for hypothesis testing yet retains the binomens used frequently by non-systematists in field guides and checklists. For example, most of the species in South America are placed in the genus *Pristimantis*, most in Central America are placed in *Craugastor*, and nearly all in the West Indies are retained in *Eleutherodactylus*. Because of the large number of species involved, we also make use of the informal categories of species series, species group, and species subgroup. We include distribution maps and images of representatives of the species groups and higher taxa. In the text we do not give authors for names of species; instead we provide a list of all species names with authors and dates, and their classification in Appendix I.

Materials and Methods

Molecular Analyses

All methods used for the collection and analysis of the new DNA sequences presented here follow those in Heinicke *et al.* (2007). The sequences have been deposited in GenBank and are EU186650–780. Localities, tissue numbers, and museum numbers for the new sequences are in Appendix II. Included among the new sequences are samples from specimens that are being described elsewhere as new species or specimens for which an accurate identification has not yet been made. Although each sequence is treated as a separate species here, several may turn out to be species already included, as suggested by some close relationships seen in the trees in the case of several pairs of sequences. These unidentified sequences will be referred to by their GenBank accession numbers or museum catalog numbers. For this study, we have added a total of 72 ingroup and eight outgroup species to the data set of Heinicke *et al.* (2007), as well as new nuclear gene sequences for eight previously-sampled taxa (Appendix II).

As in Heinicke *et al.* (2007), sequence data consisted of three overlapping sets. Partial sequences for the mitochondrial 12S (~350 bp) and 16S (~800 bp) rRNA genes were included for all 362 (344 ingroup) species. A dataset of 216 species (198 ingroup) includes the full 12S and 16S sequences, along with the intervening tRNA-Valine (~2,500 bp total). For 80 of these species (77 ingroup), data were also obtained for two nuclear exon gene regions of RAG-1 (639 bp) and Tyrosinase precursor (Tyr; 493 bp). Substantial amounts of 12S or 16S data were missing for some of the included species, due to either their not being available on GenBank or the inability to amplify these regions. In these cases the unsequenced regions were coded as missing data. In addition, one species in the 80-species set (*Eleutherodactylus counouspeus*) is missing data for the Tyr gene, and another (*Strabomantis anomalus*) could not be amplified for that gene so instead we used the Tyr sequence of a related species (*S. bufoniformis*).

Genomic DNA was extracted from frozen or ethanol-preserved tissue samples using a Qiagen DNeasy tissue extraction kit under the manufacturer's protocol. PCR amplification of samples was performed in 50- μ l reactions using AmpliTaq DNA polymerase and ThermoPol buffer (New England Biolabs). Each polymerase chain reaction for mitochondrial products contained ThermoPol buffer at 1 \times , dNTPs at 4 μ M, forward and reverse primers at 1 μ M, one unit of polymerase, and 1 μ l of extracted DNA (more for low-quality tissue). For amplification of nuclear genes, dNTP was increased to 6.6 μ M, Taq polymerase to 2.5 units, and extracted

DNA to 5 μ l. Standard reaction conditions were an initial hold for 5 min at 94°C, followed by 40 cycles of 94°C for 30 s, 50°C for 30 s, and 72°C for 60 s. After 40 cycles, a final hold of 72°C for 7 min was performed before terminating the reaction at 4°C. For low- or nonyielding samples, annealing temperature was dropped to 46°C. In some cases, a second round of PCR was performed using primer pairs inside the initially generated fragment. Primers used in PCR reactions were identical to those of Heinicke *et al.* (2007) and are listed in Appendix III. Amplified PCR products were isolated by running on agarose gels and filtering with Millipore Ultrafree-DA gel filters or by vacuum filtration using Millipore Multiscreen filters. Cycle sequencing was performed by the Pennsylvania State University Nucleic Acid Facility. All fragments were sequenced in both forward and reverse directions.

Before analyses, all chromatograms were fully inspected, and all sequences were compared against their reverse complement to detect any call errors. Embedded primer sequences were deleted from all sequence fragments before assembly or alignment. Alignments of 12S and 16S sequences were created using CLUSTAL W (Thompson *et al.* 1994) using the following scoring parameters: match (3), transition (1), transversion (0), gap opening penalty (10), gap extension penalty (5), delay divergent sequences (40%). Resulting alignments were inspected for obvious errors and compared against frog secondary structure models (including *Eleutherodactylus*) available from the European ribosomal RNA database, and modified accordingly. Regions deemed poorly aligned were excluded from analysis. In general, these are loop regions of variable sequence length greater than ~6 bases having low sequence identity (<50%), but no strict algorithm was used. Sequences for RAG-1 and Tyrosinase precursor were aligned by eye; Tyr contained no alignment gaps and all gaps in RAG-1 consisted of codon deletions with the open reading frame preserved. Final alignments for each gene are available from TreeBASE.

For all datasets, maximum likelihood analyses were performed. In addition, Bayesian and distance (NJ) methods were employed for the dataset of 80 species. For the 80-species set, three partitions (12S and 16S, RAG-1, Tyr) were introduced for the Bayesian and likelihood analyses, with model parameters unlinked across the partitions. Distance analysis was performed using MEGA 3.1 (Kumar *et al.* 2004), while Bayesian analysis used MrBayes 3.1 (Ronquist and Huelsenbeck 2003) and likelihood analyses used RAxML-VI-HPC v2.0 (Stamatankis 2006). Bayesian analysis used the GTR + I + Γ model of evolution. Neither MEGA nor RAxML implement this model; instead, TN + Γ (MEGA) and GTRMIX (RAxML) were used. The Γ parameter for the distance analysis was estimated in PAUP 4b10 (Swofford 2003). All parameters for ML and Bayesian analyses were estimated by the programs during the runs. Gaps were treated as missing data.

For each ML analysis, 100 alternative runs were performed. Model parameters in RAxML are estimated by the program and do not require input. Nonparametric bootstrap analysis (1,000 replicates) was performed to provide branch support to the most likely tree of the 100 runs for each data set. Bootstrap analysis (1,000 replicates) was also used to provide branch support for the NJ analysis. Posterior probabilities were used to determine branch support for the Bayesian analysis. The Bayesian analysis of 80 species was performed as two independent runs for 2,000,000 generations with three heated and one cold chain. Chains were sampled every 1,000 generations. The first 25% of samples were discarded as burn-in. To ensure that this was an adequate number of samples discarded, a plot of log likelihood vs. generation was produced and showed that the region of increasing log likelihood values was encompassed in the first 25% of samples. Convergence was assessed by using the program Tracer 1.3 (Rambaut and Drummond 2005) to obtain estimated sample sizes for each model parameter (six substitution frequency categories, four nucleotide frequency categories, Γ -parameter, proportion of invariant sites, tree length, and log likelihood). Estimated sample sizes of each parameter were substantially greater than 100 for the sum of both independent runs, although values for a small number of parameters were less than 100 when the independent runs were treated separately. However, the convergence metric employed by MrBayes (average standard deviation of split frequencies) was less than 0.01 (=0.006) at the conclusion of the run.

Systematic Accounts

The major part of this monograph is a taxonomic revision where new families, genera, and other taxa are described. Here, we mention some of the procedures that we used in the systematic accounts. In all cases, taxa are listed in alphabetical order.

A classification provides a way to organize species to facilitate communication and further study. At the same time, a new classification of one group, such as this one, must integrate with that of other groups, and should consider the history of the classification as it relates to stability. Above all it should reflect the evolutionary history of the organisms. For this last consideration, we relied mostly on the molecular phylogenetic analyses (Fig. 2A–D, Fig. 3A–C, Fig. 4). The species-rich analyses (Figs. 2–3) provided guidance for taxonomic decisions at lower levels (e.g., species groups and series) whereas the gene-rich analyses (Figs. 3–4) provided guidance for decisions at higher levels, although all three analyses were consulted in many cases. If we were to define taxa solely on relationships based on molecular analyses, we would not be able to classify the majority of species in the group, because so many have not yet been sequenced. Instead, we use the molecular phylogenies as primary guidance in establishing a conventional morphology-based classification that is useful for all species.

There is no biological meaning associated with any taxonomic rank or level above the species level, or at least none intended here. However, higher taxa (e.g., families) that contain too many lower taxa (e.g., species) can hinder further research simply because of their large size. Because the group in question here, with more than 850 species, is currently considered a single family, Brachycephalidae (Frost *et al.* 2006) that is larger than nearly any other family of tetrapods, our first decision was to make it more manageable by splitting the group into four families. This necessitated the creation of a higher-level taxon to contain those four families. We chose an unranked taxon to avoid putting in place yet another formal name (superfamily rank) given the volatility of anuran taxonomy in recent years (Frost *et al.* 2006) and the potential problems it might raise in dealing with existing superfamily names (e.g., Hyloidea) that may apply to this group.

Definitions of families, subfamilies, genera, and subgenera follow standardized format (Lynch 1971; Lynch & Duellman 1997). That format is essentially a numerical list of characters deemed to be important or useful in classification, although not all are necessarily diagnostic except when considered in combination. In the past, characters used in the definitions of genera and subgenera have varied because of different characters emphasized by different researchers (e.g., Savage 1987; Hedges 1989a; Lynch & Duellman 1997). Nonetheless we have attempted to standardize those definitions, at least within a genus or subgenus, for comparative purposes. Although rare, individual morphological characters that appear to have diagnostic value on their own are noted in the Remarks section of each account. This major taxonomic revision would not have been necessary if large numbers of shared derived morphological characters were already recognized in these frogs.

In cases where clades could be defined within formal taxa, we recognize the following informal taxa: series, species groups, and species subgroups. Of course, any informal taxon—including those above the family group level—does not fall under the formal rules of the code. Nonetheless, we consider all taxa in this classification as evolutionary units (monophyletic groups) except as indicated (some previously defined species groups of the genus *Pristimantis* are retained here pending further study). For consistency, we name each species series, species group, and species subgroup based on the earliest described species contained in the taxon. As more species are discovered and described and these informal taxa become larger and unmanageable, it is likely that some will be replaced with formal names (e.g., subgenera and genera) and other informal names will be created to accommodate new lower-level clades. Such is the normal evolution of a classification.

Among these informal categories, decisions on which taxonomic level (species series, species group, or species subgroup) to use, within a genus or subgenus, were based largely on convenience in classifying the species. For example, the category of species series was generally used for groups containing a large number of species requiring further subdivision (into species groups) and/or which represent deep divergences within a genus or subgenus. The category of species subgroup was used for relatively small groups of species not

requiring further subdivision at present. Within the large subgenus *Pristimantis* (*Pristimantis*), which will require more sequence data to establish a stable classification, we have continued to recognize previously defined species groups until those much needed data become available.

Definitions of species series, species groups, and species subgroups describe the potentially diagnostic aspects of the morphology of the taxon as well as some information on ecology and habits. The characters usually include body size and proportions, skin texture, coloration, and vocalization. As one would expect with such nested low-level clades, diagnostic characters for species groups in one genus may not be the same as those for another genus, and therefore this section does not have a numbered list. Because this study is based largely on a molecular phylogeny, we make no claim that any of these taxa, formal or informal, are fully diagnosable now based on morphology, but we anticipate that further study of these clades will reveal such characters in the future.

The category of subspecies has been used extensively in the past for West Indian species (Schwartz & Henderson 1991). Upon careful evaluation, we have found that some of those taxa appear to be valid species while others are not, based on observations and data collected by one of us (SBH). Herein we consider 13 of those subspecies to be distinct species.

For information contained in the systematic accounts, such as body size, coloration, distribution, and other data, we have made use of the extensive literature on this group of animals. Therefore, when a character is listed as present in a taxon, it means that we have examined the primary literature of all constituent taxa (e.g., species) for the presence of that character. Nonetheless, we do not cite each species description or intend this publication to be a bibliography or literature survey of the group. In general, we cite literature here only if it is directly relevant to aspects of the classification or a particular taxonomic decision. Distribution maps of genera and subgenera are based on maps of distributions of species by the Global Amphibian Assessment (IUCN 2006), with some modification to improve accuracy. Although we often point out geographic patterns, we do not use geography as a defining character of a taxon.

For terminology specific to “eleutherodactyline” frogs, we follow Lynch and Duellman (1997). Body size is reported as maximum snout-vent length (SVL) in adult females of each species, taken from the literature. Except in rare cases, females are larger than males. For head width (HW), we list ranges of proportions for adult females (HW/SVL x 100), taken from the literature. Numbering of digits in the hand follows conventional standards of Fingers I through IV, although we are aware that the first digit in the hand has been lost in anurans (Fabrezi & Alberch 1996). The relationship of the trigeminal nerve and adductor musculature was obtained from the literature and from dissections accomplished with the aid of Luchol’s solution; terminology follows Lynch (1986a). Nine species were dissected; all had the “S” condition of the adductor musculature. The specimens are: *Bryophryne cophites*, KU 138907; *Diasporus diademata*, KU 37467; *Dischidodactylus duidensis*, AMNH 23192; *Lynchius parkeri*, KU 181354; *Niceforonia nana*, KU 169122; *Noblella lochites*, KU 177356; *Noblella* “*peruviana*,” KU 173329; *Phrynopus montium*, KU 138880; *Psychrophrynella laplacai*, KU 154556. In the case of vocalizations of species from the West Indies, some data are based on personal observations (SBH).

Results

After alignment and removal of ambiguous regions, the 362-species dataset encompassed 1207 sites of the 12S and 16S rRNA genes. The 216-species dataset included 2578 sites of the complete 12S and 16S rRNA genes. The 80-species dataset included 3709 sites of the complete 12S and 16S rRNA genes and portions of the nuclear genes for RAG-1 and Tyrosinase. We present Maximum likelihood (ML) trees for all three datasets, respectively (Figs. 2–4), and include bootstrap confidence values on nodes. For the 80-species tree we also included neighbor-joining bootstrap values and Bayesian confidence values (posterior probabilities).

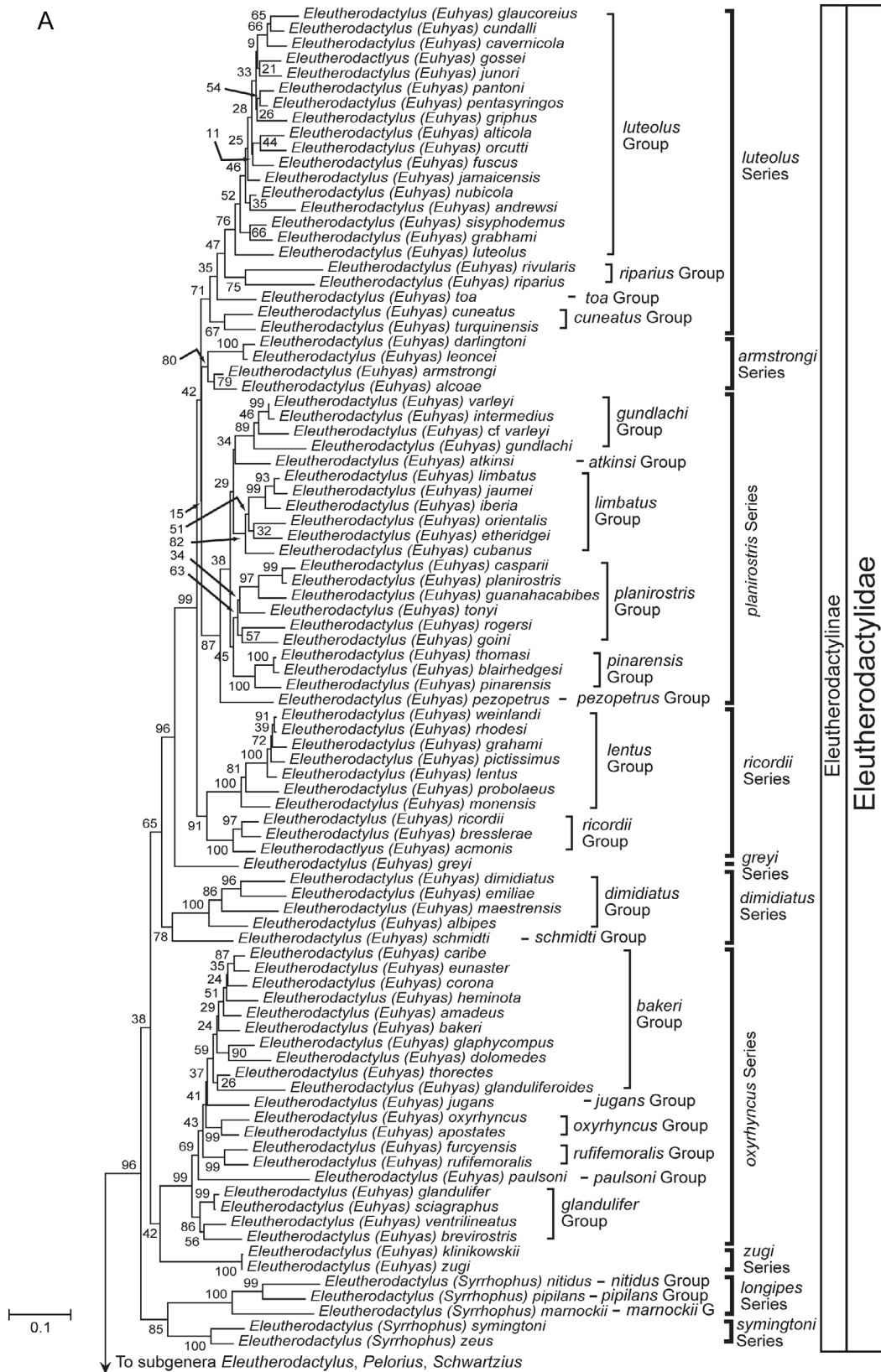


FIGURE 2. Maximum likelihood phylogeny of 362 species of frogs. The data set consists of 1,207 base pairs of aligned mitochondrial DNA sequences of the 12S rRNA and 16S rRNA genes. Bootstrap support values are shown on nodes. Classification of the species is indicated. Where species identification is not known, either the sequence accession number (continuous series of letters and numbers) or museum voucher number (letters separated from numbers) is given. (A) First segment (top) of tree. (B) Second segment of tree. (C) Third segment of tree. (D) Fourth segment (bottom) of tree.

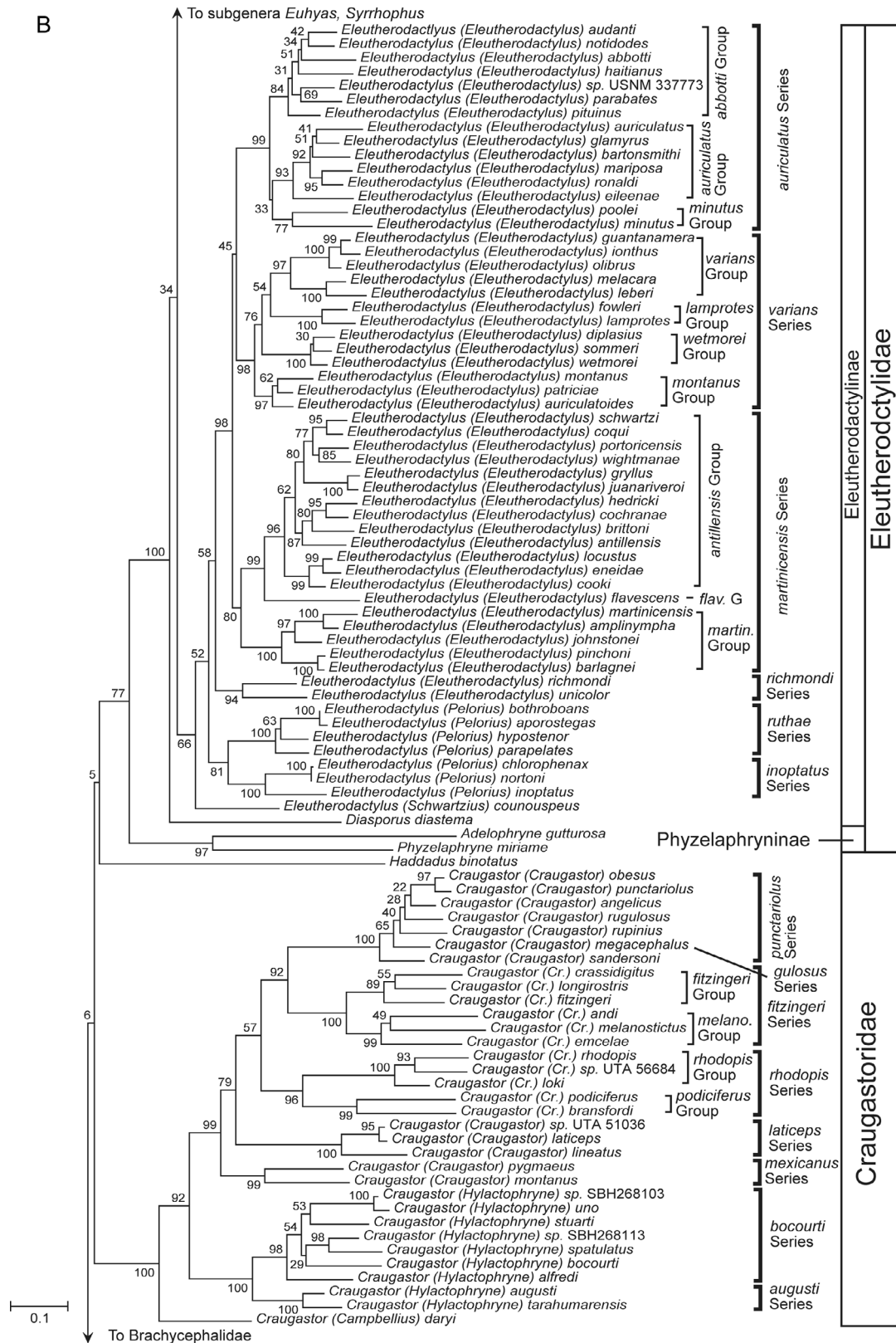


FIGURE 2 (continued).

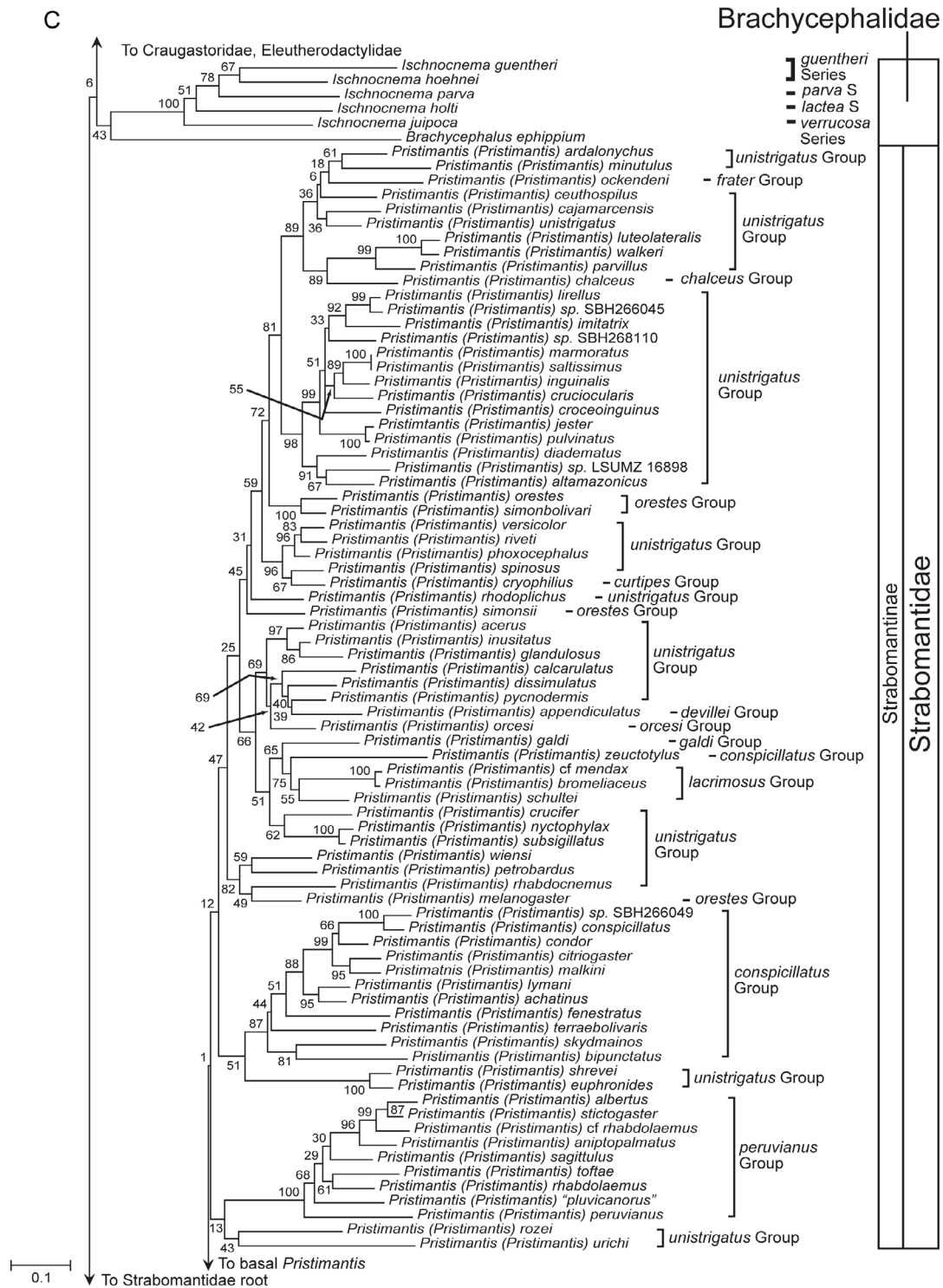


FIGURE 2 (continued).

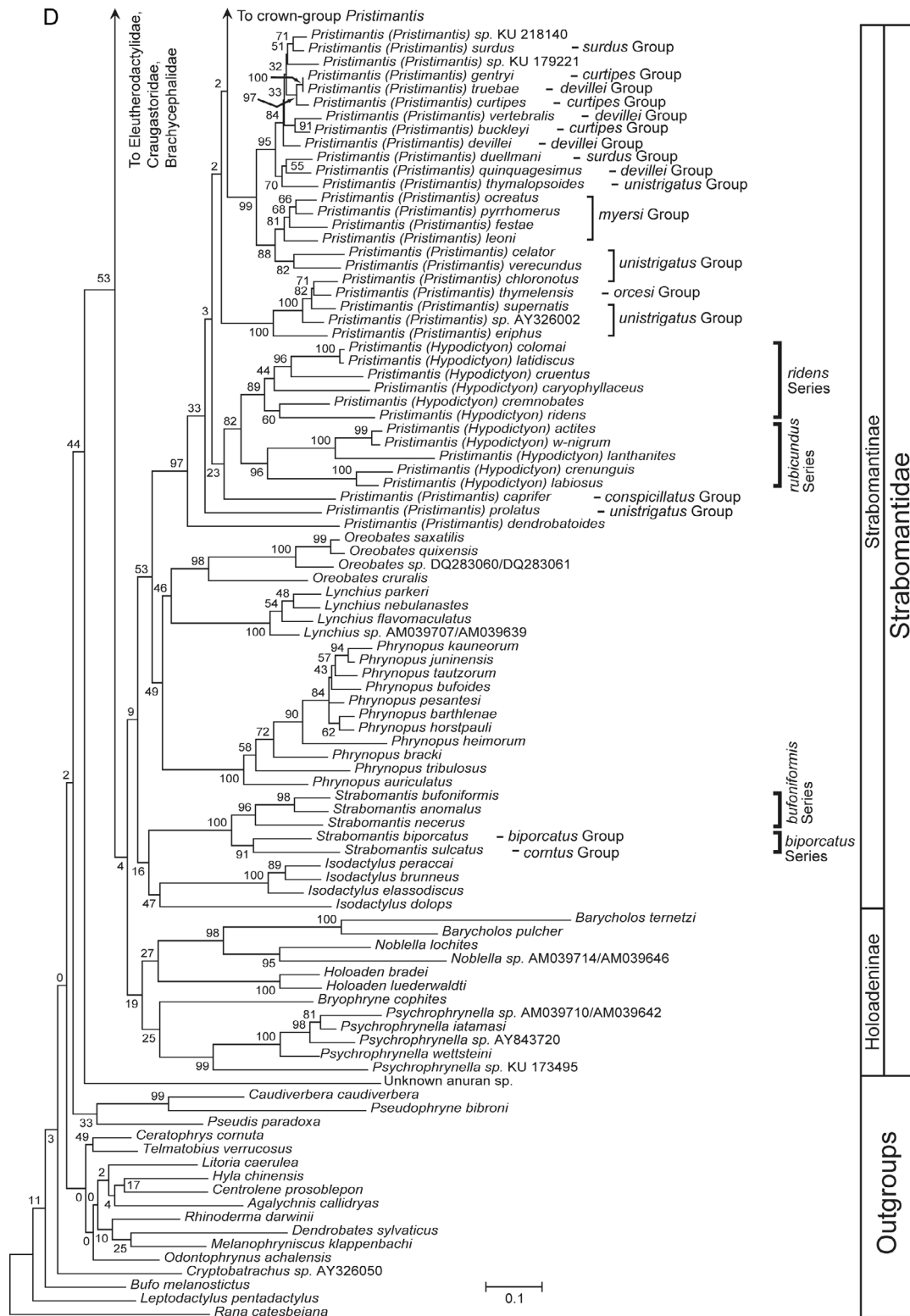


FIGURE 2 (continued).

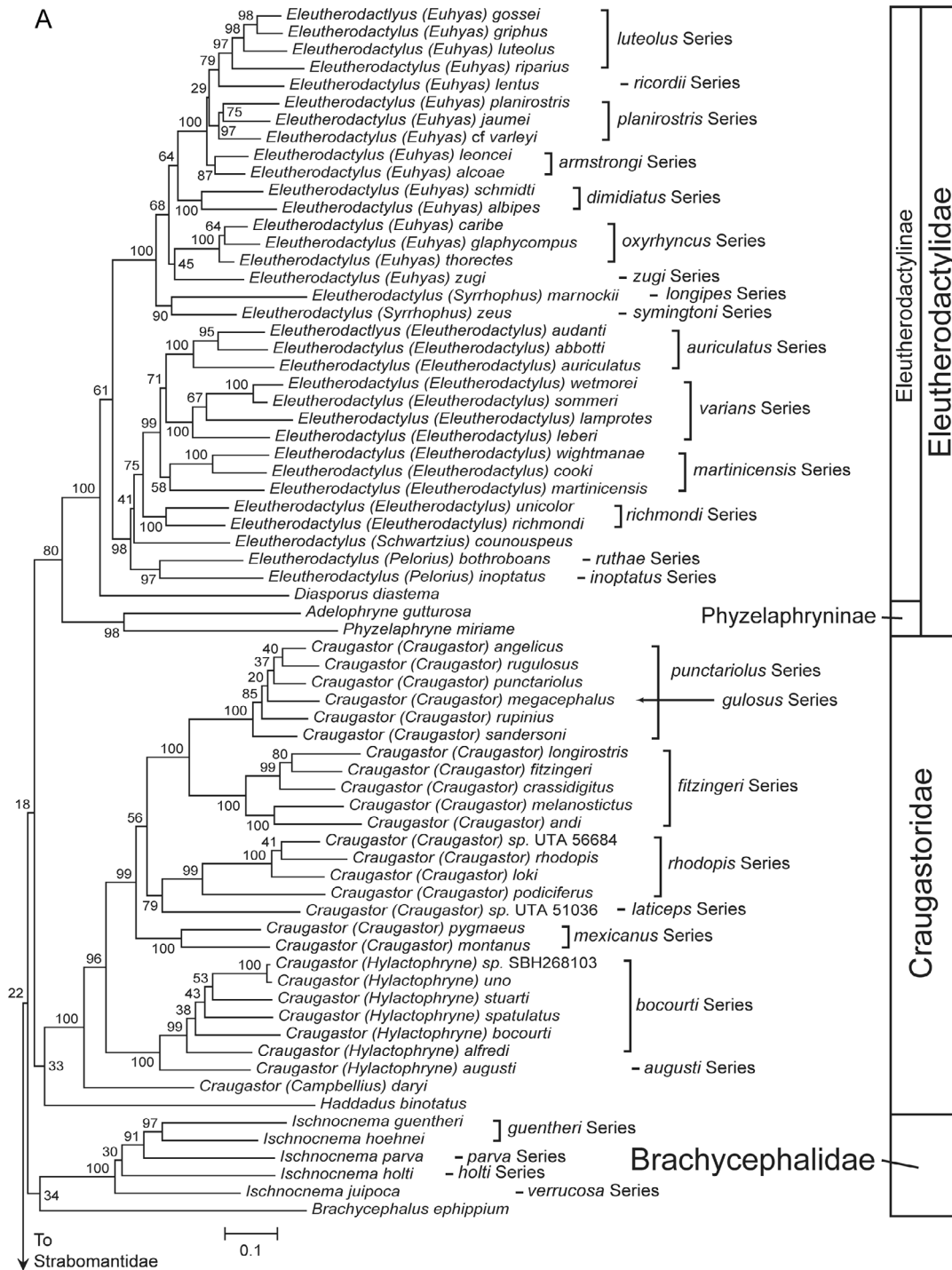


FIGURE 3. Maximum likelihood phylogeny of 216 species of frogs. The data set consists of 2578 base pairs of aligned mitochondrial DNA sequences of the 12S rRNA and 16S rRNA genes, including the intervening transfer RNA Valine. Bootstrap support values are shown on nodes. Classification of the species is indicated. (A) First segment (top) of tree. (B) Second segment (middle) of tree. (C) Third segment (bottom) of tree.

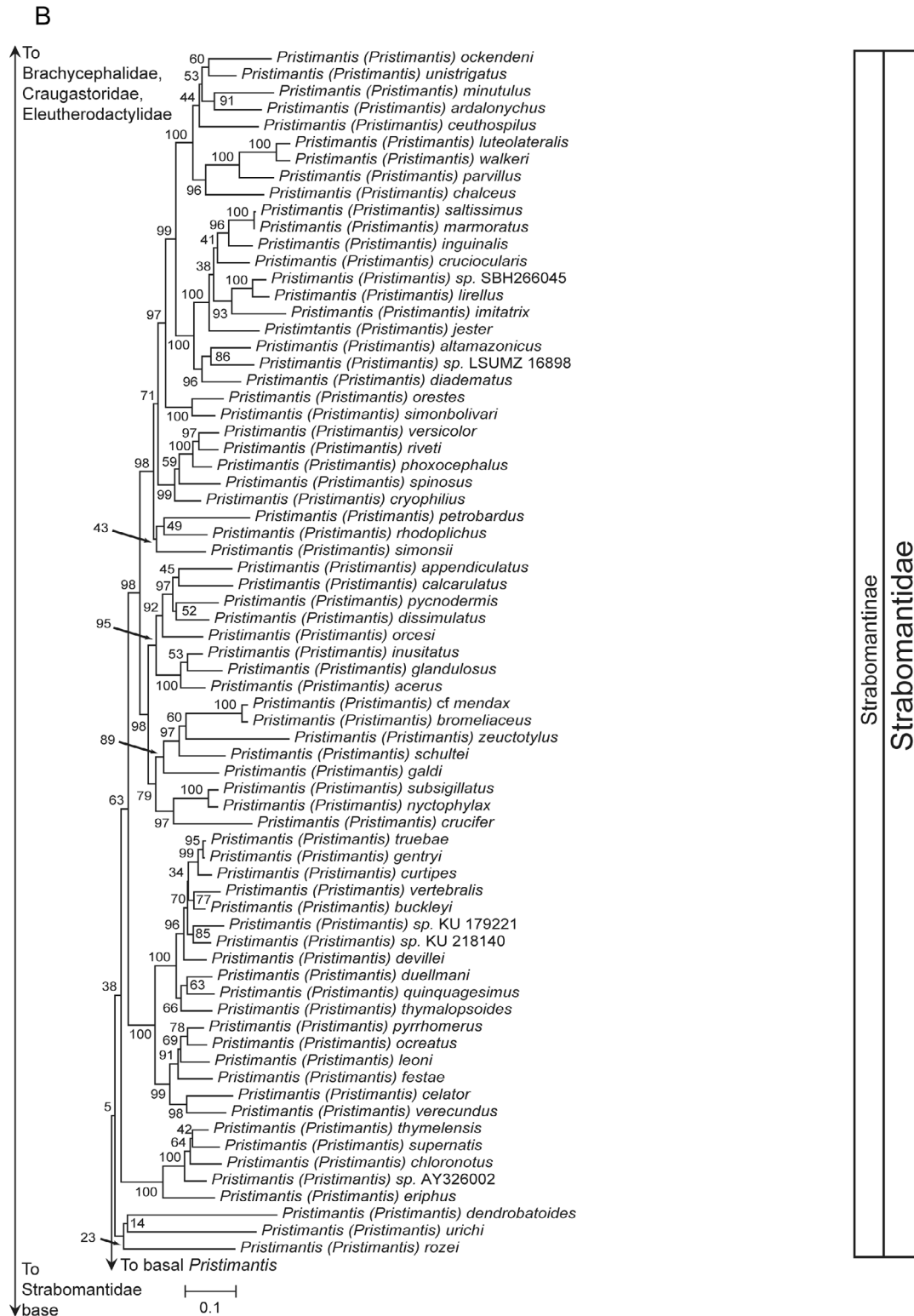


FIGURE 3 (continued).

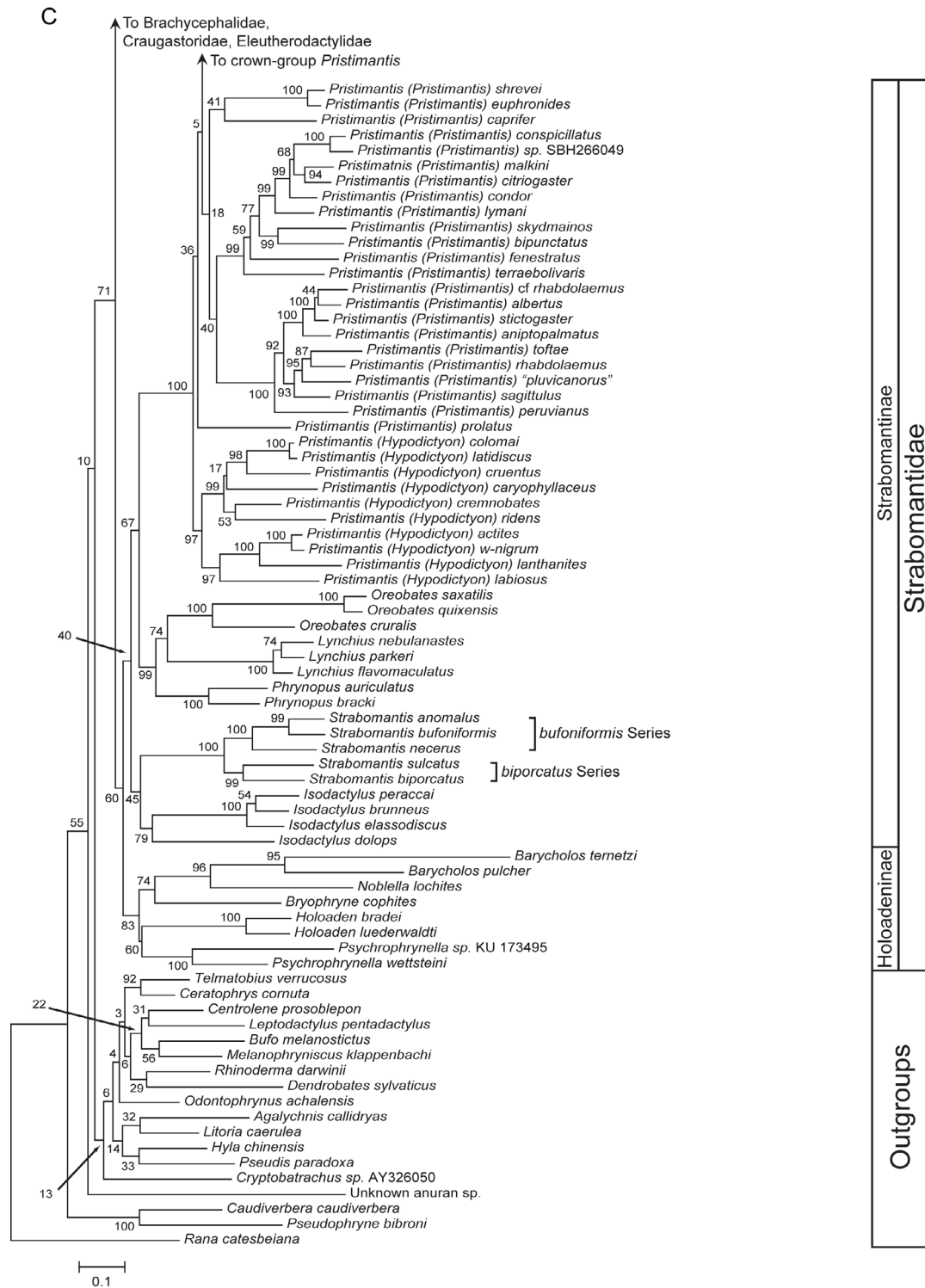


FIGURE 3 (continued).

The same four major geographic clades included in our earlier study (Heinicke *et al.* 2007) were obtained here: A Caribbean Clade (*Eleutherodactylus*), a Middle American Clade (*Craugastor*), a South American Clade (*Pristimantis*), and a Southeast Brazil Clade (*Ischnocnema*). However, the additional species and sequences clarified relationships of many poorly known taxa, identified other taxa allied to these genera, and added resolution of some deeper branches in the tree that were previously unresolved.

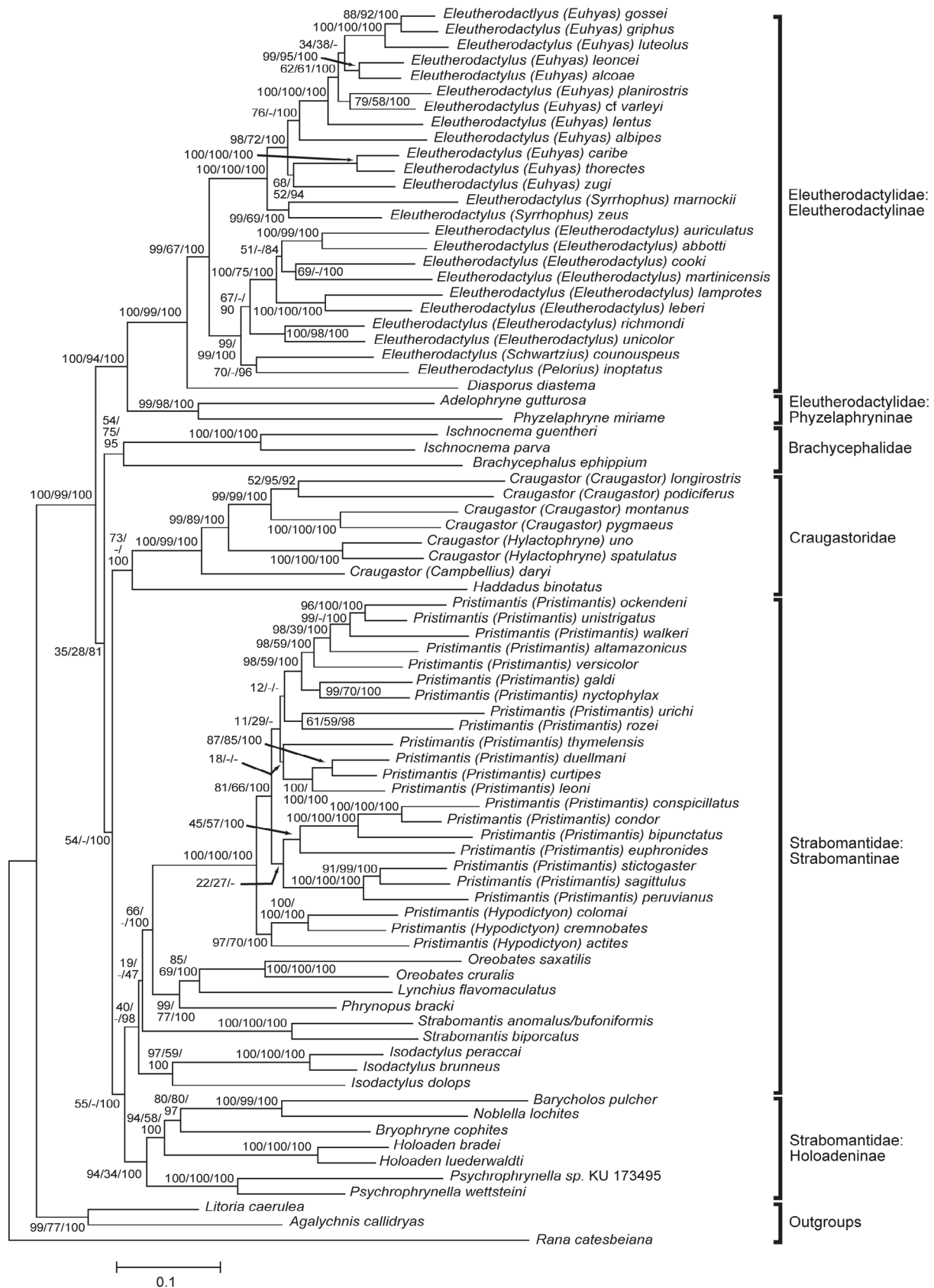


FIGURE 4. Maximum likelihood phylogeny of 80 species of frogs. The data set consists of 3709 base pairs of aligned DNA sequences, including mitochondrial DNA (12S rRNA, tRNA-Valine, and 16S rRNA) and nuclear DNA (RAG-1 and Tyr genes). Bootstrap support values and posterior probabilities (ML/NJ/Bayesian) are shown on nodes. Classification of the species is indicated.

Throughout the taxonomic accounts below, relevant aspects of the phylogenies are mentioned and discussed. As that is done, we emphasize the taxon-dense phylogeny (Fig. 2) in discussions of lower level taxa and the character-dense (with longest sequences) phylogeny (Fig. 4) in discussions of higher level taxa. The phylogeny derived from the complete 12S and 16S rRNA data set (Fig. 3) was especially useful for resolving relationships of South American and Middle American species, although it was not an advantage for the West Indian species because fewer West Indian species were sequenced for those complete genes. When the 80-species dataset is discussed, Bayesian support values will also be mentioned, while acknowledging that posterior probabilities have been criticized as inflating confidence (Suzuki *et al.* 2002; Cummings *et al.* 2003). Because the same major clades were found here, we have not re-estimated divergence times and therefore mention of such times will be from the estimates presented in our previous study (Heinicke *et al.* 2007).

Systematic Accounts

Terrarana, New Taxon

Definition.—Species in this taxon have terrestrial breeding, direct development (ovoviviparity in *Eleutherodactylus jasperi*), and embryonic egg teeth. All have arciferal (or pseudofirmisternal in a few taxa) pectoral girdles and partially fused calcanea and astragali; they lack Bidder's organs and intercalary elements in the digits. The species range in SVL from 10–11 mm in female *Brachycephalus didactylus* and *Eleutherodactylus (Euhyas) iberia* to 110 mm in female *Craugastor pelorus*.

Content.—The taxon contains four families (882 species): Brachycephalidae, Eleutherodactylidae, and two new families described below. It corresponds to the more inclusive family Brachycephalidae of Frost *et al.* (2006).

Distribution.—The taxon ranges from Texas in the USA southward throughout Mexico, Central America, and the West Indies through tropical and subtropical South America to northern Argentina (Fig. 5).

Etymology.—The name is derived from the Latin, *terra* (land) and *rana* (frog). It is used in allusion to the terrestrial breeding and direct development shared by these four families, allowing the species to successfully colonize montane forests far from standing or running water in the New World.

Remarks.—The need to recognize multiple families, and use of an unranked taxon, are discussed above (Introduction). Each of the four clades recognized here as families is defined in the latest molecular phylogeny (Fig. 4), has some morphological support (although no unambiguous shared derived characters are present), and occurs primarily in a different geographic region. Herein we restrict the family name Brachycephalidae to the genus *Brachycephalus* and its apparent close relative in southeast Brazil, *Ischnocnema*. We define the family Eleutherodactylidae, centered in the Caribbean region, to include the genus *Eleutherodactylus* and three closely related mainland genera: *Adelophryne*, *Phyzelaphryne*, and one described below. A new family is erected to contain the large genus *Craugastor* (Middle America Clade) and a small genus in Southeast Brazil. This seemingly odd pairing has some morphological support in that both genera consist primarily of species having long first fingers. The fourth and largest family is described below to include a clade of 16 genera distributed almost entirely in South America and mostly in the Andes of northwestern South America. All four of these clades recognized as families have significant support in Bayesian analyses of the data set. In maximum likelihood bootstrap analyses, only one of the four families (Eleutherodactylidae) has significant bootstrap support. Therefore, additional gene sequences will need to be collected to test the robustness of these groups.

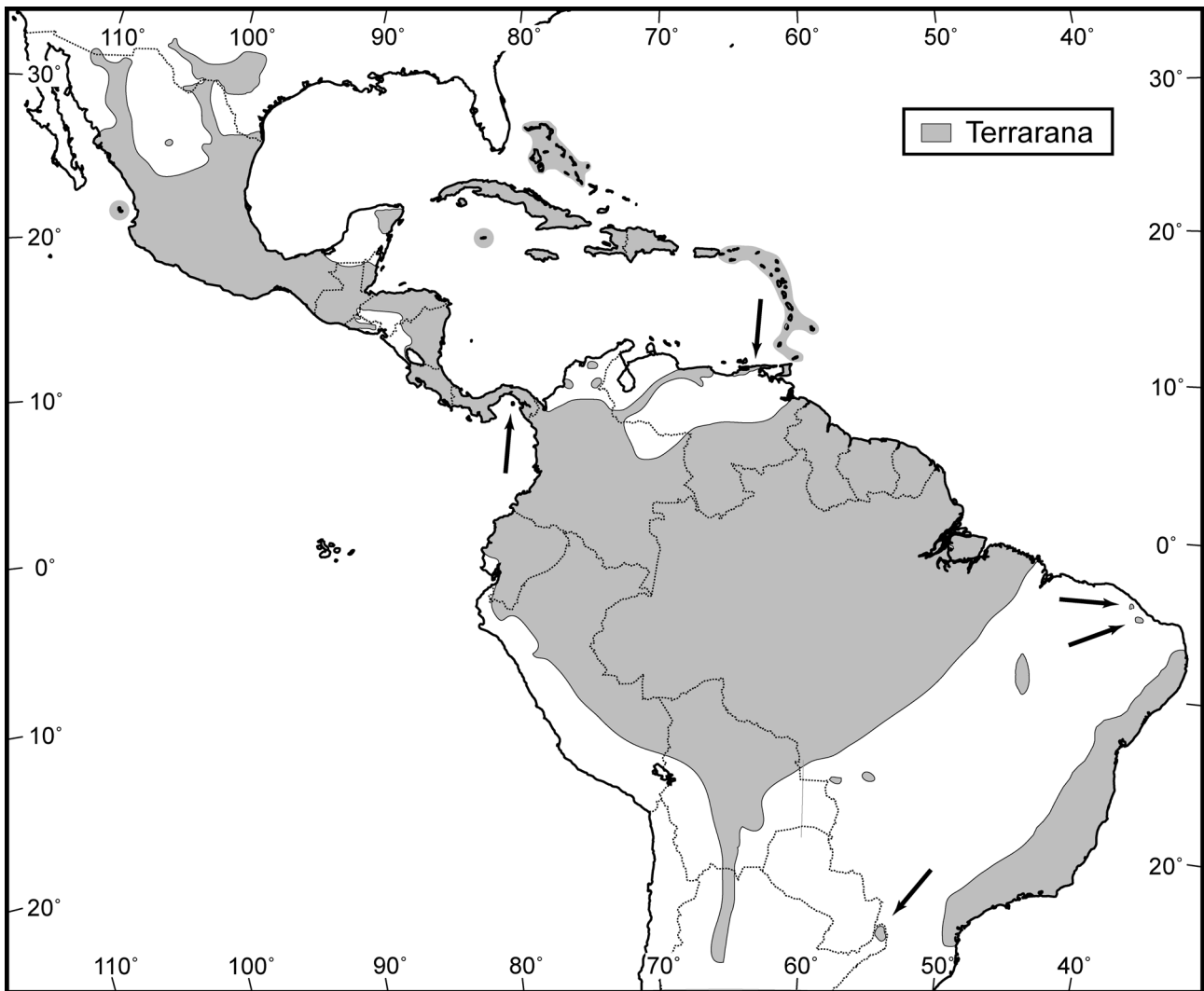


FIGURE 5. Distribution of the taxon Terrarana.

Family Brachycephalidae Günther, 1858

Brachycephalina Günther, 1858:344. Type genus: *Brachycephalus* Fitzinger, 1826:39.

Brachycephalinae—Noble, 1931:507.

Brachycephalinae (part)—Dubois, 2005b:11.

Brachycephalidae (part)—Frost *et al.* 2006:197.

Definition.—The following definition is derived principally from Alves *et al.* (2006) and Da Silva *et al.* (2007) for *Brachycephalus* and Lynch (1971, 1972) and Caramaschi and Canedo (2006) for *Ischnocnema*. Frogs of the family Brachycephalidae have: (1) sternum cartilaginous or absent; (2) vertebral shield present or absent; (3) transverse processes of posterior presacral vertebrae not broadly expanded; (4) cervical cotyles widely spaced; (5) usually eight presacral vertebrae, with usually the first and second not fused; (6) cranial elements co-ossified or not with overlying skin; (7) omosternum present; (8) sacral diapophyses rounded, barely or moderately dilated; (9) maxillary arch dentate or not; (10) alary processes of premaxillae broad at base, usually directed dorsally or posterodorsally; (11) palatal shelf of premaxilla broad or slender, indented or not; (12) pars facialis of maxilla deep, not exostosed; (13) palatal shelf of maxilla moderately broad, bearing pterygoid process or not; (14) maxillary arch usually complete; maxillae tapering posteriorly; quadratojugal

slender or absent; (15) nasals large and in contact (or not) medially; (16) nasals in contact (or not) with maxillae; (17) nasals in contact (or not) with frontoparietals; (18) frontoparietal fontanelle usually absent; (19) frontoparietals usually not exostosed; cranial crests present or absent (20) frontoparietals fused with prootics or not; (21) temporal arcade absent; (22) epiotic eminences prominent to indistinct; (23) carotid artery passing dorsal to cranial elements; (24) zygomatic ramus of squamosal broad to slender (or short), not in contact with maxilla; (25) otic ramus of squamosal short to elongate, expanded into otic plate or not; (26) squamosal-maxilla angle 44–80°; (27) columella present or absent; (28) vomers variable in size; dentigerous processes present or absent; (29) neopalatines broad, slender, or absent; (30) sphenethmoid usually entire; (31) anterior ramus of parasphenoid narrow to broad, not keeled; (32) parasphenoid alae at right angle to axis of skull or deflected posteriorly, usually not overlapped by pterygoids; (33) pterygoid lacking ventral flange; (34) occipital condyles small to large, stalked or not, widely separated medially; (35) mandible lacking odontoids; (36) terminal phalanges T-shaped, arrow-shaped, knobbed, or bearing hook-like lateral process; (37) one, two, or three phalanges in Finger IV; (38) Toe I fully developed, with short phalange, or with no phalange; (39) alary process of hyoid plate on slender or short stalk; (40) mandibular ramus of trigeminal nerve passing lateral or medial to the *m. adductor mandibulae* or passing between two slips of the muscle; (41) prominent external body glands usually absent; (42) males usually have a single, median, subgular vocal sac; (43) males having vocal slits and nonspinous nuptial pads or not; (44) fingers unwebbed; toes usually unwebbed, webbed basally, or rarely webbed extensively; (45) terminal digits expanded or not; circumferential grooves present or absent; digits apically pointed or not; (46) inner metatarsal tubercle present or absent; outer metatarsal tubercle present; (47) tympanic membrane and annulus well differentiated or not; (48) amplexus usually axillary; inguinal in some species; (49) eggs deposited in terrestrial or arboreal situations and undergo direct development; (50) SVL from 10.2 mm in females of *Brachycephalus didactylus* to 54 mm in females of *Ischnocnema guentheri*.

Content.—The family contains two genera (40 species): *Brachycephalus* with 11 species and *Ischnocnema* with 29 species.

Distribution.—The family is distributed in the Atlantic Coastal Forest in eastern Brazil and in the *Aracuaría* forest in extreme southeastern Brazil and northern Argentina (Fig. 6).

Etymology.—The familial name is derived from the Greek *brachys*, meaning short, and the Greek *kephale*, meaning head; the name refers to the small heads characteristic of the type genus.

Remarks.—The molecular phylogenies (Figs. 2–4) show a close relationship between *Brachycephalus* and *Ischnocnema*. The fact that both genera occur in southeastern Brazil probably is not coincidental. However, we have yet to identify any unique morphological characters shared by these two genera. The highly derived and miniaturized bauplan of *Brachycephalus* provides a challenge to identify such characters. The species “*Eleutherodactylus*” *binotatus* (and by association, “*E.*” *plicifer*) is shown not to be closely related to either *Brachycephalus* or *Ischnocnema* (Figs. 2–4) and herein is placed in a new genus below. Other eastern Brazilian genera included in our analyses (*Holoaden*, *Barycholos*, and *Adelophryne*) likewise do not belong to this family. Our previously defined Southeast Brazil Clade is expanded here to include *Brachycephalus* and now corresponds to the family Brachycephalidae.

Genus *Brachycephalus* Fitzinger, 1826

Brachycephalus Fitzinger 1826:39. Type species: *Bufo ephippium* Spix, 1824, by monotypy.

Ephippipher Cocteau, 1835:12. Replacement name for *Brachycephalus* Fitzinger, 1826.

Psyllophryne Izecksohn, 1971:2. Type species: *Psyllophryne didactyla* Izecksohn, 1971, by original designation. Synonymy by Kaplan (2002:227).

Definition.—Members of this genus have: (1) sternum absent; (2) usually eight presacral vertebrae; Presac-
rals IV and V, and VI and VII fused in *B. ephippium*; (3) palatal shelf of maxilla lacking pterygoid process; (4)
maxillary arch edentate, but bearing odontoids in some species; (5) neopalatines slender; absent in *B. ephip-
pium*, *ferruginus*, *hermogenesi*, *pernix*, and *pombali*; (5) columella absent; fenestra ovalis directed posteri-
orly; (6) terminal phalanges arrow-shaped; one phalange in Finger IV, no phalange or one short phalange in
Toe I; (7) terminal digits not expanded; circumferential grooves absent; digits apically pointed; (8) SVL less
than 18 mm.

Content.—Eleven species are placed in this genus: *Brachycephalus alipioi*, *brunneus*, *didactylus*, *ephip-
pium* (Fig. 7), *ferruginus*, *hermogenesi*, *izecksohni*, *nodoterga*, *pernix*, *pombali*, and *vertebralis*.

Distribution.—This genus is restricted to the Atlantic Coastal Forest in the states of R o de Janeiro, S o
Paulo, and Paran  in southeastern Brazil (Fig. 6).

Etymology.—This is the same as that for the family; the gender is masculine.

Remarks.—Based on digital morphology, Frost *et al.* (2006) suggested a close relationship between
Adelophryne, *Brachycephalus*, and *Euparkerella*. However, Da Silva *et al.* (2007) concluded that digital mor-
phology does not support a relationship between *Brachycephalus* and either *Adelophryne* or *Euparkerella*.
Molecular analyses have not included *Euparkerella*, but they confirm that *Brachycephalus* is not closely
related to *Adelophryne* (Figs. 2–4). No species groups are recognized within this genus (Alves *et al.* 2006).

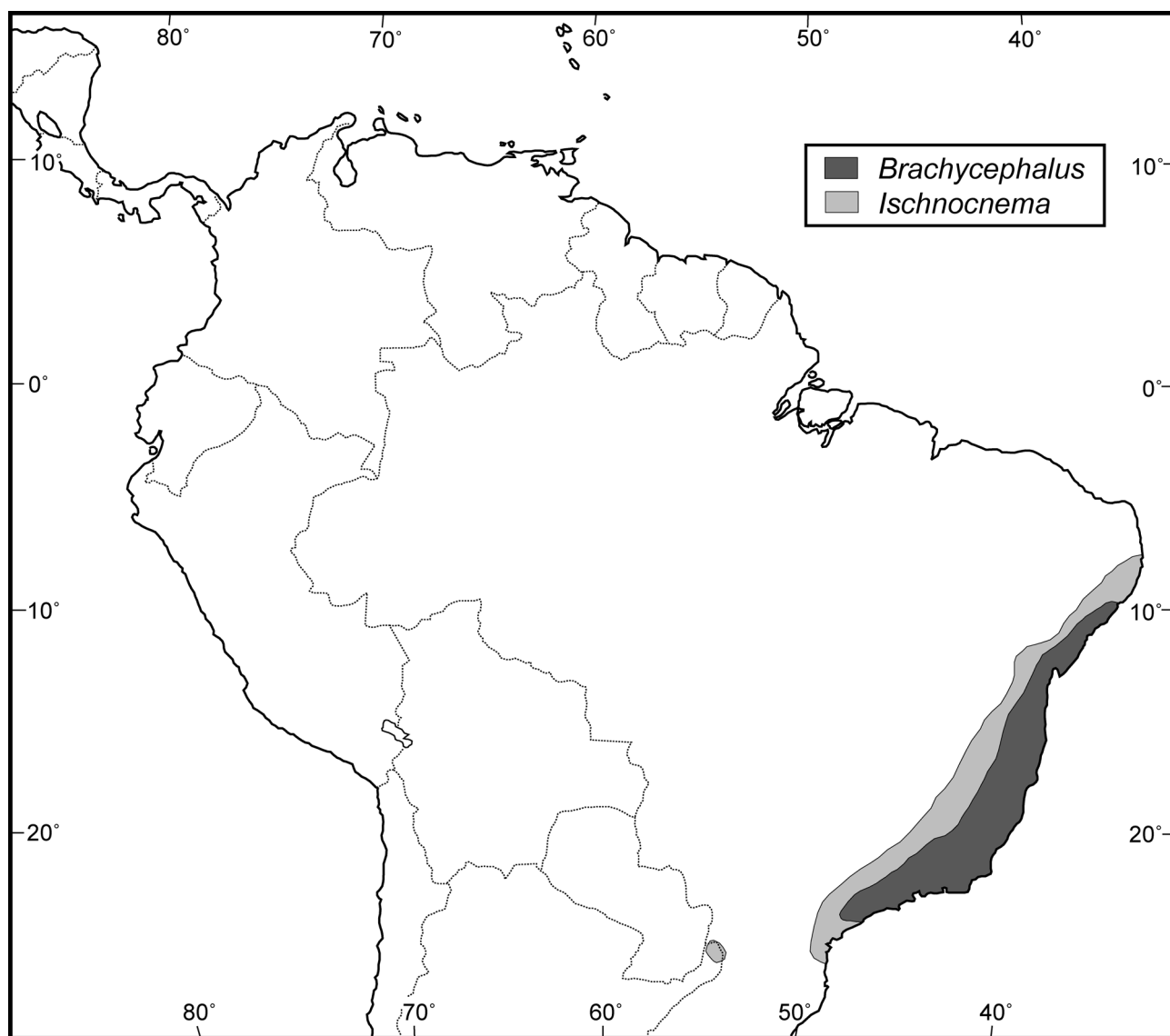


FIGURE 6. Distribution of the genera *Brachycephalus* and *Ischnocnema*, together making the Family Brachycephal-
idae. The distribution of the former completely overlaps the more inclusive distribution of the latter.

Genus *Ischnocnema* Reinhardt & Lütken, 1862

Ischnocnema Reinhardt & Lütken, 1862:239. Type species: *Leiuperus verrucosus* Reinhardt & Lütken, 1862:171.

Basanitia Miranda-Ribeiro, 1923:851. Type species: *Basanitia lactea* Miranda-Ribeiro, 1923:851, by monotypy. Synonymy by Lynch (1968b:875).

Phrynanodus Ahl, 1933:29. Type species: *Phrynanodus nanus* Ahl, 1933:29, by monotypy. Synonymy by Lynch (1968b:876).

Definition.—This genus is characterized by: (1) sternum present; (2) eight presacral vertebrae; (3) palatal shelf of maxilla bearing pterygoid process; (4) maxillary arch dentate; (5) neopalatines broad; (5) columella present; fenestra ovalis directed laterally; (6) terminal phalanges T-shaped; full complement of phalanges in digits; (7) terminal discs expanded slightly or greatly; circumferential grooves present (8) SVL from 16 mm in females of *Ischnocnema pusilla* to 54 mm in females of *I. guentheri*.

Content.—The genus contains five species series (29 species): the *Ischnocnema guentheri* (Fig. 8), *lactea*, *parva*, *ramagii*, and *verrucosa* species series.

Distribution.—The genus is widely distributed in the Atlantic Coastal Forest in eastern Brazil and in the *Aracuaria* forest in extreme southeastern Brazil and northern Argentina (Fig. 6).

Etymology.—The generic name is derived from the Greek *ischnos*, meaning slender or weak, and the Greek *kneme*, meaning calf of the leg. The name is feminine in gender.

Remarks.—Some species previously assigned to this genus are now placed in the genus *Oreobates* (Caramaschi & Canedo 2006; Padial *et al.*, In press). See also the Remarks under *Oreobates*. Heinicke *et al.* (2007) placed all but two of the species (“*E.*” *binotatus* and “*E.*” *plicifer*) in southeastern Brazil that were previously assigned to *Eleutherodactylus* into the genus *Ischnocnema*, which they also referred to as the Southeast Brazil Clade (here expanded to include *Brachycephalus*). This was done with some trepidation because they lacked sequence information for the type species, *Ischnocnema verrucosa*, and most of the other species. Nonetheless, their decision was based on the discovery of a clade of species from southeastern Brazil (*I. guentheri*, *hoehnei*, *juipoca*, and *parva*) that by implication of prior species group affiliation contains nearly half of the species that they assigned to the genus—*I. epipeda*, *erythromera*, *gualteri*, *guentheri*, *henselii*, *hoehnei*, *izecksohni*, *juipoca*, *nasuta*, *oea*, *parva*, *pusilla*, and *vinhai*. The remaining species form several clusters and previously some of those species have been placed in the same morphological species group (Lynch 1976a) along with species that Heinicke *et al.* (2007) assigned to *Ischnocnema*. A representative of one of these additional clusters, *I. holti*, is new here and it also groups with the species included in the earlier study (Fig. 2), thereby increasing the confidence that the southeast Brazil Clade is monophyletic.

The important question is whether *Ischnocnema verrucosa* is part of the Southeast Brazil Clade. In his discussion of this species, Lynch (1972) noted a resemblance to several species in southeastern Brazil. Sazima and Cardoso (1978) suggested that *Ischnocnema verrucosa* resembled “*E.*” *juipoca*, a species that was included in the study by Heinicke *et al.* (2007). The two species are similar in size, have a tuberculate dorsum (hence the Latin name *verrucosa*), short legs, small digital discs, an areolate venter, and a color pattern that includes labial and limb bars.

Heinicke *et al.* (2007) showed that *Holoaden* was not nested within the Southeast Brazil Clade and this conclusion is unchanged here with addition of a second species (Fig. 2). *Barycholos* contains a species, *B. ternetzi*, that occurs in eastern Brazil, and Campos *et al.* (2007) suggested that it might have affinities with species here placed in the Southeast Brazil Clade, based on its karyotype. However, Heinicke *et al.* (2007) showed that it is not part of the Southeast Brazil Clade defined in their molecular phylogeny.

In the following definitions of species series of *Ischnocnema* we combine elements of previous species group definitions (Lynch 1968b, 1976a; Heyer 1984) but with some differences in characters and content based on the preceding discussion and a reevaluation of the importance of various characters. As we found in the Caribbean Clade (*Eleutherodactylus*), a primary character emphasized by Lynch and Duellman (1997),

relative lengths of Toes III and V, does not seem to be useful in defining species series of *Ischnocnema*. Instead, body size and shape, relative lengths of legs and fingers, and size of digital discs are among the useful characters that we have identified for these species.



FIGURES 7–12. 7. *Brachycephalus ephippium* of the Family Brachycephalidae, from Município Campinas, São Paulo, Brazil. Photo by C. F. B. Haddad. 8. *Ischnocnema guentheri* of the *I. guentheri* Species Series, from Caparaó, Espírito Santo, Brazil. Photo by J. L. Gasparini. 9. *Ischnocnema holti* of the *I. lactea* Species Series from Brejo da Lapa Itatiaia Itamonte, São Paulo, Brazil. Photo by C. F. B. Haddad. 10. *Ischnocnema randorum* of the *I. lactea* Species Series from Santa Virgínia São Luiz de Paraitinga, São Paulo, Brazil. C. F. B. Haddad. 11. *Ischnocnema parva* of the *I. parva* Species Series, from Intervalos Copão Bonito, São Paulo, Brazil, Photo by C. F. B. Haddad. 12. *Ischnocnema verrucosa* of the *I. verrucosa* Species Series, from Município Aracruz, Espírito Santo, Brazil. Photo by C. F. B. Haddad.

The number of species that have been sampled for DNA sequence data (Heinicke *et al.* 2007) and chromosome data (Campos *et al.* 2007) is too small to be of much use in defining species series. Additional molecular and chromosomal data are needed to test these series affiliations. For convenience we use the species series rank within *Ischnocnema* to allow for finer divisions (species groups and subgroups) to be defined in the future as relationships become better resolved, especially within the larger series (*I. guentheri* and *lactea* series).

Ischnocnema guentheri Species Series

Definition.—Species in this series range in SVL from 19 mm (males only, *Ischnocnema oea*) to 54 mm (females, *I. nasuta*) and have moderately slender bodies with long legs (shank length usually > 60% SVL). The snout is acuminate in dorsal view; the tympanic membrane is differentiated. The dorsum is smooth or finely granular, and the venter usually is smooth (areolate in *I. erythromera* and *vinhai*). Nuptial pads are absent in *I. hoehnei* and unknown in several species. Finger I is approximately the same length as Finger II, and the digital discs usually are small or slightly expanded (large in *I. hoehnei* and *vinhai*).

Content.—Eleven species are placed in the series: *Ischnocnema epipeda*, *erythromera*, *gualteri*, *guentheri* (Fig. 8), *henselii*, *hoehnei*, *izecksohni*, *nasuta*, *octavioi*, *oea*, and *vinhai*.

Distribution.—The species series is widely distributed in the Atlantic Coastal Forest in southeastern Brazil from southern Bahia to Santa Catarina; one species, *I. henselii*, also occurs in *Aracuaria* forest in Rio Grande do Sul, Brazil, and Misiones, Argentina.

Remarks.—The definition and content of this series is based mainly on the work of Heyer (1984), who noted that a cluster of species within the more inclusive “*Eleutherodactylus*” *binotatus* Group of Lynch (1976a) shared several characters that suggested monophyly. He did not place *Ischnocnema hoehnei* and *I. vinhai* in the cluster but alluded to a relationship with the cluster. Heinicke *et al.* (2007) found that *I. hoehnei* was the closest relative of *I. guentheri* among the four species of the Southeast Brazil Clade they included. Therefore we have added these two species to a more inclusive *Ischnocnema guentheri* Species Series. We also include *I. octavioi* based on its smooth venter, relative finger lengths, small digital discs, and moderately long legs, and note that Bokermann (1965) associated it with an earlier version of the “*Eleutherodactylus*” *guentheri* Group. Caramaschi and Kisteumacher (1989) described *I. izecksohni* and suggested that it belonged to the “*Eleutherodactylus*” *guentheri* Group. Kwet and Solé (2005) recently resurrected *I. henselii* from the synonymy of *I. guentheri*. As more sequence data become available for this diverse species series, species groups and subgroups may be definable.

Ischnocnema lactea Species Series

Definition.—Species in this series are small to moderate in SVL and range from 18 mm (females, *I. paranaensis* and *randorum*) to 40 mm (females, *I. sambaqui*). The body is moderate or robust with short legs (shank length usually <50% SVL), and the snout is subacuminate in dorsal view. The tympanic membrane is differentiated or not; the dorsum is smooth, rugose, or tuberculate, and the venter is smooth or areolate. Nuptial pads usually are absent (minute in *I. randorum* and unknown in several species), Finger I is usually shorter than Finger II (equal in length to Finger II in several species), and at least the outer digital discs are moderate to large.

Content.—Twelve species are placed in the species series: *Ischnocnema bilineata*, *bolbodactyla*, *gehrti*, *holti* (Fig. 9), *lactea*, *manezinho*, *nigriventris*, *paranaensis*, *randorum* (Fig. 10), *sambaqui*, *spanios*, and *venancioi*.

Distribution.—The species series is distributed in the southern part of the Atlantic Coastal Forest from Rio de Janeiro to Santa Catarina in southeastern Brazil.

Remarks.—We concur with Castano and Haddad (2000) who suggested that *Ischnocnema manezinho* and *I. sambaqui* are members of the “*Eleutherodactylus*” *lactea* Group (roughly equivalent to our *Ischnocnema lactea* Species Series). We also added four other species (*I. bilineatus*, *paranaensis*, *randorum* and *spanios*) that conformed to our definition of the series. The last two species are most likely each others closest relatives (Heyer 1985). Three of the characters proposed by Lynch (1976a) to define the former “*E.*” *lacteus* Group (tympanic membrane differentiated, smooth venter, and rounded discs) are now known to be variable and not useful for defining this group. The tympanic membrane in six of the species (*I. holti*, *lactea*, *nigriventris*, *randorum*, *spanios*, and *venancioi*) is undifferentiated, and the venter of five species (*I. holti*, *nigriventris*, *randorum*, *spanios*, and *venancioi*) is areolate. Also most of the species have truncate or elliptical rather than apically rounded discs. Heinicke *et al.* (2007) did not include members of this group in their molecular phylogeny, but we have included one species (*I. holti*) in the tree presented here (Fig. 2), where it clusters with other species of *Ischnocnema*. As more sequence data become available for this diverse species series, species groups and subgroups likely will be definable.

Ischnocnema parva Species Series

Definition.—Species in this series range in SVL from 16 mm (females, *I. pusilla*) to 23 mm (females, *I. parva*); the body is robust with short legs (shank length < 50% SVL) and the snout is rounded in dorsal view. The upper half of the tympanic membrane is undifferentiated. The dorsum and venter are smooth, and nuptial pads are absent; Finger I is approximately the same length as Finger II, and the digital discs are small and pointed.

Content.—Two species, *Ischnocnema parva* (Fig. 11) and *pusilla* are placed in this group.

Distribution.—The species series occurs in the Atlantic Coastal Forest in the states of Rio de Janeiro and São Paulo in southeastern Brazil.

Remarks.—Heinicke *et al.* (2007) included *Ischnocnema parva* in their molecular phylogeny. It clustered with two members of the *Ischnocnema guentheri* Species Series (*I. guentheri* and *hoehnei*), which because of the limited sampling only indicated that this series is more closely related to the *Ischnocnema guentheri* Species Series than to “*Eleutherodactylus*” *binotatus*. With more taxa (Fig. 3) it still clusters with the *guentheri* series.

Ischnocnema ramagii Species Series

Definition.—Species in this series range in SVL from 22 mm (sex unknown, *I. ramagii*) to 36 mm (females, *I. paulodutraii*). The frogs are moderate in shape (not slender or particularly robust) and have moderately long legs; the snout is subacuminate in dorsal view. The tympanic membrane is differentiated; the dorsum is finely granular, and the venter is areolate. The condition of the nuptial pads is unknown. Finger I is much longer than Finger II, and at least the outer digital discs are large.

Content.—Two species, *Ischnocnema paulodutraii* and *ramagii*, are placed in this series.

Distribution.—The species series occurs in the isolated remnants of Atlantic Coastal Forest in the states of Paraíba, Pernambuco, and Bahia in eastern Brazil.

Remarks.—As noted by Lynch (Lynch 1976a), these two species are unusual among South American eleutherodactylids in having a long first finger combined with large digital discs. With the placement of two species (“*E.*” *binotatus* and “*E.*” *plicifer*) in a new genus, these are the only species of *Ischnocnema* with Finger I much longer than Finger II. Heinicke *et al.* (2007) did not include a member of the *Ischnocnema ramagii* Species Series in their molecular phylogeny. Although the long first finger may indicate a close relationship

with "*Eleutherodactylus*" *binotatus*, members of the *Ischnocnema ramagii* Species Series have an areolate venter, large digital discs, and a smooth dorsum, in contrast to a smooth venter, small digital discs, and longitudinal dermal ridges on the dorsum in "*E.*" *binotatus* and "*E.*" *plicifer*. We tentatively place these two species in *Ischnocnema*.

Ischnocnema verrucosa Species Series

Definition.—Species in this series range in SVL from 21 mm (males only, *I. juipoca*) to 26 mm (females, *I. verrucosa*). The body is moderate in shape with short legs (shank length < 55% SVL), and the snout is subacuminate in dorsal view. The tympanic membrane differentiated or not; the dorsum is tuberculate, and the venter is areolate. The condition of the nuptial pads is unknown. Finger I is approximately the same length as Finger II, and the digital discs are small.

Content.—Two species, *Ischnocnema juipoca* and *verrucosa* (Fig. 12), are placed in this series.

Distribution.—The distribution of the species series is disjunct in the Atlantic Coastal Forest in the states of Espírito Santo, Minas Gerais, and São Paulo in southeastern Brazil.

Remarks.—As noted above in the remarks for the genus, these two species share a suite of characters. Heinicke *et al.* (2007) included one species (*I. juipoca*) in their molecular phylogeny, where it appeared as a basal member of the Southeast Brazilian Clade (*Ischnocnema*).

Family Craugastoridae, New Family

Eleutherodactylinae (part) Lutz, 1954:157.

Eleutherodactylini—Lynch, 1971:142 [Tribe].

Brachycephalinae (part)—Dubois, 2005b:4.

Brachycephalidae (part)—Frost *et al.*, 2006.

Type genus.—*Craugastor* Cope, 1862:153.

Definition.—Frogs of the family Craugastoridae have: (1) sternum cartilaginous; (2) vertebral shield lacking; (3) transverse processes of posterior presacral vertebrae not broadly expanded; (4) cervical cotyles widely spaced; (5) eight presacral vertebrae, Presacrals I and II not fused; (6) cranial elements not co-ossified with overlying skin; (7) omosternum present; (8) sacral diapophyses rounded or barely dilated; (9) maxillary arch usually dentate; teeth blunt, pedicellate; (10) alary processes of premaxillae broad at base, usually directed dorsally or posterodorsally; (11) palatal shelf of premaxilla usually broad, indented or not; (12) pars facialis of maxilla usually deep, not exostosed; (13) palatal shelf of maxilla moderately broad, bearing pterygoid process or not; (14) maxillary arch complete; maxillae tapering posteriorly; quadratojugal slender; (15) nasals usually large with broad median contact; (16) nasals usually not in contact with maxillae or pterygoids; (17) nasals not in contact with frontoparietals; (18) frontoparietal fontanelle usually absent; (19) frontoparietals usually not exostosed; cranial crests present or not; (20) frontoparietals fused with prootics or not; (21) temporal arcade absent; (22) epiotic eminences prominent to indistinct; (23) carotid artery passing dorsal to cranial elements; (24) zygomatic ramus of squamosal broad to slender, usually not in contact with maxilla; (25) otic ramus of squamosal short to elongate, expanded into otic plate or not; (26) squamosal-maxilla angle 44–67°; (27) columella present; fenestra ovalis directed laterally; (28) vomers variable in size; (29) neopalatines broad; (30) sphenethmoid entire; (31) anterior ramus of parasphenoid narrow to broad, not keeled; (32) parasphenoid alae at right angle to axis of skull or deflected posteriorly, usually not overlapped by pterygoids; (33) pterygoid lacking ventral flange; anterior ramus not reaching neopalatine, except in some *Craugastor*; (34) occipital condyles small to large, stalked or not, widely separated medially; (35) mandible lacking odontoids; (36) ter-

minal phalanges T-shaped; (37) three phalanges in Finger IV; (38) Toe I fully developed and free; (39) alary process of hyoid plate on slender stalk or not; (40) mandibular ramus of trigeminal nerve passing lateral to the *m. adductor mandibulae* (“S” condition) in *Haddadus*, passing medially (“E” condition) in *Craugastor*; (41) prominent external body glands absent; (42) males having single, median, subgular vocal sac or not (absent in some *Craugastor*); (43) males having vocal slits and nonspinous nuptial pads or not; (44) fingers unwebbed; toes usually unwebbed or webbed basally, but webbing extensive in some *Craugastor*; (45) terminal digits expanded with pads set off by distinct circumferential grooves; (46) inner and outer metatarsal tubercles present, inner tubercle not spade-like; (47) tympanic membrane and annulus usually well differentiated; (48) amplexus axillary; (49) eggs deposited in terrestrial or arboreal situations and undergoing direct development; (50) range in SVL from 18 mm in female *Craugastor pygmaeus* to 110 mm in female *Craugastor pelorus*.

Content.—The family contains two genera and 113 species.

Distribution.—This family is represented by one genus in southwestern USA, Mexico, Central America, and northwestern South America and another genus in southeastern Brazil (Fig. 13).

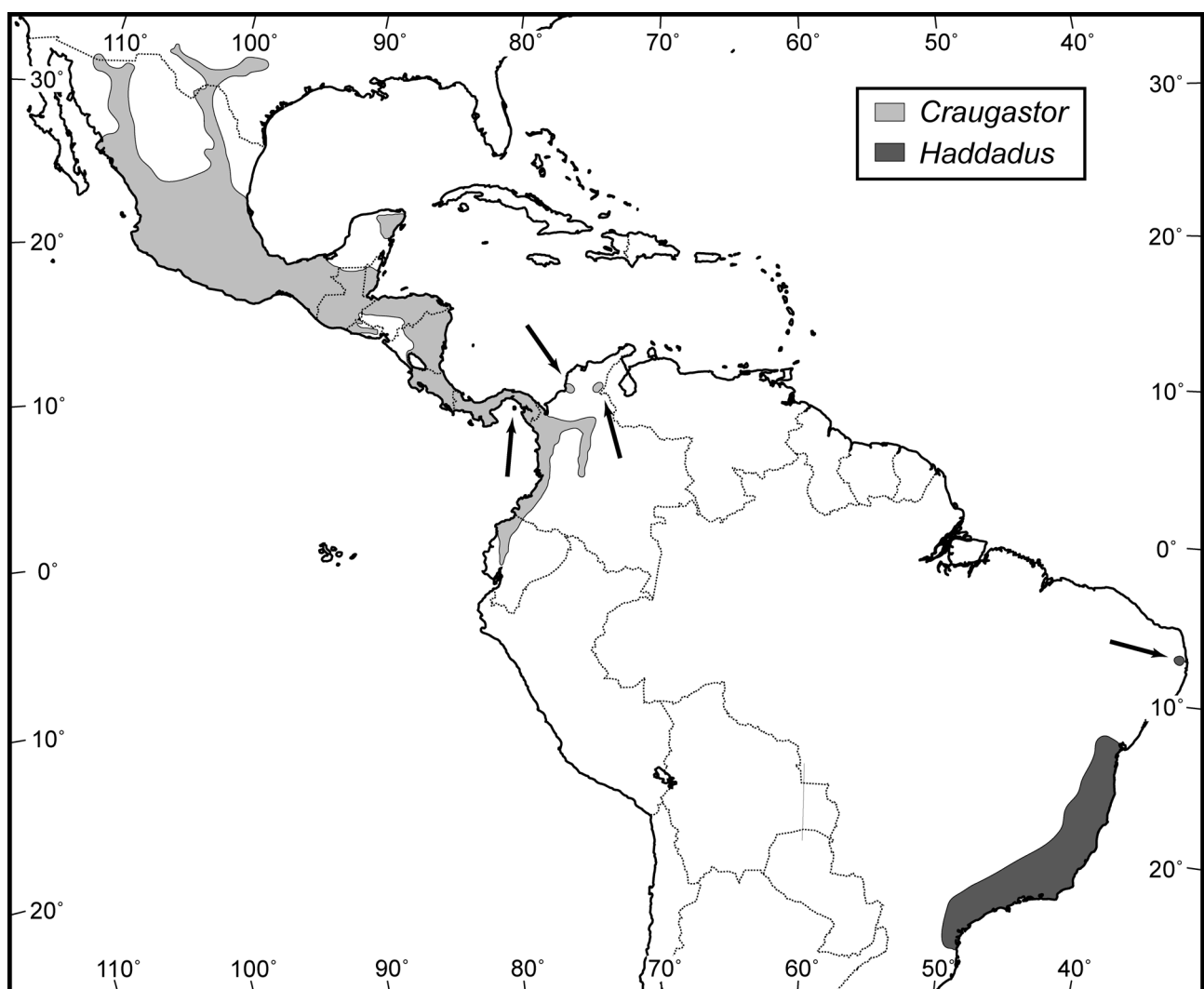


FIGURE 13. Distribution of the two genera comprising the Family Craugastoridae: *Craugastor* and *Haddadus*.

Remarks.—This family joins two genera, *Craugastor* (the Middle American Clade) and a small genus of two Brazilian species described below (“*Eleutherodactylus*” *binotatus* and “*E.*” *plicifer*), based primarily on their close relationship in our earlier molecular phylogeny (Heinicke *et al.* 2007) and here (Fig. 3–4). Support

for the family is moderately strong (73%), in the molecular phylogeny (Fig. 4) and the Bayesian posterior probability is 100%. Although their current ranges are widely separated, the divergence occurred 59–31 million years ago (Ma) (Heinicke *et al.* 2007), prior to the major Andean uplift and when the landscape was much different.

A long first finger (longer than Finger II) is uncommon in Terrarana, and this condition apparently is a shared derived trait of Craugastoridae. It is present in both species of the new genus from Brazil and in most species of *Craugastor*, including those groups branching basally in the tree (Figs. 2–4). In contrast, it is present in only three species in the subgenus *Pelorius* of the large family Eleutherodactylidae. Within Brachycephalidae, a long first finger exists in only two species of *Ischnocnema* (*ramagii* series). Some earlier accounts (Lynch 1976a; Lynch & Duellman 1997) reported a long first finger for the “*Eleutherodactylus guentheri* Group” (= *Ischnocnema*), but Heyer (1984) noted that Finger I and II were subequal in many species, with “*E. binotatus* and “*E. plicifer* being exceptions in having distinctly long first fingers. In the large South American clade, the first finger is longer than the second in only 30–40 or so additional species in the former *conspicillatus*, *discoidalis*, *dolops*, *nigrovittatus*, and *sulcatus* groups of “*Eleutherodactylus*” (Lynch & Duellman 1997), which are apportioned into several genera below.

Genus *Craugastor* Cope, 1862

Craugastor Cope, 1862:153. Type species: *Hylodes fitzingeri* Schmidt, 1857:12, by subsequent designation by Dunn and Dunn, 1940:71.

Leiyla Keferstein, 1868:296. Type species *Leiyla güntherii* Keferstein, 1868:296, by monotypy. Synonymy with *Hylodes* (*sensu lato*) by Boulenger (1882:198), and with *Eleutherodactylus* by Savage (1974:290).

Microbatrachylus Taylor, 1940a:499. Type species *Eleutherodactylus hobartsmithi* Taylor, 1936, by monotypy. Synonymy by Lynch (1965:8).

Definition.—Frogs of the genus *Craugastor* are characterized by (1) head narrower than, or as wide as, body, width 31–55% of SVL; (2) tympanic membrane usually differentiated and sexually dimorphic (larger in males), although status of sexual dimorphism not determined in the subgenus *Hylactophryne* (see below); (3) cranial crests absent, except in *C. gulosus* Species Series; (4) dentigerous processes present, triangular or transverse, reduced or absent in the *C. mexicanus* Species Series; (5) “E” condition of adductor muscle; (6) digital discs narrow (with pointed discs on some toes in *C. laticeps* species series) to expanded and truncate; circumferential grooves present; terminal phalanges T-shaped; (7) Finger I longer than Finger II, except I = II or I < II in some members of the subgenus *Hylactophryne* and the *C. fitzingeri*, *C. mexicanus* and *C. rhodopis* Species Series; (8) Toe III longer than Toe V, except Toe V longer than Toe III in some species of the subgenus *Hylactophryne*; (9) subarticular tubercles projecting or not; (10) dorsum smooth to tuberculate; (11) venter smooth, granular, or areolate; (12) range in SVL 18 mm in female *C. pygmaeus* to 110 mm in female *C. pelorus*.

Content.—The genus contains three subgenera and 111 species.

Distribution.—The genus ranges from southern Arizona and western Texas, USA, through Mexico and Central America into northwestern Colombia (Figs. 13–14).

Etymology.—The generic name presumably is derived from the Greek *kreas*, meaning fleshy, and the Greek *gaster*, meaning stomach. The name has been used as masculine.

Remarks.—This major clade of eleutherodactylid frogs has been recognized since Lynch’s (1986a) discovery of the different patterns of jaw musculature in “*Eleutherodactylus*.” Independent analyses of molecular data (Crawford & Smith 2005; Frost *et al.* 2006; Heinicke *et al.* 2007) showed *Craugastor*, for the most part, to be a well-supported clade. However, the most recent analysis (Heinicke *et al.* 2007) discovered that some South American species assigned to this genus, those in the *C. anomalus* and *C. bufoniformis* species

groups, were misclassified; thus they were removed from *Craugastor* and placed in the genus *Limnophys* (now placed in *Strabomantis*; see below). This further strengthens the geographic distinction of the genus *Craugastor*, which is almost entirely associated with Middle America. Herein, we also transfer “*Eleutherodactylus*” *biporcatus* from *Craugastor* to *Strabomantis* (see below); this necessitates a change from the *Craugastor biporcatus* Species Group to the *Craugastor gulosus* Species Series. Only four species of *Craugastor* are known to occur in South America and in all four cases they are also distributed in Central America and their South American distribution is confined to the extreme northwest part of the continent (Fig. 13). See Remarks under *Pristimantis* (*Yunganastes*) concerning the position of species allied with *Pristimantis fraudator*.

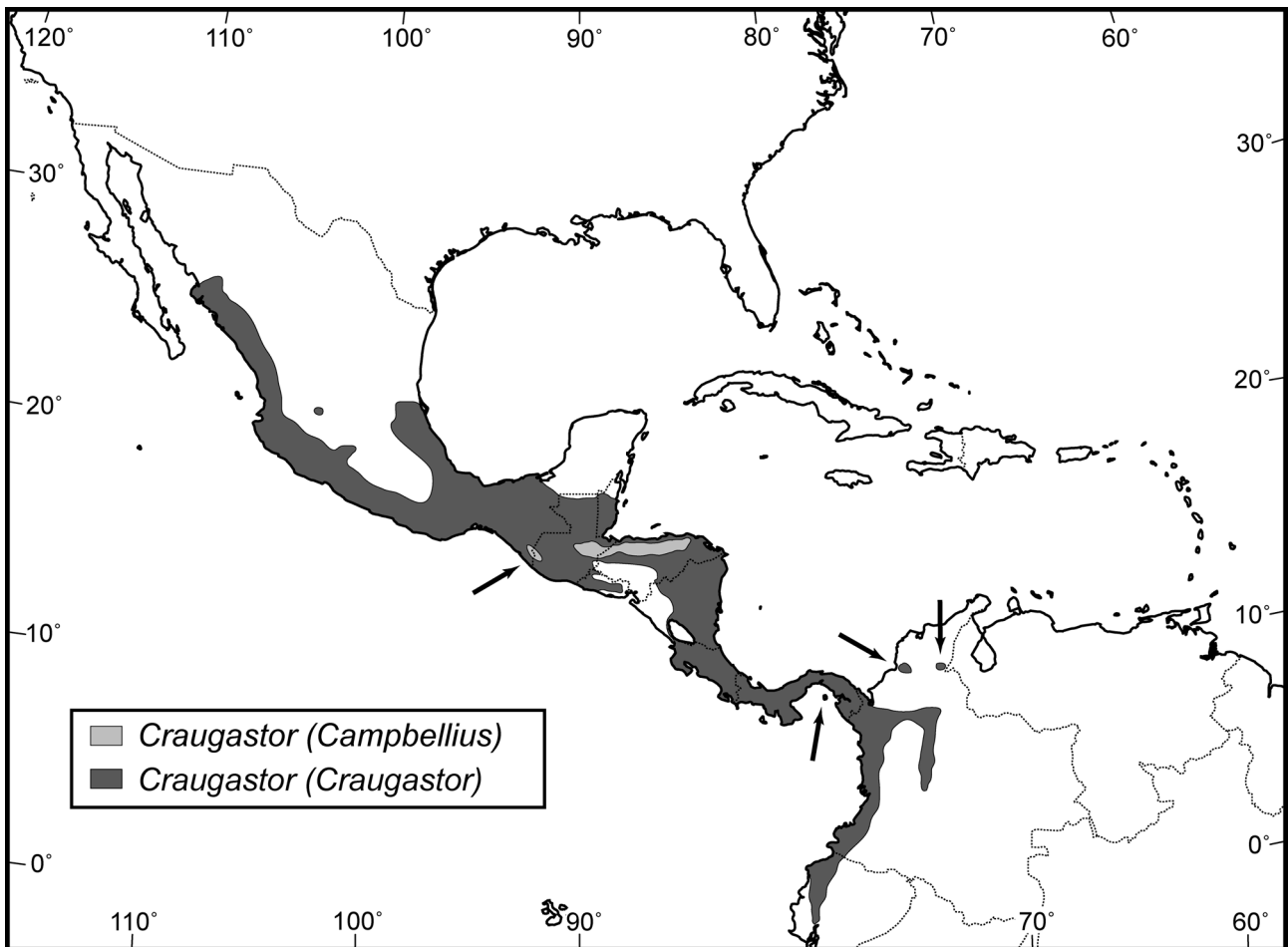


FIGURE 14. Distribution of the subgenera *Campbellius* and *Craugastor*, Genus *Craugastor*, Family Craugastoridae. The distribution of *Campbellius* is completely within that of *Craugastor*.

Species series and group assignments within the assemblage of species recognized herein as the genus *Craugastor* have had a complicated history, perhaps more so than in any other currently recognized genus of terraranan frogs. For example, the groups recognized by Savage (1987) differ substantially from those recognized by Lynch (2000). These and more recent arrangements (Savage 2002) are partly at odds with the molecular phylogenetic evidence (Crawford & Smith 2005; Heinicke *et al.* 2007), although taxon sampling was an issue in previous molecular studies. The study by Crawford and Smith (2005) and this study (Fig. 2) each sampled approximately one-third of the species, although the species sampled were not all the same. Different genes were used and therefore the sequences from the earlier study could not be used here. In contrast to the considerable chromosome variation in the Caribbean Clade (genus *Eleutherodactylus*) (Bogart 1981; Bogart

& Hedges 1995), the chromosomes of most species of *Craugastor* that have been sampled show relatively little variation in diploid number (18–24), with most being 20 or 22 (Savage 1987). Until more species of *Craugastor* are sampled, it will be difficult to assess the diagnostic value of chromosome variation.

There is one inconsistency between the two previous molecular phylogenies of *Craugastor*, in which more than 10 species were included (Crawford & Smith 2005; Heinicke *et al.* 2007), that requires clarification. The sequence of *C. mexicanus* used by Heinicke *et al.* (2007) clustered with *C. rhodopis* (*C. rhodopis* Species Series) and not with the two other species of the *C. mexicanus* Species Series (*C. montanus* and *C. pygmaeus*). That sequence came from the study of Darst and Cannatella (2004) where it was identified as “*Eleutherodactylus rhodopis*.” However, the current identification of that sequence (AY326006) in GenBank is *C. mexicanus*. Based on the tree of Heinicke *et al.* (2007), the original identification as a member of the *C. rhodopis* Species Series would appear to be correct, and the voucher specimen (Museum of Natural History, University of Texas, Arlington) is likewise identified as *C. rhodopis*.

In the study by Crawford and Smith (2005), an unexpected result involved the close clustering of “*E. megacephalus*” (*C. gulosus* Species Series) and “*E. ranoides*” of the former “*C. rugulosus* Group” (= herein the *C. punctariolus* Species Series). The genetic distance separating them is smaller than the distance separating some samples of the same species elsewhere in their tree and is suggestive of two closely related species of the same group rather than two species series representing a total of 38 species. Those authors did not comment on this unusual result. Unfortunately Heinicke *et al.* (2007) did not include a representative of the *C. gulosus* Species Series, and they used different genes. We have examined the specimen of *C. megacephalus* (FMNH 257714) used by Crawford and Smith and have confirmed its identification. Moreover, we have now sequenced a different specimen of *C. megacephalus* and six species of the *C. punctariolus* Species Series (Fig. 2). They all cluster very tightly in the tree, agreeing with the initial result of Crawford and Smith (2005). Based on this new tree with expanded taxonomic coverage, either the *C. gulosus* and *C. punctariolus* series are distinct and extremely closely related, or there is no justification for recognizing the two clades of species. Because we included only a single species of the *C. gulosus* Species Series, we are unable to distinguish between these two possibilities and therefore we maintain the distinction of these two species series.

We recognize subgenera, species series, and species groups within the genus *Craugastor* based largely on our new molecular phylogeny (Fig. 2), but also considering previous morphological and molecular studies. The previous sequence analyses all agree that species allied with *Craugastor milesi* represent a basal lineage within the genus, which we designate here as a new subgenus. A second subgenus, *Hylactophryne*, is recognized for the lineage of species consisting of the former “*Eleutherodactylus alfredi*” and “*E. augusti*” species groups of Lynch (2000), which is the next most basal lineage in the genus. The remaining species are placed in the subgenus *Craugastor*.

Subgenus *Campbellius*, New Subgenus

Type species.—*Eleutherodactylus stadelmani* Schmidt, 1936:44.

Definition.—Frogs of the subgenus *Campbellius* are characterized by (1) head moderate to wide, width 37–49% of SVL; (2) tympanic membrane undifferentiated in females, differentiated or not in males; (3) cranial crests absent; (4) dentigerous processes present, triangular or transverse; (5) “E” condition of adductor muscle; (6) digital discs expanded; circumferential grooves present; terminal phalanges T-shaped; (7) Finger I longer than Finger II; (8) Toe III longer than Toe V; (9) subarticular tubercles not projecting; (10) dorsum rugose and tuberculate; (11) venter smooth to slightly areolate; (12) range in SVL from 22 mm in *C. saltuarius* (males only) to 65 mm in female *C. daryi*.

In addition, species in this subgenus have a robust body, a rounded snout in dorsal view, and vocal slits (except in *C. omoensis*). An inner tarsal fold is absent, and the toes are moderately webbed, with distinct lateral fringes or keels. Most species have pale paracloacal bars. Members of this subgenus are riparian and

retreat under water when disturbed.

Content.—This subgenus includes 13 species: *Craugastor* (*Campbellius*) *adamastes*, *chrysozetetes*, *cruzi*, *daryi* (Fig. 15), *epochthidius*, *fecudus*, *matudai*, *miles*, *myllomyllon*, *omoaensis*, *salutarius*, *stadelmani*, and *trachydermus*.



FIGURES 15–20. 15. *Craugastor* (*Campbellius*) *daryi* from 3.8 km E Purulhá, Baja Verapaz, Guatemala. Photo by J. A. Campbell. 16. *Craugastor* (*Craugastor*) *crassidigitus* of the *C. fitzingeri* Species Group from 14 km N San Isidro del General, San José, Costa Rica. Photo by W. E. Duellman. 17. *Craugastor* (*Craugastor*) *fitzingeri* of the *C. fitzingeri* Species Group from Barro Colorado Island, Panama, Panama. Photo by W. E. Duellman. 18. *Craugastor* (*Craugastor*) *andi* of the *C. melanostictus* Species Group from Río Claro, 910 m, Bocas del Toro, Panama. Photo by W. E. Duellman. 19. *Craugastor* (*Craugastor*) *gollmeri* of the *C. laticeps* Species Series from Cerro Bruja Trail, Panama, Panama. Photo by W. E. Duellman. 20. *Craugastor* (*Craugastor*) *aphanus* of the *C. gulosus* Species Series from 11.6 km WSW Santo Tomás, Izabal, Guatemala. Photo by J. A. Campbell.

Distribution.—The subgenus is distributed in montane cloud forests at elevations of 150–2000 m in Guatemala and Honduras (Fig. 14).

Etymology.—This genus group name honors Jonathan A. Campbell, University of Texas (Arlington), in recognition of his many significant contributions to the herpetology of Middle America.

Remarks.—This subgenus corresponds to the former “*Eleutherodactylus milesi*” Species Group (McCranie *et al.* 1989; Campbell 1994; Lynch 2000; McCranie & Wilson 2002). As with the *Craugastor punctariolus* Species Series, these frogs are largely riparian in habits. The molecular phylogenetic evidence suggests that this subgenus is the most basal lineage in the genus (Crawford & Smith 2005; Heinicke *et al.* 2007). We refrain from recognizing species series or species groups because no phylogenetic analysis has been made of these species and there has been no proposal for subdivisions within the former “*Eleutherodactylus milesi*” Species Group. Crawford and Smith (2005) included two species (*C. daryi* and *C. trachydermus*) and this study and Heinicke *et al.* (2007) included one species (*C. daryi*) in their molecular phylogenetic analyses. Many species of these streamside frogs have disappeared from their habitats and some may be extinct (McCranie & Wilson 2002).

Subgenus *Craugastor* Cope, 1862

Craugastor Cope, 1862:153. Type species: *Hylodes fitzingeri* Schmidt, 1857:12, by subsequent designation by Dunn and Dunn, 1940:71.

Leiyla Kieferstein, 1868:296. Type species *Leiyla güintherii* Kieferstein, 1868:296, by monotypy. Synonymy with *Hylodes (sensu lato)* by Boulenger (1882:198), and with *Eleutherodactylus* by Savage (1974:290).

Microbatrachylus Taylor, 1940a:499. Type species *Eleutherodactylus hobartsmithi* Taylor, 1936, by monotypy. Synonymy by Lynch (1965:8).

Definition.—Frogs of the subgenus *Craugastor* are characterized by (1) head narrower than, or as wide as, body, width 31–55% of SVL; (2) tympanic membrane differentiated and sexually dimorphic (larger in males); (3) cranial crests absent, except in *C. gulosus* Species Series; (4) dentigerous processes present, triangular or transverse; reduced or absent in the *C. mexicanus* Species Series; (5) “E” condition of adductor muscle; (6) terminal discs narrow (with pointed discs on some toes in *C. laticeps* species series) to expanded and truncate; circumferential grooves present; terminal phalanges T-shaped; (7) Finger I longer than Finger II, except I equals II or I is shorter than II in some members of *C. fitzingeri*, *C. mexicanus* and *C. rhodopis* Species Series; (8) Toe III longer than Toe V; (9) subarticular tubercles not projecting, except in some members of *C. laticeps*, *C. mexicanus* and *C. rhodopis* Species Series; (10) dorsum smooth to tuberculate; (11) venter smooth, granular, or areolate; (12) range in SVL from 18 mm in female *C. pygmaeus* to 110 mm in female *C. pelorus*.

Content.—The subgenus contains 77 species placed in six species series.

Distribution.—The subgenus ranges from Mexico through Central America into northwestern Colombia (Fig. 14).

Etymology.—As for the genus.

Remarks.—This subgenus contains all of the species of the genus *Craugastor* that are not included in the smaller subgenera *Campbellius* and *Hylactophryne*. Molecular phylogenies (Crawford & Smith 2005; Heinicke *et al.* 2007), including those presented here (Figs. 2–3) indicate that this subgenus is monophyletic. See Remarks for the genus *Craugastor* for discussion of the major divisions within the genus and recent taxonomic changes.

Craugastor (Craugastor) fitzingeri Species Series

Definition.—Species in this series are slender in body shape (long-limbed) and moderate to large in SVL, ranging from 31 mm (females, *C. monnichorum*) to 86 mm (females, *C. andi*). They have narrow to moderately wide heads (width 34–44% SVL) lacking cranial crests; the dorsum is smooth or slightly shagreen or tuberculate with low folds, and the venter is smooth or granular. The snout is subacuminate in dorsal view. The tympanic membrane is differentiated or not; vocal slits are present; nuptial pads are usually present. Finger I is longer or shorter than Finger II and the digits, especially on Fingers III and IV, have moderate to large digital discs; an inner tarsal fold is usually present, and plantar tubercles are absent. The toes are slightly to extensively webbed. Coloration is variable, but most have dark bars on the hind limbs. Most species are arboreal.

Content.—The species series (13 species) includes two species groups: the *Craugastor (Craugastor) fitzingeri* and *melanostictus* species groups.

Distribution.—The species series is distributed from northeastern Honduras southeastward through Nicaragua, Costa Rica, and Panama to northwestern Colombia.

Remarks.—This is one of the most studied assemblages of terraranan frogs. Previous versions, referred to as the *fitzingeri* group or series (Lynch 1976a; Lynch & Myers 1983; Lynch 1986a; Miyamoto 1986; Savage 1987; Lynch & Duellman 1997), bear almost no resemblance to the species series recognized here; some former members now reside in different genera. Savage *et al.* (2004) reviewed the complex taxonomic history of this group, and it is not repeated here. The content of the species series recognized here corresponds most closely to that recognized by Savage *et al.* (2004). Nonetheless, the relationships determined here (Fig. 2) do not agree with earlier phylogenetic analyses, including that most recent one.

Crawford and Smith (2005) analyzed five of the 13 species in their molecular phylogenetic study, although none of the seven montane species (distributions above 1000 meters) previously associated with this series (*Craugastor andi*, *cuaquero*, *emcelae*, *melanostictus*, *monnichorum*, *phasma*, and *rayo*) was included. Our molecular phylogeny (Fig. 2) includes three of the montane species (*C. andi*, *emcelae*, and *melanostictus*) and three of the predominantly lowland species (*C. crassidigitus*, *fitzingeri*, and *longirostris*). Remarkably, these two groups of species form two clades in our phylogeny, even though previous analyses did not reveal such a dichotomy. An association of montane species appeared in the analysis of Savage *et al.* (2004), including the three in our tree, but their montane clade excluded a montane species (*C. phasma*). Their lowland species did not form a group (Savage *et al.* 2004).

Besides altitudinal differences, the three lowland species in our tree also have wider distributions that extend into eastern Panama and South America whereas the montane species are restricted to Costa Rica and western Panama. In morphology, the lowland species have a dorsal texture that is slightly rugose or tuberculate whereas the montane species have a mostly smooth dorsum. Also, the lowland species have moderate to extensive toe webbing (none or basal webbing in the montane species, except moderate in *C. andi*) and an unpatterned venter (marked with gray or black pigment in the montane species). These same distributional and morphological characters also hold for most of the other lowland and montane species in the *C. fitzingeri* Species Series that were not included in our molecular phylogeny. In the West Indies, where species relationships are best known (see below), closely related species also tend to occur at similar elevations, resulting in clades of upland species and clades of lowland species. Considering all of the evidence, we recognize these two divisions within the *C. fitzingeri* Species Series as the *C. fitzingeri* Species Group and the *C. melanostictus* Species Group. Although by necessity, the names of these species groups have appeared in past literature, they should not be confused with earlier versions of these groups because their content is different.

Craugastor (Craugastor) fitzingeri Species Group

Definition.—Species in this group are slender in body shape (long-limbed) and moderate to large in SVL, ranging from 48 mm (females, *C. crassidigitus*) to 74 mm (females, *C. raniformis*). They have narrow to moderately wide heads (width 34–41% SVL) lacking cranial crests; the dorsum is finely or moderately tuberculate and rugose, and the venter is smooth (granular in *C. tabasarae*). The snout is subacuminate in dorsal view. The tympanic membrane is differentiated in both sexes; vocal slits and nuptial pads are present, except in *C. tabasarae*. Finger I is longer or shorter than Finger II, and the digits, especially on Fingers III and IV, have moderately enlarged discs. An inner tarsal fold is present or not; plantar tubercles are absent, and the toes are moderately to extensively webbed. Coloration is variable, but most are brown dorsally and have unmarked white or yellow venter. Most species are arboreal; known calls have been described as a series of chirps, mews, or clacks.

Content.—The species group includes six species: *Craugastor (Craugastor) crassidigitus* (Fig. 16), *fitzingeri* (Fig. 17), *longirostris*, *raniformis*, *tabasarae*, and *talamancae*.

Distribution.—The species group is distributed at elevations of 0–2000 m from northeastern Honduras southeastward through Nicaragua, Costa Rica, Panama, northwestern Colombia, to southwestern Ecuador.

Remarks.—See Remarks for the *Craugastor fitzingeri* Species Series for a discussion of the taxonomic history of this assemblage and justification for erecting this species group, which should not be confused with groups of the same name used in earlier literature. All of the included species in this group occur at or near sea level, except for *C. tabasarae* (600–800 m). In contrast, all species in the *C. melanostictus* Species Group occur above 910 m elevation. Savage *et al.* (2004) associated *C. tabasarae* with montane species, although Crawford and Smith (2005) found it to be the closest relative of *C. longirostris*, a lowland species. Thus the group allocation of this species is uncertain.

Craugastor (Craugastor) melanostictus Species Group

Definition.—Species in this group are slender in body shape (long-limbed) and moderate to large in SVL, ranging from 31 mm (females, *C. monnichorum*) to 86 mm (females, *C. andi*). They have moderate to wide heads (width 36–44% SVL) lacking cranial crests; the dorsum is smooth or slightly shagreen or rugose, and the venter is smooth (granular in *C. melanostictus*). The snout is subacuminate in dorsal view. The tympanic membrane is differentiated or not; vocal slits and nuptial pads are present. Finger I is longer or shorter than Finger II, and the digits, especially on Fingers III and IV, have moderate to large digital discs. An inner tarsal fold is present (absent in *C. melanostictus*); plantar tubercles are absent, and the toes are slightly webbed (moderately webbed in *C. andi* and *rayo*). Coloration is variable, but most or all have a heavily marked or mottled (with black) venter. Most species are arboreal; calls are mostly unknown, although the call of *C. andi* is described as a “deep guttural glug”.

Content.—The species group includes seven species: *Craugastor (Craugastor) andi* (Fig. 18), *cuaquero*, *emcelae*, *melanostictus*, *monnichorum*, *phasma*, and *rayo*.

Distribution.—The species group is distributed at elevations of 900–2700 m in montane Costa Rica and montane western Panama.

Remarks.—See Remarks for the *Craugastor fitzingeri* Species Series for a discussion of the taxonomic history of this assemblage and justification for erecting this species group. We include the montane species (1850 m elevation) *C. phasma* in this group, although Savage *et al.* (2004) did not include it in their montane clade because they considered it to be most closely related to *C. talamancae*, a lowland species. We include *C. phasma* in our *C. melanostictus* Species Group because it agrees in other ways with species in this group, as in the possession basal toe webbing (not moderate or extensive) and dark pigment on the venter.

Craugastor (Craugastor) laticeps Species Series

Definition.—Species in this series are mostly slender with long legs but *Craugastor laticeps* is robust) and range in SVL from 34 mm (females, *C. coffeus*) to 80 mm (females, *C. laticeps*). They have moderate to wide heads (width 34–49% SVL) lacking cranial crests. The dorsum is weakly granular, commonly with one or more series of distinct tubercles, including a postorbital, supratympanic, two or more paravertebrals, and two suprascapular tubercles on each side; some have a suprascapular fold across the back, and the venter is smooth. The eighth presacral and sacral vertebrae are fused. The snout is acuminate in dorsal view, but subacuminate in *C. laticeps*. The tympanic membrane is differentiated in both sexes; vocal slits and nuptial pads are absent. The digital discs are small to moderate in size; some are pointed apically. An inner tarsal fold is present; plantar tubercles are present or absent, and the toes are slightly to moderately webbed. Coloration is variable, but most have an hourglass or X-shaped middorsal blotch with smaller lateral blotches and usually a distinct dark facemask (solid or blotched) extending onto the anterior flank and bordered above by a narrow pale line. Most species are terrestrial and usually found on the forest floor, often by day. Vocalization is unknown.

Content.—The species series includes nine species: *Craugastor (Craugastor) chac*, *coffeus*, *gollmeri* (Fig. 19), *greggi*, *laticeps*, *lineatus*, *mimus*, *noblei*, and *rostralis*.

Distribution.—The species series is distributed throughout Middle America, from southern Mexico to Panama.

Remarks.—This species series corresponds mostly to the “*Eleutherodactylus gollmeri*” Species Group (Savage 1987; Lynch 2000; McCranie & Wilson 2002; Savage 2002; Crawford & Smith 2005), although we use the earlier name “*laticeps*.” These frogs represent a radiation of moderate to large species that inhabit the forest floor and leaf litter. The fusion of the eighth presacral and sacral vertebrae is a defining character (Lynch 2000), except that it also is present in *C. daryi*, which was shown by Crawford and Smith (2005) not to be in their “*E. gollmeri* Species Group.” Although Lynch (2000) placed “*E. greggi*” in the “*E. gollmeri* Species Group,” he noted that it differed in several ways from other members of the group. Crawford and Smith (2005) examined six of the nine species in this series.

Craugastor (Craugastor) gulosus Species Series

Definition.—Species in this series are robust and range from 44 mm (females, *C. aphanus*) to 103 mm (females, *C. gulosus*). They have relatively wide heads, width 39–55% SVL, with paired frontoparietal crests visible externally as cranial crests in adults of most species; the venter is smooth. In dorsal view the snout is rounded; the tympanic membrane is differentiated in both sexes, and males lack vocal slits and nuptial pads. The digital discs are small; an inner tarsal fold and plantar tubercles are absent, and the toes are not webbed. Coloration is variable, but most have dark reticulations enclosing yellow, orange, or red spots on the belly and ventral surfaces of the limbs. These species are terrestrial and inhabit leaf litter on the forest floor. Vocalizations are unknown.

Content.—The species series includes five species: *Craugastor (Craugastor) aphanus* (Fig. 20), *C. gulosus*, *C. megacephalus*, *C. opimus*, and *C. rugosus*.

Distribution.—The species series is distributed from eastern Guatemala through Honduras, Nicaragua, Costa Rica, and Panama to northwestern Colombia.

Remarks.—This species series was reviewed recently, as the “*Eleutherodactylus biporcatus* Species Group,” by Savage and Myers (2002), who retained the Venezuelan species “*Eleutherodactylus biporcatus*” in this largely Middle American group while recognizing that it differs substantially in structure and chromosomes from other members. Herein, we place “*E.*” *biporcatus* in the genus *Strabomantis* (see below) and recognize the remaining assemblage as the *Craugastor (Craugastor) gulosus* Species Series. See Remarks for the

genus *Craugastor* (above) concerning the close relationship between *C. ranoides* (*C. punctariolus* Species Series) and *C. megagephalus* (*C. gulosus* Species Series) found by Crawford and Smith (2005). Crawford and Smith's (2005) analysis included one (*C. megagephalus*) of the five species in this series.

Craugastor (*Craugastor*) *mexicanus* Species Series

Definition.—Species in this series are robust with short legs, and range in SVL from 18 mm (females, *C. pygmaeus*) to 44 mm (females, *C. saltator*). They have narrow to moderately wide heads, width 38–45% SVL. The dorsum is smooth to tuberculate, and the venter is smooth or areolate; in most species the dentigerous processes of the vomers are small, concealed, or absent, but they are well developed in *C. occidentalis*. In dorsal view the snout is rounded to subacuminate; vocal slits and nuptial pads are absent. Finger I is slightly shorter than, equal to, or longer than Finger II. The digital discs are small; an inner tarsal fold is absent. Plantar tubercles are absent or barely evident, and the toes are not webbed. Coloration is variable, but most are uniform brown or have a poorly developed pattern. Most species are active on the forest floor. The call has been described as “faint” (*C. occidentalis*).

Content.—The species series includes seven species: *Craugastor* (*Craugastor*) *hobartsmithi*, *mexicanus*, *montanus*, *occidentalis*, *omiltemanus*, *pygmaeus* (Fig. 21), and *saltator*.



FIGURES 21–24. 21. *Craugastor* (*Craugastor*) *pygmaeus* of the *C. mexicanus* Species Series from 30 km N San Gabriel Mixtepec, Oaxaca, Mexico. 22. *Craugastor* (*Craugastor*) *podociferus* of the *C. podociferus* Species Group, *C. podociferus* Species Series, from Rama Sur Río Las Vueltas, Heredia, Costa Rica. 23. *Craugastor* (*Craugastor*) *rhodopis* of the *C. rhodopis* Species Group, *C. podociferus* Species Series, from South slope Volcán San Martín, Veracruz, Mexico. 24. *Craugastor* (*Craugastor*) *rugulosus* of the *C. punctariolus* Species Series from South slope Volcán San Martín, Veracruz, Mexico. All photos by W. E. Duellman.

Distribution.—The species series is distributed primarily in western and southern Mexico, with one species extending into Guatemala.

Remarks.—This species series and the next are remnants of the former “*Eleutherodactylus rhodopis*” and “*E. omiltemanus*” species groups (Lynch 2000); he reviewed the complicated and confusing history of these groups and the relationships of species associated with “*E. bransfordii*,” “*E. mexicanus*,” and “*E. rhodopis*” and resolved some nomenclatural problems. Crawford and Smith (2005) included 13 of the 18 species in the two series (as recognized here) and presented molecular phylogenetic evidence for a different arrangement of species to groups that bore little resemblance to former arrangements. They identified three clades of species: a northern clade (their “*E. rhodopis* Species Group”) composed of “*E. rhodopis*” and “*E. loki*,” a southern clade (their “*E. bransfordii* Species Group”) composed of six described and two undescribed species, and another northern clade (“*E. mexicanus* Species Group”) composed of five described and one undescribed species. The first two clades were found to be closest relatives whereas the relationship of that pair to the third clade and other species groups was unresolved.

We recognize the first and second clades as the *Craugastor rhodopis* and *C. podiciferus* species groups and place them in the *C. rhodopis* Species Series. We recognize the third clade as the *C. mexicanus* Species Series. Although Crawford and Smith (2005) did not define these three newly discovered clades morphologically, or allocate species to them that were not included in their study, we have attempted to do so here. The two series seem to differ in condition of the vomerine teeth—small, concealed, or absent (*C. mexicanus* Species Series) versus large and prominent (*C. rhodopis* Species Series). The two species groups of the *C. rhodopis* Species Series have structural and coloration differences (see below). Lynch (2000) mentioned black mesorchia (mesentery around testes) as a character of possible diagnostic value, but apparently it is not found in all of the species of the group referred herein to the *C. mexicanus* Species Series. The taxon “*Eleutherodactylus saltator*” was placed in the synonymy of “*E. mexicanus*” by Lynch (2000) but the sample of that species used by Crawford and Smith (2005) clustered with another species (“*E. pygmaeus*”), therefore supporting recognition of *C. saltator* as a valid species, assuming the identifications are correct. The *C. mexicanus* Species Series, as defined here, appears to represent the basal clade within the subgenus *Craugastor* (Figs. 2–3).

Craugastor (Craugastor) rhodopis Species Series

Definition.—Species in this series are robust with short legs and range from 22 mm (females, *C. lauraster* and *C. stejnegerianus*) to 46 mm (females, *C. rhodopis*). They have narrow to moderately wide heads, width 31–44% SVL; the dorsum is rugose and tuberculate, and the venter is smooth or areolate. The dentigerous processes of the vomers are large and prominent. The snout is rounded to subacuminate in dorsal view. Vocal slits are absent (present in *C. bransfordii*, and *C. podiciferus*), and nuptial pads are absent (present in *C. bransfordii*, *C. underwoodi*, and in the *C. rhodopis* Species Group). The digital discs are small. An inner tarsal fold is absent or weakly developed; plantar tubercles are absent or inconspicuous, and the toes are not webbed. Coloration is variable (see below). Most species are terrestrial and usually are found on the forest floor during the day. Known vocalizations have been described as a chirp, squeak, or trill.

Content.—The species series includes two species groups (10 species): the *Craugastor (Craugastor) podiciferus* and *rhodopis* species groups.

Distribution.—The species series is distributed from eastern and southern Mexico to western Panama.

Remarks.—This species series contains remnants of the previous “*Eleutherodactylus rhodopis* Species Group” or Series (Lynch 2000; Savage 2002) as discussed in the Remarks section of the *Craugastor mexicanus* Species Series (see above).

Craugastor (Craugastor) podiciferus Species Group

Definition.—Species in this series are robust with short legs and range in body shape and SVL from 22 mm (females, *C. lauraster* and *C. stejnegerianus*) to 40 mm (females, *C. podiciferus*). They have narrow to moderately wide heads, width 31–44% SVL. The dorsum is rugose and tuberculate, and the venter is areolate. The snout is rounded to subacuminate in dorsal view; vocal slits are absent (present in *C. bransfordii*, and *C. podiciferus*), and nuptial pads are absent (present in *C. bransfordii* and *C. underwoodi*). Finger I is shorter than, or equal to, Finger II, and the digits have small discs. An inner tarsal fold is absent or inconspicuous; plantar tubercles are absent or not evident, and the toes are not webbed. Coloration is variable, but most are uniform or mottled brown with a yellow venter. Most species are active on the forest floor. Known vocalizations have been described as a chirp, squeak, or trill.

Content.—The species group includes eight species: *Craugastor (Craugastor) bransfordii*, *jota*, *lauraster*, *persimilis*, *podiciferus* (Fig. 22), *polyptychus*, *stejnegerianus*, and *underwoodi*.

Distribution.—The species group is distributed from eastern Honduras to western Panama.

Remarks.—This species group contains remnants of the previous “*Eleutherodactylus rhodopis* Species Group” or Series (Lynch 2000; Savage 2002), and corresponds to the “*E. bransfordii* Species Group” of Crawford and Smith (2005), as discussed in the Remarks section of the *Craugastor mexicanus* Species Series (see above). Savage (2002) resurrected “*E. polyptychus*” from the synonymy of “*E. bransfordii*.”

This species group is the southern counterpart of the *C. rhodopis* Species Group. Besides geography and DNA sequences, these two groups can be distinguished by ventral skin texture (weakly areolate or areolate versus smooth in the *C. rhodopis* Species Group), relative finger length (Finger I shorter than, or equal to, Finger II versus Finger I slightly longer than Finger II), and ventral ground coloration (yellow versus white). Also, with the exception of one large member of the southern group, *C. podiciferus* (40 mm SVL), the two groups are distinguished by body size (22–30 mm versus 38–46 mm in the *C. rhodopis* Species Group).

Craugastor (Craugastor) rhodopis Species Group

Definition.—Members of this group have narrow to moderately wide heads, width $\pm 36\%$ SVL. The dorsum is rugose and tuberculate, and the venter is smooth. The snout is subacuminate in dorsal view. Vocal slits are absent, but nuptial pads are present. Finger I is slightly longer than Finger II; the digits have small discs. An inner tarsal tubercle or vague fold is present; plantar tubercles are absent or inconspicuous, and the toes not webbed. Dorsally, the color pattern is complex and polymorphic; venter is white with dark flecks. Most species are terrestrial and usually found on the forest floor by day. Vocalization is unknown.

Content.—The species group includes two species: *Craugastor (Craugastor) loki* and *rhodopis* (Fig. 23).

Distribution.—The species group is distributed from eastern and southern Mexico, south through Guatemala, Belize, El Salvador, and Honduras.

Remarks.—This species group contains remnants of the previous “*Eleutherodactylus rhodopis* Species Group” or Series (Lynch 2000; Savage 2002), and corresponds to the “*E. rhodopis* Species Group” of Crawford and Smith (2005), as discussed in the Remarks section of the *Craugastor mexicanus* Species Series (see above). See also the Remarks section of the *C. podiciferus* Species Group for characters distinguishing that species group from this group. Although there are only two described species in this group, molecular data support the existence of several undescribed species, including some currently recognized as *C. rhodopis*. One such sample is included in our analysis (Fig. 2–3).

Craugastor (Craugastor) punctariolus Species Series

Definition.—Species in this series are robust in body shape and large in SVL, ranging from 50 mm (females, *C. emleni*) to 110 mm (females, *C. pelorus*), although one species, *E. olanchano*, is known only from small (30 mm SVL) males. They have moderate to wide heads (width 32–47% SVL) lacking cranial crests; the dorsum is smooth to rugose to strongly tuberculate, and the venter is smooth. The snout in dorsal view is rounded, subacuminate, or subelliptical; a tympanic membrane is differentiated in both sexes. Vocal slits present or absent; nuptial pads are present or absent. The digits have small to large digital discs; an inner tarsal fold is present, but plantar tubercles are absent. The toes are slightly to nearly fully webbed. In coloration, these frogs are variable, but most have scattered areas of body with rusty or reddish color, a series of alternating pale and dark lip bars, a pale interocular spot bordered by a dark interocular bar, and sometimes a narrow cream to red middorsal line. Most species are terrestrial and are found in riparian habitats; their calls are unknown or poorly known.

Content.—The species series includes 33 species: *Craugastor (Craugastor) amniscola*, *anciano*, *angelicus*, *aurilegulus*, *azueroensis*, *berkenbuschii*, *brocchi*, *catalinae*, *charadra*, *emleni*, *escoces*, *fleischmanni*, *inachus*, *laevissimus*, *merendonensis*, *obesus*, *olanchano*, *palenque*, *pechorum*, *pelorus*, *pozo*, *psephosypharus*, *punctariolus*, *ranoides*, *rhyacobatrachus*, *rivulus*, *rugulosus* (Fig. 24), *rupinius*, *sabrinus*, *sandersoni*, *taurus*, *vocalis*, and *vulcani*.

Distribution.—The species series is distributed from Mexico to western Panama.

Remarks.—This species series represents a large radiation of large, robust, riparian species formerly called the “*E. rugulosus* Group” (the series name *punctariolus* is used here because it predates *rugulosus*). Campbell and Savage (2000) divided the species into four clusters based on presence and absence of vocal slits and nuptial pads. However, they emphasized that those clusters probably do not correspond to evolutionary groups, and therefore we do not recognize any species groups within this large series. Crawford and Smith (2005) included one of the 33 species in this series in their molecular phylogeny and Heinicke *et al.* (2007) included two species. An additional four species have been included here (Fig. 2). As mentioned in the Remarks on the genus, this series, as currently defined, appears to be polyphyletic with respect to at least some members of the *C. gulosus* Species Series.

As of June 2007 the only known extant member of this series is a population of *Craugastor ranoides* in Costa Rica. According to J. R. Mendelson (pers. comm.), *C. punctariolus* was common in the vicinity of El Valle, Panama in 2005; this population died out from chytrid fungus infections early in 2006, but some individuals remain in captivity at the El Valle Amphibian Conservation Center, Atlanta Botanical Garden, and Zoo Atlanta. The presumed near extinction of this clade likely has been caused by the chytrid fungus.

Subgenus *Hylactophryne* Lynch, 1968

Hylactophryne Lynch, 1968a:511. Type species: *Hylodes augusti* Dugés, in Brocchi, 1879:21. Synonymized with “*Eleutherodactylus*” by Lynch (1968:255).

Definition.—Frogs of the subgenus *Hylactophryne* are characterized by (1) head narrower than, or as wide as, body; head width, 33–45% SVL, although broad (49%) in *C. uno*; (2) tympanic membrane differentiated; status of sexual dimorphism not established (see below); (3) cranial crests absent; (4) dentigerous processes of vomers triangular or transverse, reduced or absent in at least two species (*C. cyanochthebius* and *C. nefrens*); (5) “E” condition of adductor muscle; (6) digital discs large (especially on outer two fingers), truncate or notched; circumferential grooves present; terminal phalanges T-shaped; (7) Finger I shorter or longer than Finger II; (8) Toe V longer than Toe III (except in *C. augusti* and *C. tarahumaraensis*); (9) subarticular tubercles not projecting; (10) dorsum usually granular, rarely smooth or tuberculate; (11) venter smooth (granular

in *C. batrachylus*); (12) range in SVL 16 mm in *C. galacticorhinus* (male only) to 95 mm in female *C. augusti*.

In addition, species in this subgenus are moderate in body shape, but robust in *C. augusti* and have a subacuminate snout in dorsal view. Vocal slits and nuptial pads are present or absent. An inner tarsal fold and plantar tubercles are present or not; the toes are barely webbed if at all. Coloration is variable, but in most species the dorsum is tan or brown with an olive or green hue, and the venter is white, grayish-white, or unpigmented. These arboreal frogs are commonly encountered in trees and bushes at night, although one species (*C. augusti*) is a rock and cliff-dweller. The calls are largely unrecorded; where known they have been described as a soft “peep” (*C. galacticorhinus*), barking (*C. augusti*), and a low growl, a low chuckle, single clicks, and a multi-note laugh (*C. polymniae*).

Content.—This subgenus includes 21 species in the *Craugastor* (*Hylactophryne*) *augusti* and *bocourti* species series.

Distribution.—The subgenus is distributed from southern border regions of the United States (southeast Arizona, southern New Mexico, and central and southwest Texas) through most of central and southern Mexico and central Guatemala to northwestern Honduras (Fig. 25).

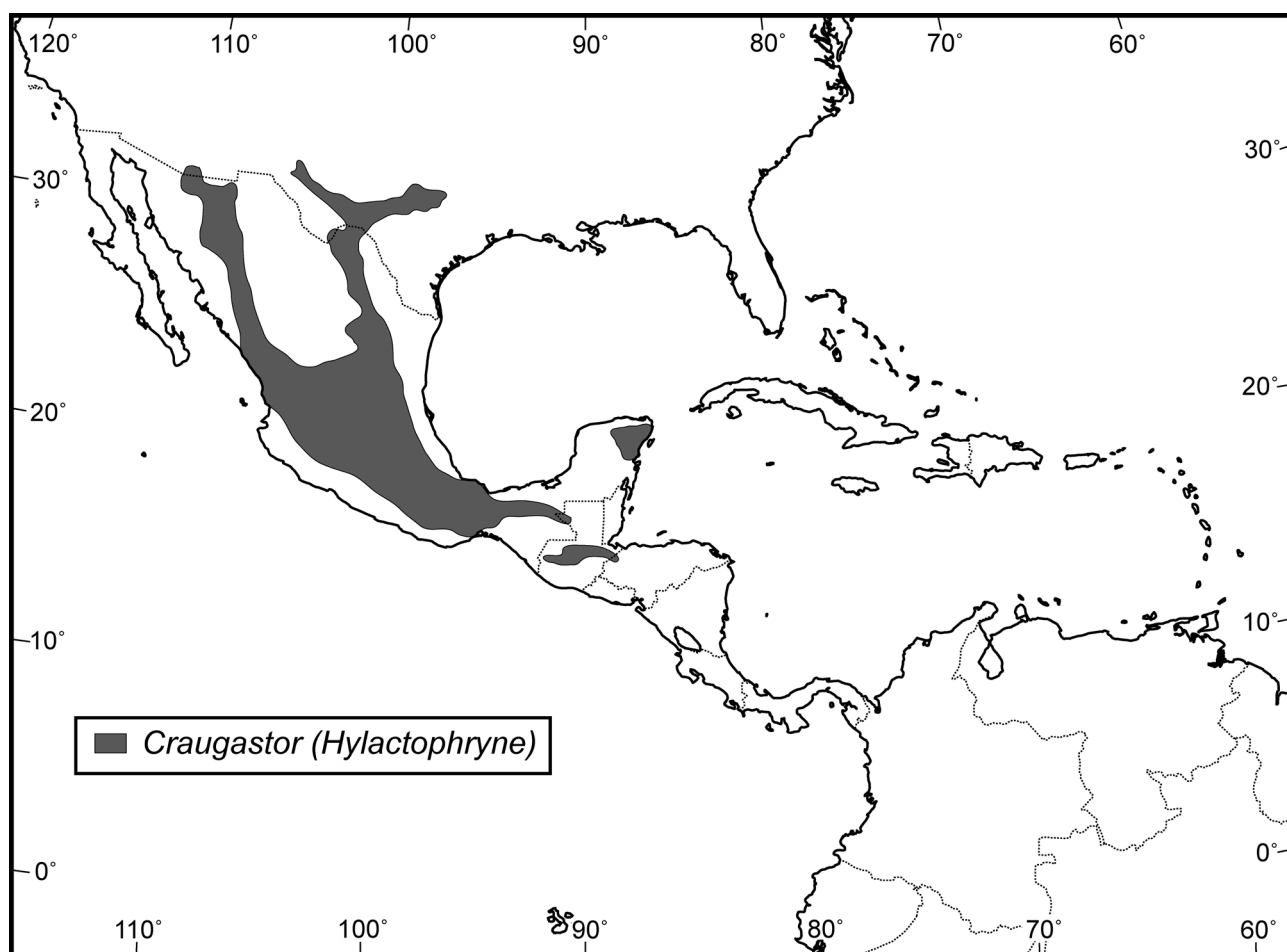


FIGURE 25. Distribution of the Subgenus *Hylactophryne*, Genus *Craugastor*, Family Craugastoridae.

Etymology.—The subgeneric name is derived from the Greek *hylacto*, meaning barking, and the Greek *phryne*, meaning toad, in allusion to the vocalization of *C. augusti*. The name is masculine in gender.

Remarks.—This subgenus combines the previous “*Eleutherodactylus augusti*” and “*E. alfredi*” species groups (Lynch 2000). These two groups were found to be closely related in two independent molecular phylogenies (Crawford & Smith 2005; Heinicke *et al.* 2007). We continue to recognize these two units here as species series. Because *C. bocourti* is an older name than *C. alfredi*, we refer to the larger of these two series as the *C. bocourti* Species Series. In so doing, the several recognized subgroups within the former “*E. alfredi* Species Group,” namely the *alfredi*, *decoratus*, and *spatulatus* subgroups (Lynch 1966; Lynch 1967b; Smith 2005), might be considered as species groups. We refrain from doing so here because many species have been added to this assemblage since those subdivisions were described and it is unclear where some of the new additions (e.g., *C. batrachylus* and *C. uno*) would fit. Also, molecular phylogenies (Crawford & Smith 2005; Heinicke *et al.* 2007; and here) have included only a few of these species.

Sexual dimorphism in tympanum size, with males having a larger tympanum than females, was considered a diagnostic character in *Craugastor* that defined a monophyletic assemblage including most species except those placed here in the subgenus *Hylactophryne* (Lynch 2000), which includes mostly the former “*E. alfredi* Species Group.” Crawford and Smith (2005) also associated the lack of sexual dimorphism in tympanum size as a characteristic of the “*E. alfredi* Species Group.” However, Campbell *et al.* (1989), in discussing the “*E. alfredi* Species Group,” stated that “the relative size of the tympanum is also usually sex dependent, being larger in males of most species.” It is possible that the small number of specimens of most of the species in the group (some are known only from males) has contributed to this confusion.

Craugastor uno previously has been unassigned to series or group (Lynch 2000). Our molecular phylogeny clearly shows that it is a member of the *Craugastor (Hylactophryne) bocourti* Series (Figs. 2–3). Relevant characters are its large and truncate digital discs and distribution. We also include the species *Craugastor batrachylus* in this subgenus, although we have not sampled it. Previously, it was placed in the predominantly South American “*Eleutherodactylus unistrigatus* Species Group” in part because of its granular venter and long fifth toe (Lynch & Duellman 1997). However, its northern distribution (Mexico) is at odds with that assignment, and members of the *Craugastor* subgenus *Hylactophryne* typically have a long fifth toe.

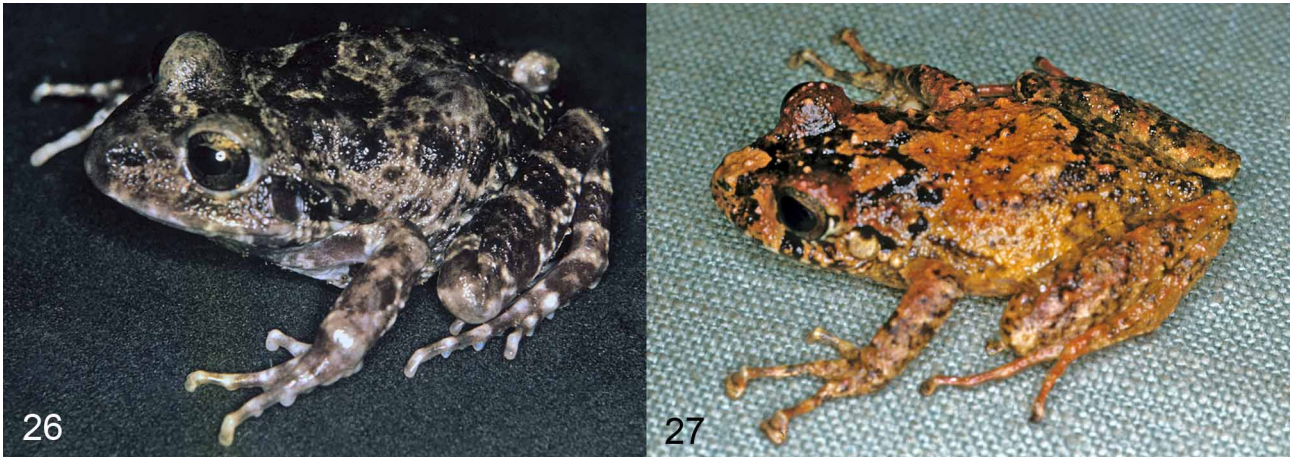
Craugastor (Hylactophryne) augusti Species Series

Definition.—Species in this series are robust and range in SVL from 43 mm (females, *C. tarahumaraensis*) to 95 mm (females, *C. augusti*). They have moderately wide heads, width 41–45% SVL, lacking cranial crests. The dorsum is granular, and the venter is smooth. The snout is subacuminate in dorsal view, and the tympanic membrane is differentiated in both sexes. Vocal slits are present; nuptial pads are absent. The digital discs are small; Finger I is longer than Finger II, and Toe V is shorter than Toe III. An inner tarsal fold is absent, and plantar tubercles are present; the toes are unwebbed. Coloration is variable, but most have distinct dark spots or blotches on the body and bars on the limbs. Both species are rock and cliff-dwellers, often seen on exposed rocks. The call is a barking sound (*C. augusti*) or “quack” (*C. tarahumaraensis*).

Content.—The species series includes two species: *Craugastor (Hylactophryne) augusti* (Fig. 26) and *tarahumaraensis*.

Distribution.—The species series is distributed from the southern border regions of the United States (southeast Arizona, southern New Mexico, and central and southwest Texas) through most of central Mexico to the Isthmus of Tehuantepec.

Remarks.—This species series represents the former “*E. augusti* Species Group” (see Remarks above for subgenus *Hylactophryne*). Geographic variation in morphology, calls, and DNA sequences of the wide-ranging *C. augusti* (Zweifel 1956; Goldberg *et al.* 2004) suggest that it may be a complex of species.



FIGURES 26–27. 26. *Craugastor (Hylactophryne) augusti* of the *C. augusti* Species Series from Agua del Obispo, Guerrero, Mexico. Photo by W. E. Duellman. 27. *Craugastor (Hylactophryne) spatulatus* of the *C. bocourti* Species Series from 3 km SW Huatusco, Veracruz, Mexico. Photo by W. E. Duellman.

Craugastor (Hylactophryne) bocourti Species Series

Definition.—Species in this series are moderate in body shape and range in SVL from 16 mm (males only, *C. galacticorhinus*) to 63 mm (females, *C. uno*). They have moderate to wide heads, width 33–49% SVL, lacking cranial crests. The dorsum is smooth or granular; and the venter usually is smooth (areolate in *C. batrachylus*, *guerreroensis*, and *spatulatus*). The snout is subacuminate or truncate in dorsal view; the tympanic membrane is differentiated in both sexes. Vocal slits and nuptial pads are present or absent; the digital discs are large and truncate or notched. Finger I is shorter than Finger II, and Toe V is longer than Toe III. An inner tarsal fold is present, and plantar tubercles are present or absent; the toes are unwebbed or slightly webbed basally. Coloration is variable, but in most species the dorsum is tan or brown with an olive or green hue, and the venter is white, grayish-white, or unpigmented. These frogs are encountered in trees and bushes at night. The calls of most species have not been recorded; the known calls have been described as a soft “peep” (*C. galacticorhinus*) or a low growl, a low chuckle, single clicks, and a multi-note laugh (*C. polymniae*).

Content.—The species series includes 19 species: *Craugastor (Hylactophryne) alfredi*, *batrachylus*, *bocourti*, *campbelli*, *cyanochthebius*, *decoratus*, *galacticorhinus*, *glaucus*, *guerreroensis*, *megalotympanum*, *nefrens*, *polymniae*, *silvicola*, *spatulatus* (Fig. 27), *stuarti*, *taylori*, *uno*, *xucanebi*, *yucatanensis*.

Distribution.—The species series is distributed from east-central and west-central Mexico and the Yucatan Peninsula through southern Mexico and central Guatemala, to northwestern Honduras.

Remarks.—This species series represents the former “*E. alfredi* Species Group,” but with the addition of several species (see Remarks above for subgenus *Hylactophryne*).

Genus *Haddadus*, New Genus

Type species.—*Rana binotata* Spix, 1824:31.

Definition.—This craugastorid genus is characterized by (1) head narrower than body; (2) tympanic membrane differentiated; (3) cranial crests absent; (4) dentigerous processes of vomers prominent; (5) “S” condition of adductor muscle; (6) small terminal discs on digits, bearing circumferential grooves; terminal phalanges narrow, T-shaped; (7) Finger I longer than Finger II; (8) Toe III equal in length or slightly shorter

than Toe V; (9) subarticular tubercles not projecting; (10) dorsum smooth to granular with longitudinal ridges; (11) venter smooth to granular; (11) range in SVL 17 mm in only known specimen of *H. plicifer* to 64 mm in females of *H. binotatus*.

Content.—The genus contains two species, *Haddadus binotatus* (Fig. 28) and *Haddadus plicifer*.



FIGURE 28. *Haddadus binotatus* from Pisinguaba, São Paulo, Brazil. Photo by C. F. B. Haddad.

Distribution.—The genus is distributed in Atlantic Coastal Forest in eastern and southern Brazil, from the state of Pernambuco south to the state of Rio Grande do Sul (Fig. 13).

Etymology.—This new genus is named for Célio F. B. Haddad, Universidade Estadual Paulista (UNESP), Brazil, in recognition of his contributions to the systematics of Brazilian amphibians.

Remarks.—Lynch (1968b) placed species of “*Eleutherodactylus*” from southern Brazil in four species groups (see additional discussion under *Ischnocnema*). He considered “*E.*” *binotatus* distinct enough from the other species to warrant its own species group defined primarily by a disproportionately long first finger and separate from the “*E.*” *guentheri* Species Group. Later, he placed less emphasis on the length of Finger I by combining the “*E.*” *binotatus* and “*E.*” *guentheri* species groups (Lynch 1976a). Heyer (1984) disagreed and removed “*E.*” *binotatus* from a core group of “*Eleutherodactylus*” in southeastern Brazil, which he called the “*Eleutherodactylus*” *guentheri* cluster, in effect renewing emphasis on finger length, although he did not attempt a classification of species other than those in the “*E.*” *guentheri* cluster. He pointed out that the relative lengths of Fingers I and II of species in that cluster was variable, with some having slightly longer and others slightly shorter first fingers. Frost *et al.* (2006) discussed the position of “*E.*” *binotatus*, but taxon sampling of terraranans was insufficient to draw any robust conclusions.

Heinicke *et al.* (2007) distinguished a Southeast Brazil Clade of “*Eleutherodactylus*” including “*E.*” *guentheri*, *hoehnei*, *juipoca*, and *parvus*, but not “*E.*” *binotatus*, which appeared elsewhere in the tree. They did not include “*E.*” *plicifer* or other species of the genus from southern Brazil. Since then we have added “*E.*” *holti*, which joins the Southeast Brazil Clade (Fig. 2). In our evaluation here of the Southeast Brazil Clade (*Ischnocnema*) and its content, we find that the character of relative finger length (I versus II) may be of diagnostic significance, with nearly all species in that Clade having Finger I shorter than, or equal to Finger II, except for the two species of the *Ischnocnema ramagii* Species Group, in which Finger I is longer than Finger II. Although it is possible that those two species should be transferred to *Haddadus*, they agree in other ways with *Ischnocnema* and therefore we place them in that latter genus (see above). We also note that the diploid chromosome count of *H. binotatus*, $2n=22$ (Beçak & Beçak 1974), is a number commonly encountered among species of *Craugastor* (DeWeese 1976).

Family Eleutherodactylidae Lutz, 1954

Eleutherodactylinae (part) Lutz, 1954:157. Type genus *Eleutherodactylus* Duméril and Bibron, 1841:620.

Eleutherodactylini (part)—Lynch, 1971:142 [Tribe].

Brachycephalinae (part)—Dubois, 2005b:4.

Brachycephalidae (part)—Frost *et al.*, 2006.

Definition.—Frogs of the family Eleutherodactylidae have: (1) sternum cartilaginous; (2) vertebral shield lacking; (3) transverse processes of posterior presacral vertebrae not broadly expanded; (4) cervical cotyles widely spaced; (5) eight presacral vertebrae, Presacrals I and II not fused; (6) cranial elements not co-ossified with overlying skin; (7) omosternum present; (8) sacral diapophyses rounded or barely dilated; (9) maxillary arch usually dentate; teeth blunt, pedicellate; (10) alary processes of premaxillae broad at base, usually directed dorsally or posterodorsally; (11) palatal shelf of premaxilla usually broad, indented or not; (12) pars facialis of maxilla usually deep, not exostosed; (13) palatal shelf of maxilla moderately broad, bearing pterygoid process or not; (14) maxillary arch complete; maxillae tapering posteriorly; quadratojugal slender; (15) nasals usually large with broad median contact; (16) nasals usually not in contact with maxillae or pterygoids; (17) nasals not in contact with frontoparietals; (18) frontoparietal fontanelle usually absent; (19) frontoparietals usually not exostosed; cranial crests present in some *Eleutherodactylus*; (20) frontoparietals fused with prootics or not; (21) temporal arcade absent; (22) epiotic eminences prominent to indistinct; (23) carotid artery passing dorsal to cranial elements; (24) zygomatic ramus of squamosal broad to slender, usually not in contact with maxilla; (25) otic ramus of squamosal short to elongate, expanded into otic plate or not; (26) squamosal-maxilla angle 44–67°; (27) columella present, except in fenestra ovalis directed laterally; (28) vomers variable in size; dentigerous processes absent in *Eleutherodactylus* (*Syrrhophus*), and some diminutive species of *Eleutherodactylus* (*Euhyas*); (29) neopalatines usually broad; slender in *Eleutherodactylus* (*Syrrhophus*); (30) sphenethmoid usually entire, divided in some *Eleutherodactylus* (*Syrrhophus*); (31) anterior ramus of parasphenoid narrow to broad, not keeled; (32) parasphenoid alae at right angle to axis of skull or deflected posteriorly, usually not overlapped by pterygoids; (33) pterygoid lacking ventral flange; anterior ramus not reaching neopalatine; (34) occipital condyles small to large, stalked or not, widely separated medially; (35) mandible lacking odontoids; (36) terminal phalanges T-shaped; (37) usually three phalanges in Finger IV (two in some *Adelophryne*); (38) Toe I fully developed and free; (39) alary process of hyoid plate on slender stalk or not; (40) mandibular ramus of trigeminal nerve passing lateral to the *m. adductor mandibulae* (condition unknown in *Adelophryne*); (41) prominent external body glands usually absent; lumbar glands in some *Eleutherodactylus*; (42) males having single or paired subgular vocal sac, single pectoral vocal sac, or no vocal sac; (43) males having vocal slits (or not) and no nuptial pads; (44) fingers unwebbed; toes usually unwebbed or webbed basally, but webbing extensive in some *Eleutherodactylus*; (45) terminal digits usually expanded with pads set off by distinct circumferential grooves; digits apically pointed in *Adelophryne* and some *Diasporus*; grooves present only laterally in *Phyzelaphryne*; (46) inner and outer metatarsal tubercles present, inner tubercle not spade-like; (47) tympanic membrane and annulus well differentiated or not; (48) amplexus axillary; (49) eggs deposited in terrestrial or arboreal situations and undergoing direct development; ovoviviparity exists in at least *Eleutherodactylus* (*Eleutherodactylus*) *jasperi*; (50) range in SVL from 10.5 mm in female *Eleutherodactylus* (*Euhyas*) *iberia* to 88 mm in female *Eleutherodactylus* (*Pelorius*) *inoptatus*.

Content.—There are 199 species placed in four genera, and five subgenera.

Distribution.—The family is distributed throughout the West Indies, peninsular Florida (either native or introduced) and from southern Texas (USA) south to northwestern Ecuador; other genera are discontinuously distributed in northeastern South America and in the Amazon Basin (Fig. 29).

Remarks.—Support for the family in the molecular phylogeny (Fig. 4) is significant in the ML (96%) and Bayesian (100%) analyses. Use and authorship of the family-group name needs to be clarified. The first name created for Eleutherodactylidae was Cornuferinae by Noble (1931). Based on the proposal by Zweifel (1966)

the International Commission of Zoological Nomenclature changed the type species of the genus *Cornufer*, which antedates *Eleutherodactylus*, and thus transferred Cornuferinae to Ranoidea. Taylor (1940b) used the name eleutherodactylid. However, Taylor did not explicitly use it as a family-group name; the name could have been validated under Article 11.7.2 of the Code of Zoological Nomenclature only if it had been published before 1900, Latinized later (e.g., by Lutz), and credited to Taylor by subsequent authors. Because the name was published in 1940 and was never credited to Taylor, it cannot be credited to him now.

Our current molecular phylogenies (Fig. 2–4) contain three taxa that were not present in any earlier study including our own (Heinicke *et al.* 2007), and they proved to be critical for defining this family. “*Eleutherodactylus diastema*” turned out to be a close relative of the Caribbean Clade (*Eleutherodactylus*), and therefore we place most species of the former “*Eleutherodactylus diastema* Group” in a new genus, with the exception of two species identified as belonging to the genus *Pristimantis* (see below). Together, the new genus and *Eleutherodactylus* are placed in the subfamily Eleutherodactylinae. We also included representatives of *Adelophryne* and *Phyzelaphryne*. They form a closely related pair, which in turn is the closest relative of the subfamily Eleutherodactylinae. For that reason we recognize this clade as a new subfamily, described below.

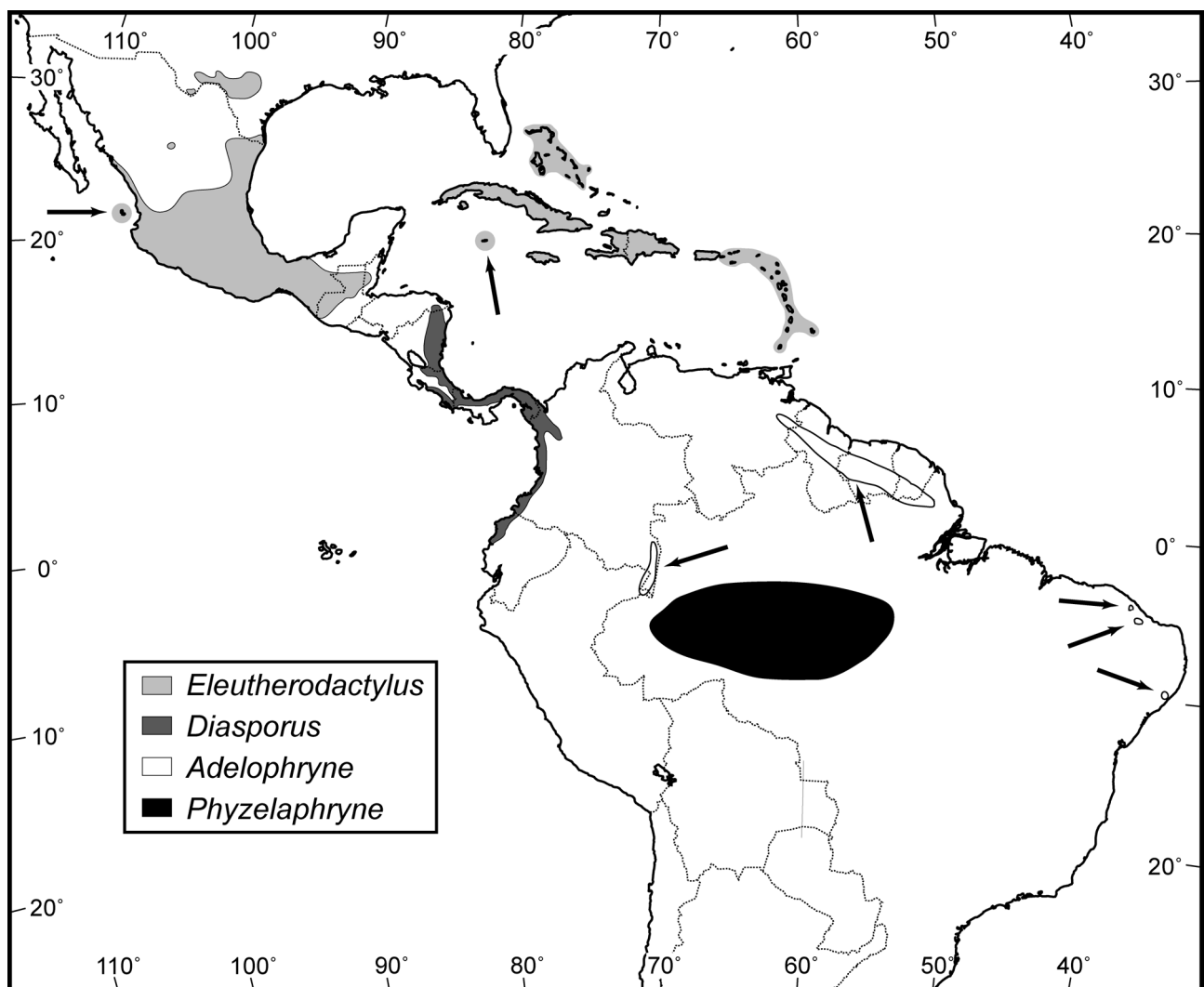


Figure 29. Distribution of the four genera comprising the Family Eleutherodactylidae: *Diasporus* and *Eleutherodactylus* (Subfamily Eleutherodactylinae), and *Adelophryne* and *Phyzelaphryne* (Subfamily Phyzelaphryninae).

Subfamily Eleutherodactylinae Lutz 1954

Eleutherodactylinae (part) Lutz, 1954:157. Type genus *Eleutherodactylus* Duméril and Bibron, 1841:620.

Definition.—These are eleutherodactylid frogs that have expanded terminal digits on the fingers and toes; the discs are rounded or truncate (apically pointed in some members of the new genus described below), and the circumferential grooves are complete; Finger IV always has three phalanges. The species are terrestrial or arboreal (some *Pelorius* are fossorial) and range in size from 10.5 mm in female *Eleutherodactylus* (*Euhyas*) *iberia* to 88 mm in female *Eleutherodactylus* (*Pelorius*) *inoptatus*.

Content.—The 193 currently recognized species are placed in two genera—a new genus (described below) and *Eleutherodactylus*, the latter with five subgenera.

Distribution.—The subfamily is distributed throughout the West Indies, peninsular Florida (either native or introduced) and from southern Texas (USA) south to northwestern Ecuador (Fig. 29).

Remarks.—With the exception of the inclusion of the new genus, this subfamily is equivalent to the genus *Eleutherodactylus* in the sense of Heinicke *et al.* (2007).

Genus *Diasporus*, New Genus

Type species.—*Lithodytes diastema* Cope, 1876:155.

Definition.—Frogs of the genus *Diasporus* are characterized by: (1) head distinct from body; head width 32–41% SVL; (2) tympanic membrane usually differentiated; membrane not differentiated but annulus visible beneath skin in *Diasporus gularis*; (3) cranial crests absent; (4) dentigerous processes of vomer usually prominent (absent in *E. hylaeformis*); (5) “S” condition of adductor musculature (contra Starrett 1968); (6) digital discs expanded with or without lanceolate or papillate tips; circumferential grooves present; terminal phalanges T-shaped; (7) Finger I shorter than Finger II; (8) Toe V much longer than Toe III; (9) subarticular tubercles not projecting; (10) dorsum smooth to rugose; (11) venter coarsely areolate; (12) range in SVL from 10.9 mm in male *E. quidditus* to 26 mm in female *E. hylaeformis*. Additionally, the left lobe of the liver is long and pointed whereas the right lobe is smaller and rounded (liver shape examined in *D. diastema*, *hylaeformis*, and *vocator*).

Content.—Eight species—*Diasporus anthrax*, *diastema* (Fig. 30), *gularis*, *hylaeformis*, *quidditus*, *tigrillo*, *tinker*, and *vocator*—are assigned to this genus.



FIGURE 30. *Diasporus diastema* from Cerro La Campana, Panama, Panama. Photo by W. E. Duellman.

Distribution.—These frogs inhabit humid lowland and montane forests from eastern Honduras through Panama to the Pacific versant of Colombia and northwestern Ecuador (Fig. 29).

Etymology.—The generic name is from the Greek *diaspora* (a dispersion from). The gender is masculine. It is used here in allusion to the close relationship of this mainland group to the Caribbean Clade, inferring an ancient dispersal event.

Remarks.—Support for the subfamily in the molecular phylogeny (Fig. 4) is significant in the ML (100%) and Bayesian (100%) analyses. Those analyses revealed that *Diasporus diastema* is the closest relative of the Caribbean clade (= *Eleutherodactylus*), whereas *Pristimantis chalceus*, previously associated with *D. diastema* in the “*Eleutherodactylus diastema* Group” (Lynch 2001), is deeply imbedded in the South American clade containing *Pristimantis*, and most closely related to species in the subgenus *Pristimantis*. This led us to erect a genus for *diastema* while retaining *chalceus* in *Pristimantis*. However, we were faced with allocating the remaining species of the former “*E. diastema* Group” to these two genera. Fortunately, some morphological characters provided the needed guidance. Members of the genus *Diasporus* have oval palmar tubercles and prominent vomerine teeth; also they are like some West Indian *Eleutherodactylus* by having)(-shaped gular folds. Lynch (2001) noted that: “Such folds also are found in several small species from Cuba and Hispaniola, which caused Dunn (1926) to posit a relationship between the Middle American and some Caribbean taxa.” However, Lynch (2001) noted that “*E. chalceus*” and “*E. scolodiscus*” differed from the others by having bifid palmar tubercles, weakly developed vomerine teeth, and by not having)(-shaped gular folds. We recognize these two species as members of the *Pristimantis (Pristimantis) chalceus* Species Group.

Genus *Eleutherodactylus* Duméril & Bibron, 1838

Cornufer Tschudi, 1838:28. Type species: *Cornufer unicolor* Tschudi, 1838:28, by monotypy. Synonymy by Zweifel, 1966:23.

Eleutherodactylus Duméril & Bibron, 1841:620. Type species: *Hylodes martinicensis* Tschudi, 1838:37, by monotypy. Official list of generic names, 1978.

Definition.—Members of the genus *Eleutherodactylus* can be defined as eleutherodactylid frogs having: (1) head narrow or moderate; (2) tympanic membrane differentiated; (3) cranial crests absent (present in *E. inoptatus* Group of subgenus *Pelorius*); (4) dentigerous process of vomers present (absent in subgenus *Syrrhophus* and several diminutive Cuban species of the subgenus *Euhyas*); (5) “S” condition of the adductor muscles; (6) terminal discs on digits present, bearing well-defined circumferential grooves, supported by T-shaped terminal phalanges; (7) Finger I usually shorter than Finger II (about equal to Finger II in the subgenus *Syrrhophus* and longer than Finger II in some species of the subgenus *Pelorius*); (8) Relative length of Toe III and Toe V variable, but Toe V longer than Toe III in most species of subgenera *Eleutherodactylus* and *Pelorius* and Toe V shorter than Toe III in most species of the subgenera *Euhyas* and *Syrrhophus*; (9) subarticular tubercles prominent; (10) texture of skin on dorsum variable; (11) texture of skin on venter variable; (12) range in SVL from 11 mm in female *E. iberia* to 88 mm in female *E. inoptatus*.

Content.—One hundred and eighty-five species are placed in five subgenera.

Distribution.—The genus is distributed throughout the West Indies, peninsular Florida (either native or introduced) and southern Texas, USA, Mexico, Belize, and Guatemala (Fig. 29).

Etymology.—The generic name is derived from the Greek *eleutheros*, meaning free, and the Greek *dactylos*, meaning finger or toes, in reference to the absence of webbing between the digits. The generic name is masculine in gender.

Remarks.—Support for the genus in the molecular phylogeny (Fig. 4) is significant in the ML (99%) and Bayesian (100%) analyses. This was once the largest genus of vertebrates, but its content was restricted to a smaller Caribbean-centered clade of species in a recent molecular phylogenetic analysis (Heinicke *et al.* 2007;

and here). The four subgenera proposed in an earlier allozyme analysis (Hedges 1989a) were largely corroborated in that recent analysis, and therefore they are maintained here (the group recognized as the subgenus *Eleutherodactylus* here was considered the “*auriculatus* section” of the subgenus *Eleutherodactylus* in that earlier study). Frost *et al.* (2006) considered those subgenera to be distinct genera, but that was under a prior assumption of phylogenetic relationships unsupported by the analyses of Heinicke *et al.* (2007) and here (Figs. 2–4). Our DNA sequence analyses (Heinicke *et al.* 2007) also revealed that one species from Hispaniola, *E. counouspeus*, is not a member of those subgenera. Morphologically, it also does not neatly fit into any of the named subgenera. For these reasons, we erect a fifth subgenus for this species (see below).

Definitions and content for the pre-existing subgenera are modified from that proposed by Lynch and Duellman (1997). The differences mainly involve species in which conflicts existed among external morphological characters, internal morphological characters, and molecular data sets and these are discussed in the remarks section of each subgenus. The major difference between the previous classifications (Savage 1987; Joglar 1989; Lynch & Duellman 1997; Frost *et al.* 2006) and this classification is the recognition here of the Caribbean Clade (genus *Eleutherodactylus*) that excludes a close relationship between the eastern Caribbean clade (formerly *E. auriculatus* Group or *E. auriculatus* Section) and a large component of South American species (formerly the “*E.*” *unistrigatus* Group). DNA sequence analyses (Heinicke *et al.* 2007) revealed that the external morphological characters that had previously suggested a link between these groups, such as enlarged digital tips, Toe V longer than Toe III, and an areolate venter are convergent.

The molecular phylogeny (Fig. 4) defines an Eastern Caribbean Clade (99% support) consisting of the subgenera *Eleutherodactylus*, *Pelorius*, and the new subgenus, and a Western Caribbean Clade (100% support) consisting of the subgenera *Euhyas* and *Syrrhophus*. At least one morphological character, liver shape, is consistent with this higher-level arrangement of subgenera. The liver shape character showed an association with the allozyme data (Hedges 1989a). Species of the Western Caribbean Clade have a long and pointed left lobe of the liver whereas species in the Eastern Caribbean Clade have shorter and rounded left lobes, similar to their right lobes. The phylogenetic position of *Diasporus*, as the closest relative of the Caribbean Clade, provides the opportunity to examine polarity of this liver shape character. *Diasporus* has a long and pointed left lobe suggesting that the alternative condition, rounded lobes of equal size (Eastern Caribbean Clade), is derived in *Eleutherodactylus*. Liver shape has yet to be surveyed extensively outside of Eleutherodactylidae. Immunological data supported the Western Caribbean Clade of *Syrrhophus* and *Euhyas* (Hass & Hedges 1991); support also appeared in earlier sequence analyses of small numbers of species (Crawford & Smith 2005; Frost *et al.* 2006). Even prior to the molecular studies, the association of *Syrrhophus* with a Cuban *Eleutherodactylus* was found in a phylogenetic analysis of morphological data (Heyer 1975).

Several other characters may not be diagnostic but nonetheless help to define the Eastern and Western Clades. Species of the Western Caribbean Clade are generally ground-dwelling (terrestrial) or saxicolous, lack an external vocal sac, and often have inguinal glands and Toe V shorter than Toe III. In contrast, species of the Eastern Caribbean Clade are mostly arboreal, have external vocal sacs (except the subgenus *Pelorius*), lack inguinal glands, and usually have Toe V longer than Toe III. In vocalization, most species in the Western Caribbean Clade have soft chirping-type calls whereas most in the Eastern Caribbean Clade have loud whistle-type calls. Not all species conform to this generalization, but the difference can be striking if, for example, one compares the species in Jamaica (17 native species, all of the Western Caribbean Clade) with those in Puerto Rico (16 native species, all of the Eastern Caribbean Clade). This difference even appears to extend to the sex of the parent that guards the egg clutch—male in Puerto Rico and female in Jamaica (Townsend 1996).

The definition of species series and species groups of West Indian *Eleutherodactylus* was last attempted nearly two decades ago (Hedges 1989a). Unfortunately, allozyme data were available for only about one-half of the species and therefore many species were left unassigned to species group or series. This problem was rectified in the recent DNA study (Heinicke *et al.* 2007), where nearly all species were sampled. Additional species are included here (Fig. 2). These new data, together with morphological data, have allowed us to com-

pletely reorganize and redefine the classification of the West Indian species in this genus; this reorganization is presented below in the accounts of the subgenera. In doing so, we have emphasized clades that are strongly supported in the molecular phylogenies (Figs. 2–4), and which, additionally, have morphological and geographic support. In almost all cases, the taxa defined here reflect phylogenetic groupings based on the previous (Heinicke *et al.* 2007) and current (Figs. 2–4) DNA sequence analyses.

Subgenus *Eleutherodactylus* Duméril & Bibron, 1838

Cornufer Tschudi, 1838:28. Type species: *Cornufer unicolor* Tschudi, 1838:28, by monotypy. Synonymy by Zweifel (1966:23).

Eleutherodactylus Duméril & Bibron, 1841:620. Type species: *Hylodes martinicensis* Tschudi, 1838:37, by monotypy. Official list of generic names, 1978.

Ladailadne Dubois, 1987:23. Type species: *Eleutherodactylus jasperi* Drewry and Jones, 1976:161. Synonymy by Hedges (1989a:327).

Definition.—Members of the subgenus *Eleutherodactylus* can be defined as eleutherodactylid frogs having: (1) head narrow; (2) tympanic membrane differentiated; (3) cranial crests absent; (4) dentigerous process of vomers present; (5) “S” condition of the adductor muscles; (6) terminal discs on digits expanded, bearing well-defined circumferential grooves, supported by T-shaped terminal phalanges; (7) Finger I shorter than Finger II; (8) Toe V longer than Toe III; (9) subarticular tubercles prominent; (10) texture of skin on dorsum usually smooth; (11) texture of skin on venter usually areolate; (12) range in SVL 17 mm in female *E. brittoni* to 80 mm in female *E. karlschmidti*. Additionally, the two lobes of the liver are approximately the same length and shape.

Content.—Fifty-four species are placed in the subgenus.

Distribution.—The subgenus is distributed naturally throughout the West Indies, excluding Jamaica, although its natural occurrence on some islands in the Lesser Antilles is not yet established (distinguished from human introductions). In terms of species density, it is the only (or predominate) group on the eastern islands (Lesser Antilles, Virgin Islands, Puerto Rico, and the North Paleoisland (region north of the Cul de Sac-Valle de Neiba) of Hispaniola (Fig. 31).

Etymology.—As for genus.

Remarks.—See the Remarks under the genus *Eleutherodactylus* for a discussion of the taxonomic history of the subgenera. This subgenus received only moderately strong support (70%) in the molecular phylogeny (Fig. 4), although the node excluding the *Eleutherodactylus richmondi* Species Series was significant (100%). Molecular data were unavailable for *E. lentus* (Virgin Islands) when it was previously assigned to the subgenus *Eleutherodactylus* based on its liver shape (Hedges 1989a). Now, DNA sequence analyses (Heinicke *et al.* 2007) (Fig. 2) show that it is the easternmost species of the subgenus *Euhyas*. The ground-dwelling Puerto Rican species *E. richmondi* was originally placed in the *E. ricordii* Group (now subsumed into the subgenus *Euhyas*) based on morphological traits (Schwartz 1976; Joglar 1989), but was placed in the *E. auriculatus* section of the subgenus *Eleutherodactylus* by Hedges (1989a). Lynch and Duellman (1997) claimed that this was done “inexplicably” and assigned it once again to the subgenus *Euhyas*. However, the reason that Hedges (1989a) placed it in the *E. auriculatus* section was because *E. richmondi* was found to cluster in his molecular phylogenetic tree with other members of the *E. auriculatus* section, and was found to have the same liver shape (short and rounded left lobe) and vocal sac condition (external) as species in the *E. auriculatus* section (subgenus *Eleutherodactylus*). The recent DNA sequence analysis also places this species in the subgenus *Eleutherodactylus*. The unusual ground-dwelling habits of *E. richmondi* (nearly all other Puerto Rican species are arboreal) probably influenced a suite of morphological traits that led to this confusion, causing it to converge with the predominantly terrestrial species of the Western Caribbean Clade.

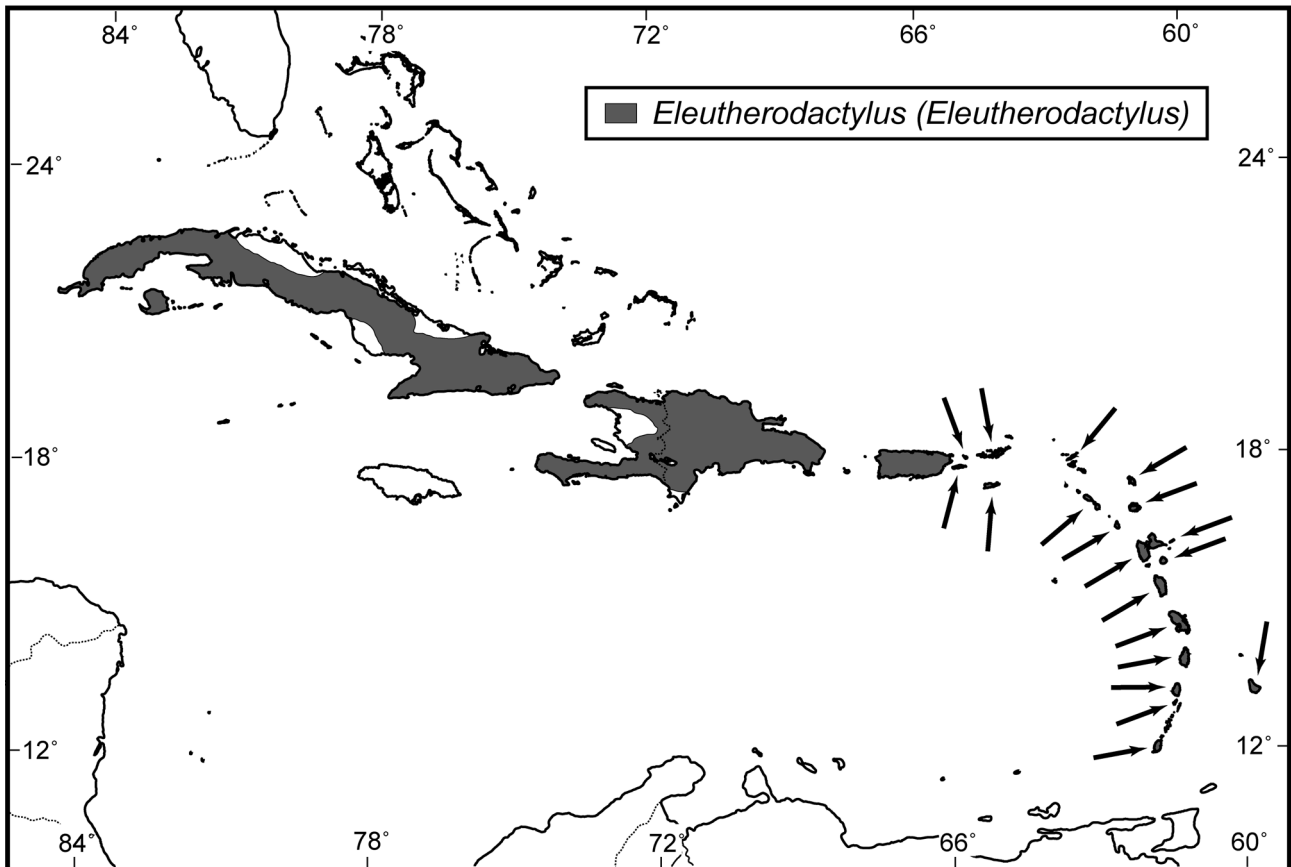


FIGURE 31. Distribution of the Subgenus *Eleutherodactylus*, Genus *Eleutherodactylus*, Subfamily Eleutherodactylinae, Family Eleutherodactylidae.

In their assignment of species to subgenus, Lynch and Duellman (Lynch & Duellman 1997) listed assignments for nine other West Indian species (besides *E. richmondi*) that differed from the assignments made by Hedges (Hedges 1989a; Hedges & Thomas 1992) based on allozyme data and liver shape. They moved the following species of the subgenus *Euhyas* to the subgenus *Eleutherodactylus*: *E. amadeus*, *bakeri*, *corona*, *eunaster*, *glanduliferoides*, and *thorectes*. They also moved the following species of the subgenus *Eleutherodactylus* to the subgenus *Euhyas*: *E. minutus*, *parabates*, and *unicolor*. In all of these cases, the species possess lengths of Toe V (relative to Toe III) that disagree with their taxonomic placement by allozyme data and liver shape. However, the recent DNA sequence results (Figs. 2–4) support the original assignments and show substantial homoplasy in the character of the relative lengths of Toes III and V. Most of the nine species have ecological habits that are unusual for their subgenus—arboreal for the normally terrestrial subgenus *Euhyas* and terrestrial (*E. unicolor*) for the normally arboreal subgenus *Eleutherodactylus*. Therefore the relative lengths of the toes seems to be an adaptive feature related to climbing, which is perhaps not surprising. Therefore, based on DNA sequences, relative toe lengths do not seem to be as closely correlated with phylogeny in *Eleutherodactylus* as they do in *Pristimantis*.

Eleutherodactylus (Eleutherodactylus) auriculatus Species Series

Definition.—Species in this series are mostly small, ranging in SVL from 19 mm (female *E. minutus*) to 36 mm (female *E. mariposa*). They lack a distinct narrowing of the body in the neck region (see *Eleutherodactylus*-

lus varians Species Series). Most are tan or brown and lack bright colors or bold markings. They are arboreal but usually are found on small bushes and herbaceous plants and rarely high in trees. Most have a repetitious mating call made up of hollow- or metallic-sounding clicks and snaps, constant in frequency and rarely whistle-like.

Content.—Three species groups (16 species) are placed in this series: the *Eleutherodactylus* “*Eleutherodactylus*” *abbotti*, *auriculatus*, and *minutus* species groups.

Distribution.—This species series is distributed on the islands of Cuba and Hispaniola (including Haiti and the Dominican Republic).

Remarks.—This species series received significant support (99%) in the molecular phylogeny (Fig. 2). A comparison between this series and the *E. varians* Species Series (see below) is pertinent because both are broadly sympatric on Cuba and Hispaniola. The average maximum size of the species in the *E. auriculatus* Species Series is 26.5 mm, compared with 36.5 mm for the *E. varians* Species Series. Also, species in the latter series have a distinct neck (narrowing of the body posterior to the head). In addition to these differences in size and body shape, these two large radiations have segregated ecologically; the former occurs on small plants and the latter primarily higher in trees and bromeliads. The vocalizations of the two species series also differ; species in the *E. auriculatus* Species Series usually produce a continuous series of hollow or metallic clicks that are constant in frequency, whereas species in the other series usually have a loud whistle-like call composed of notes that change frequency (Hedges *et al.* 1992).

Eleutherodactylus (Eleutherodactylus) abbotti Species Group

Definition.—Species in this group are uniformly small in size, ranging in SVL from 21 mm (female *E. haitianus*) to 29 mm (female *E. pituinus*), have a finely and irregularly granular dorsum that often includes a pair of slightly concave dorsolateral folds, and relatively narrow heads (34.1–37.4% SVL).

Content.—Seven species are placed in the group. Five of those were previously recognized as species: *Eleutherodactylus abbotti* (Fig. 32), *audanti*, *haitianus*, *parabates*, and *pituinus*. Two were described as subspecies of *E. audanti* (Schwartz 1966) and are elevated here to species status: *Eleutherodactylus (Eleutherodactylus) melatrigonum* and *Eleutherodactylus (Eleutherodactylus) notidodes*. An additional species is being described from the Sierra de Neiba (SBH, in preparation).

Distribution.—The species group is distributed in Haiti and the Dominican Republic on the island of Hispaniola.

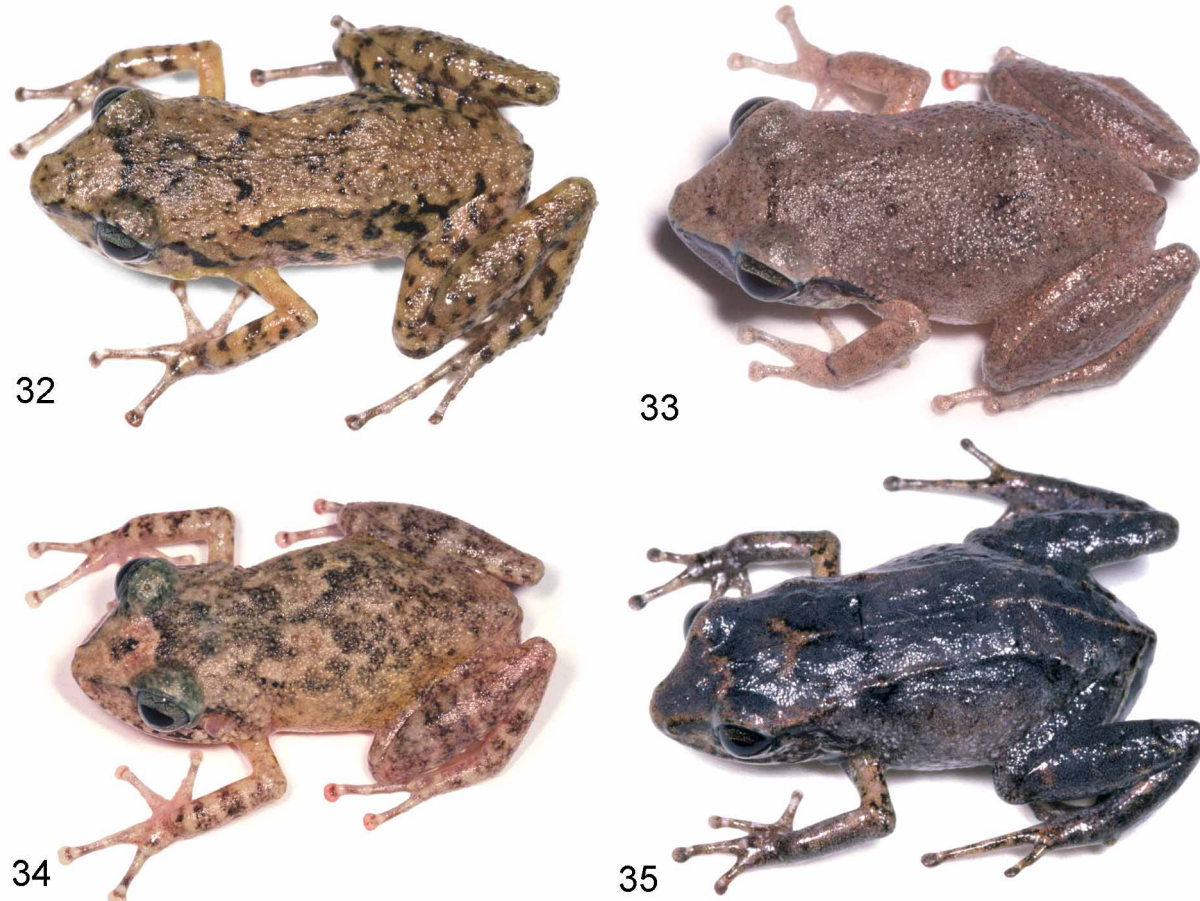
Remarks.—This group is the major radiation of species of the *Eleutherodactylus auriculatus* Species Series on Hispaniola. It received moderately strong support (84%) in the molecular phylogeny (Fig. 2). Six of the species, including the most divergent, occur only in upland areas of the North Paleoisland, suggesting that this paleoisland was important in the evolution of the group.

Schwartz (1966) described two subspecies of *E. audanti* on Hispaniola, and one of us (SBH) has field experience with both taxa and the nominate subspecies. All three subspecies have disjunct distributions, separated by intervening areas with no known populations and no evidence of intergradation among the subspecies. Besides consistent pattern and structural differences (Schwartz 1966), they also have different mating calls. By criteria currently used to distinguish different species of the genus *Eleutherodactylus*, these three subspecies should be recognized as distinct species; therefore we have elevated them to species level.

This leaves the species *E. audanti* as occurring only in three disjunct regions on the Hispaniolan South Paleoisland—the Sierra de Baoruco, the Massif de La Selle, and The Massif de al Hotte. These require further study to determine if differentiation has occurred among these isolates. One of us (SBH) has noticed that most individuals collected from the Massif de la Selle are erythristic. Also, individuals of *E. audanti*, normally an abundant species in its habitat, were rarely encountered on several expeditions to both the north and south

slopes of the Massif de la Hotte. Instead, arboreal species of the normally terrestrial subgenus *Euhyas*, of the same size as *E. audanti*, were abundant; this suggests possible competition.

Schwartz (1964) considered *E. parabates* to be most closely related to *E. jugans* (here placed in the subgenus *Euhyas*) because both are small, dark, and have robust body shapes. However, liver shape and phylogenetic analyses of proteins (Hedges 1989a) indicated that it was convergent with *E. jugans* and a member of the subgenus *Eleutherodactylus*. Lynch and Duellman (1997) placed *E. parabates* in the subgenus *Euhyas*. However, phylogenetic analyses of DNA sequences (Heinicke *et al.* 2007) confirm that it belongs in the subgenus *Eleutherodactylus* and is convergent with *E. jugans*. Also, despite its robust body shape inferring terrestrial habits (typical of the subgenus *Euhyas*), it has short dentigerous processes of the vomers, an external vocal sac, and arboreal habits, all typical of the subgenus *Eleutherodactylus* and not the subgenus *Euhyas*.



FIGURES 32–35. **32.** *Eleutherodactylus (Eleutherodactylus) abbotti* of the *E. abbotti* Species Group, *E. auriculatus* Species Series, from 27 km N Los Pinos, Elias Piña, Dominican Republic. Photo by S. B. Hedges. **33.** *Eleutherodactylus (Eleutherodactylus) auriculatus* of the *E. auriculatus* Species Group, *E. auriculatus* Species Series, from Soroa, Pinar del Rio, Cuba. Photo by S. B. Hedges. **34.** *Eleutherodactylus (Eleutherodactylus) mariposa* of the *E. auriculatus* Species Group, *E. auriculatus* Species Series, from 5.4 km WSW La Tagua, Guantánamo, Cuba. Photo by S. B. Hedges. **35.** *Eleutherodactylus (Eleutherodactylus) minutus* of the *E. minutus* Species Group, *E. auriculatus* Species Series, from 37 km SE Constanza, La Vega, Dominican Republic. Photo by S. B. Hedges.

Eleutherodactylus (Eleutherodactylus) auriculatus Species Group

Definition.—Species in this group are small to moderate in size, ranging in SVL from 23 mm (female *E. principalis*) to 36 mm (female *E. mariposa*), have a finely and evenly granular dorsum, and have relatively wide heads (39.5–43.8% SVL).

Content.—Seven species are placed in the group: *Eleutherodactylus (Eleutherodactylus) auriculatus* (Fig. 33), *bartonsmithi*, *eileenae*, *glamyrus*, *mariposa* (Fig. 34), *principalis*, and *ronaldi*.

Distribution.—The species group is endemic to Cuba.

Remarks.—This species group represents one of the two major radiations of species of the subgenus *Eleutherodactylus* on Cuba, the other being the *E. varians* Species Group of the *E. varians* Species Series. See Remarks under *E. auriculatus* Species Series (above) for a discussion of their morphological and ecological differences. This species group received moderately strong support (93%) in the molecular phylogeny (Fig. 2).

The distinction here between the Cuban radiation (*E. auriculatus* Species Group) and major Hispaniolan radiation (*E. abbotti* Species Group) of the *E. auriculatus* Species Series, as reflected in the molecular phylogeny is born out in the non-overlapping difference in head shape and to a lesser degree in dorsal skin textures.

Eleutherodactylus (Eleutherodactylus) minutus Species Group

Definition.—Species in this group are variable in SVL, with one being small (female *E. minutus*, 19 mm) and the other being moderate in size (female *E. poolei*, 34 mm). They have relatively narrow heads (34.1–37.5% SVL).

Content.—Two species are placed in the group: *Eleutherodactylus (Eleutherodactylus) minutus* (Fig. 35) and *poolei*.

Distribution.—The species group is distributed in Haiti and the Dominican Republic on the island of Hispaniola.

Remarks.—This species group received moderately strong support (77%) in the molecular phylogeny (Fig. 2). A comparison between this species group and the *E. abbotti* Species Group is pertinent because they are sympatric on Hispaniola and their distributions are primarily centered on the North Paleoisland (north of the Cul de Sac, Valle de Neiba). In body size, the two species of this group are both smaller (*E. minutus*) and larger (*E. poolei*) than those of the *E. abbotti* Species Group. Also, their calls are different from each other and from those of the *E. abbotti* Species Group. The latter have calls typical of the *E. auriculatus* Species Series in being constant in frequency and repetitious. The call of *E. minutus* is a high-pitched rising whistle and that of *E. poolei* is a two-note electronic-sounding “eenk-eenk;” both calls are unusual for species in the *E. auriculatus* Species Series.

Eleutherodactylus (Eleutherodactylus) martinicensis Species Series

Definition.—Species in this series are moderate in body shape and variable in SVL, ranging from 17 mm (female *E. juanriveroi*) to 58 mm (female *E. coqui*). Except for one species (*E. hedricki*), they lack a distinct narrowing of the body in the neck region (present in the *Eleutherodactylus varians* Species Series). They are variable in coloration; some are brightly colored (red, yellow, or green) although most are tan or brown with variable patterns. Most species are arboreal, but *E. barlagnei* is riparian and *E. cooki* is cavernicolous. Most species have a relatively loud mating call that is whistle-like or has a whistle-like component.

Content.—Three species groups (20 species) are placed in this series: the *Eleutherodactylus (Eleutherodactylus) antillensis*, *flavescens*, and *martinicensis* species groups.

Distribution.—This species series is distributed on islands in the eastern Caribbean, including eastern Hispaniola, the Puerto Rican Bank, St. Croix, and the Lesser Antilles. Two species (*E. coqui* and *E. johnstonei*) have been widely introduced outside this range.

Remarks.—This species series received moderately strong support (80%) in the molecular phylogeny

(Fig. 2). That phylogeny also shows that the *E. flavescens* and *E. antillensis* species groups are closest relatives, of the three included species groups in the series. The phylogenetic position of the Lesser Antillean radiation, the *E. martinicensis* Species Group, is somewhat surprising from a biogeographic standpoint because of its nested position within the Eastern Caribbean Clade (Fig. 2). This suggests dispersal from west to east, estimated to have occurred 15–20 Ma (Heinicke *et al.* 2007). However, there is no geologic evidence that the Lesser Antilles, which are volcanic, were ever interconnected by land and therefore dispersal was most likely by flotsam. Moreover, ocean currents now and in the past have flowed predominantly from east to west (Hedges 2006b). This suggests that currents flowed differently in the past, perhaps associated with a clockwise Caribbean gyre, or that larger areas of land were exposed (facilitating dispersal) during sea level low stands, or both.

Eleutherodactylus (Eleutherodactylus) antillensis Species Group

Definition.—Species in this group have 26 chromosomes (Bogart 1981). They range in SVL from 17 mm (female *E. juanriveroi*) to 58 mm (female *E. coqui*) and are arboreal in habits (*E. cooki* is cave-dwelling).

Content.—Four species subgroups (14 species) are placed in the group: the *Eleutherodactylus (Eleutherodactylus) antillensis*, *gryllus*, *locustus*, and *wightmanae* subgroups.

Distribution.—The species group is distributed on the Puerto Rican Bank and St. Croix. One species (*E. coqui*) has been introduced into Florida, Hawaii, Guam, and other locations, and *E. antillensis* has been introduced into Panama.

Remarks.—This group is the major radiation of species of the subgenus *Eleutherodactylus* on Puerto Rico. All species have large digital discs and climb on vegetation or, in the case of *E. cooki*, on rock faces in boulder caves. It received significant support (96%) in the molecular phylogeny (Fig. 2). It shares the island with the three species of the *Eleutherodactylus (Eleutherodactylus) richmondi* Species Group, which have 30 chromosomes and are more terrestrial in habits. We recognize four species subgroups of this species group, primarily based on the phylogenetic analysis (Heinicke *et al.* 2007; and here). The first of those is not well defined based on other information, but the remaining three subgroups have some support from body shape, coloration, and vocalization.

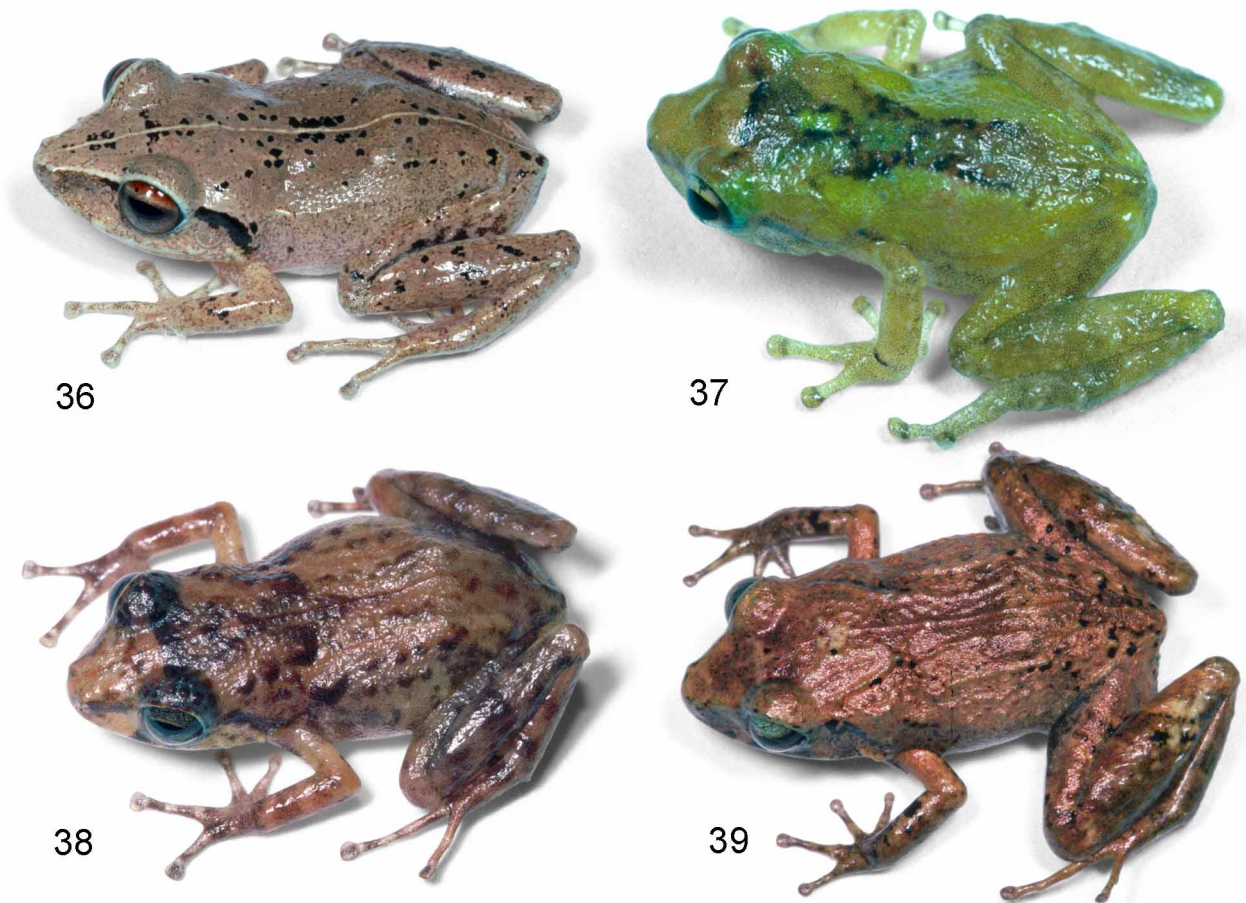
Eleutherodactylus (Eleutherodactylus) antillensis Species Subgroup

Definition.—Species in this subgroup are small to moderate, ranging in SVL from 19 mm (female *E. brittoni*) to 35 mm (female *E. antillensis* and *E. hedricki*). They are moderate in body shape and have small to large digital discs, rounded to ovate in shape. They are variable in coloration and vocalization.

Content.—Four species are placed in the subgroup: *Eleutherodactylus (Eleutherodactylus) antillensis* (Fig. 36), *brittoni*, *cochranae*, and *hedricki*.

Distribution.—The species subgroup is distributed on the Puerto Rican Bank and St. Croix; *E. antillensis* has been introduced into Panama.

Remarks.—This is the most weakly-defined subgroup from the standpoint of non-molecular information. It received moderately strong support (87%) in the molecular phylogeny (Fig. 2). The call of *Eleutherodactylus brittoni* consists of sharply rising whistles (Drewry & Rand 1983), and the second note of the *E. antillensis* call is also a sharply rising whistle (more so than the corresponding notes of *E. coqui*, *portoricensis*, and *schwartzii*).



FIGURES 36–39. 36. *Eleutherodactylus (Eleutherodactylus) antillensis* of the *E. antillensis* Species Subgroup, *E. antillensis* Species Group, *E. auriculatus* Species Series, from 1.5 km S Isla Verde Airport, San Juan, Puerto Rico. Photo by S. B. Hedges. 37. *Eleutherodactylus (Eleutherodactylus) gryllus* of the *E. gryllus* Species Subgroup, *E. antillensis* Species Group, *E. auriculatus* Species Series, from El Yunque Peak, Puerto Rico. Photo by S. B. Hedges. 38. *Eleutherodactylus (Eleutherodactylus) locustus* of the *E. locustus* Species Subgroup, *E. antillensis* Species Group, *E. auriculatus* Species Series, from 3.8 km S and 0.3 km E of El Yunque Peak, Puerto Rico. Photo by S. B. Hedges. 39. *Eleutherodactylus (Eleutherodactylus) wightmanae* of the *E. wightmanae* Species Subgroup, *E. antillensis* Species Group, *E. auriculatus* Species Series, from 1.3 km S and 1.1 km E El Yunque Peak, Puerto Rico. Photo by S. B. Hedges.

Eleutherodactylus (Eleutherodactylus) gryllus Species Subgroup

Definition.—Species in this subgroup are small, ranging in SVL from 17 mm (female *E. juanriveroi*) to 23 mm (female *E. jasperi*). They are dorsoventrally flattened in body shape and have relatively short legs and rounded digital discs. They usually have green or yellow on the body. Their calls are variable.

Content.—Three species are placed in the subgroup: *Eleutherodactylus (Eleutherodactylus) gryllus* (Fig. 37), *jasperi*, and *juanriveroi*.

Distribution.—The species subgroup is distributed on Puerto Rico.

Remarks.—This subgroup is a small radiation of small, green or yellow species that have depressed bodies and occupy arboreal niches, including bromeliads. It received significant support (100%) in the molecular phylogeny (Fig. 2). The group contains an ovoviviparous species (*Eleutherodactylus jasperi*) which is considered critically endangered and possibly extinct (IUCN 2007).

Eleutherodactylus (Eleutherodactylus) locustus Species Subgroup

Definition.—Species in this subgroup are small to large, ranging in SVL from 24 mm (female *E. locustus*) to 54 mm (female *E. cooki*). They are moderate in body shape with relatively large eyes, long legs, and large, ovate digital discs. In coloration, they are usually dark (brown or dark brown). In vocalization, they emit a call with multiple (usually >5), evenly spaced notes of the same frequency.

Content.—Three species are placed in the subgroup: *Eleutherodactylus (Eleutherodactylus) cooki*, *eneidae*, and *locustus* (Fig. 38).

Distribution.—The species subgroup is restricted to Puerto Rico.

Remarks.—This subgroup is a small radiation of dark, gracile species with large eyes and ovate digital discs. It received significant support (99%) in the molecular phylogeny (Fig. 2).

Eleutherodactylus (Eleutherodactylus) wightmanae Species Subgroup

Definition.—Species in this subgroup are small to large, ranging in SVL from 23 mm (female *E. wightmanae*) to 58 mm (female *E. coqui*). They are moderate in body shape (almost robust in *E. wightmanae*), and have rounded to slightly ovate digital discs. In coloration, they are variable, but often have red, reddish, or salmon color on the body. The call consists of two types of notes, including one or more initial low frequency monotonic notes followed by one or more higher frequency notes, each rising moderately in frequency.

Content.—Four species are placed in the subgroup: *Eleutherodactylus (Eleutherodactylus) coqui*, *portoricensis*, *schwartzii*, and *wightmanae* (Fig. 39).

Distribution.—The species subgroup is distributed on the Puerto Rican Bank and St. Croix. One species (*E. coqui*) has been introduced into Florida, Hawaii, Guam, and other locations.

Remarks.—This subgroup is a small radiation of mostly large species with loud, two-note calls (“coqui”). It received moderately strong support (77%) in the molecular phylogeny (Fig. 2). *Eleutherodactylus wightmanae* does not fit neatly into that description. However, the call structure of that species, which is a variation on the basic two-note call (Drewry & Rand 1983), and reddish coloration (in some specimens) could be viewed as characters tying it to this group, in addition to the evidence from molecular phylogeny.

Eleutherodactylus (Eleutherodactylus) flavescens Species Group

Definition.—The single species is moderate in SVL (females, 41 mm), has a yellow vocal sac, large and indented digital discs, and is the only representative of the *Eleutherodactylus martinicensis* Species Series in Hispaniola.

Content.—A single species is placed in this group: *Eleutherodactylus (Eleutherodactylus) flavescens* (Fig. 40).

Distribution.—The species group occurs in the Dominican Republic on the eastern one-third of Hispaniola.

Remarks.—This species is the closest relative of the *E. antillensis* Species Group in phylogenetic analyses of DNA sequences (Heinicke *et al.* 2007).

Eleutherodactylus (Eleutherodactylus) martinicensis Species Group

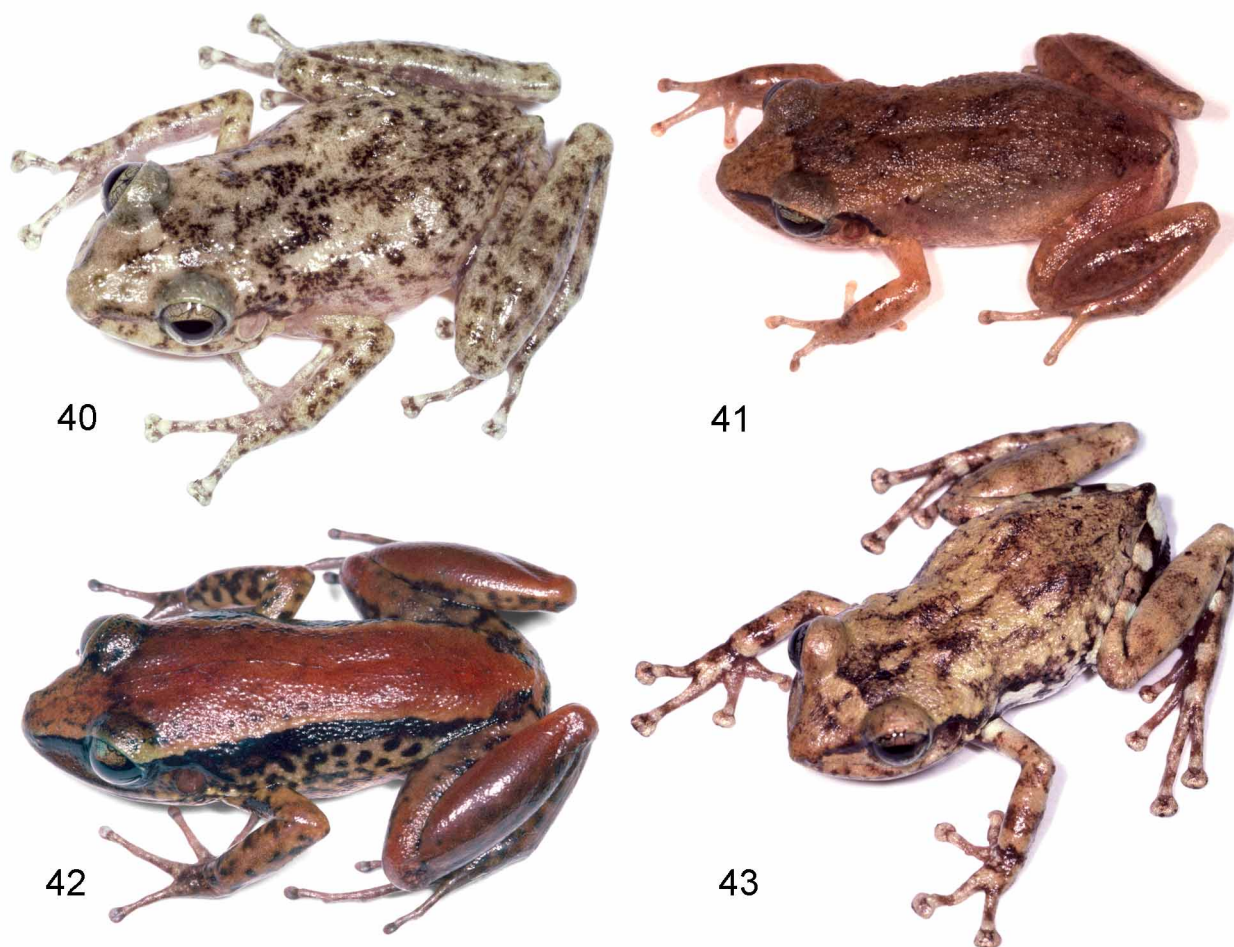
Definition.—Species in this group have 28 chromosomes (Kaiser *et al.* 1994). They range in SVL from 20

mm (female *E. pinchoni*) to 50 mm (female *E. amplinympha*) and are arboreal, except that *E. barlagnei* is stream-dwelling.

Content.—Five species are placed in the group: *Eleutherodactylus* (*Eleutherodactylus*) *amplinympha*, *barlagnei*, *johnstonei*, *martinicensis* (Fig. 41), and *pinchoni*.

Distribution.—The species group is distributed in the Lesser Antilles. One species (*E. johnstonei*) has been introduced into Jamaica and Venezuela.

Remarks.—This group is a small radiation of species of the genus *Eleutherodactylus* in the Lesser Antilles. It received significant support (100%) in the molecular phylogeny (Fig. 2). Two species, *E. johnstonei* and *E. martinicensis*, occur on multiple islands and their wider distributions are believed to be the result of introductions (Kaiser 1992), although their natural distributions have yet to be determined. Two species in the genus *Pristimantis* (see below) occur on islands in the southernmost Lesser Antilles (St. Vincent and Grenada).



FIGURES 40–43. 40. *Eleutherodactylus* (*Eleutherodactylus*) *flavescens* of the *E. flavescens* Species Group, *E. auriculatus* Species Series, from 2 km N Boca de Yuma, La Altagracia, Dominican Republic. Photo by S. B. Hedges. 41. *Eleutherodactylus* (*Eleutherodactylus*) *martinicensis* of the *E. martinicensis* Species Group, *E. auriculatus* Species Series, from Roseau, Dominica. Photo by S. B. Hedges. 42. *Eleutherodactylus* (*Eleutherodactylus*) *richmondi* of the *E. richmondi* Species Series, from 1.3 km S and 1.1 km E El Yunque Peak, Puerto Rico. Photo by S. B. Hedges. 43. *Eleutherodactylus* (*Eleutherodactylus*) *lamprotes* of the *E. lamprotes* Species Group, *E. varians* Species Series, from 2–3 km S Castillon, Grand'Anse, Haiti. Photo by S. B. Hedges.

Eleutherodactylus (Eleutherodactylus) richmondi Species Series

Definition.—Species in this series have 30 chromosomes (Bogart 1981). They are robust in body shape and variable in SVL, ranging from 17 mm (female *E. unicolor*) to 80 mm (female *E. karlschmidti*). They lack a distinct narrowing of the body in the neck region (see *Eleutherodactylus varians* Species Series). They range from dark brown (*E. unicolor*) to reddish brown (*E. richmondi*) to dark brown with yellow mottling (*E. karlschmidti*). These frogs are terrestrial; *E. karlschmidti* occupies rocky stream-side habitats. The mating calls are variable, although none is whistle-like.

Content.—Three species are placed in this series: *Eleutherodactylus (Eleutherodactylus) karlschmidti*, *richmondi* (Fig. 42), and *unicolor*.

Distribution.—This species series is endemic to Puerto Rico.

Remarks.—This species series is the smaller of two radiations of species of the subgenus *Eleutherodactylus* on Puerto Rico. It received moderately strong support (94%) in the molecular phylogeny (Fig. 2). The major radiation is the *Eleutherodactylus antillensis* Species Group. Besides sharing the same chromosome number, similarities in their karyotype suggest a close relationship. All other Puerto Rican species have 26 chromosomes (Bogart 1981).

See Remarks for the subgenus *Eleutherodactylus* (above) for discussion of confusion surrounding the classification of *E. richmondi*. Morphologically, that species and *E. unicolor* are similar with stocky bodies, narrow snouts, and small digital discs. The third species, *E. karlschmidti*, is much larger and has large digital discs, not outwardly similar to the other two species. However, the chromosomes of *E. karlschmidti* and *richmondi* suggest a close relationship (Bogart 1981). One of the three species in this series, *E. karlschmidti*, is a large riparian species that is considered critically endangered and possibly extinct (IUCN 2007).

Eleutherodactylus (Eleutherodactylus) varians Species Series

Definition.—Species in this series are moderate in SVL, ranging from 28 mm (*E. olibrus* and *E. staurometopon*, males only) to 44 mm (females of *E. montanus*). They have a narrowing of the body in the neck region distinguishing their relatively wide head from the rest of the body. Most are tan, brown, or greenish-brown, uniform or mottled, and usually lack bright colors or bold markings (except *E. lamprotes* which has orange flash markings). These frogs are arboreal and usually are found high in trees, frequently in bromeliads. Most have a whistle-like call, commonly composed of a note that rises in frequency.

Content.—Four species groups (15 species) are placed in this series: the *Eleutherodactylus (Eleutherodactylus) lamprotes*, *montanus*, *varians*, and *wetmorei* species groups.

Distribution.—This species series is distributed on the islands of Cuba and Hispaniola (including Haiti and the Dominican Republic).

Remarks.—This species series is one of two major assemblages of species of the subgenus *Eleutherodactylus* on Cuba and Hispaniola, with the other being the *E. auriculatus* Species Series. It received significant support (98%) in the molecular phylogeny (Fig. 2). See Remarks for the *E. auriculatus* Species Series (above) about how these two species series differ in morphology and ecology.

Eleutherodactylus (Eleutherodactylus) lamprotes Species Group

Definition.—Species in this group are moderate in SVL, ranging from 29 mm (females, *E. lamprotes*) to 33 mm (females, *E. fowleri*), have large eyes, and large, rounded digital discs. The dorsum is mostly tan or brown, occasionally with mottling (*E. lamprotes*). Both species dwell in bromeliads.

Content.—Two species are placed in the group: *Eleutherodactylus (Eleutherodactylus) fowleri* and *lamprotes* (Fig. 43).

Distribution.—The species group occurs in southern Haiti and southern Dominican Republic on the island of Hispaniola.

Remarks.—This species group received significant support (100%) in the molecular phylogeny (Fig. 2). The two included species are allopatric; *E. lamprotes* occupies the Massif de la Hotte and *E. fowleri* occurs on the Massif de la Selle and western portion of the Sierra de Baoruco. These three massifs make up the Hispaniolan South Paleo-island.

Eleutherodactylus (Eleutherodactylus) montanus Species Group

Definition.—Species in this montanus are moderate in SVL, ranging from 33 mm (females, *E. auriculatoides*) to 44 mm (females, *E. montanus*), and have moderately expanded and rounded digital discs. In dorsal coloration, they vary from being uniformly tan or brown to having yellowish-green vermiculations. One species (*E. auriculatoides*) inhabits bromeliads in trees, whereas the two high elevation species are often found under objects on the ground, and call from the ground, rocks, or low on vegetation.

Content.—Three species are placed in the group: *Eleutherodactylus (Eleutherodactylus) auriculatoides*, *montanus* (Fig. 44), and *patricae*.

Distribution.—The species group is endemic to the Cordillera Central of the Dominican Republic on the island of Hispaniola.

Remarks.—This species group received significant support (97%) in the molecular phylogeny (Fig. 2). The three included species are regionally sympatric, although one species (*E. auriculatoides*) occurs at lower elevations than the other two species. The Cordillera Central is part of the Hispaniolan North Paleo-island.

Eleutherodactylus (Eleutherodactylus) varians Species Group

Definition.—Species in this group are moderate in SVL, ranging from 28 mm (males only, *E. olibrus* and *staurometopon*) to 40 mm (females, *E. ionthus*), moderate in shape, and have large and rounded digital discs. In dorsal coloration, most are tan, brown, or greenish-brown, and some have mottling or a bold pattern. All but one species (*E. leberi*) have been found in bromeliads during the day, males have been observed calling from bromeliads and leaves of trees (or rarely rocks) at night, often high above the ground.

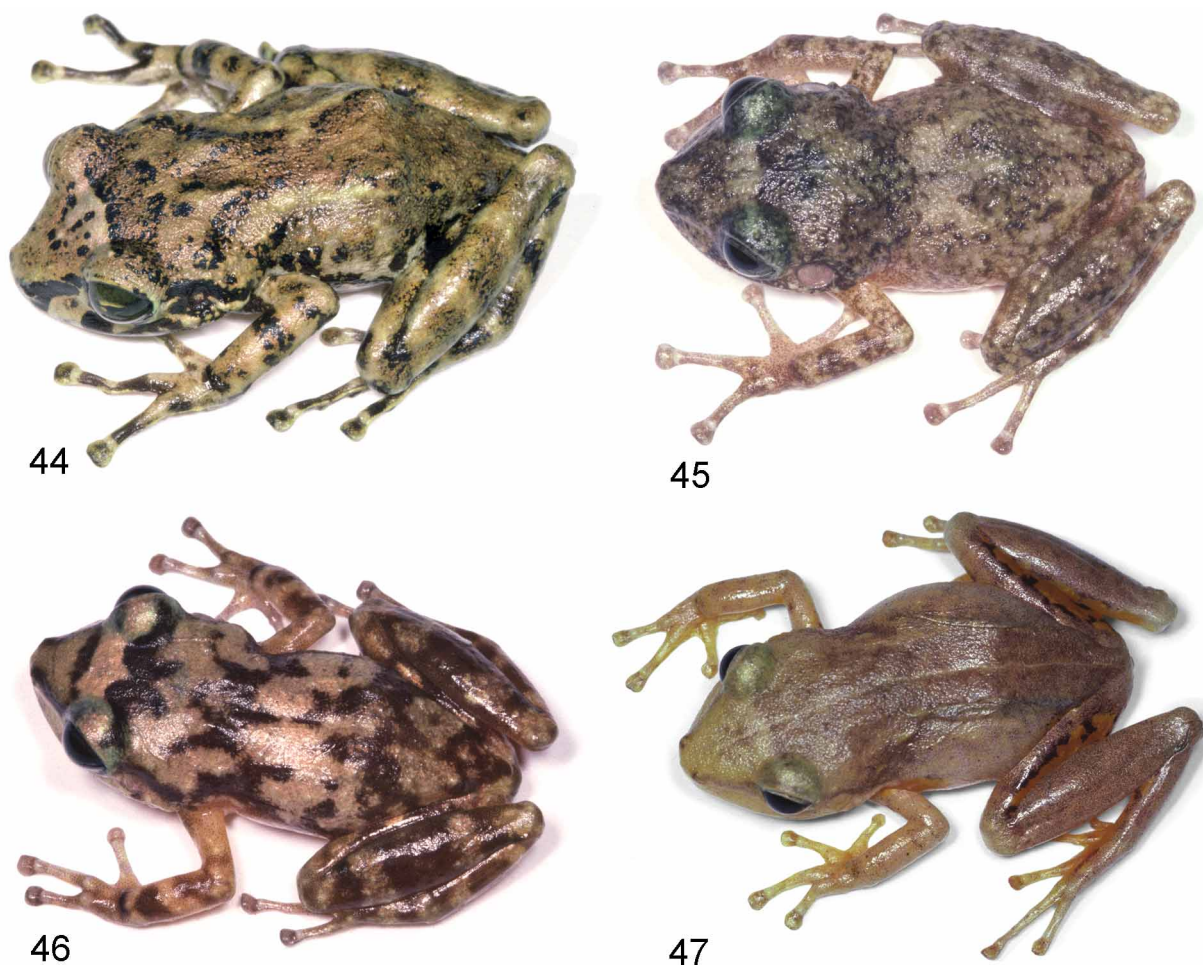
Content.—Two species subgroups (seven species) are placed in the group: the *Eleutherodactylus (Eleutherodactylus) leberi* and *varians* subgroups.

Distribution.—The species group is endemic to Cuba.

Remarks.—This species group is one of the two major radiations of species of the subgenus *Eleutherodactylus* on Cuba, the other being the *E. auriculatus* Species Group of the *E. auriculatus* Species Series. It received significant support (97%) in the molecular phylogeny (Fig. 2). See Remarks under *E. auriculatus* Species Series (above) for a discussion of the morphological and ecological differences of this species group and the *E. auriculatus* Species Group.

Species in the two subgroups of the *Eleutherodactylus (Eleutherodactylus) varians* Species Group are remarkably similar in appearance and habits. They are highly arboreal and frequent bromeliads. The molecular phylogeny defines these two subgroups, and the *E. leberi* subgroup is further supported by a shared chromosome number ($2N = 24$), unique among Cuban species (Bogart 1981; Hedges *et al.* 1992). The species in the *E. varians* subgroup are united by their calls, which are higher in frequency and similar in quality. The calls of *E. leberi* and *E. melacara* differ in number of notes, yet they possess lower frequency calls than other

species in the group (Hedges *et al.* 1992). Species within each of the two subgroups are allopatric, yet the two species subgroups are sympatric.



FIGURES 44–47. 44. *Eleutherodactylus (Eleutherodactylus) montanus* of the *E. montanus* Species Group, *E. varians* Species Series, from 13 km NW La Horma, La Vega, Dominican Republic. Photo by S. B. Hedges. 45. *Eleutherodactylus (Eleutherodactylus) leberi* of the *E. leberi* Species Subgroup, *E. varians* Species Group, *E. varians* Species Series, from 1.5 km WSW La Tabla, Santiago de Cuba, Cuba. Photo by S. B. Hedges. 46. *Eleutherodactylus (Eleutherodactylus) olibrus* of the *E. varians* Species Subgroup, *E. varians* Species Group, *E. varians* Species Series, from Soroa, Pinar del Rio, Cuba. Photo by S. B. Hedges. 47. *Eleutherodactylus (Eleutherodactylus) wetmorei* of the *E. wetmorei* Species Group, *E. varians* Species Series, from 8 km NW Port Salut, Sud, Haiti. Photo by S. B. Hedges.

Eleutherodactylus (Eleutherodactylus) leberi Species Subgroup

Definition.—Species in this subgroup are moderate in SVL, ranging from 33 mm (females, *E. leberi*) to 36 mm (females, *E. melacara*). They have 24 chromosomes and a relatively low frequency call (2.0–2.3 kilohertz). If the call of *E. melacara* is shown to have two components, as is suggested by an audiospectrogram (Hedges *et al.* 1992), this would be another character shared with *E. leberi*.

Content.—Two species are placed in this subgroup: *Eleutherodactylus (Eleutherodactylus) leberi* (Fig. 45) and *melacara*.

Distribution.—The species group is restricted to the Sierra Maestra in eastern Cuba.

Remarks.—This species subgroup received significant support (100%) in the molecular phylogeny (Fig. 2). See remarks below under *Eleutherodactylus (Eleutherodactylus) varians* Species Subgroup for a comparison of the two subgroups of the *E. varians* Species Group.

Eleutherodactylus (Eleutherodactylus) varians Species Subgroup

Definition.—Species in this subgroup are moderate in SVL, ranging from 28 mm (males only, *E. olibrus* and *staurometopon*) to 40 mm (females, *E. ionthus*). They have 18, 26, or 28 chromosomes and a relatively high frequency call (2.4–2.8 kilohertz) composed of a series of multiple notes, each with one frequency component, compared with other Cuban species in the subgenus where individual notes have multiple components (Hedges *et al.* 1992).

Content.—Five species are placed in the subgroup. Three of those were previously recognized as species: *Eleutherodactylus guantanamera*, *ionthus*, and *varians*. Two were described as subspecies of *E. varians* (Schwartz 1958c, 1960) and are elevated here to species status: *Eleutherodactylus (Eleutherodactylus) olibrus* (Fig. 46) and *Eleutherodactylus (Eleutherodactylus) staurometopon*.

Distribution.—The species subgroup is endemic to Cuba.

Remarks.—This species subgroup received significant support (100%) in the molecular phylogeny (Fig. 2). Schwartz (1958c, 1960) described three subspecies of *E. varians* on Cuba. Hedges *et al.* (1992) discussed their differences and elevated one of those taxa (*E. ionthus*) to full species status. The decision to leave the other taxa unchanged was made only because the focus of that study was on species from eastern Cuba. The other two taxa, elevated here, occur in western Cuba (*E. olibrus*) and on Isla de Juventud (*E. staurometopon*). Their specific status is supported by morphological, pigmentation, and call differences, and their ranges are disjunct with no evidence of intergradation.

Eleutherodactylus (Eleutherodactylus) wetmorei Species Group

Definition.—Species in this group are moderate in SVL, ranging from 33 mm (females, *E. wetmorei*) to 36 mm (females, *E. sommeri*), and have large and rounded digital discs. They are uniformly tan or grayish-tan dorsally, and the concealed areas of the groin and hindlimbs are orange or red. All species call from bromeliads or leaves of trees, often high above the ground, and have a loud, two-note call.

Content.—Three species are placed in the group. One of these, *Eleutherodactylus wetmorei* (Fig. 47), was previously recognized as a species. The other two were described as subspecies of *E. wetmorei* (Schwartz 1968, 1973, 1977) and are elevated here to species status: *Eleutherodactylus (Eleutherodactylus) diplasius* and *Eleutherodactylus (Eleutherodactylus) sommeri*.

Distribution.—The species group is distributed in Haiti and the Dominican Republic on the island of Hispaniola.

Remarks.—This species group is a small radiation of closely related species in Hispaniola. It received significant support (100%) in the molecular phylogeny (Fig. 2). A fourth taxon, *Eleutherodactylus wetmorei ceraemerus*, was described by Schwartz (1968). One of us (SBH) has had field experience with all four taxa. They have minor but significant structural and call differences and differ especially in the pattern of their flash markings on the concealed areas of the groin and hindlimbs. The ranges of two of the species, *E. diplasius* and *E. wetmorei*, contact in the Massif de la Hotte of Haiti, and specimens from the area of contact show no signs of intergradation. Another species, *E. sommeri*, occurs far to the north in Haiti and the Dominican Republic, on the North Paleoisland of Hispaniola. There is no evidence of intergradation with the species to the south (Schwartz 1977). For these reasons, we recognize these three taxa as full species. However, we leave the status of *E. w. ceraemerus* unchanged because of the identification of two populations showing intergradation with *E. w. wetmorei* (Schwartz 1977). Nonetheless, the overall differences between those two subspecies exist, and further study may justify recognition of *E. w. ceraemerus* as a full species.

Subgenus *Euhyas* Fitzinger, 1843

Euhyas Fitzinger, 1843:31. Type species: *Hylodes ricordii* Duméril & Bibron, 1841:623, by original designation.

Sminthillus Barbour & Noble, 1920:402. Type species: *Phyllobates limbatus* Cope, 1862:154, by original designation.

Synonymy by Hedges (1989a:318).

Definition.—Members of the subgenus *Euhyas* can be defined as eleutherodactylid frogs having: (1) head narrow; (2) tympanic membrane differentiated, prominent, and large in most species; (3) cranial crests absent; (4) dentigerous processes of vomers present (absent in several diminutive Cuban species); (5) “S” condition of the adductor muscles; (6) terminal discs on digits expanded, bearing well-defined circumferential grooves, supported by T-shaped terminal phalanges; (7) Finger I usually shorter than Finger II; (8) Toe V usually shorter than Toe III, although longer than Toe III in several arboreal species (e.g., *E. amadeus*, *E. bakeri*, *E. corona*, *E. eunaster*, *E. glanduliferoides*, and *E. thorectes*); (9) subarticular tubercles prominent; (10) texture of skin on dorsum variable; (11) texture of skin on venter usually smooth; (12) range in SVL from 11 mm in female *E. iberia* to 64 mm in female *E. greyi*. Additionally, the left lobe of the liver is long and pointed whereas the right lobe is smaller and rounded.

Content.—The subgenus contains eight species series, 20 species groups, five species subgroups, and 95 species.

Distribution.—*Euhyas* is widely distributed throughout the Greater Antilles (except mainland Puerto Rico), Bahamas Islands, Virgin Islands, and Cayman Islands (Fig. 48). It has been introduced into Florida, Louisiana, and Hawaii in the USA.

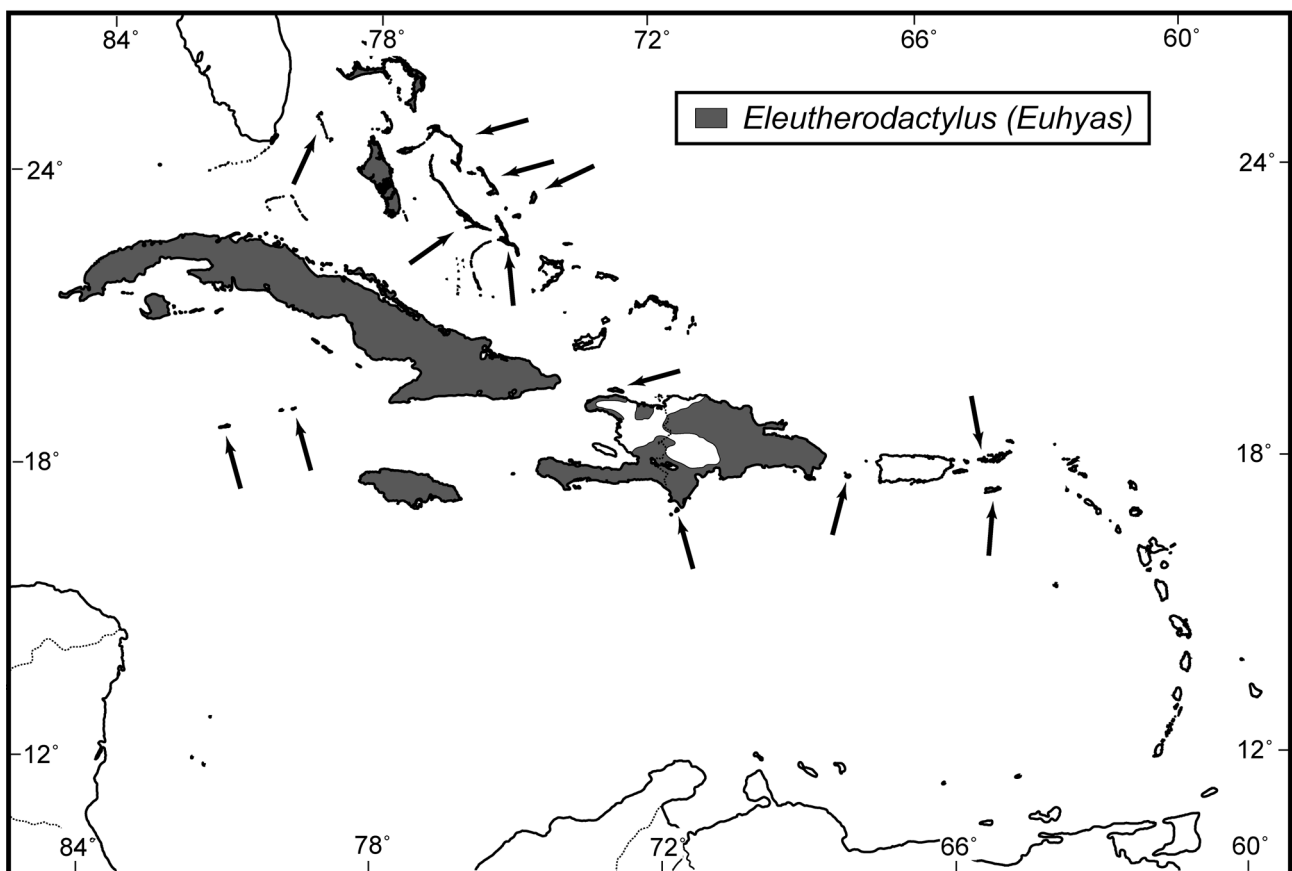


FIGURE 48. Distribution of the Subgenus *Euhyas*, Genus *Eleutherodactylus*, Subfamily Eleutherodactylinae, Family Eleutherodactylidae.

Etymology.—The generic name is derived from the Greek *eu*, meaning true, and the Greek mythological character *hyas*, used in reference to a treefrog. The name is feminine in gender.

Remarks.—See the Remarks under the genus *Eleutherodactylus* for a discussion of the taxonomic history of the subgenera. This subgenus received significant support (98%) in the molecular phylogeny (Fig. 4). See above (under subgenus *Eleutherodactylus*) for discussion of the ten species whose placement in this subgenus has been controversial. Sexual size dimorphism is more pronounced in this subgenus than in the other West Indian subgenera; males of most species are considerably smaller than females. Moreover, species in the subgenus *Euhyas* often lack an external vocal sac and even vocal slits, and their mating calls tend to be less noisy and include irregular chirps and clicks rather than whistles common to the subgenus *Eleutherodactylus*. Calling sites also differ; most species are terrestrial (e.g., ground, rocks, and streams) rather than arboreal as in most members of the other West Indian subgenera (more than half of the species of *Peorius* call from the ground or below ground). The major difference in liver shape noted previously (Hedges 1989a) agrees virtually completely with recent DNA sequence evidence (Heinicke *et al.* 2007). Members of this subgenus and those species in the genus *Diasporus* and the subgenus *Syrrophus* that have been examined have livers with long, pointed left lobes whereas species in the Eastern Caribbean Clade (subgenera *Eleutherodactylus*, *Pelorius*, and *Schwartzius*) have livers in which both lobes are short and rounded (apparently the derived state).

Eleutherodactylus (Euhyas) armstrongi Species Series

Definition.—Species in this series are moderate in body shape and moderate in SVL, ranging from 37 mm (females, *E. alcoae*) to 45 mm (females, *E. leoncei*). All have large, ovate digital discs, and most have long legs (*E. alcoae* has short legs). In coloration, they are variable (yellows, reds, greens, and browns), although two species (*E. darlingtoni* and *leoncei*) have a pair of pale scapular bars resembling quotation marks. In habits, they vary from ground dwelling (*E. darlingtoni* and *leoncei*) to rock dwelling (*E. alcoae*) and tree and bromeliad dwelling (*E. armstrongi*). Vocalization (unknown in *E. darlingtoni*) ranges from soft, irregular chirps (*E. alcoae* and *leoncei*) to a loud, metallic “peng” (*E. armstrongi*).

Content.—Four species are placed in the species series: *Eleutherodactylus (Euhyas) alcoae*, *armstrongi* (Fig. 49), *darlingtoni*, and *leoncei*.

Distribution.—The species series is distributed in southern Hispaniola, including Haiti and the Dominican Republic.

Remarks.—This species series received moderately strong support (80%) in the molecular phylogeny (Fig. 2). The evolutionary history of this series seems to be confined to the region of the Massif de la Selle and Sierra de Baoruco, including the Barahona Peninsula. This has resulted in a pair of allopatric species (*E. darlingtoni* and *leoncei*) at high elevations and a pair of mostly allopatric (partly sympatric) species (*E. alcoae* and *armstrongi*) at low to moderate elevations. Previously, *E. darlingtoni* and *leoncei* were considered to be sympatric (Schwartz & Henderson 1991) but the status of the two species was reassessed and the distributions were revised (Hedges 1992). The distribution of one species (*E. armstrongi*) consists of two isolated regions separated by tens of kilometers. The habits of the two ground-dwelling species (*E. darlingtoni* and *E. leoncei*) are not well known, and their large digital discs suggest that they climb and probably do so mostly on rocks.

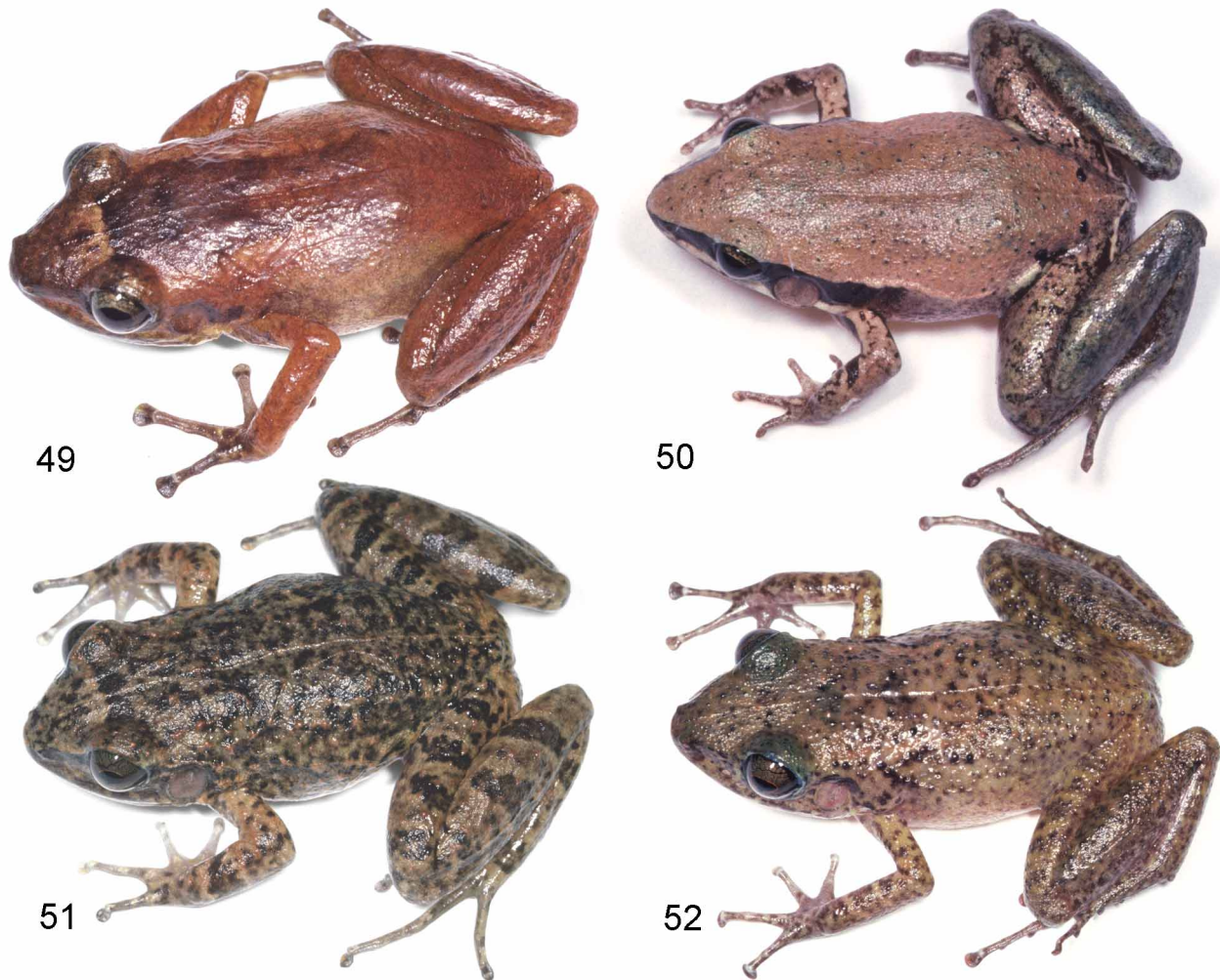
Eleutherodactylus (Euhyas) dimidiatus Species Series

Definition.—Species in this series are robust in body shape and moderate to large in SVL, ranging from 27 mm (females, *E. emiliae*) to 58 mm (females, *E. dimidiatus*). Most are tan, brown, or greenish-brown, and one (*E. albipes*) has limbs with red or orange. The calls of these terrestrial species are variable, but most emit a faint, short sound.

Content.—Two species groups (seven species) are placed in this series: the *Eleutherodactylus* (*Euhyas*) *dimidiatus* and *schmidti* species groups.

Distribution.—This species series occurs on Cuba and Hispaniola (including Haiti and the Dominican Republic).

Remarks.—This species series received moderately strong support (78%) in the molecular phylogeny (Fig. 2). The series includes two island radiations (species groups) of related, robust, ground-dwelling species. The Cuban radiation (*E. dimidiatus* Species Group) contains forest floor species whereas the Hispaniolan radiation (*E. schmidti* Species Group) contains streamside species.



FIGURES 49–52. 49. *Eleutherodactylus* (*Euhyas*) *armstrongi* of the *E. armstrongi* Species Series, from 13 km SSW La Guazara, Barahona, Dominican Republic. Photo by S. B. Hedges. 50. *Eleutherodactylus* (*Euhyas*) *dimidiatus* of the *E. dimidiatus* Species Group, *E. dimidiatus* Species Series, from Soroa, Pinar del Rio, Cuba. Photo by S. B. Hedges. 51. *Eleutherodactylus* (*Euhyas*) *schmidti* of the *E. schmidti* Species Group, *E. dimidiatus* Species Series, from north slope of Loma Nalga de Maco, Elias Piña, Dominican Republic. Photo by S. B. Hedges. 52. *Eleutherodactylus* (*Euhyas*) *greyi* of the *E. greyi* Species Series, from north slope of Pico de Potrerillo, Sancti Spiritus, Cuba. Photo by S. B. Hedges.

Eleutherodactylus (*Euhyas*) *dimidiatus* Species Group

Definition.—Species in this group are robust in body shape and small to moderate in SVL, ranging from 27 mm (females, *E. emiliae*) to 45 mm (females, *E. dimidiatus*). All have short fingers with small digital discs. Two species (*E. albipes* and *E. emiliae*) have short hind limbs, whereas the other two (*E. dimidiatus* and *E.*

maestrensis) have long hind limbs. Typically these frogs are tan or brown, and have a weakly or well-developed dark face mask that may extend posterior to the forelimb. Most of these terrestrial species emit a faint chirping sound (Díaz *et al.* 2005).

Content.—Four species are placed in the group: *Eleutherodactylus (Euhyas) albipes*, *dimidiatus* (Fig. 50), *emiliae*, and *maestrensis*.

Distribution.—The species group is endemic to Cuba.

Remarks.—This species group received significant support (100%) in the molecular phylogeny (Fig. 2). Schwartz (1958b) described the subspecies *Eleutherodactylus dimidiatus amelasma* from Western Cuba, but Díaz *et al.* (2005) did not consider the taxon to be valid based on data from morphology and vocalization. Nonetheless, there seems to be a geographic gap between the eastern and western populations, and molecular analyses are needed to determine if there has been genetic differentiation.

Eleutherodactylus (Euhyas) schmidti Species Group

Definition.—Species in this group are robust in body shape and moderate to large in SVL, ranging from 43 mm (females, *E. limbensis*) to 58 mm (females, *E. rucillensis*). They have slight webbing present between their toes and are variable in coloration. They are most commonly encountered on rocks and the ground adjacent to mountain streams; some individuals have been found in the water. The call of most species is a short, faint, “mew” noise.

Content.—Three species are placed in the group. One of those, *Eleutherodactylus (Euhyas) schmidti* (Fig. 51), was previously recognized as a species, whereas two have been recognized as subspecies of *E. schmidti* (Schwartz 1970) and are elevated here to species status—*Eleutherodactylus (Euhyas) limbensis* and *Eleutherodactylus (Euhyas) rucillensis*.

Distribution.—The species group is distributed in central and northern Hispaniola (including Haiti and the Dominican Republic).

Remarks.—This species group represents a small island radiation of streamside frogs in Hispaniola. Schwartz (1970) reviewed the available material and redefined the previously described subspecies. The Haitian taxon (*E. limbensis*), which is isolated from the other two, is slightly smaller, has a different color pattern, and males have shorter legs than males of the other two species. The two species inhabiting the Cordillera Central of the Dominican Republic, *E. rucillensis* and *E. schmidti*, differ greatly in body size (58 mm versus 46 mm, respectively), have different leg proportions, and different coloration (Schwartz 1970). Their ranges are in broad contact; yet there is no substantial evidence of intergradation. Accordingly, we recognize *E. limbensis* and *rucillensis* as full species. One of us (SBH) is aware of an undescribed species belonging to this group from the Sierra de Neiba in the Dominican Republic.

Eleutherodactylus (Euhyas) greyi Species Series

Definition.—The single species in this series is moderate in body shape and large in SVL (females, 64 mm). It has a tuberculate dorsum, long legs, and large, ovate digital discs. The dorsal coloration is variable but usually tan, yellowish-grey, or greenish gray with small dark spots. It is primarily rock dwelling, but also has been encountered on the forest floor and on river talus. It has a two-note call, with the second note higher in frequency than the first.

Content.—This species series contains a single species, *Eleutherodactylus (Euhyas) greyi* (Fig. 52).

Distribution.—This species occurs in central Cuba.

Remarks.—The vocalization and habits of this species were recently described by Díaz *et al.* (2007b).

Eleutherodactylus (Euhyas) luteolus Species Series

Definition.—Species in this series are robust to moderate in body shape and small to large in SVL, ranging from 18 mm (females, *E. griphus* and *sisyphodemus*) to 59 mm (females, *E. cuneatus*). Leg length and digital disc size varies among species. Coloration is variable, and many taxa exhibit pattern polymorphism. The Cuban species are associated with streams, whereas the Jamaican species occupy diverse habitats. The calls include the typical chirps and mews characteristic of the subgenus *Euhyas* as well as some with hollow rapping or knocking noises.

Content.—Four species groups (22 species) are placed in this species series: the *Eleutherodactylus (Euhyas) cuneatus*, *luteolus*, *riparius*, and *toa* species groups.

Distribution.—The species series occurs on Cuba and Jamaica.

Remarks.—This species series received moderately strong support (71%) in the molecular phylogeny (Fig. 2). It includes the Jamaican radiation of *Eleutherodactylus (E. luteolus* Species Group) and the five Cuban species that are their closest relatives. Because Jamaica and Cuba were not connected geologically during the Cenozoic, the only way that the Jamaican radiation could have originated was from dispersal over water of a Cuban species. A riparian species would be more likely than others to be washed out of a river with flotsam, and therefore it is relevant that the five Cuban species in this series are the only riparian species in Cuba.

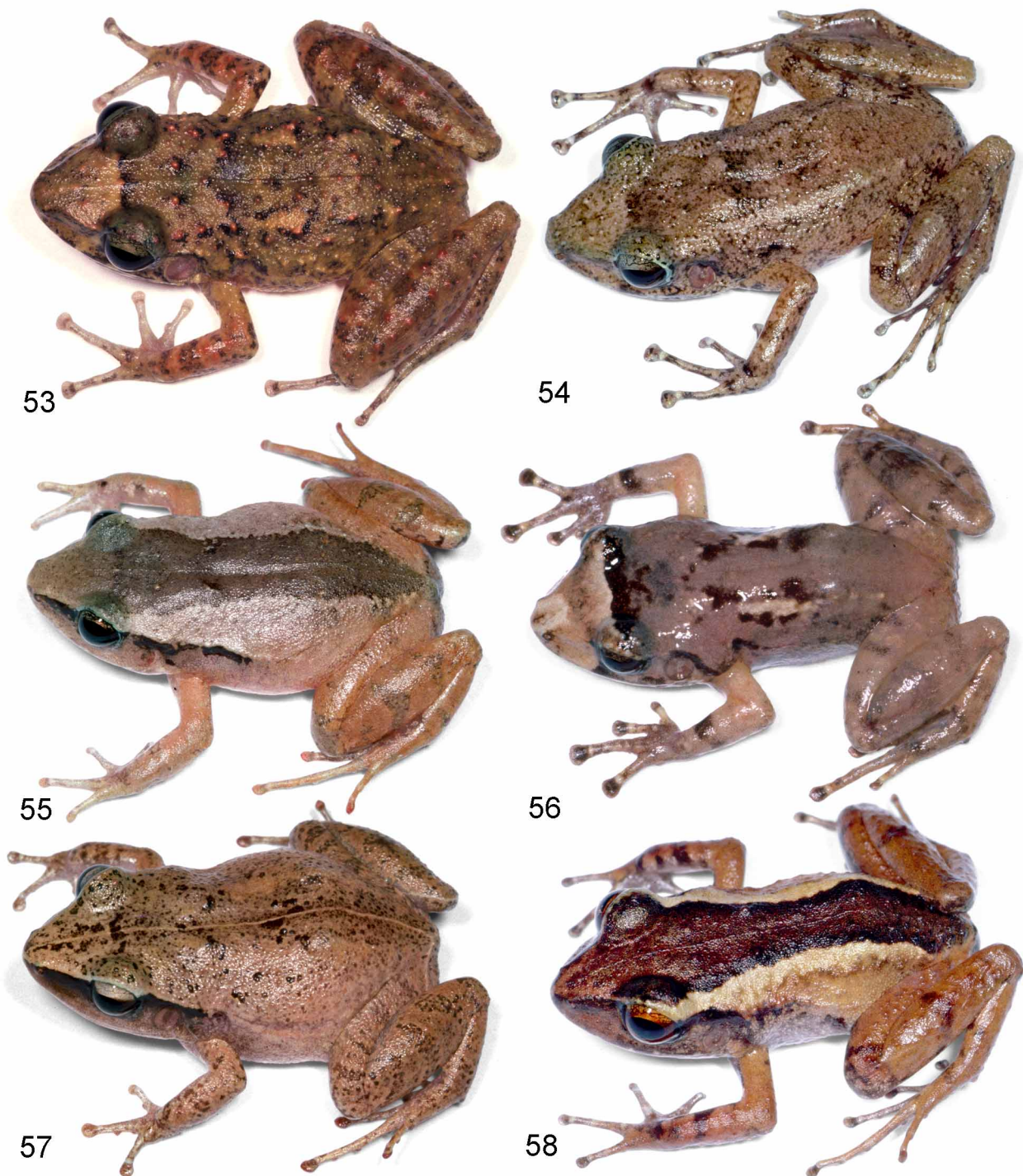
Eleutherodactylus (Euhyas) cuneatus Species Group

Definition.—Species in this group are robust in body shape and large in SVL, ranging from 53 mm (females, *E. turquinensis*) to 59 mm (females, *E. cuneatus*). They have moderate to long legs, moderate to large digital discs, and toe webbing (*E. turquinensis*). They are primarily reddish-brown, grayish brown, and greenish brown with pattern polymorphism. They occupy mountain streams and adjacent habitats; *E. cuneatus* is less aquatic than *E. turquinensis* and also occurs in forests away from streams. The call is a “chirp” that either descends (*E. cuneatus*) or rises slightly (*E. turquinensis*) in frequency (Hedges *et al.* 1995).

Content.—Two species are placed in the group: *Eleutherodactylus (Euhyas) cuneatus* (Fig. 53) and *E. turquinensis*.

Distribution.—The species group is restricted in eastern Cuba.

Remarks.—This species group received moderate support (67%) in the molecular phylogeny (Fig. 2). It includes a pair of closely related, sympatric riparian species. The confused taxonomic history of *Eleutherodactylus cuneatus* was reviewed elsewhere (Estrada & Hedges 1998). Other stream-associated species in Cuba are *E. riparius* and *E. rivularis*, (*E. riparius* Species Group) and *E. toa* (*E. toa* Species Group). Although it might seem appropriate to place all five riparian species in the same group, they differ considerably in morphology. The species in this group are larger than those in the *E. riparius* Species Group, have a tubercular dorsum (not rugose), and have large digital discs (not small). The single species in the *E. toa* Species Group is small and has a tuberculate dorsum and areolate venter. Neither these two groups nor the *E. toa* group are closest relatives in the molecular phylogeny, but more sequence data will be needed to resolve the details of those relationships.



FIGURES 53–58. 53. *Eleutherodactylus (Euhyas) cuneatus* of the *E. cuneatus* Species Group, *E. luteolus* Species Series, from southwest slope of Pico Turquino at Pico Cardero, Santiago de Cuba, Cuba. Photo by S. B. Hedges. 54. *Eleutherodactylus (Euhyas) cundalli* of the *E. cundalli* Species Subgroup, *E. luteolus* Species Group, *E. luteolus* Species Series, from Quick Step, Trelawny, Jamaica. Photo by S. B. Hedges. 55. *Eleutherodactylus (Euhyas) gossei* of the *E. gossei* Species Subgroup, *E. luteolus* Species Group, *E. luteolus* Species Series, from 2.9 km N Port Maria, St. Mary, Jamaica. Photo by S. B. Hedges. 56. *Eleutherodactylus (Euhyas) jamaicensis* of the *E. jamaicensis* Species Subgroup, *E. luteolus* Species Group, *E. luteolus* Species Series, from 4.2 km W Ecclesdown, Portland, Jamaica. Photo by S. B. Hedges. 57. *Eleutherodactylus (Euhyas) luteolus* of the *E. luteolus* Species Subgroup, *E. luteolus* Species Group, *E. luteolus* Species Series, from 7.0 km WSW Old Hope, Westmoreland, Jamaica. Photo by S. B. Hedges. 58. *Eleutherodactylus (Euhyas) nubicola* of the *E. nubicola* Species Subgroup, *E. luteolus* Species Group, *E. luteolus* Species Series, from 1.3 km W Hardwar Gap, St. Andrew, Jamaica. Photo by S. B. Hedges.

Eleutherodactylus (Euhyas) luteolus Species Group

Definition.—Species in this group are robust to moderate in body shape and small to moderate in SVL, ranging from 18 mm (females, *E. griphus* and *E. sisyphodemus*) to 49 mm (females, *E. nubicola*). Leg length and digital disc size varies among species. They are variable in coloration; distinctive pattern polymorphisms are shared among the species (Schwartz & Fowler 1973; Crombie 1977, 1986). These species occupy a diversity of habitats, including leaf litter, caves, bromeliads, and streams. The calls are variable and include the typical chirps and mews characteristic of the subgenus *Euhyas* as well as some with hollow rapping or knocking noises.

Content.—Five species subgroups (17 species) are placed in this species group: *Eleutherodactylus (Euhyas) cundalli*, *gossei*, *jamaicensis*, *luteolus*, and *nubicola* species subgroups.

Distribution.—The species group is endemic to Jamaica.

Remarks.—This species group received moderately strong support (76%) in the molecular phylogeny (Fig. 2), although it received significant support (100%) in the higher-level tree with fewer taxa and longer sequences (Fig. 4). This species group includes all native species of the genus *Eleutherodactylus* on Jamaica and represents an adaptive radiation in the true sense, inasmuch as the included species occupy a great diversity of habitats and show obvious adaptations to those habitats (Hedges 1989b). Although originally identified by protein variation (Hedges 1989a, 1989b), this species group has support from albumin immunology (Hass & Hedges 1991), chromosome variation (Bogart & Hedges 1995), and DNA sequence analyses (here). The DNA sequence data were insufficient to resolve relationships of species within the species group; longer sequences will be needed. The subgroups recognized here are based on relationships defined in the earlier analyses of protein variation, albumin immunology, and chromosomes.

Eleutherodactylus (Euhyas) cundalli Species Subgroup

Definition.—Species in this group are moderate in body shape and moderate in SVL, ranging from 38 mm (females, *E. cavernicola* and *E. glaucoreius*) to 45 mm (females, *E. cundalli*). They have relatively large eyes, long legs, long digits, and moderate to large digital discs. They are variable in coloration. All are commonly found on rocks, and at least two (*E. cavernicola* and *E. cundalli*) are encountered in caves. Calls consist of irregular series of chirps and ticks.

Content.—Three species are placed in the species subgroup: *Eleutherodactylus (Euhyas) cavernicola*, *cundalli* (Fig. 54), and *glaucoreius*.

Distribution.—The species subgroup is restricted to Jamaica.

Remarks.—This species subgroup represents a trio of long-legged, large-disced, allopatric species that occupy rocky and cave habitats on Jamaica. At least one species (*E. cundalli*) has a unique reproductive behavior (froglet transport) among terraranan frogs (Diesel *et al.* 1995).

Eleutherodactylus (Euhyas) gossei Species Subgroup

Definition.—Species in this subgroup are robust in body shape and small to moderate in SVL, ranging from 18 mm (females, *E. griphus*) to 44 mm (females, *E. pantoni*). They have relatively short legs, short digits, and small digital discs. The dorsal ground color usually is tan, brown, grayish-brown, or reddish-brown; they have red or orange in the concealed areas of the groin and hindlimbs. These frogs are usually encountered on the ground, or more rarely, on low vegetation and rocks. The calls include a muffled whistle or series of hollow sounding notes.

Content.—Five species are placed in the subgroup: *Eleutherodactylus (Euhyas) fuscus*, *gossei* (Fig. 55), *junori*, *pantoni*, and *pentasyringos*.

Distribution.—The species subgroup is endemic to Jamaica.

Remarks.—This species subgroup includes a pair of mostly allopatric (partially sympatric in one small region) species, *E. pantoni* and *E. pentasyringos*, that have yellow or orange bellies. It also includes a trio of sympatric species, *E. fuscus*, *E. gossei*, and *E. junori* that differ in body size and lack yellow or orange bellies.

Eleutherodactylus (Euhyas) jamaicensis Species Subgroup

Definition.—The single species in this group has a depressed body and moderate SVL (females, 30 mm). It has large, rounded digital discs. The dorsal ground color is dark brown, tan, or gray, commonly with a pair of pale dorsolateral marks, and capable of changing colors (dark to pale). This frog lives exclusively in bromeliads. The call is a series of short chirps.

Content.—One species is placed in the subgroup: *Eleutherodactylus (Euhyas) jamaicensis* (Fig. 56).

Distribution.—The species subgroup occurs on Jamaica.

Remarks.—This species was found to be most closely related to the *Eleutherodactylus cundalli* and *E. nubicola* subgroups (Hedges 1989b; Bogart & Hedges 1995).

Eleutherodactylus (Euhyas) luteolus Species Subgroup

Definition.—Species in this subgroup are robust in body shape and small to moderate in SVL, ranging from 18 mm (females, *E. sisymphodemus*) to 29 mm (females, *E. grabhami*). They have short limbs and small to large digital discs. They are variable in coloration. One species (*E. sisymphodemus*) lives in leaf litter; the other two climb on vegetation and rocks. The calls are a faint, insect like buzz (*E. sisymphodemus*) or whistle-like peep.

Content.—Three species are placed in the subgroup: *Eleutherodactylus (Euhyas) grabhami*, *luteolus* (Fig. 57), and *sisymphodemus*.

Distribution.—The species subgroup is restricted to Jamaica.

Remarks.—This species subgroup is the most divergent of the subgroups and contains species that are the least similar to one another, yet they are united by several types of genetic data (Hedges 1989b; Bogart & Hedges 1995), including partial support from DNA sequence data (Heinicke *et al.* 2007). Their greater morphological divergence may reflect their longer period of diversification on Jamaica (i.e., earlier divergences among species compared with the other species subgroups in Jamaica).

Eleutherodactylus (Euhyas) nubicola Species Subgroup

Definition.—Species in this subgroup are robust in body shape and small to moderate in SVL, ranging from 18 mm (females, *E. griphus*) to 49 mm (females, *E. nubicola*). Most have relatively short legs and small digital discs, although one species (*E. orcutti*) has large digital tips and webbing between the toes. They are variable in coloration. All are terrestrial, except for *E. orcutti*, which inhabits streams. The calls vary from chirps to raspy notes and faint whistles.

Content.—Five species are placed in the subgroup: *Eleutherodactylus (Euhyas) alticola*, *andrewsi*, *griphus*, *nubicola* (Fig. 58), and *orcutti*.

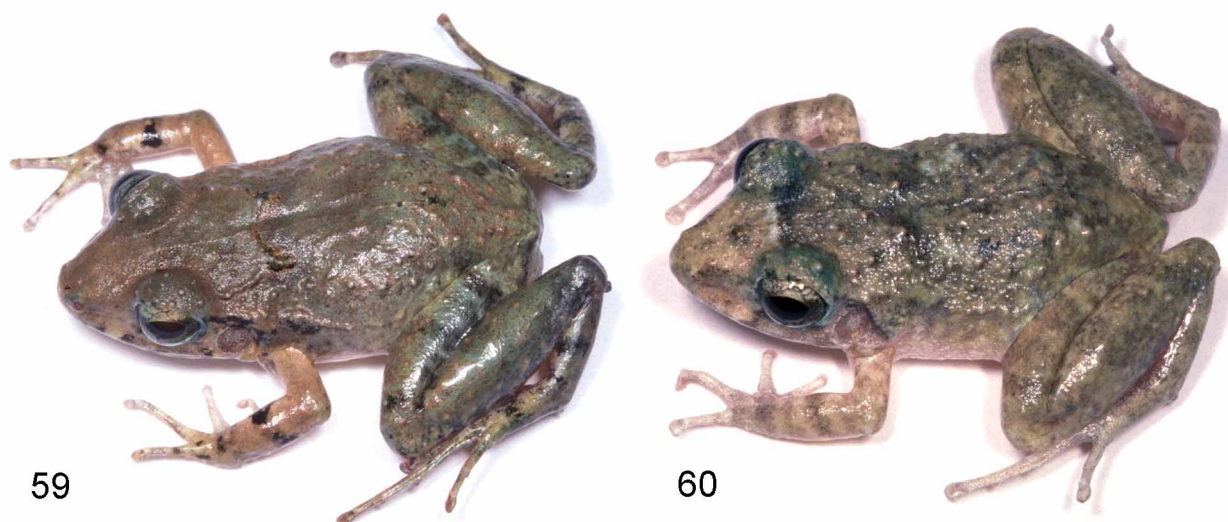
Distribution.—The species subgroup is endemic to Jamaica.

Remarks.—Based on distribution, the diversification of this species group occurred in eastern Jamaica (the Blue Mountains), with a single species (*E. griphus*) occurring in the Cockpit Country of western Jamaica.

Eleutherodactylus (Euhyas) riparius Species Group

Definition.—Species in this group are robust in body shape and moderate in SVL, ranging from 31 mm (females, *E. rivularis*) to 42 mm (females, *E. riparius*). They have a rugose dorsum and W-shaped suprascapular fold, long legs, and small digital discs. They are primarily gray, grayish brown, or olive brown and exhibit pattern polymorphism (uniform, mottled, and striped) in one species. These frogs usually occur along the edges of streams. They emit one or a few chirps (Estrada & Hedges 1998; Díaz *et al.* 2001).

Content.—Two species are placed in the group: *Eleutherodactylus riparius* (Fig. 59) and *rivularis*.



FIGURES 59–60. 59. *Eleutherodactylus (Euhyas) riparius* of the *E. riparius* Species Group, *E. luteolus* Species Series, from Soroa, Pinar del Rio, Cuba. Photo by S. B. Hedges. 60. *Eleutherodactylus (Euhyas) toa* of the *E. toa* Species Group, *E. luteolus* Species Series, from 7.7 km N Imias, Guantánamo, Cuba. Photo by S. B. Hedges.

Distribution.—The species group is distributed in Cuba.

Remarks.—This species group received moderately strong support (75%) in the molecular phylogeny (Fig. 2). It includes a pair of closely related, sympatric riparian species. *Eleutherodactylus riparius* is a common, wide-ranging species found throughout most of Cuba and formerly called *E. cuneatus*. The confused taxonomic history of *E. cuneatus* was reviewed elsewhere (Estrada & Hedges 1998). Other Cuban stream-associated species are *E. turquinensis* (*E. cuneatus* Species Group) and *E. toa* (*E. toa* Species Group). See Remarks (above) under *Eleutherodactylus (Euhyas) cuneatus* Species Group concerning relationships and differences among the five riparian species of Cuba.

Eleutherodactylus (Euhyas) toa Species Group

Definition.—The species in this group is robust in body shape and moderate in SVL (females, 33 mm). It has a tuberculate dorsum, an areolate venter, long legs, and digital discs of moderate size. The dorsum is either pale whitish tan, yellowish green, or greenish gray, with several pattern polymorphisms. Most individuals of this terrestrial species have been collected in pine forest, although some have been found along streams; this

leads to the impression, along with its streamlined and robust habitus, that it may be adapted to streamside situations. Vocalization is unknown.

Content.—A single species is placed in the group: *Eleutherodactylus (Euhyas) toa* (Fig. 60).

Distribution.—The species is distributed in eastern Cuba.

Remarks.—Other Cuban stream-associated species are *E. cuneatus* and *E. turquinensis* (*E. cuneatus* Species Group) and *E. riparius* and *E. rivularis* (*E. riparius* Species Group). See Remarks (above) under *Eleutherodactylus (Euhyas) cuneatus* Species Group concerning relationships and differences among the five riparian species of Cuba.

Eleutherodactylus (Euhyas) oxyrhynchus Species Series

Definition.—Species in this series are variable in body shape and in SVL, ranging from 15 mm (females, *E. thorectes*) to 43 mm (females, *E. apostates*). They are variable in coloration. These frogs are terrestrial or arboreal; they inhabit streams, marshes, bromeliads, rocks, and caves. Their calls span the spectrum of variation from faint chirps to loud whistles.

Content.—Six species groups (21 species) are placed in this series: the *Eleutherodactylus (Euhyas) bakeri*, *glandulifer*, *jugans*, *oxyrhynchus*, *paulsoni*, and *ruffifemoralis* species groups.

Distribution.—This species series is distributed in southern Hispaniola, including Haiti and the Dominican Republic.

Remarks.—This species series received significant support (99%) in the molecular phylogeny (Fig. 2). It is the major adaptive radiation of species of the subgenus *Euhyas* on Hispaniola. Compared with the similar-sized major radiation on Cuba, the *Eleutherodactylus (Euhyas) planirostris* Species Series (23 species), species in this Hispaniolan radiation seem to be adapted to more habitats. In particular, this radiation of frogs has exploited arboreal habitats, an aspect of the environment not utilized by the *E. planirostris* Species Series (see below). A possible explanation for this difference, supported by the branching order in the molecular phylogeny (Fig. 2), is that the arboreal subgenus *Eleutherodactylus* colonized Cuba and filled arboreal niches, thereby excluding the *E. planirostris* series from those niches prior to the colonization of the South Paleoisland of Hispaniola by the *E. oxyrhynchus* Species Series. Thus, the *E. oxyrhynchus* Species Series was free to expand into those vacant arboreal niches on the South Paleoisland. The comparatively modest presence of the arboreal subgenus (*Eleutherodactylus*) on the South Paleoisland probably can be attributed to its later arrival, after *Euhyas* had filled most of the arboreal niches.

Eleutherodactylus (Euhyas) bakeri Species Group

Definition.—Species in this group are moderate in body shape and small to moderate in SVL, ranging from 15 mm (females, *E. thorectes*) to 35 mm (females, *E. bakeri*). Most have moderate to large digital discs (small in *E. glanduliferoides* and *E. thorectes*). Coloration is variable; most are shades of tan, brown, and reddish brown and are polymorphic in pattern (Hedges *et al.* 1987). All of the species are arboreal, and several frequent bromeliads. Surprisingly, the two species with small digital tips also climb, but only in low vegetation. One species, *E. glaphycompus*, also calls from limestone rocks. Their calls vary, but most species emit a loud whistle-like noise.

Content.—Eleven species are placed in the group: *Eleutherodactylus (Euhyas) amadeus*, *bakeri* (Fig. 61), *caribe*, *corona*, *dolomedes*, *eunaster*, *glanduliferoides*, *glaphycompus*, *heminota*, *semipalmatus*, and *thorectes*.

Distribution.—This species group is distributed in southern Hispaniola, including Haiti and the Dominican Republic.



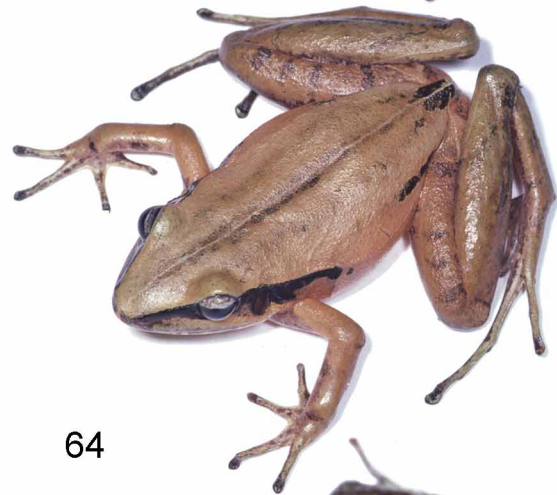
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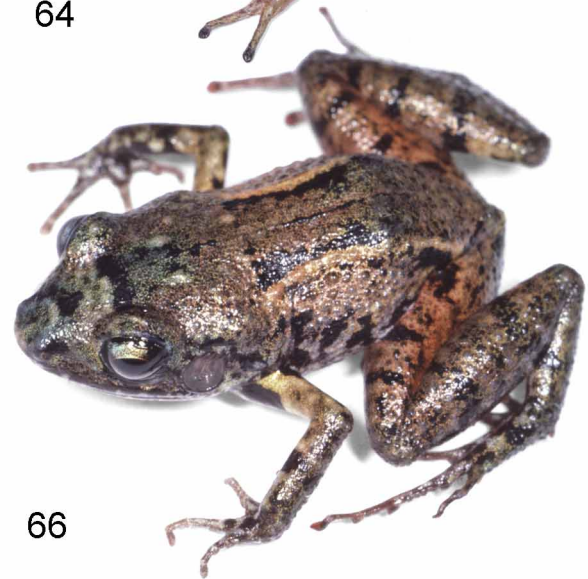
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FIGURES 61–66. **61.** *Eleutherodactylus (Euhyas) bakeri* of the *E. bakeri* Species Group, *E. oxyrhincus* Species Series, from 11.7 km S and 1.7 km E Marché Léon, Grand’Anse, Haiti. Photo by S. B. Hedges. **62.** *Eleutherodactylus (Euhyas) glandulifer* of the *E. glandulifer* Species Group, *E. oxyrhincus* Species Series, from south slope of Pic Formon, Sud, Haiti. Photo by S. B. Hedges. **63.** *Eleutherodactylus (Euhyas) jugans* of the *E. jugans* Species Group, *E. oxyrhincus* Species Series, from 8.0 km NW Sequin, Sud’Est, Haiti. Photo by S. B. Hedges. **64.** *Eleutherodactylus (Euhyas) oxyrhincus* of the *E. oxyrhincus* Species Group, *E. oxyrhincus* Species Series, from 1.5 km S Castillon, Grand’Anse, Haiti. Photo by S. B. Hedges. **65.** *Eleutherodactylus (Euhyas) paulsoni* of the *E. paulsoni* Species Group, *E. oxyrhincus* Species Series, from 5.8 km S Pestel, Grand’Anse, Haiti. Photo by S. B. Hedges. **66.** *Eleutherodactylus (Euhyas) rufifemoralis* of the *E. rufifemoralis* Species Group, *E. oxyrhincus* Species Series, from 2 km S Tejunde, Barahona, Dominican Republic. Photo by S. B. Hedges).

Remarks.—This species group received moderate support (59%) in the molecular phylogeny (Fig. 2). It is an unusual radiation of arboreal species within the otherwise predominantly ground- and rock-dwelling subgenus *Euhyas*. The enlarged, rounded digital discs seem to be associated with climbing abilities. Their resemblance to species in the mostly arboreal subgenus *Eleutherodactylus* also includes the short dentigerous processes of the vomers and loud, whistle-like calls of some of the species. It has been suggested that the size of the vomerine processes is correlated with feeding habits: short for soft-bodied prey such as dipterans and lepidopterans that might be encountered in arboreal situations and longer (with more teeth) for hard-bodied prey such as coleopterans and orthopterans that might be encountered more frequently in terrestrial situations (Hedges 1989a).

Protein analyses and liver shape (Hedges 1989a) first revealed this radiation and its remarkable convergence, although Lynch and Duellman (Lynch & Duellman 1997) were not convinced and relegated more than half of the species in this group (*Eleutherodactylus amadeus*, *bakeri*, *corona*, *eunaster*, *glanduliferoides*, *glaphycompus*, and *thorectes*) to the subgenus *Eleutherodactylus*. They did this primarily based on variation in relative length of the fifth toe compared to the third toe, a character that they singled out as being of high systematic value. However, the recent DNA sequence analyses (Heinicke *et al.* 2007) now confirm the original allocations using proteins and liver shape, indicating that the toe character is part of the convergence and thus not a useful character in this group.

The two small species with small digital tips, *E. glanduliferoides* and *E. thorectes*, are least like other members of this group, and not surprisingly they are the most divergent members in the molecular phylogeny (Fig. 2). However, more molecular data are needed to resolve the relationships of these species.

Eleutherodactylus (Euhyas) glandulifer Species Group

Definition.—Species in this group are robust in body shape and small to moderate in SVL, ranging from 21 mm (females, *E. sciagraphus*) to 36 mm (females, *E. glandulifer*). Three have short snouts, short legs, and small digital discs in contrast to *E. glandulifer*. Coloration is mostly dark shades of brown and green. These frogs are terrestrial, although the large digital discs of *E. glandulifer* suggest that it also climbs. Vocalization is variable.

Content.—Four species are placed in the group: *Eleutherodactylus (Euhyas) brevirostris*, *glandulifer* (Fig. 62), *sciagraphus*, and *ventrilineatus*.

Distribution.—The species group is restricted to the Massif de la Hotte, on the eastern end of the Tiburon Peninsula of Haiti, on the island of Hispaniola.

Remarks.—This species group received moderate support (86%) in the molecular phylogeny (Fig. 2). It is a small radiation of robust, dark, terrestrial species in the Massif de la Hotte.

Eleutherodactylus (Euhyas) jugans Species Group

Definition.—The single species in this group is robust in body shape and moderate in SVL (females, 33 mm). It has short legs and small digital discs. It is usually brown, reddish brown, or orange-brown. The call of this terrestrial species is a series of soft, raspy notes.

Content.—A single species is placed in the group: *Eleutherodactylus (Euhyas) jugans* (Fig. 63).

Distribution.—The species is distributed in the Massif de la Selle of Haiti and the western end of the adjacent Sierra de Baoruco in the Dominican Republic, in southern Hispaniola.

Remarks.—For discussion of the confusion in relationships between this species and *E. parabates*, see above in Remarks of *Eleutherodactylus (Eleutherodactylus) abbotti* Species Group. In addition, this species

was considered to be closely related to *E. ventrilineatus*, a similarly dark, robust species in the Massif de la Hotte (Schwartz 1964). However, the DNA sequence evidence (Fig. 2) shows that the two species are not close relatives and are convergent in appearance.

Eleutherodactylus (Euhyas) oxyrhyncus Species Group

Definition.—Species in this group are robust in body shape and moderate to large in SVL, ranging from 43 mm (females, *E. apostates*) to 55 mm (females, *E. oxyrhyncus*). They have relatively long snouts, long legs, and small digital discs. Sexual size dimorphism is pronounced; males are much smaller than females (e.g., approximately one-half the length and a small fraction of the mass) and may represent the most extreme sexual size dimorphism within the family. They are variable in color and pattern, although the ground color is usually tan, brown, or gray-brown. The calls of these terrestrial frogs are either soft, raspy notes (*E. apostates*) or chirps (*E. oxyrhyncus*).

Content.—Two species are placed in the group: *Eleutherodactylus (Euhyas) apostates* and *E. oxyrhyncus* (Fig. 64).

Distribution.—The species group is distributed on the Tiburon Peninsula in southern Hispaniola, including the Massif de la Hotte and the Massif de la Selle of Haiti.

Remarks.—This species group received significant support (99%) in the molecular phylogeny (Fig. 2). It is a pair of long-snouted, long-legged, terrestrial species that in many ways resemble, convergently, species in the *Eleutherodactylus (Euhyas) dimidiatus* Species Group of Cuba. In the Massif de la Hotte, *E. oxyrhyncus* is the more abundant of the two species on the North Slope whereas *E. apostates* is the most abundant, if not the only species of the pair, on the South Slope. The two species are sympatric at least at Castillon in the northern portion of mountain range. One of us (SBH) has noted differences in the geographic isolates of *E. oxyrhyncus* in the Massif de la Hotte compared with those in the Massif de la Selle that may warrant recognition of the latter isolate as a separate species.

Eleutherodactylus (Euhyas) paulsoni Species Group

Definition.—The single species in this group is moderate in body shape and small in SVL (females, 26 mm). It has small (slightly expanded) digital discs and a noticeably and evenly tuberculate dorsum. The dorsum is mottled brown, usually with a pinkish wash in the posterior half of the body. The call of this terrestrial frog is unknown.

Content.—A single species is placed in the group: *Eleutherodactylus (Euhyas) paulsoni* (Fig. 65).

Distribution.—This species is restricted to Haitian Tiburon Peninsula in southern Hispaniola.

Remarks.—This is one of two predominantly lowland species in the entire *Eleutherodactylus oxyrhyncus* Species Series; the other is *E. caribe*, known only from a single brackish marsh in Haiti.

Eleutherodactylus (Euhyas) rufifemoralis Species Group

Definition.—Species in this group are moderate in body shape and small to moderate in SVL, ranging from 18 mm (females, *E. rufifemoralis*) to 37 mm (females, *E. furcyensis*). They have small digital discs. The ground color is gray or brown; the snout is bluish gray, and the concealed areas of the limbs and groin are red or orange. These frogs are terrestrial. The call of *E. furcyensis* is an irregular series of soft ticks and peeps.

Content.—Two species are placed in the group: *Eleutherodactylus (Euhyas) furcyensis* and *rufifemoralis* (Fig. 66).

Distribution.—This species group is distributed in southern Hispaniola, including Haiti and the Dominican Republic.

Remarks.—This species group received significant support (99%) in the molecular phylogeny (Fig. 2). It is an allopatric pair of closely related species occupying a connected pair of mountain ranges, the Massif de la Selle (Haiti) and Sierra de Baoruco (Dominican Republic) in Hispaniola.

Eleutherodactylus (Euhyas) planirostris Species Series

Definition.—Species in this series are variable in body shape and small to large in SVL, ranging from 11 mm (females, *E. iberia*) to 62 mm (females, *E. pinarensis*). The included species have small to large digital discs. They are variable in coloration. Most are terrestrial or saxicolous and have calls consisting of a series of chirps.

Content.—Six species groups (23 species) are placed in this series: the *Eleutherodactylus (Euhyas) atkinsi*, *gundlachi*, *limbatus*, *pezopetrus*, *pinarensis*, and *planirostris* species groups.

Distribution.—The species series is distributed on Cuba, the Cayman Islands, and the Bahamas. Whether the presence of *E. planirostris* in southern Florida is natural or through human introduction is debated. However, the presence of *E. planirostris* in other areas (e.g., northern Florida, Georgia, Louisiana, Mississippi, Hawaii, and the Lesser Antilles) is from human introduction.

Remarks.—This species series received moderately strong support (87%) in the molecular phylogeny (Fig. 2). It is a large and diverse radiation of terrestrial and saxicolous species that evolved almost entirely on Cuba. As such, it is the largest single adaptive radiation of frogs on Cuba. All other adaptive radiations of frogs of the subgenus *Euhyas* in Cuba include only 2–4 species. See Remarks above under *Eleutherodactylus (Euhyas) oxyrhynchus* Species Series for ecological and evolutionary comparison of these two major species series on neighboring islands.

Eleutherodactylus (Euhyas) atkinsi Species Group

Definition.—The single species in this group is robust in body shape and moderate in SVL (females, 43 mm). It has small digital discs. It is reddish-brown, tan, or gray with dark spots in the groin and on the thighs. This terrestrial species emits a series of chirps.

Content.—A single species is placed in the group: *Eleutherodactylus (Euhyas) atkinsi* (Fig. 67).

Distribution.—The species is restricted to Cuba.

Remarks.—This species has an unusually broad distribution throughout Cuba and has adapted well to human modifications of natural habitats. A subspecies, *E. a. estradai*, occurs in extreme eastern Cuba, adjacent to the range of *E. a. atkinsi*. The status of this taxon is in need of assessment.

Eleutherodactylus (Euhyas) gundlachi Species Group

Definition.—Species in this group are robust in body shape and small in SVL, ranging from 14 mm (females, *E. tetajulia*) to 23 mm (females, *E. gundlachi*). They have short snouts, short legs, short digits, and small digital discs, although *E. gundlachi* is moderate in all of those characters. Several species (*E. adelus*, *gundlachi*, and *varleyi*) have a distinctly tuberculate dorsum. The dorsum is mostly gray, brown, or grayish brown with or without pale dorsolateral stripes. Most species are found on the ground, but *E. adelus* and *E. varleyi* inhabit grasses, and *E. gundlachi* occurs on the ground or among rocks. The calls of most species consist of a faint chirping noise with species-specific differences (Estrada & Hedges 1996b; Díaz *et al.* 2003).



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FIGURES 67–72. 67. *Eleutherodactylus (Euhyas) atkinsi* of the *E. atkinsi* Species Group, *E. planirostris* Species Series, from Golf Course, Guantanamo Bay Naval Station, Cuba. Photo by S. B. Hedges. 68. *Eleutherodactylus (Euhyas) varleyi* of the *E. gundlachi* Species Group, *E. planirostris* Species Series, from 2 km N La Muniación, Guantánamo, Cuba. Photo by S. B. Hedges. 69. *Eleutherodactylus (Euhyas) limbatus* of the *E. limbatus* Species Group, *E. planirostris* Species Series, from Soroa, Pinar del Rio, Cuba. Photo by S. B. Hedges. 70. *Eleutherodactylus (Euhyas) pezopetrus* of the *E. pezopetrus* Species Group, *E. planirostris* Species Series, from 1.5 km NE La Cantera, Santiago de Cuba, Cuba. Photo by S. B. Hedges. 71. *Eleutherodactylus (Euhyas) pinarensis* of the *E. pinarensis* Species Group, *E. planirostris* Species Series, from 12.4 km ESE Playa Girón, Matanzas, Cuba. Photo by S. B. Hedges. 72. *Eleutherodactylus (Euhyas) planirostris* of the *E. planirostris* Species Group, *E. planirostris* Species Series, from 2.9 km NW Port Maria, St. Mary, Jamaica. Photo by S. B. Hedges.

Content.—Five species are placed in the group: *Eleutherodactylus (Euhyas) adelus*, *gundlachi*, *intermedius*, *tetajulia*, and *varleyi* (Fig. 68).

Distribution.—The species group is distributed on Cuba.

Remarks.—This species group received moderately strong support (89%) in the molecular phylogeny (Fig. 2). The soft calls and relatively cryptic behavior of these species, which may call from cavities (e.g., *E. intermedius* and *E. tetajulia*) or beneath grass and leaf litter (*E. adelus* and *E. varleyi*) suggest that there are more, as yet unnamed species in this group awaiting discovery.

Eleutherodactylus (Euhyas) limbatus Species Group

Definition.—Species in this group are mostly robust in body shape and small in SVL, ranging from 11 mm (females, *E. iberia*) to 19 mm (females, *E. etheridgei*). Body shapes vary greatly, from robust (most species) to indented at midbody (*E. orientalis*) to slender with a long snout (*E. jaumei*); all have short legs. In all species, digital discs are small, and in all except *E. etheridgei* digits are distinctly short. All species except *E. etheridgei* have pale dorsolateral stripes. Most of these terrestrial species emit a faint chirping noise that is species-specific.

Content.—Six species are placed in the group: *Eleutherodactylus (Euhyas) cubanus*, *etheridgei*, *iberia*, *jaumei*, *limbatus* (Fig. 69), and *orientalis*.

Distribution.—The species group is distributed on Cuba; all species except *E. limbatus*, which is island-wide, are endemic to eastern Cuba.

Remarks.—This species group received moderately strong support (82%) in the molecular phylogeny (Fig. 2). It is a radiation of diminutive, short-legged, terrestrial species that evolved in eastern Cuba and have one wide-ranging member (*E. limbatus*). The inclusion here of *E. etheridgei* differs from previous characterizations of the group (Estrada & Hedges 1996a; Estrada & Alonso 1997) and is based primarily on the molecular phylogeny (Heinicke *et al.* 2007). However, that species also is small, short-legged, and has a slight midbody constriction that is more or less evident in other members of the group. One species in the group, *E. iberia*, is the smallest tetrapod in the northern hemisphere and is similar in size to the smallest tetrapod in the southern hemisphere, *Brachycephalus didactylus* (Estrada & Hedges 1996a).

Eleutherodactylus (Euhyas) pezopetrus Species Group

Definition.—The single species in this group is moderate in body shape and SVL (females, 49 mm). It has long legs, long digits, and large, ovate digital discs. The dorsal ground color is tan or greenish tan with brown mottling, pale dorsolateral stripes, or pale sacral blotches, and patches of orange tubercles on the dorsum. It is encountered on and around rocks and cliff faces. The call (a chirping sound) is a one- to three-notes (Díaz *et al.* 2007b).

Content.—A single species is placed in the group: *Eleutherodactylus (Euhyas) pezopetrus* (Fig. 70).

Distribution.—The species is endemic to eastern Cuba.

Remarks.—In size and body shape, this species resembles members of the *Eleutherodactylus cuneatus* Species Group of the *E. luteolus* Species Series, and has been compared with *E. cuneatus* (Díaz *et al.* 2007b). However, the molecular phylogeny (Heinicke *et al.* 2007) indicates that the resemblance is the result of convergence, and that this species is an unusually large member of the *E. planirostris* Species Series. The pattern polymorphisms (mottling and dorsolateral stripes) bear a greater resemblance to those in the *E. planirostris* Species Series and thereby support the molecular phylogeny.

Eleutherodactylus (Euhyas) pinarensis Species Group

Definition.—Species in this group are moderate in body shape and small to large in SVL, ranging from 30 mm (females, *E. blairhedgesi*) to 62 mm (females, *E. pinarensis*). They have a tuberculate dorsum, long digits, and large, ovate digital discs. The dorsum usually is tan, yellowish tan, or greenish brown with mottling or other markings. These primarily rock-dwelling frogs emit a series of one- to three-note trills (Díaz *et al.* 2007b).

Content.—Three species are placed in the group: *Eleutherodactylus (Euhyas) blairhedgesi*, *pinarensis* (Fig. 71), and *thomasi*.

Distribution.—The species group is distributed on Cuba.

Remarks.—This species group received significant support (100%) in the molecular phylogeny (Fig. 2). It is a small radiation of tuberculate, saxicolous species that emit trills. One species (*E. thomasi*) is composed of three subspecies with disjunct distributions; these may be distinct species.

Eleutherodactylus (Euhyas) planirostris Species Group

Definition.—Species in this group are somewhat flattened in body shape and small to moderate in SVL, ranging from 23 mm (females, *E. guanahacabibes*) to 37 mm (females, *E. goini*). They have a tuberculate dorsum with or without a slight middorsal ridge, moderate to long legs, and digital discs of moderate size. The dorsum usually is tan, yellowish tan, greenish tan, or brown with two major pattern polymorphisms—mottled or pale dorsolateral stripes. They are primarily ground dwelling and rock dwelling, and most species emit an irregular series of faint chirps.

Content.—Seven species are placed in the group: *Eleutherodactylus (Euhyas) casparii*, *goini*, *guanahacabibes*, *planirostris* (Fig. 72), *rogersi*, *simulans*, and *tonyi*.

Distribution.—The species group is distributed on Cuba, the Cayman Islands, and the Bahamas. Whether the presence of *E. planirostris* in southern Florida is natural or through human introduction is debated. However, the presence of *E. planirostris* in other areas (e.g., northern Florida, Georgia, Louisiana, Mississippi, Hawaii, and the Lesser Antilles) is from human introduction.

Remarks.—This species group received moderate support (63%) in the molecular phylogeny (Fig. 2). It is a moderate-sized radiation of mostly small, tuberculate, and ground-dwelling species with pattern polymorphisms and which are almost entirely allopatric in distribution. Their wide distribution and ability to successfully invade new areas (at least in one species, *E. planirostris*) probably derives from desiccation resistance (Stewart & Martin 1980). Several of the included species were previously considered subspecies of *E. planirostris* (Schwartz 1974) but have since been elevated to species status (Estrada & Hedges 1997; Heinicke *et al.* 2007).

Eleutherodactylus (Euhyas) ricordii Species Series

Definition.—Species in this series are robust or moderate in body shape and small to moderate in SVL, ranging from 24 mm (females, *E. lucioi*) to 48 mm (females, *E. michaelschmidi*). They have small to slightly expanded digital discs. The dorsum usually is tan, yellowish tan, greenish tan, or reddish tan with either dark mottling or pale dorsolateral stripes. These frogs are primarily ground dwelling and rock dwelling. Most species emit a series of faint chirps that differ among species.

Content.—Two species groups (14 species) are placed in this series: the *Eleutherodactylus (Euhyas) lentus* and *ricordii* species groups.

Distribution.—This species series is distributed on Cuba, Hispaniola, Mona Island, and the Virgin Islands.

Remarks.—This species series received moderately strong support (91%) in the molecular phylogeny (Fig. 2). The two included species groups of this series each have more restricted geographic distributions, with the *Eleutherodactylus lentus* Species Group occupying the eastern islands in the Antilles and the *E. ricordii* Species Group distributed in the west (Cuba). Given this allopatric distribution and their close relationships (Heinicke *et al.* 2007), it can be inferred that they arose by either dispersal or vicariance between Cuba and Hispaniola.

Eleutherodactylus (Euhyas) lentus Species Group

Definition.—Species in this group are moderate in body shape and small to moderate in SVL, ranging from 24 mm (male only, *E. lucioi*) to 43 mm (females, *E. pictissimus*). Most have depressed bodies and small to slightly expanded digital discs. The dorsal ground color commonly is yellowish tan, with a reddish wash in some species, and a polymorphic pattern (typically dark mottling or pale dorsolateral lines). Most of these terrestrial species emit a faint chirping noise that is species specific.

Content.—Ten species are placed in the group. Nine of those previously were recognized as species—*Eleutherodactylus (Euhyas) grahami*, *lentus* (Fig. 73), *lucioi*, *monensis*, *pictissimus* (Fig. 74), *probolaeus*, *rhodesi*, *warreni*, and *weinlandi*. One was described as a subspecies of *E. weinlandi* and is elevated here to species status—*Eleutherodactylus (Euhyas) paralius*.

Distribution.—The species group is distributed on Hispaniola, Mona Island, and the Virgin Islands.

Remarks.—This species group received significant support (100%) in the molecular phylogeny (Fig. 2). It is a moderate (probably large when fully understood) radiation of terrestrial species; their distributions center on the Hispaniolan North Paleoisland, Mona Island, and the Virgin Islands. The absence of a species in this group from Puerto Rico is odd, because it leaves a major distributional hiatus between Mona Island (*E. monensis*) and the Virgin Islands (*E. lentus*). Previously, *E. richmondi* was considered to be that Puerto Rican link, but that species is unquestionably a member of the subgenus *Eleutherodactylus* (see discussion above under Remarks for that subgenus). It is possible that a species of this group once occurred on Puerto Rico (not unlikely considering land connections during the Pleistocene) and was outcompeted by *E. richmondi*, which is somewhat similar ecologically, or other members of the subgenus *Eleutherodactylus*.

Schwartz (1965a; Schwartz 1976) described two subspecies of *E. weinlandi* on Hispaniola, both of which “are exceptionally distinct in numerous details of size, pattern, and coloration” (Schwartz 1976). In the case of *E. w. chersonesodes*, he found evidence of intergradation with *E. w. weinlandi* in a “compact” region where their distributions joined. However, the taxon recognized here as a full species, *E. paralius*, has not been found to intergrade with either of the other taxa despite close proximity of their ranges. Two subspecies of *E. pictissimus* also were described (Schwartz 1965a); additional study is needed to determine their taxonomic status. One of us (SBH) has collected both *E. pictissimus* and *weinlandi* throughout Hispaniola, and has encountered many specimens that do not conform to either species, suggesting that species group is larger than currently recognized.

Eleutherodactylus (Euhyas) ricordii Species Group

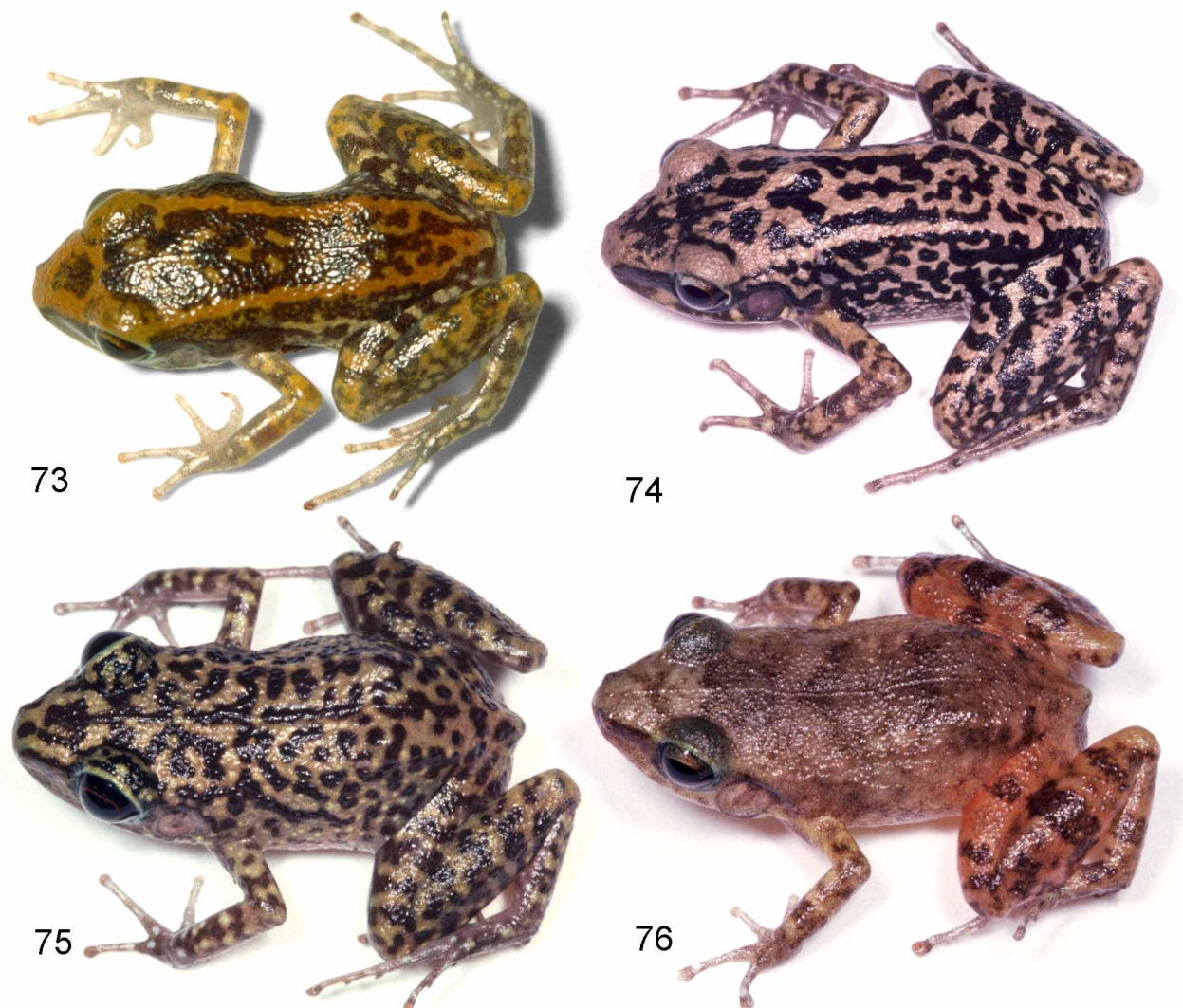
Definition.—Species in this group are robust in body shape and small to moderate in SVL, ranging from 25 mm (females, *E. acmonis*) to 48 mm (females, *E. michaelschmidi*). They have an evenly, mildly tuberculate (granular) dorsum with a slightly raised middorsal ridge, small to slightly expanded digital discs, and rela-

tively large and dark eyes. The dorsum usually is tan, yellowish tan, greenish tan, or reddish tan with distinctive dark brown or black spots, blotches, or mottling, with or without pale dorsolateral stripes. Most of these primarily ground-dwelling and rock-dwelling species emit a series of faint chirps, with species-specific differences (Díaz *et al.* 2007b).

Content.—Four species are placed in the group: *Eleutherodactylus (Euhyas) acmonis*, *bresslerae*, *michaelschmidi*, and *ricordii* (Fig. 75).

Distribution.—The species group is restricted to eastern Cuba.

Remarks.—This species group received significant support (100%) in the molecular phylogeny (Fig. 2). In many ways these species resemble those in the *Eleutherodactylus planirostris* Species Group of the *E. planirostris* Species Series. For many years *E. planirostris* was considered a subspecies of *E. ricordii*. Both groups consist of small- to moderate-sized, ground- and rock-dwelling species with patterns of mottling and dorsolateral stripes. The members of the *E. planirostris* Species Group appear more flattened in body shape, although that trait is difficult to measure. Also, members of the *E. ricordii* Species Group appear to have darker eyes that are relatively larger than those of species in the other group.



FIGURES 73–76. **73.** *Eleutherodactylus (Euhyas) lentus* of the *E. lentus* Species Group, *E. ricordii* Species Series, from St. Croix, U.S. Virgin Islands. Photo by S. B. Hedges. **74.** *Eleutherodactylus (Euhyas) pictissimus* of the *E. lentus* Species Group, *E. ricordii* Species Series, from 5.8 km S Pestel, Grand'Anse, Haiti. Photo by S. B. Hedges. **75.** *Eleutherodactylus (Euhyas) ricordii* of the *E. ricordii* Species Group, *E. ricordii* Species Series, from 1–2 km E Boca de Yumurí, Guantánamo, Cuba. Photo by S. B. Hedges. **76.** *Eleutherodactylus (Euhyas) zugii* of the *E. zugii* Species Series, from Soroa, Pinar del Río, Cuba. Photo by S. B. Hedges.

Eleutherodactylus (Euhyas) zugii Species Series

Definition.—Species in this series are robust in body shape and small in SVL, ranging from 19 mm (females, *E. zugii*) to 27 mm (females, *E. klinikowskii*). The dorsum has irregular, low tubercles and commonly a slight middorsal ridge. The legs are relatively short, and digital discs are small to moderate in size. The dorsum is pinkish tan, tan, or brown, and with pattern polymorphism (dorsolateral stripes or dark mottling). These frogs have been encountered on the ground and climbing on rocks and vegetation around rocky outcrops. Their calls consist of a series of faint insect-like clicks or chirps.

Content.—Three species are placed in the group. Two of these were previously recognized as species: *Eleutherodactylus (Euhyas) klinikowskii* and *zugii* (Fig. 76). The third was described as a subspecies of *E. zugii* (Schwartz 1960) and is elevated here to species status—*Eleutherodactylus (Euhyas) erythroproctus*.

Distribution.—This species series is restricted to western Cuba.

Remarks.—This species group received significant support (100%) in the molecular phylogeny (Fig. 2). It is a radiation of small ground and rock-dwelling species in western Cuba. We recognize *Eleutherodactylus erythroproctus* as a full species because of its structural differences from *E. zugii*; it has short, rather than long, vomerine tooth rows (Schwartz 1960). Also it is geographically isolated from *E. zugii* with no evidence of intergradation. We place *E. klinikowskii* in this species series based on a close relationship with *E. zugii* in the DNA sequence analyses (Heinicke *et al.* 2007), even though the two species have not been considered close relatives in the past (additional material of both species needs to be compared, because the genetic difference is unusually low for valid species). However, certain structural and pattern elements are shared among the three species, but not necessarily in all specimens. These include a narrow middorsal ridge, a wide shank bar, dorsolateral stripes, and narrow dorsal cross-bars that are slightly chevron shaped.

Subgenus *Pelorius* Hedges, 1989

Pelorius Hedges, 1989:329. Type species: *Leptodactylus inoptatus* Barbour, 1914:252, by original designation.

Definition.—Members of the subgenus *Pelorius* can be defined as eleutherodactylid frogs having: (1) head narrow; (2) tympanic membrane differentiated; (3) cranial crests present or absent; (4) dentigerous process of vomers present; (5) “S” condition of the adductor muscles; (6) terminal discs on digits expanded, bearing well-defined circumferential grooves, supported by T-shaped terminal phalanges; (7) Finger I longer than Finger II (shorter than Finger II in *E. chlorophenax*, *E. hypostenor*, and *E. nortoni*); (8) Toe V longer than Toe III; (9) subarticular tubercles prominent; (10) texture of skin on dorsum usually smooth (tuberculate in *E. nortoni*); (11) texture of skin on venter smooth; (12) range in SVL from 48 mm in female *E. aporostegus* to 88 mm in female *E. inoptatus*. All have internal, subgular vocal sacs (Hedges & Thomas 1987) and the two lobes of the liver are approximately the same length and shape.

Content.—The subgenus contains two species series (nine species): the *Eleutherodactylus (Pelorius) inoptatus* and *ruthae* Species Series.

Distribution.—The genus is endemic to the island of Hispaniola in the West Indies (Fig. 77).

Etymology.—The subgeneric name is derived from the Greek adjective *pelorios*, meaning huge or prodigious; the name, which is masculine, was proposed in reference to the comparative large sizes of the included species.

Remarks.—See the Remarks under the genus *Eleutherodactylus* for a discussion of the taxonomic history of the subgenera. This subgenus received moderately strong support (81%) in the molecular phylogeny (Fig. 2). Lynch (1996b) and Lynch and Duellman (1997) questioned the monophyly of *Pelorius*, but that subgenus is supported by allozyme data (Hedges 1989a) and by DNA sequence data (Fig. 2). Even before those studies,

it was recognized as a monophyletic species group of *Eleutherodactylus* based on external morphological traits (Schwartz 1965b; Hedges & Thomas 1987).

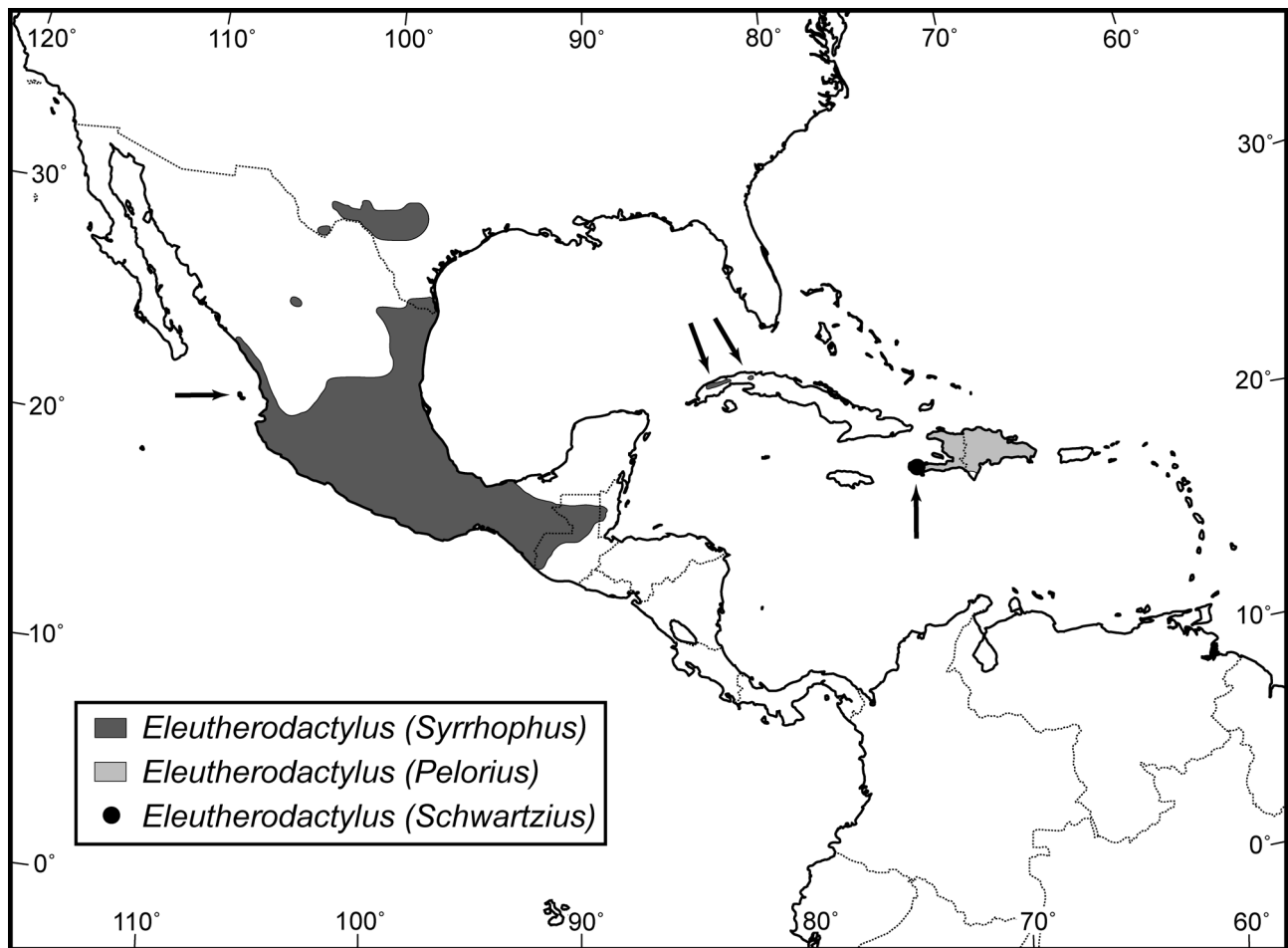


FIGURE 77. Distribution of the subgenera *Pelorius* and *Schwartzius* (Hispaniola), and the Subgenus *Syrrhophus* (Cuba, North America, and Central America), Genus *Eleutherodactylus*, Subfamily Eleutherodactylinae, Family Eleutherodactylidae. The distribution of *Schwartzius* is completely within that of *Pelorius*.

Eleutherodactylus (Pelorius) inoptatus Species Series

Definition.—Species in this series are large, ranging in SVL from 66 mm (females, *E. nortoni*) to 88 mm (females, *E. inoptatus*), sexually dimorphic in size and robust in shape. They have moderately to greatly enlarged digital discs, cranial crests, an otic shelf on the cranium, and bars on the shanks that are not chevron-shaped; they lack dermal cornification on the tip of the snout. Normally they do not burrow in the ground or call from underground cavities.

Content.—Three species are placed in the series: *Eleutherodactylus (Pelorius) chlorophenax*, *inoptatus* (Fig. 78), and *nortoni* (Fig. 79).

Distribution.—The species series is distributed throughout the countries of the Dominican Republic and Haiti on the island of Hispaniola.

Remarks.—This species series received significant support (100%) in the molecular phylogeny (Fig. 2). This series was initially defined by Hedges (1989a), based on protein variation and body size. Lynch (1996b) identified additional osteological characters, and Heinicke *et al.* (2007) added DNA sequence evidence. One species, *Eleutherodactylus chlorophenax*, is poorly known. It was described from a single specimen from the

north slope of the Massif de La Hotte, and no additional specimens have been collected in that region. Hedges and Thomas (1987) collected a specimen on the south slope of the La Hotte but were unable to record its call.



FIGURES 78–81. **78.** *Eleutherodactylus (Pelorius) inoptatus* of the *E. inoptatus* Species Series, from 13 km SSW La Guazara, Barahona, Dominican Republic. Photo by S. B. Hedges. **79.** *Eleutherodactylus (Pelorius) nortoni* of the *E. inoptatus* Species Series, from 6.5 km SW Seguin, Sud’Est, Haiti. Photo by S. B. Hedges. **80.** *Eleutherodactylus (Pelorius) aporostegus* of the *E. ruthae* Species Series, from 5–6 km NW Les Platons, Sud, Haiti. Photo by S. B. Hedges. **81.** *Eleutherodactylus (Schwartzius) counouspeus* from 13.5 km N Camp Perrin, Sud, Haiti. Photo by S. B. Hedges.

Eleutherodactylus (Pelorius) ruthae Species Series

Definition.—Species in this series are moderate to large in SVL, ranging from 48 mm (females, *E. aporostegus*) to 58 mm (females, *E. ruthae*), and apparently are not sexually dimorphic in size, although females of only one species are known. They are robust in shape with a shovel-shaped snout with an unpigmented dermal cornification on the tip, moderately enlarged digital discs, and bars on the shanks that are chevron-shaped. They lack cranial crests and an otic shelf on the cranium. Normally they burrow in the ground or call from underground cavities

Content.—Six species are placed in the series. Three of those were previously recognized as a species: *Eleutherodactylus (Pelorius) hypostenor*, *parapelates*, and *ruthae*. Three additional taxa have been recognized

as subspecies of *E. ruthae* (Schwartz 1965b) and are elevated here to species status—*Eleutherodactylus (Pelorius) aporostegus* (Fig. 80), *Eleutherodactylus (Pelorius) bothroboans*, and *Eleutherodactylus (Pelorius) tychathrous*.

Distribution.—The species series is distributed in disjunct populations within the countries of the Dominican Republic and Haiti on the island of Hispaniola.

Remarks.—This species series received significant support (100%) in the molecular phylogeny (Fig. 2). Schwartz (1965b) described three subspecies of *E. ruthae* from Hispaniola. These have disjunct distributions separated by intervening areas with no known populations and no evidence of intergradation among the subspecies. They have pattern differences, non-overlapping structural differences (e.g., leg proportions), and different mating calls (Schwartz 1965b). By criteria currently used to distinguish different species of the genus *Eleutherodactylus*, these three subspecies are recognized as distinct species here. Based on call differences in other isolated populations of this complex, it is likely that additional species remain to be discovered and described (Hedges & Thomas 1987).

This series was initially defined by Hedges (1989a) as a species group based on protein variation, body size, and leg pattern. Lynch (1996b) identified additional osteological characters, and sequence evidence was added by Heinicke *et al.* (2007) and here (Fig. 2). The largest species, *E. tychathrous*, is known only from the holotype collected 45 years ago, and the distributions of all of the species are spotty. Males construct and call from enclosed underground chambers that have no surface evidence or exit hole. One of us (SBH) observed this behavior in a captive specimen, in which it used its snout and all four limbs to construct the chamber. Hatchlings of *E. aporostegus* were encountered inside a chamber that was opened (Schwartz 1965b); presumably they lay eggs in the chambers. Only a few females, all of *E. ruthae*, are known; these were encountered above ground. All known specimens of the remaining five species are males that were secured while they were vocalizing from their underground chambers.

Subgenus *Schwartzius*, New Subgenus

Type species.—*Eleutherodactylus counouspeus* Schwartz 1964:2.

Definition.—The sole member of the subgenus *Schwartzius* can be defined as an eleutherodactylid frog having: (1) head narrow; (2) tympanic membrane differentiated; (3) cranial crests absent; (4) dentigerous process of vomers present; (5) “S” condition of the adductor muscles; (6) terminal discs on digits expanded, bearing well-defined circumferential grooves, supported by T-shaped terminal phalanges; (7) Finger I shorter than Finger II; (8) Toe V shorter than Toe III; (9) subarticular tubercles prominent; (10) texture of skin on dorsum smooth; (11) texture of skin on venter smooth; (12) maximum SVL 57 mm in female *Eleutherodactylus (Schwartzius) counouspeus*.

Content.—This subgenus includes only one Haitian species, *Eleutherodactylus (Schwartzius) counouspeus* (Fig. 81).

Distribution.—The subgenus is found only at the western end of the Haitian Tiburon peninsula of southwestern Hispaniola (Fig. 77).

Etymology.—This new subgenus is named in memory of Albert Schwartz (1923–1992) for his contributions to the herpetology of the West Indies.

Remarks.—This subgenus is required to accommodate *Eleutherodactylus (Schwartzius) counouspeus*, which branches basally within the Eastern Caribbean Clade of *Eleutherodactylus* according to DNA sequence analysis (Heinicke *et al.* 2007) (Fig. 2). Morphologically, it has a suite of characters that support this basal position and exclude it from either subgenus in the clade (*Eleutherodactylus* or *Pelorius*). In the original description, (Schwartz 1964) placed it in the “*Eleutherodactylus*” *ricordii* Group (now part of the subgenus *Euhyas*), probably because of its smooth venter and rock-dwelling habits, although this was not explicitly

stated. In the allozyme analysis by Hedges (1989a), it was too divergent from all other species to associate it with any subgenus, and therefore it was left “unassigned to series” within the *auriculatus* section (= subgenus *Eleutherodactylus*). This was done because the vomerine tooth rows are short (usually long in the subgenus *Euhyas*), the vocal sac is external (although not prominent; vocal sac is internal or absent in most species of *Euhyas*), and the liver has a short, rounded left lobe (long and pointed in *Euhyas*). Joglar (1989) also associated *E. counouspeus* with the subgenus *Eleutherodactylus* (the West Indian portion of his “*Eleutherodactylus*” *unistrigatus* Group). However, Lynch and Duellman (Lynch & Duellman 1997) returned the species to the subgenus *Euhyas*, apparently based on the presence of a short Toe V relative to Toe II. From this discussion, it can be seen that this species does not fit readily in any named subgenus, and therefore its phylogenetic position as a basal branch in the Eastern Caribbean Clade was not unexpected. The characters allying it with *Euhyas*, such as a smooth venter, inguinal glands (contra Schwartz 1964), and short Toe V, can be interpreted as primitive characters shared with the Western Caribbean Clade.

Subgenus *Syrrhophus* Cope, 1878

Epirhexis Cope, 1866b:96. Type species: *Batrachyla longipes* Baird, 1859:35, by original designation. Suppression of generic name requested by Lynch (1967a:313–315); officially suppressed 1974.

Syrrhophus Cope, 1878:253. Type species: *Syrrhophus marnockii* Cope, 1878:253, by monotypy. Official list of generic names 1974.

Malachylodes Cope, 1879:264. Type species: *Malachylodes guttilatus* Cope, 1879:264, by monotypy. Synonymy by Boulenger (1888:206).

Tomodactylus Günther, 1900:219. Type species: *Tomodactylus amulae* Günther, 1900:219. Synonymy by Hedges (1989a:318).

Definition.—Members of the subgenus *Syrrhophus* can be defined as eleutherodactylid frogs having: (1) head narrow or wide; (2) tympanic membrane differentiated; (3) cranial crests absent; (4) dentigerous process of vomers small or absent; (5) “S” condition of the adductor muscles; (6) terminal discs on digits expanded, bearing well-defined circumferential grooves, supported by T-shaped terminal phalanges; (7) Finger I about equal in length to Finger II (slightly shorter or slightly longer than Finger II in various species); (8) Toe V shorter than Toe III; (9) subarticular tubercles prominent; (10) texture of skin on dorsum variable; (11) texture of skin on venter variable; (12) range in SVL from 19 mm in males of *E. pallidus* to 83 mm in females of *E. zeus*. Additionally, the left lobe of the liver is long and pointed whereas the right lobe is smaller and rounded.

Content.—Two species series (six species groups and 26 species) are recognized: the *Eleutherodactylus* (*Syrrhophus*) *longipes* and *symingtoni* species series.

Distribution.—The subgenus occurs from southern Texas, USA through Mexico to Belize and Guatemala (Fig. 77). Two species, *Eleutherodactylus* (*Syrrhophus*) *symingtoni* and *zeus*, occur in western Cuba.

Etymology.—The subgeneric name is derived from the Greek *syrrhaptos*, meaning sewn together, in reference to the united outer metatarsals, or in reference to the condition of “the nasal bones [in forming] a close continuous roof” (Cope 1878).

Remarks.—See the Remarks under the genus *Eleutherodactylus* for a discussion of the taxonomic history of the subgenera. This subgenus received moderately strong support (85%) in the molecular phylogeny (Fig. 2). In the previous DNA sequence study, it was discovered that two species from western Cuba formerly placed in the subgenus *Euhyas*, *E. symingtoni* and *E. zeus*, clustered with *E. marnockii* in the molecular phylogeny (Heinicke *et al.* 2007). For this reason, they were transferred to the subgenus *Syrrhophus*. Their presence in Cuba supports the inference that mainland members of the subgenus *Syrrhophus* arose through dispersal from Cuba. Because in both Cuban species (each others’ closest relatives) the dentigerous processes of the vomers are present (absent in mainland species of the subgenus), it can be inferred that they represent a basal branch of the *Syrrhophus* radiation. Our new phylogeny (Fig. 2) now includes representatives of three

mainland species groups of the subgenus and they form a monophyletic group (100% support), further supporting the definition of a mainland clade (*E. longipes* Species Series). Although it removes the absence of dentigerous processes as defining character of the subgenus, it is relevant that those two Cuban species have short processes, whereas most species of *Euhyas* have long processes. They are so short that the original describer (Schwartz 1958a) debated as to whether they should be placed in the “*Eleutherodactylus auriculatus*” group (= current subgenus *Eleutherodactylus*). A second character allying them with the mainland species of the subgenus *Syrrhophus* is the relative length of the first and second fingers. In the subgenus *Euhyas*, the first finger is normally shorter than the second, whereas in mainland *Syrrhophus* it is variable but the two fingers are approximately equal in length (Lynch & Duellman 1997). In the two Cuban species of the subgenus, they are approximately equal in length as well. Lynch and Duellman (1997) defined species in the subgenus *Syrrhophus* as lacking sexual size dimorphism, yet females are larger than males in all nine species that had measurements of four or more specimens of each sex (Lynch 1970).

The species groups currently recognized for this subgenus were defined by Lynch (1970), with the addition of the species formerly placed in the genus *Tomodactylus*. Hedges (1989a) recognized two higher level groupings as species series: the *longipes* species series (species formerly placed in the genus *Syrrhophus*) and the *nitidus* species series (species formerly placed in the genus *Tomodactylus*). Our new molecular phylogeny (Fig. 2) shows that the distinction of the former genera *Syrrhophus* and *Tomodactylus* was artificial, because *E. nitidus* (“*Tomodactylus*”) appears in a nested position among species of the former genus “*Syrrhophus*”. Therefore, we recognize only a mainland clade (*E. longipes* Species Series, with six species groups) and a Cuban clade (*E. symingtoni* Species Series).

Eleutherodactylus (Syrrhophus) longipes Species Series

Definition.—Species in this series are robust to moderate in body shape and small to moderate in SVL, ranging from 19 mm (males only, *E. pallidus*) to 40 mm (females, *E. longipes*). Dentigerous process of the vomers and compact lumbar glands are absent.

Content.—Six species groups (24 species) are placed in this species series: the *Eleutherodactylus* (*Syrrhophus*) *leprus*, *longipes*, *marnockii*, *modestus*, *nitidus*, and *pipilans* species groups.

Distribution.—The species series is distributed from southern Texas, USA through Mexico to Belize and Guatemala. Most species occur at low to moderate elevations.

Remarks.—This species series corresponds to the content of the combined genera *Syrrhophus* and *Tomodactylus*, as was previously recognized (Lynch 1970). In the accounts of the species groups, we use the same character definitions as were used by Lynch (1970).

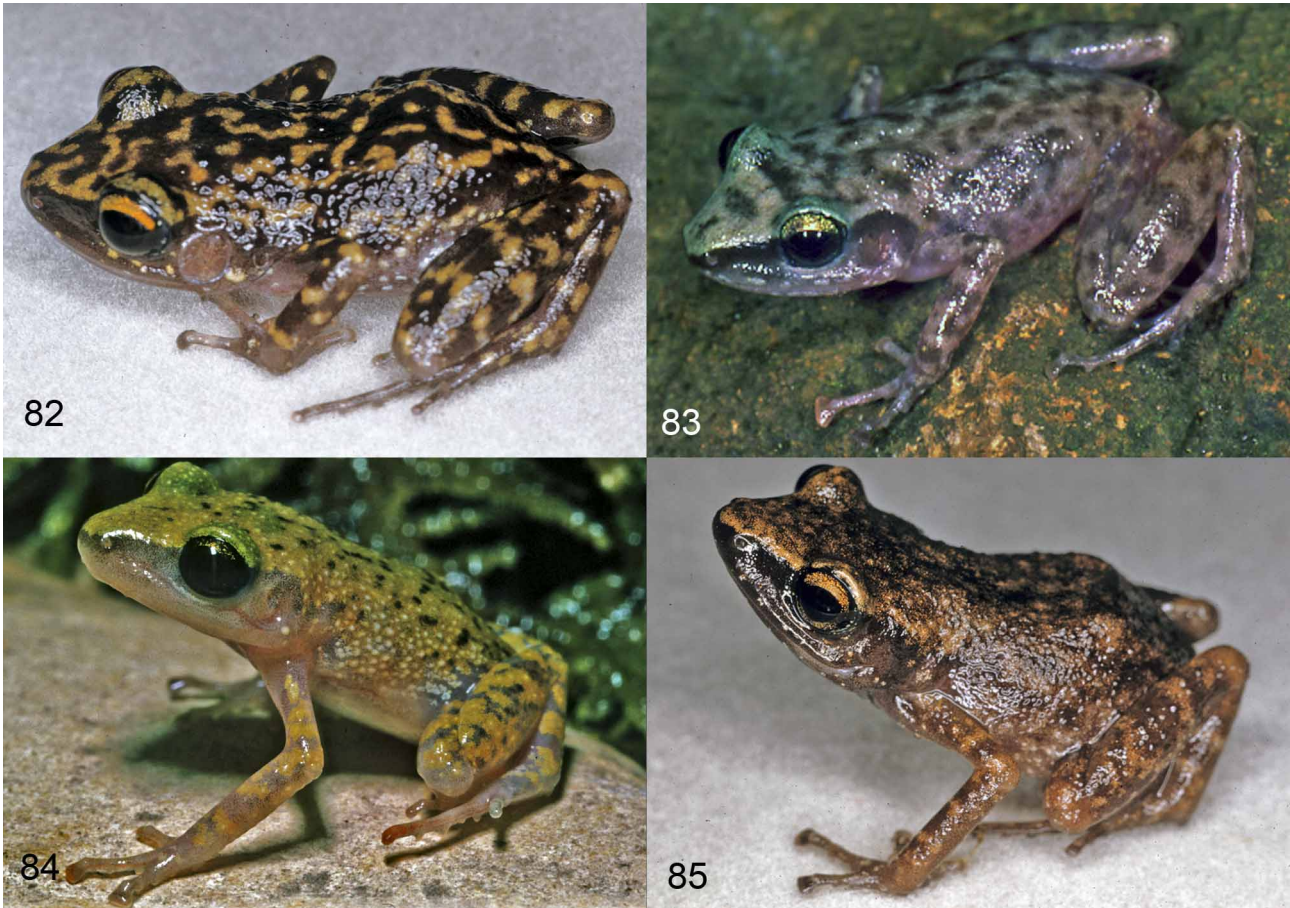
Eleutherodactylus (Syrrhophus) leprus Species Group

Definition.—Species in this group are robust to moderate in body shape and small in SVL, ranging from 24 mm (males only, *E. rubrimaculatus*) to 29 mm (females, *E. leprus*). The snout is acuminate or subacuminate, the first finger is slightly shorter or slightly longer than the second, the digits lack distinct lateral fringes, the digital discs are small, and the outer metatarsal tubercle is conical.

Content.—Three species are placed in the group: *Eleutherodactylus (Syrrhophus) cystignathoides*, *leprus* (Fig. 82), and *rubrimaculatus*.

Distribution.—The species group is distributed from southern Texas (USA) and eastern Mexico to the Isthmus of Tehuantepec and northern Guatemala and Belize.

Remarks.—The definition of this species series is adapted from Lynch (1970).



FIGURES 82–85. **82.** *Eleutherodactylus (Syrrhophus) leprus* of the *E. leprus* Species Group, *E. longipes* Species Series, from San Andres Tuxtla, Veracruz, Mexico. Photo by W. E. Duellman. **83.** *Eleutherodactylus (Syrrhophus) dennisi* of the *E. longipes* Species Group, *E. longipes* Species Series, from El Panehan Cave, 4.8 km N Antiguo Morelos, Tamaulipas, Mexico. Photo by J. A. Campbell. **84.** *Eleutherodactylus (Syrrhophus) marnockii* of the *E. marnockii* Species Group, *E. longipes* Species Series, from San Marcos, Texas. Photo by D. G. Barker. **85.** *Eleutherodactylus (Syrrhophus) teretistes* of the *E. modestus* Species Group, *E. longipes* Species Series, from 5 km NW Tepic, Nayarit, Mexico. Photo by W. E. Duellman.

Eleutherodactylus (Syrrhophus) longipes Species Group

Definition.—Species in this group are robust to moderate in body shape and moderate in SVL, ranging from 32 mm (females, *E. dennisi*) to 40 mm (females, *E. longipes*). The snout is acuminate, the first finger is slightly shorter than the second, the digits bear lateral fringes, the digital discs are large and ovate, and the outer metatarsal tubercle is not conical.

Content.—Two species are placed in the group: *Eleutherodactylus (Syrrhophus) dennisi* (Fig. 83) and *longipes*.

Distribution.—The species group occurs in the Sierra Madre Oriental from central Nuevo León to northern Hidalgo in eastern Mexico.

Remarks.—The definition of this species group is adapted from Lynch (1970).

Eleutherodactylus (Syrrhophus) marnockii Species Group

Definition.—Species in this group are robust in body shape and small to moderate in SVL, ranging from 20 mm (*E. verruculatus*) to 35 mm (females, *E. marnockii*). The snout is rounded, the first finger is slightly shorter or equal in length to the second, the digits lack lateral fringes, the digital discs are moderate to large in size and rounded or truncate in outline, and the outer metatarsal tubercle is not conical.

Content.—Four species are placed in the group: *Eleutherodactylus (Syrrhophus) guttilatus*, *marnockii* (Fig. 84), *verrucipes*, and *verruculatus*.

Distribution.—The species group is distributed primarily on the Mexican Plateau and in the Sierra Madre Oriental of central and eastern Mexico, from southern Texas (USA) west to central Durango and south to Hidalgo and west-central Veracruz, Mexico.

Remarks.—The definition of this species group is adapted from Lynch (1970). Firschein (1954) considered “*Syrrhophus*” *verruculatus* to be a *nomen dubium* which should be omitted from lists of valid species. Lynch and Duellman (1997) followed this recommendation, although Frost *et al.* (2006) recognized it as valid. Firschein (1954) considered it a *nomen dubium* because he found errors in the type locality and because all specimens allocated to this species, other than the type, were done so in error. Firschein (1954) said that he was “inclined to believe that the type belonged to some other genus of the family Leptodactylidae.” However, he did not examine the type (nor have we done so) and noted that E. R. Dunn’s examination of the type revealed that it lacks vomerine teeth and lumbar glands. However, considering the type locality, these characters would place it within *Syrrhophus*. For these reasons, we continue to recognize this species as valid. It may well be a valid species represented by a single specimen. Also, the error in the type locality (Huatusco, Veracruz, Mexico) was relatively minor (a misspelling of one letter), and there was good evidence, as Firschein conceded, that it was collected in that region of Mexico. We tentatively assign *E. verruculatus* to the *E. marnockii* Species Group based on its large digital discs and skin texture (tuberculate dorsum and areolate belly), as noted in the original description. The only other species of the *E. longipes* Species Series with a tuberculate dorsum and areolate venter is *E. verrucipes*, also in this species group.

Eleutherodactylus (Syrrhophus) modestus Species Group

Definition.—Species in this group are robust to moderate in body shape and small in SVL, ranging from 19 mm (males only, *E. pallidus*) to 27 mm (females, *E. interorbitalis*). The snout is subacuminate, the first finger is slightly shorter than the second, the digits bear poorly defined lateral fringes, the digital discs are moderate to large and truncate in outline, and the inner metatarsal tubercle is twice as large (or larger) as the outer metatarsal tubercle.

Content.—Five species are placed in the group: *Eleutherodactylus (Syrrhophus) interorbitalis*, *modestus*, *nivicolimae*, *pallidus*, and *teretistes* (Fig. 85).

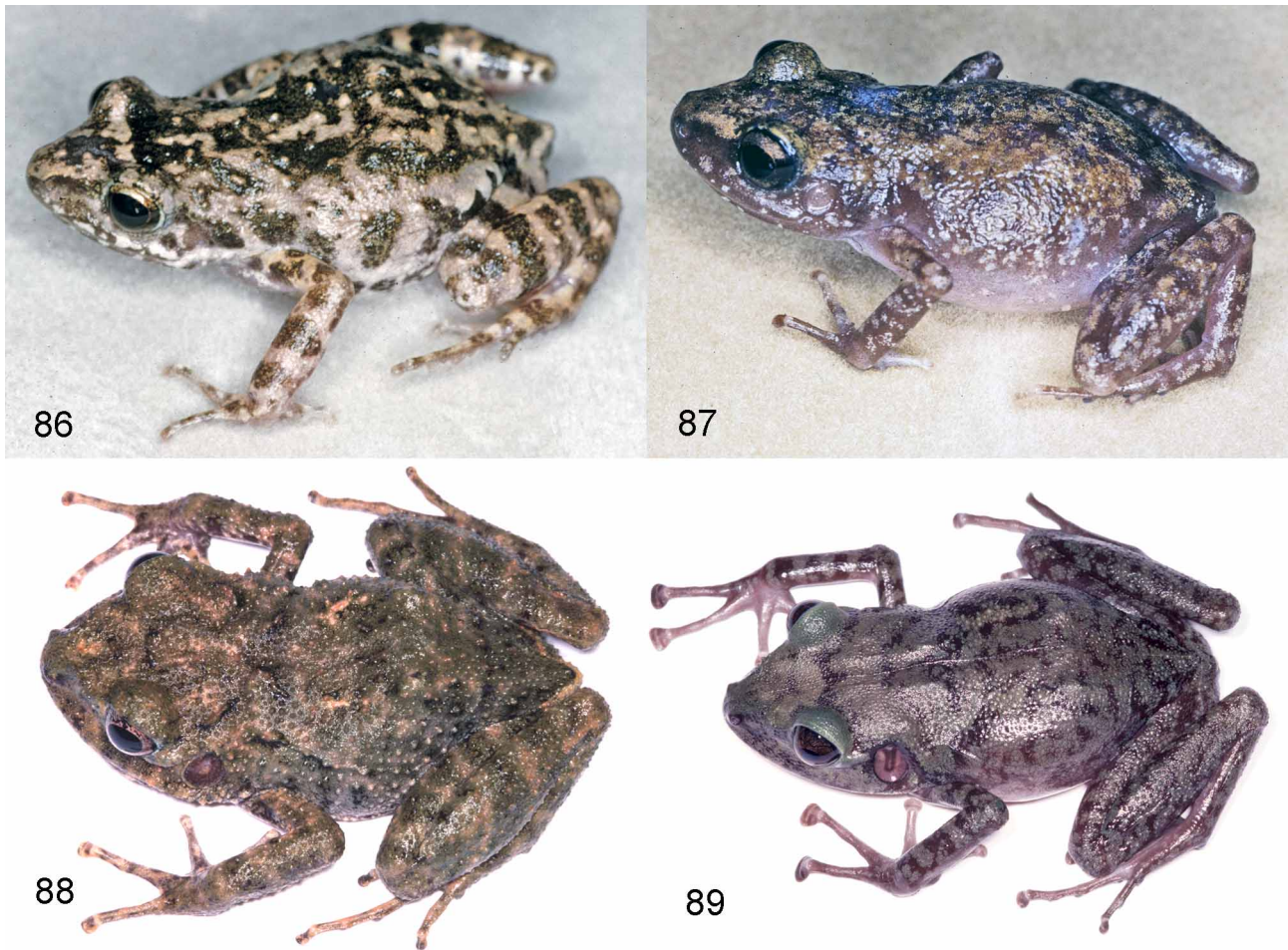
Distribution.—The species group is distributed in the Pacific lowlands and the Sierra Madre Occidental of western Mexico, from Sinaloa and Durango south to Colima, and includes the Tres Marias Islands.

Remarks.—The definition of this species group is adapted from Lynch (1970).

Eleutherodactylus (Syrrhophus) nitidus Species Group

Definition.—Species in this group are robust to moderate in body shape and small to moderate in SVL, ranging from 23 mm (males, *E. rufescens*) to 32 mm (males, *E. saxatilis*). They have relatively short legs and a granular (areolate) venter. Dentigerous processes of the vomers are absent. Compact lumbar glands are present.

Content.—Nine species are placed in this species group: *Eleutherodactylus (Syrrophus) albolabris*, *angustidigitum*, *dilatatus*, *grandis*, *maurus*, *nitidus* (Fig. 86), *rufescens*, *saxatilis*, and *syristes*.



FIGURES 86–89. **86.** *Eleutherodactylus (Syrrophus) nitidus* of the *E. nitidus* Species Series, from 2.4 km N Huajintlán, Morelos, Mexico. Photo by W. E. Duellman. **87.** *Eleutherodactylus (Syrrophus) pipilans* of the *E. pipilans* Species Group, *E. longipes* Species Series, from 1 km S Bochil, Chiapas, Mexico. Photo by W. E. Duellman. **88.** *Eleutherodactylus (Syrrophus) symingtoni* of the *E. symingtoni* Species Series, from Soroa, Pinar del Rio, Cuba. Photo by S. B. Hedges. **89.** *Eleutherodactylus (Syrrophus) zeus* of the *E. symingtoni* Species Series, from San Vicente, Pinar del Rio, Cuba. Photo by S. B. Hedges.

Distribution.—Central, west-central, and southern Mexico from the Sierra Madre Occidental in southwest Durango south Oaxaca.

Remarks.—This species group corresponds to the content of the genus *Tomodactylus* as was previously recognized (Lynch 1970). It was distinguished from “*Syrrophus*” (= the *Eleutherodactylus (Syrrophus) longipes* Species Series) primarily by the presence of compact lumber glands (Lynch 1968a, 1971). It is recognized as a species group here rather than a species series because of the phylogenetic results (Fig. 2) showing that it is more closely related to one species group (*E. pipilans*) of the former genus *Syrrophus* than to another species group (*E. marnockii*) of that former genus.

Hedges (1989a) provided the replacement name *Eleutherodactylus maurus* (for *E. fuscus* Davis and Dixon 1955, preoccupied by *E. fuscus* Lynn and Dent 1943). Dixon (1957) suggested four groupings within the assemblage that is referred to here as the *Eleutherodactylus (Syrrophus) nitidus* Species Group. One of those groups included the species *E. angustidigitum*, *E. grandis*, and *E. maurus*. However, the remaining three

groups included single species, and the subsequently described species, *E. rufescens* and *E. saxatilis*, also do not fit readily into those four groups. Rather than recognize five or six species subgroups for these nine species, we have chosen not to recognize any divisions within the species group until a review or phylogenetic analysis is undertaken.

Eleutherodactylus (Syrhophus) pipilans Species Group

Definition.—The single species in this group is robust in body shape and small in SVL (females, 29 mm). The snout is subacuminate, the first finger is equal in length to the second, the digits lack lateral fringes, the digital discs are small, and the metatarsal tubercles are subequal in size.

Content.—A single species is placed in the group: *Eleutherodactylus (Syrhophus) pipilans* (Fig. 87).

Distribution.—The species is distributed from south-central Mexico (states of Mexico, Guerrero, Oaxaca, and Chiapas) to southwestern Guatemala.

Remarks.—The definition of this species group is adapted from Lynch (1970).

Eleutherodactylus (Syrhophus) symingtoni Species Series

Definition.—Species in this series are moderate in body shape and large in SVL, ranging from 69 mm (females, *E. symingtoni*) to 83 mm (females, *E. zeus*). The dentigerous processes of the vomers are short. Lumbar glands are absent. The dorsum is tuberculate (heavily so in *E. symingtoni*), with one or more canthal spines. They have long digits, and digital disc size varies from small (*E. symingtoni*) to large (*E. zeus*). The dorsum is either dark brown to brown (*E. symingtoni*) or olive-brown to bluish-brown (*E. zeus*). These terrestrial frogs mostly inhabit rocks. The calls consist of a low-frequency whistle-like noise (Díaz *et al.* 2007b).

Content.—Two species are placed in this species series: *Eleutherodactylus (Syrhophus) symingtoni* (Fig. 88) and *zeus* (Fig. 89).

Distribution.—The species series is restricted to low to moderate elevations in western Cuba.

Remarks.—This species series received significant support (100%) in the molecular phylogeny (Fig. 2). These two sympatric species are large, have short vomerine dentigerous processes, and share distinctive canthal tubercles, traits that indicate that they are close relatives (Schwartz 1958a).

Subfamily Phyzelaphryinae, New Subfamily

Type genus.—*Phyzelaphryne* Heyer, 1977:152.

Definition.—In these small eleutherodactylid frogs the terminal digits are not or barely expanded; the digits are pointed apically; the circumferential grooves are weak or in *Phyzelaphryne* evident only laterally; Finger IV has three phalanges (only two in some *Adelophryne*). The species are inhabitants of terrestrial leaf litter and none exceeds 20 mm in SVL.

Content.—The two genera contain six species.

Distribution.—The species have discontinuous distributions in northeastern Brazil, the Guianan Region, and the Amazon Basin in South America (Fig. 29).

Remarks.—The molecular support (Fig. 4) for this subfamily is significant (99%). It supports the suggestion of a close relationship of the two genera by Hoogmoed and Lescure (1984), based on sharing of slightly expanded terminal discs that have incomplete circumferential grooves and pointed tips.

Genus *Adelophryne* Hoogmoed and Lescure, 1984

Adelophryne Hoogmoed and Lescure, 1984:92. Type species: *Adelophryne adiaastola* Hoogmoed and Lescure, 1984:95, by original designation.

Definition.—These minute eleutherodactylid frogs are characterized by: (1) head no wider than body; (2) tympanic membrane differentiated; (3) cranial crests absent; (4) dentigerous processes of vomers small, transverse; (5) condition of adductor muscle unknown; (6) terminal discs on digits barely expanded, apically pointed, with circumferential grooves and discs; terminal phalanges knobbed or barely T-shaped; (7) Finger I shorter than Finger II; Finger IV with two (*A. adiaastola* and *pachydactyla*) or three (*A. baturitensis*, *gutturosa*, and *maranguapensis*) phalanges; (8) Toes III longer than Toe V; (9) subarticular tubercles not projecting; (10) dorsum smooth; (11) venter smooth; (12) maximum SVL in females 17 mm.

Content.—Five species are presently recognized: *Adelophryne adiaastola*, *baturitensis*, *gutturosa* (Fig. 90), *maranguapensis*, and *pachydactyla*.

Distribution.—The genus has a discontinuous distribution in eastern and northeastern Brazil and in the Guiana Shield Region in northeastern South America, and in the upper Amazon Basin (Fig. 29).

Etymology.—The generic name is derived from the Greek *adelos*, meaning unseen, unknown, or obscure, and the Greek *phryne*, meaning toad. The genus is feminine in gender.

Remarks.—These minute frogs inhabit leaf litter. Hoogmoed *et al.* (1994) provided a review of the genus and a key to the species. Until now, none of the species has been included in a molecular phylogenetic analysis.



FIGURES 90–91. 90. *Adelophryne gutturosa* from La Laja, Bolívar, Venezuela. Photo by César Barrio A. 91. *Phyzelaphryne miriamae* from 40 km S Manaus, Amazonas, Brazil. Photo by J. P. Caldwell.

Genus *Phyzelaphryne* Heyer, 1977

Phyzelaphryne Heyer, 1977:152. Type species: *Phyzelaphryne miriamae* Heyer, 1977:153, by original designation.

Definition.—This genus of eleutherodactylid is characterized by: (1) head not as wide as body; (2) tympanic membrane differentiated; (3) cranial crests absent; (4) dentigerous processes of vomers distinct, transverse; (5) “S + E” condition of adductor muscle; (6) terminal discs on digits not expanded, acuminate on Fingers III and IV and on toes; circumferential grooves present laterally; terminal phalanges T-shaped; (7) Finger I slightly shorter than Finger II about equal in length; (8) Toe III longer than Toe V; (9) subarticular tubercles protruding moderately; (10) dorsum shagreen; (11) venter smooth; (12) SVL to 20 mm in females.

Content.—One species is recognized: *Phyzelaphryne miriamae* (Fig. 91).

Distribution.—The single species occurs in the drainages of the Rio Madeira and Rio Tapajos in Amazonian Brazil (Fig. 29).

Etymology.—The generic name is derived from the Greek *phyzelos*, meaning shy, and the Greek *phryne*, meaning toad. The name is feminine in gender.

Remarks.—See comments in the subfamily account concerning the close relationship of this genus to *Adelophryne*. Until now, this genus has not been included in any molecular phylogenetic analysis.

Family Strabomantidae, New Family

Eleutherodactylinae (part) Lutz, 1954:157. Type genus *Eleutherodactylus* Duméril and Bibron, 1841:620.

Eleutherodactylini (part)—Lynch, 1971:142 [Tribe].

Brachycephalinae (part)—Dubois, 2005b:4.

Brachycephalidae (part)—Frost *et al.* 2006.

Type genus.—*Strabomantis* Peters, 1863:405.

Definition.—Frogs of the family Strabomantidae have: (1) sternum cartilaginous; (2) vertebral shield lacking; (3) transverse processes of posterior presacral vertebrae not broadly expanded; (4) cervical cotyles widely spaced; (5) eight presacral vertebrae, Presacrals I and II not fused; (6) cranial elements not co-ossified with overlying skin; (7) omosternum present; (8) sacral diapophyses rounded or barely dilated; (9) maxillary arch usually dentate; teeth blunt, pedicellate; (10) alary processes of premaxillae broad at base, usually directed dorsally or posterodorsally; (11) palatal shelf of premaxilla usually broad, indented or not; (12) pars facialis of maxilla usually deep, not exostosed; (13) palatal shelf of maxilla moderately broad, bearing pterygoid process or not; (14) maxillary arch complete; maxillae tapering posteriorly; quadratojugal slender; (15) nasals usually large with broad median contact; (16) nasals usually not in contact with maxillae or pterygoids; (17) nasals not in contact with frontoparietals; (18) frontoparietal fontanelle usually absent; (19) frontoparietals usually not exostosed; cranial crests present in *Strabomantis*, and some *Pristimantis*; (20) frontoparietals fused with prootics or not; (21) temporal arcade absent; (22) epiotic eminences prominent to indistinct; (23) carotid artery passing dorsal to cranial elements; (24) zygomatic ramus of squamosal broad to slender, usually not in contact with maxilla; (25) otic ramus of squamosal short to elongate, expanded into otic plate or not; (26) squamosal-maxilla angle 44–67°; (27) columella present, except in *Euparkerella* and *Holoaden*; fenestra ovalis directed laterally; (28) vomers variable in size, greatly reduced in *Euparkerella*; dentigerous processes absent in *Euparkerella*, *Noblella*, and most *Phrynopus* and *Psychrophrynella*; (29) neopalatines usually broad; slender in *Euparkerella*, *Holoaden*, *Phrynopus*, and *Psychrophrynella*; bearing odontoid ridge in *Oreobates*; (30) sphenethmoid usually entire, divided in *Euparkerella*; (31) anterior ramus of parasphenoid narrow to broad, not keeled; (32) parasphenoid alae at right angle to axis of skull or deflected posteriorly, usually not overlapped by pterygoids; (33) pterygoid lacking ventral flange; anterior ramus not reaching neopalatine, except in *Oreobates*; (34) occipital condyles small to large, stalked or not, widely separated medially; (35) mandible lacking odontoids; (36) terminal phalanges T-shaped, knobbed, or bearing hook-like lateral process (*Euparkerella*); (37) usually three phalanges in Finger IV (two in *Noblella myrmecoides*); Finger IV reduced or absent in *Euparkerella*; (38) Toe I fully developed and free; (39) alary process of hyoid plate on slender stalk or not; process absent in *Euparkerella* and *Holoaden*; (40) mandibular ramus of trigeminal nerve passing lateral to the *m. adductor mandibulae*, passing medially in some *Strabomantis*, anterior to the *m. adductor mandibulae* in *Pristimantis (Yunganastes)*, passing between two slips of the muscle in *Noblella myrmecoides*; (41) prominent external body glands usually absent, entire dorsum with glands in *Holoaden*, and inguinal glands in *Euparkerella*, and inguinal and axillary glands in *Oreobates*; (42) males usually having single, median, subgular vocal sac (absent in *Holoaden*, unknown in *Atopophrynus*); (43) males having vocal slits

and nonspinous nuptial pads or not; (44) fingers unwebbed; toes usually unwebbed or webbed basally, but webbing extensive in some *Strabomantis*; (45) terminal digits usually expanded with pads set off by distinct circumferential grooves; digits apically pointed in *Euparkerella*, *Geobatrachus* and *Noblella*; grooves absent in *Barycholos*, *Bryophryne*, *Euparkerella*, *Geobatrachus*, *Holoaden*, *Lynchi*, *Noblella*, *Oreobates*, *Phrynopus*, and *Psychrophrynella*; (46) inner and outer metatarsal tubercles present, inner tubercle not spade-like; (47) tympanic membrane and annulus well differentiated or not; (48) amplexus axillary, inguinal in at least some *Phrynopus*; (49) eggs deposited in terrestrial or arboreal situations and undergoing direct development; (50) range in SVL from 13 mm and 14 mm in male *Pristimantis imitatrix* and *Psychrophrynella boettgeri*, respectively, to 106 mm in female *Strabomantis cheiroplethus*.

Content.—There are 530 species placed in two subfamilies and 16 genera, one of which contains three subgenera.

Distribution.—Fourteen genera are restricted to tropical and subtropical South America as far south as northwestern Argentina; the family is most diverse in western South America and is meagerly represented in eastern Brazil. *Pristimantis* and *Strabomantis* extend into Central America (to Honduras and Costa Rica, respectively) and the former extends into the Lesser Antilles (Fig. 92).

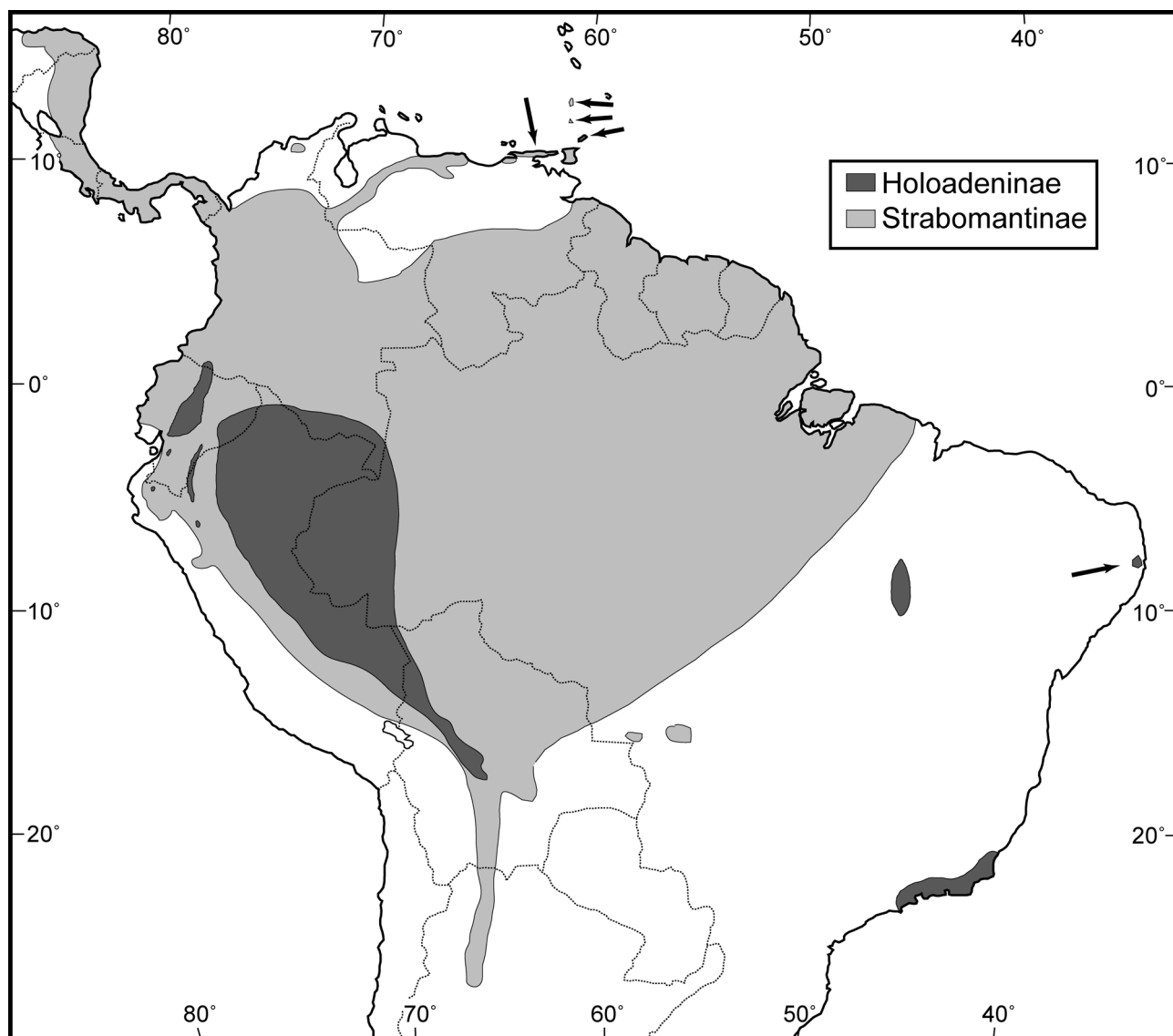


FIGURE 92. Distribution of the two subfamilies comprising the Family Strabomantidae: Strabomantinae completely overlaps that of Holoadeninae in western South America.

Remarks.—This family received moderate support (55%) in the ML molecular phylogeny (Fig. 4) and the Bayesian posterior probability was 100%. It is a more inclusive South American Clade than was defined in our earlier work (Heinicke *et al.* 2007) and includes all South American terraranans except a few species in the Craugastoridae and Eleutherodactylidae and the Southeast Brazil Clade (Brachycephalidae) of 40 species. The vast majority of strabomantids are associated with the Andean uplift in the western and northwestern part of the continent. Five of the recognized genera—*Atopophrynus* (1 species), *Dischidodactylus* (2 species), *Euparkerella* (4 species), *Geobatrachus* (1 species), and *Niceforonia* (3 species)—are not included in the molecular analyses because tissues were not available for our use. *Niceforonia* and the monotypic *Atopophrynus* and *Geobatrachus* are endemic to Andean Colombia, and the two species of *Dischidodactylus* are known from two tepuis in southern Venezuela. Until now, *Niceforonia* has been a synonym of the strabomantid genus *Phrynopus*. The remaining four genera are placed here in Strabomantidae principally on the basis of geography.

Each of the four species of *Euparkerella* has a restricted distribution in the Atlantic Coastal Forest in southeastern Brazil. Members of this genus differ from other strabomantids in several morphological characters (absence of a columella, greatly reduced vomers, divided sphenethmoid, structure of terminal phalanges, and reduction or loss of Finger IV), whereas they share some features, especially phalangeal reduction, with *Brachycephalus* (Izecksohn 1988; Giaretta & Sawaya 1998). In contrast, Heyer (1975) found that *Euparkerella* and *Holoaden* (a strabomantid) were closest relatives in a phylogenetic analysis of morphological data. Molecular sequence data will be needed to confirm the position of this enigmatic genus.

Subfamily Holoadeninae, New Subfamily

Type Genus.—*Holoaden* Miranda-Ribeiro, 1920:319.

Definition.—These are strabomantid frogs that have narrow terminal digits on the fingers and toes and lack circumferential grooves (present distally in *Noblella*); the toes are apically pointed in *Euparkerella* and some *Noblella*, and the terminal phalanges are knob-shaped (*Bryophryne*, *Holoaden*, and *Psychophrynella*), hook-shaped (*Euparkerella*), or weakly T-shaped (*Barycholos* and *Noblella*). The tympanic membrane is differentiated only in *Barycholos*, *Noblella*, and *Psychophrynella boettgeri*. These terrestrial frogs range in SVL from 14 mm in male *Psychophrynella boettgeri* to 48 mm in female *Holoaden*.

Content.—The 37 currently recognized species are placed in six genera.

Distribution.—The subfamily is confined to South America; it occurs on the Pacific lowlands of Ecuador and southern Colombia, in the Andes of southern Ecuador, Peru, and Bolivia, and in the Amazon Basin; two genera (*Euparkerella* and *Holoaden*) are endemic to the Atlantic Coastal Forest in southeastern Brazil (Fig. 92–94).

Remarks.—This subfamily received moderately strong support (94%) in the ML molecular phylogeny (Fig. 4) and the Bayesian posterior probability was 100%.

Genus *Barycholos* Heyer, 1969

Barycholos Heyer, 1969:6. Type species: *Leptodactylus pulcher* Boulenger, 1898:122, by original designation.

Definition.—This genus is characterized by: (1) head as broad as body; (2) tympanic membrane differentiated; (3) cranial crests absent; (4) dentigerous processes of vomers small, transverse; (5) “S” condition of adductor muscle; (6) terminal discs on fingers not expanded, those of toes slightly expanded, round; circumferential grooves absent; terminal phalanges weakly T-shaped; (7) Finger I longer than Finger II; (8) Toe III

longer than Toes V; (9) subarticular tubercles projecting; (10) dorsum smooth with short, longitudinal ridges; (11) venter smooth; (12) SVL to 31 mm in females.

Content.—Two species are placed in this genus: *Barycholos pulcher* (Fig. 95) and *ternetzi*.

Distribution.—One species occurs on the Pacific lowlands of Ecuador and the other inhabits highlands and lowlands in eastern Brazil from Maranhão to Goiás and Mato Grosso (Fig. 93).

Etymology.—The generic name is derived from the Greek *baruxolos*, meaning savage, in reference to Jay M. Savage. The genus is masculine in gender.

Remarks.—This genus was originally placed in Leptodactylinae by Heyer (1969) and Lynch (1971), because of the condition of the body style of the pectoral girdle. Heyer (1975) found that *Barycholos* was allied with “*Eleutherodactylus*” and, later, Lynch (1980) determined that *Barycholos* was most closely related to a then member of the “*Eleutherodactylus*” *discoidalis* Group, “*E.*” *nigrovittatus* (here placed in the strabomantine genus *Isodactylus*). *Barycholos ternetzi* was included in the phylogenetic analyses of molecular data by Heinicke *et al.* (2007). Here, both species were included and they were found to be each others closest relatives (100% support), supporting the continued recognition of this genus (Fig. 2). Based on the molecular phylogeny (Fig. 4), *Barycholos* is closely related to *Noblella*. Unlike other holoadenines, these genera display weakly T-shaped terminal phalanges.

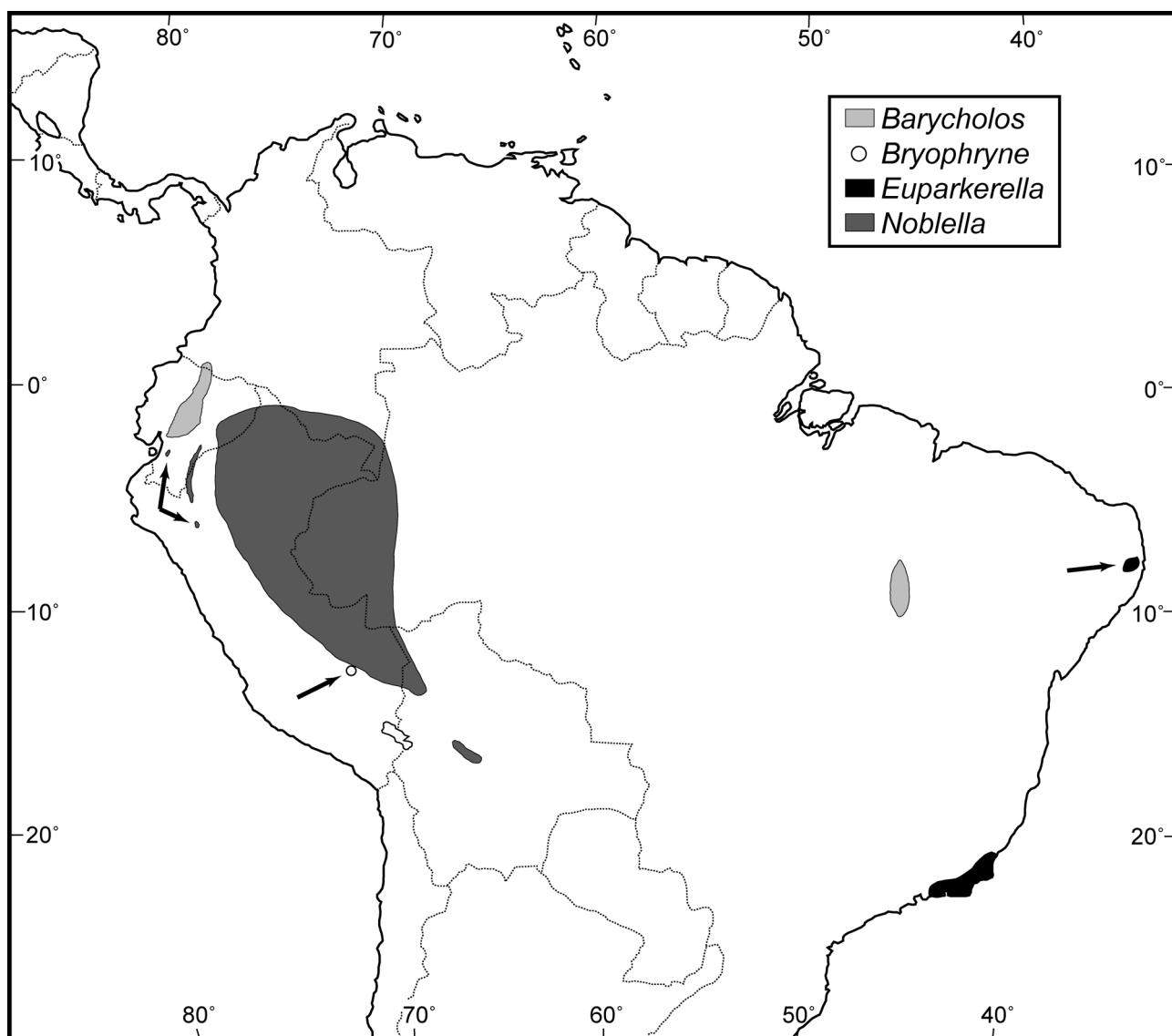


FIGURE 93. Distribution of the genera *Barycholos*, *Bryophryne*, *Euparkerella*, and *Noblella*, Subfamily Holoadeninae, Family Strabomantidae.

Genus *Bryophryne*, New Genus

Phrynopus (in part)—Lynch, 1975a:8.

Type species.—*Phrynopus cophites* Lynch, 1975a:16.

Definition.—This genus is characterized by (1) head narrow, not as wide as body; (2) tympanic membrane, tympanic annulus, columella, and cavum tympanicum absent (3) cranial crests absent; (4) dentigerous processes of vomers absent; (5) “S” condition of adductor muscle; (6) tips of digits narrow, rounded; circumferential grooves absent; terminal phalanges knob-shaped; (7) Finger I shorter than Finger II; (8) Toes III and V about equal in length; (9) subarticular tubercles not projecting; (10) dorsum finely areolate; (11) venter coarsely areolate; (12) SVL to 29.3 mm.

Content.—This genus contains two species: *Bryophryne bustamantei* and *cophites* (Fig. 96).

Distribution.—The genus occurs at elevations of 2900–4120 m in the Cordillera Oriental in the Departamento de Cusco in southern Peru (Fig. 93).

Etymology.—The generic name is derived from the Greek *bryon* meaning moss and the Greek *phrynos*, meaning toad. The name is feminine in gender and refers to a common habitat of these species.

Remarks.—At a time when some frogs now placed in *Bryophryne*, *Lynchius*, *Niceforonia*, *Phrynopus*, and *Psychrophrynella* were considered to be congeneric, *Bryophryne* (then *Phrynopus*) *cophites* was considered to be closely related to species of “*Phrynopus*” now placed in *Psychrophrynella* (Lynch 1975a; Cannatella 1984). Our analyses of sequence data (Figs. 3–4) reveal that *Bryophryne* is the closest relative of a clade containing *Barycholos* and *Noblella lochites* within the Holoadeninae, with moderately strong support (81%) in the ML phylogeny (Fig. 4) and significant (97%) Bayesian support. The Holoadeninae also contains *Psychrophrynella* but not *Lynchius*, *Niceforonia*, and *Phrynopus*; the last three genera are in Strabomantinae.

Genus *Euparkerella* Griffiths, 1959

Euparkerella Griffiths, 1959:477. Type species: *Sminthillus brasiliensis* Parker, 1926:201, by original designation.

Definition.—This genus of relatively small species is characterized by: (1) head narrower than body; (2) tympanic membrane and annulus absent; (3) cranial crests absent; (4) dentigerous processes of vomers absent; (5) “S” condition of adductor muscle; (6) discs on digits small, pointed; circumferential grooves absent; terminal phalanges with small, hook-like lateral processes; Finger IV reduced or absent; (7) Fingers I and II about equal in length; (8) Toe III slightly longer than Toe V; (9) subarticular tubercles not projecting; (10) dorsum finely granular; (11) venter areolate; (12) SVL to 20 mm in females.

Content.—The genus contains four species: *Euparkerella brasiliensis*, *cochranae* (Fig. 97), *robusta*, and *tridactyla*.

Distribution.—The distribution is restricted to the Atlantic Coastal Forest in southeastern Brazil (Fig. 93).

Etymology.—The generic name, a patronym for H. W. Parker, who named the type species, has the Greek prefix *eu-*, meaning true, and the Greek suffix *-ella*, a diminutive form. The gender is feminine.

Remarks.—The phylogenetic relationships of these small frogs are unknown, and this genus has not been included in any molecular phylogeny. The similarity in reduction of Finger IV is like that in some species of *Noblella*. The presence of inguinal glands is shared with some species of *Syrrhophus*. The reduction in the number of phalanges and of entire digits, as seen in *Euparkerella*, was compared with the even greater reduction in *Brachycephalus* (including *Psyllophryne*) by Izechsohn (1988) and Giaretta and Sawaya (1998). These possible relationships await much needed analyses of molecular data. Until then, we place this genus tentatively in the subfamily Holoadeninae, in part based on its association with *Holoaden* in some early phylogenetic analyses of morphological data (Heyer 1975).

Genus *Holoaden* Miranda-Ribeiro, 1920

Holoaden Miranda-Ribeiro, 1920:319. Type species: *Holoaden lüderwaldti* Miranda-Ribeiro, 1920:319, by monotypy.

Definition.—Frogs of the genus *Holoaden* are characterized by: (1) Head not as wide as body; (2) tympanic membrane and annulus absent; (3) cranial crests absent; (4) dentigerous processes of vomers prominent, transverse; (5) “S” condition of adductor muscle; (6) discs on digits small, rounded; circumferential grooves absent; terminal phalanges knob-shaped; (7) Finger I longer than Finger II; (8) Toe III longer than Toe V; (9) subarticular tubercles not protuberant; (10) dorsum highly glandular; (11) venter areolate; (12) SVL to 48 mm in females.

Content.—Two species are recognized in the genus: *Holoaden bradei* and *luederwaldti* (Fig. 98).

Distribution.—*Holoaden* is endemic to the Atlantic Coastal Forest in southeastern Brazil (Fig. 94).

Etymology.—The generic name is derived from the Greek *holos*, meaning whole or entire, and the Greek *aden*, meaning gland. The name refers to the dorsum being covered with pustular glands. The gender is neuter.

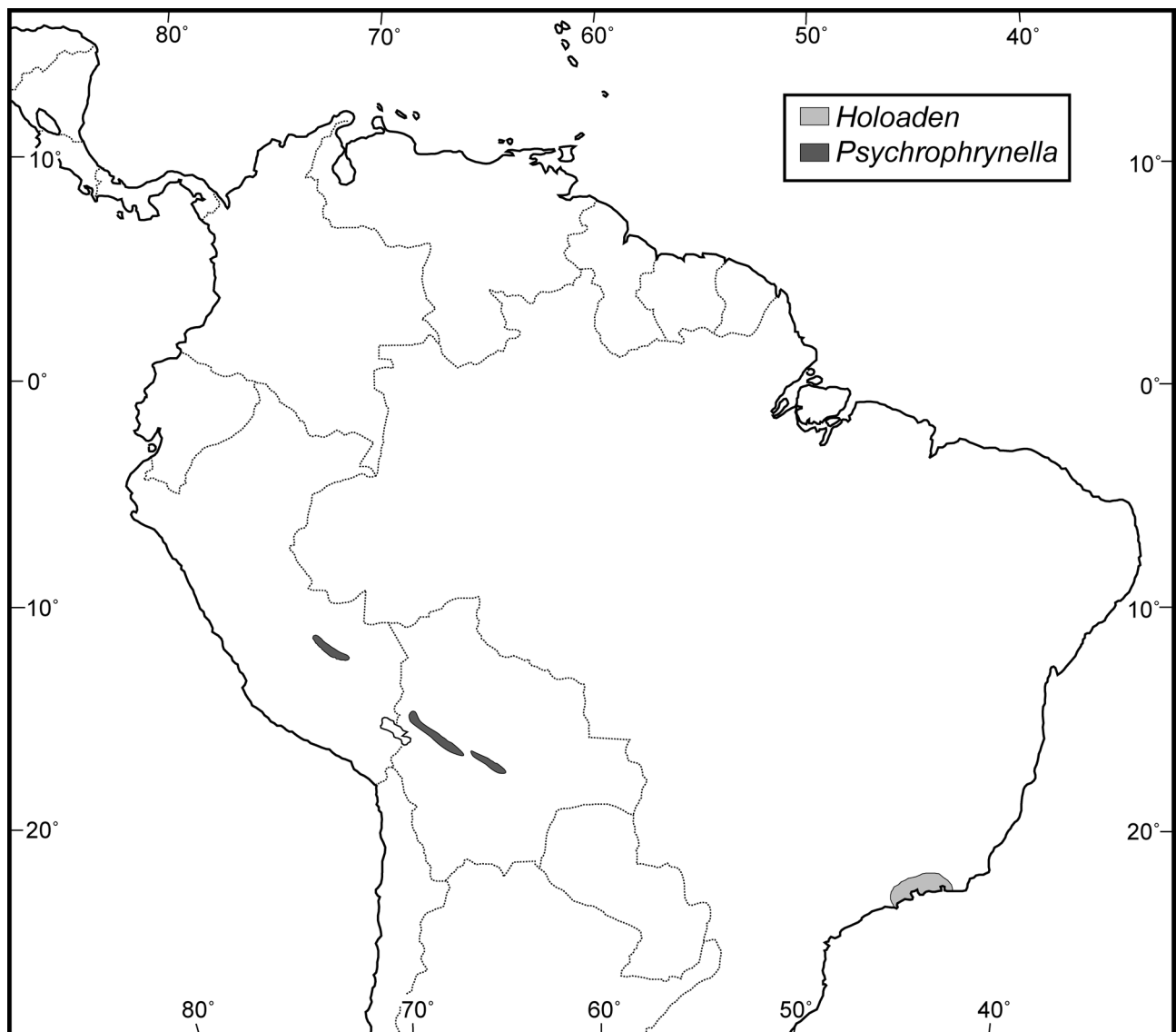


FIGURE 94. Distribution of the genera *Holoaden* and *Psychrophrynella*, Subfamily Holoadeninae, Family Strabomantidae.

Remarks.—In the phylogenetic analyses of molecular data presented by Heinicke *et al.* (2007), *Holoaden bradei* was associated with various species of *Phrynopus* or *Phrynopus* and *Barycholos ternetzi*. Here we have included the other species, *H. luederwaldti*, and it clusters with *H. bradei* as expected (Fig. 2). In our tree of mitochondrial and nuclear gene sequences (Fig. 4) the genus *Holoaden* clusters, with significant ML (96%) and Bayesian (100%) support, with the clade containing *Barycholos*, *Noblella*, and *Bryophryne*. The genus is unique among strabomantid frogs in having many rounded glands on the dorsum.



FIGURES 95–100. **95.** *Barycholos pulcher* from Estación Biológica Río Palenque, Los Rios, Ecuador. Photo by William E. Duellman. **96.** *Bryophryne cophites* from Abra Acanacu, Vusco, Peru. Photo by W. E. Duellman. **97.** *Euparkerella cochranæ* from Magé, Rio de Janeiro, Brazil. Photo by I. Sazima. **98.** *Holoaden luederwaldti* from Campos do Jordão, São Paulo, Brazil. Photo by I. A. Martins. **99.** *Noblella myrmecoides* from Quebrada Vásquez, Loreto, Peru. Photo by W. W. Lamar. **100.** *Psychrophrynella* sp. from Abra Acanacu, Cusco, Peru. Photo by W. E. Duellman.

Genus *Noblella* Barbour, 1930

Noblella Barbour, 1930:81. Type species *Sminthillus peruvianus* Noble, 1921:1, by original designation.
Phyllonastes Heyer, 1977:151. Type species: *Euparkerella myrmecoides* Lynch, 1976b:50, by original designation. Synonymy by De la Riva *et al.*, 2008:0.

Definition.—Species of *Noblella* are strabomantid frogs having: (1) head no wider than body; (2) tympanic membrane differentiated (except in *N. duellmani*); (3) cranial crests absent; (4) dentigerous processes of vomers absent; (5) “S” condition of adductor muscle; (6) terminal discs on digits not or barely expanded; discs and circumferential grooves present distally (except in *N. duellmani*); terminal phalanges narrowly T-shaped; (7) Finger I shorter than, or equal in length to, Finger II; Finger IV containing only two phalanges in *N. carrascoicola*, *lochites*, *myrmecoides*, and *ritarasquinae*; (8) Toe III shorter than Toe V; tips of at least Toes III–IV acuminate; (9) subarticular tubercles not protruding; (10) dorsum pustulate or shagreen; (11) venter smooth; (12) SVL less than 22 mm.

Content.—Eight species are recognized: *Noblella carrascoicola*, *duellmani*, *heyeri*, *lochites*, *lynchi*, *myrmecoides* (Fig. 99), *peruviana*, and *ritarasquinae*.

Distribution.—Seven species occur in the Andes from extreme southern Ecuador to central Bolivia, and one species occurs in the Amazonian lowlands of Ecuador, Peru, and extreme western Brazil (Fig. 93).

Etymology.—The generic name is a patronym for Gladwyn K. Noble, who described the first species (*N. peruviana*). The name is feminine in gender.

Remarks.—For the past three decades these small frogs have been recognized as *Phyllonastes*, a generic name proposed by Heyer (1977) for the small Amazonian species formerly known as *Euparkerella myrmecoides* Lynch (1976). Subsequently additional species were discovered and named. De la Riva *et al.* (2008) discovered that *Sminthillus peruvianus* Noble, 1921, was not a *Phrynopus*, a genus in which it has been placed for many years (Lynch 1975a), but instead possessed the features characteristic of frogs recognized as *Phyllonastes*. Consequently, they considered *Smithillus peruvianus* Noble, the type species of *Noblella* Barbour, 1930, to be congeneric with *Phyllonastes*, for which *Noblella* is an earlier name.

As noted by Lehr *et al.* (2004), *Noblella duellmani* lacks some features characteristic of other members of the genus—viz. discs and circumferential grooves on digits, tympanum, and suprainguinal spots. In these regards this species is like members of the genus *Phrynopus*; however, it has pointed tips of digits and an inner tarsal tubercle, features unique to *Noblella*.

The generic status and phylogenetic relationships of *Noblella* are unresolved. Using molecular data (12s and 16s mitochondrial genes), Lehr *et al.* (2005) created a maximum likelihood tree of 13 species of “*Phrynopus*,” in which an undetermined species of “*Phyllonastes*” from Departamento de San Martín, Peru, was the closest relative of *Phrynopus* (= *Isodactylus*) *brunneus* from Ecuador. This species is closest to *Noblella lochites* in our molecular phylogeny (Fig. 2). We have included only *N. lochites* in our more comprehensive analyses (Fig. 4) and it appears as the closest relative of *Barycholos* in Holoadeninae, with significant ML (100%) and Bayesian (100%) support.

Genus *Psychrophrynella*, New Genus

Phrynopus (part)—Lynch, 1975a:8.

Type species.—*Phrynopus bagrecito* Lynch, 1986b:428.

Definition.—The small frogs of the genus *Psychrophrynella* are characterized by (1) head narrow, not as wide as body; (2) differentiated tympanic membrane and tympanic annulus usually absent (annulus visible beneath skin in some species; differentiated tympanic membrane in *P. boettgeri*); (3) cranial crests absent; (4)

dentigerous processes of vomers usually absent; (5) "S" condition of adductor muscle; (6) tips of digits narrow, rounded, or bulbous, not expanded; circumferential grooves absent; terminal phalanges knob-shaped; nuptial pads are absent; (7) Finger I shorter, equal to, or greater than Finger II; (8) Toe V usually slightly longer than Toe III; (9) subarticular tubercles not projecting; (10) dorsum smooth, granular, or shagreen; (11) venter finely granular, granular, or coarsely granular, although smooth in *P. pinguis*; (12) SVL in ranging from 14.0 mm in *P. boettgeri* to 33.4 mm in *P. wettsteini*.

Content.—Nineteen species are recognized at this time: *Psychrophrynella adenopleura*, *ankohuma*, *bagrecito*, *boettgeri*, *chacaltaya*, *condoriri*, *guillei*, *harveyi*, *iani*, *iatamasi*, *illampu*, *illimani*, *kallawaya*, *katantika*, *kempffi*, *pinguis*, *quimsacruzis*, *saltator*, and *wettsteini*. The population of the species formerly known as "*Phrynopus*" *peruvianus* from Abra Acanacu, Peru, is an undescribed species of "*Phrynopus*" (= *Psychrophrynella*) (Fig. 100)(De la Riva et al., 2008).

Distribution.—The genus, as now recognized, occurs at elevations of 1830–4190 m in the Cordillera Oriental of the Andes in southern Peru and Bolivia (Fig. 94).

Etymology.—The generic name is derived from the Greek *psychros* meaning cold and the Greek *phrynos* meaning toad with the Greek diminutive suffix *ella*. The name is feminine in gender and is used in allusion to the cold environments inhabited by these small frogs.

Remarks.—Of the species herein placed in *Psychrophrynella*, *P. iatamasi* and *wettsteini*, plus three unnamed species are contained in a southern Peru-Bolivian clade that is distinct from *Phrynopus* in central Peru in our molecular phylogeny (Fig. 2). In an analysis of 12S and 16S mitochondrial genes of more species of *Phrynopus* (*sensu lato*) these same species plus *Psychrophrynella boettgeri* form a well-supported clade (E. Lehr, pers. comm.). In fact, in our analyses of both nuclear and mitochondrial genes (Figs. 4), *Psychrophrynella* is associated with *Barycholos*, *Bryophryne*, and *Holoaden* in Holoadeninae, in contrast to the association of *Phrynopus* with *Oreobates* in Strabomantinae. *Psychrophrynella* appears to be the basal genus within the Holoadeninae.

For the past three decades our definition of "*Phrynopus peruvianus*" has been based on the description by Lynch (1975a) of specimens from Abra Acanacu, Departamento de Cusco, Peru. According to De la Riva et al. (2008), who compared the type series of *Sminthillus peruvianus* with specimens from Abra Acanacu, the latter are not conspecific with *Sminthillus peruvianus*, which they consider to be congeneric with *Phyllonastes*. Thus the specific name *peruvianus* is not applicable to the frogs herein referred to that species, nor is the generic name *Noblella* available for these high Andean frogs, because *Noblella* is a senior synonym of *Phyllonastes* (De la Riva et al. 2008).

Subfamily Strabomantinae, New Subfamily

Type genus.—*Strabomantis* Peters, 1863:405.

Definition.—These are strabomantid frogs that have expanded terminal digits on the fingers and toes (except *Isodactylus*, *Lynchius*, *Niceforonia*, and *Phrynopus*) and have circumferential grooves (absent in *Lynchius*, *Niceforonia*, and *Phrynopus*). The terminal phalanges are T-shaped (knob-shaped in *Lynchius*, *Niceforonia*, *Oreobates*, and *Phrynopus*). The tympanic membrane usually is differentiated. Most species are arboreal, but others (e.g., *Geobatrachus*, *Niceforonia*, *Lynchius*, and *Phrynopus*) are secretive and terrestrial, whereas some of the large species of *Strabomantis* are riparian; SVL varies from 13 mm in male *Pristimantis imitatrix* to 106 mm in *Strabomantis cheiroplethus*.

Content.—The 493 currently recognized species are placed in 10 genera, one of which has two subgenera.

Distribution.—This subfamily is widespread in tropical South America, where it is most diverse in the Andean regions of Colombia, Ecuador, and Peru. It extends as far south as northwestern Argentina; although

it is reasonably diverse in northeastern South America, it does not occur in the Atlantic Coastal Forest of Brazil. *Pristimantis* and *Strabomantis* extend into Central America (to Honduras and Costa Rica, respectively) and the former extends into the Lesser Antilles (Figs. 92, 101–103).

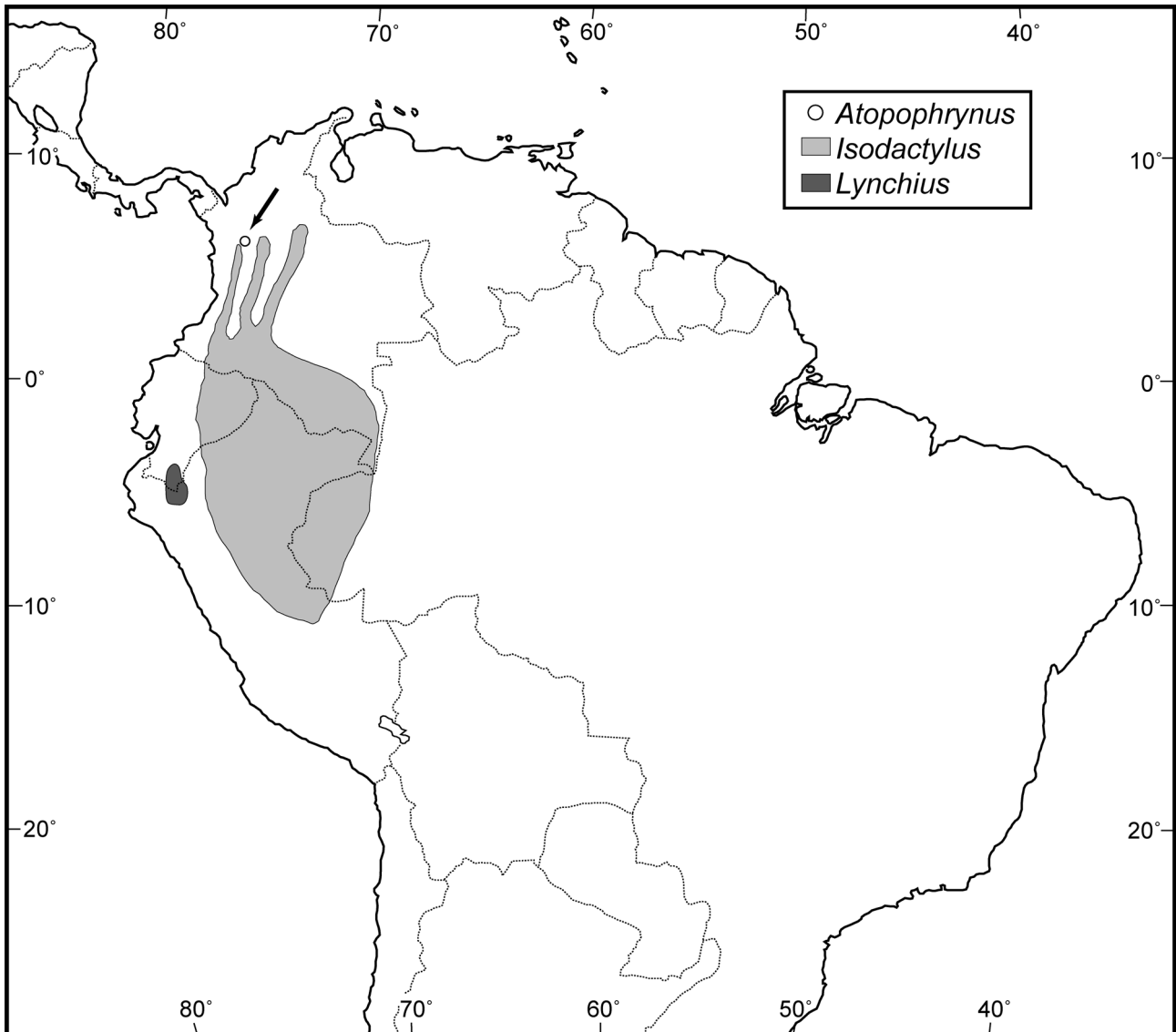


FIGURE 101. Distribution of the genera *Atopophrynus*, *Isodactylus*, and *Lynchius*, Subfamily Strabomantinae, Family Strabomantidae.

Remarks.—This is largest clade of Terrarana, but because of the absence of tissues several small, but distinctive, genera (e.g., *Atopophrynus*, *Dischidodactylus*, *Geobatrachus*, *Niceforonia*) are not included in the molecular analyses, so their relationships are unknown. Likewise, because of the absence of tissues, *Pristimantis* and *Phrynopus* of diverse phenetic species groups are not represented. Moreover, we are aware of many undescribed species, especially of *Pristimantis*. Therefore, the present analyses and resulting classification must be regarded as an initial effort waiting to be expanded and refined.

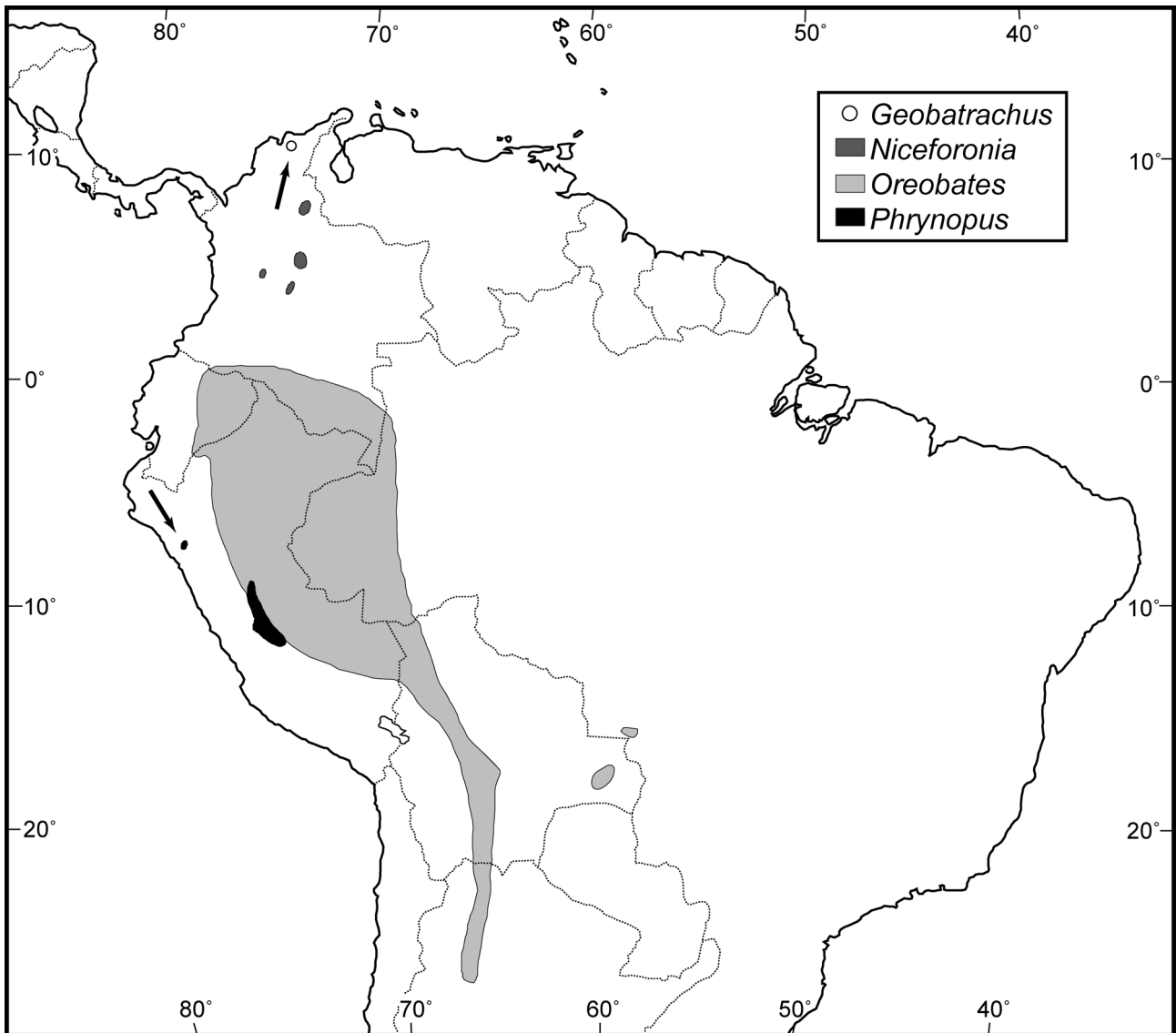


FIGURE 102. Distribution of the genera *Geobatrachus*, *Niceforonia*, *Oreobates*, and *Phrynopus*, Subfamily Strabomantinae, Family Strabomantidae. The distribution of *Oreobates* completely encompasses that of *Phrynopus* in southern Peru.

Genus *Atopophrynus* Lynch & Ruiz-Carranza, 1982

Atopophrynus Lynch & Ruiz-Carranza, 1982:557. Type species: *Atopophrynus syntomopus* Lynch & Ruiz-Carranza, 1982:557, by original designation.

Definition.—This genus is characterized by (1) head narrow; (2) tympanic membrane and annulus absent; (3) cranial crests absent; (4) dentigerous processes of vomers absent; (5) “S = E” condition of adductor muscle; (6) terminal discs expanded (absent on Finger I); circumferential groove present; terminal phalanges T-shaped; (7) Finger 1 shorter than Finger II; (8) Toes III and V about equal in length; Toe I weak, concealed externally and adherent to Toe II; toes three-fourths webbed; (9) subarticular tubercles not projecting; (10) dorsum smooth; (11) venter smooth; (12) SVL less than 20 mm in females.

Content.—The genus contains a single species: *Atopophrynus syntomopus* (Fig. 104).

Distribution.—*Atopophrynus* is known only from the crest of the Cordillera Central in Departamento de

Antioquia, Colombia (Fig. 101).

Etymology.—The generic name is derived from the Greek *atopos*, meaning strange or out of place, and the Greek *phryne*, meaning toad. The genus is masculine in gender.

Remarks.—This monotypic genus originally was placed in Dendrobatidae by Lynch & Ruiz-Carranza (1982). Myers & Ford (1986) unequivocally removed it from that family; their detailed observations on myology and osteology led them to consider the genus to be a sister taxon to *Geobatrachus*. Both monotypic genera share certain unique features among strabomantine frogs—concealed Toe I and a pair of slender anterior processes on each hyale of the hyoid. Neither genus has been included in any molecular phylogenetic analysis, so their placement in Strabomantinae is tentative. However, we place this pair of genera in this subfamily because one or both has T-shaped terminal phalanges, expanded terminal digits, and digital disks with circumferential grooves.

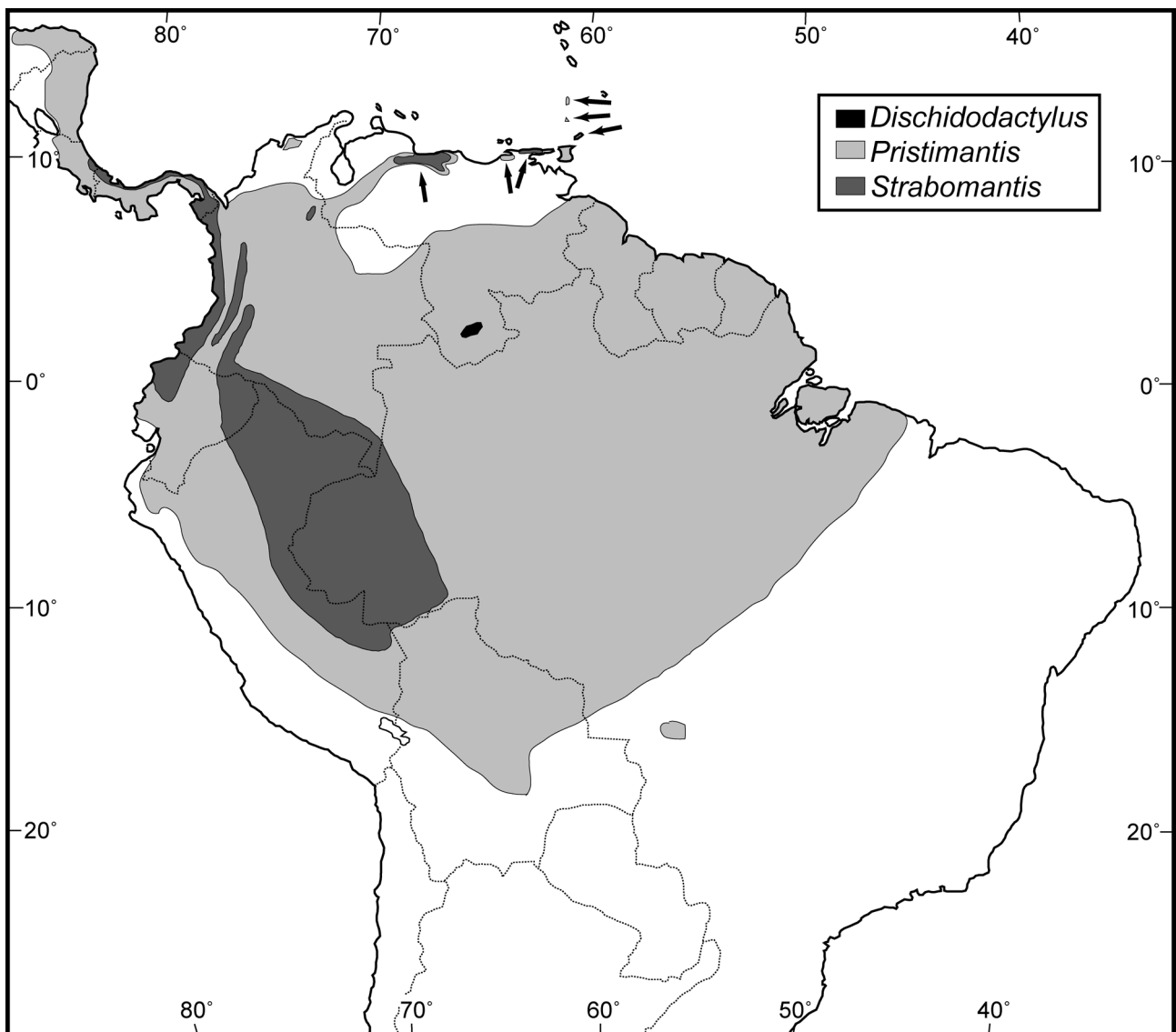
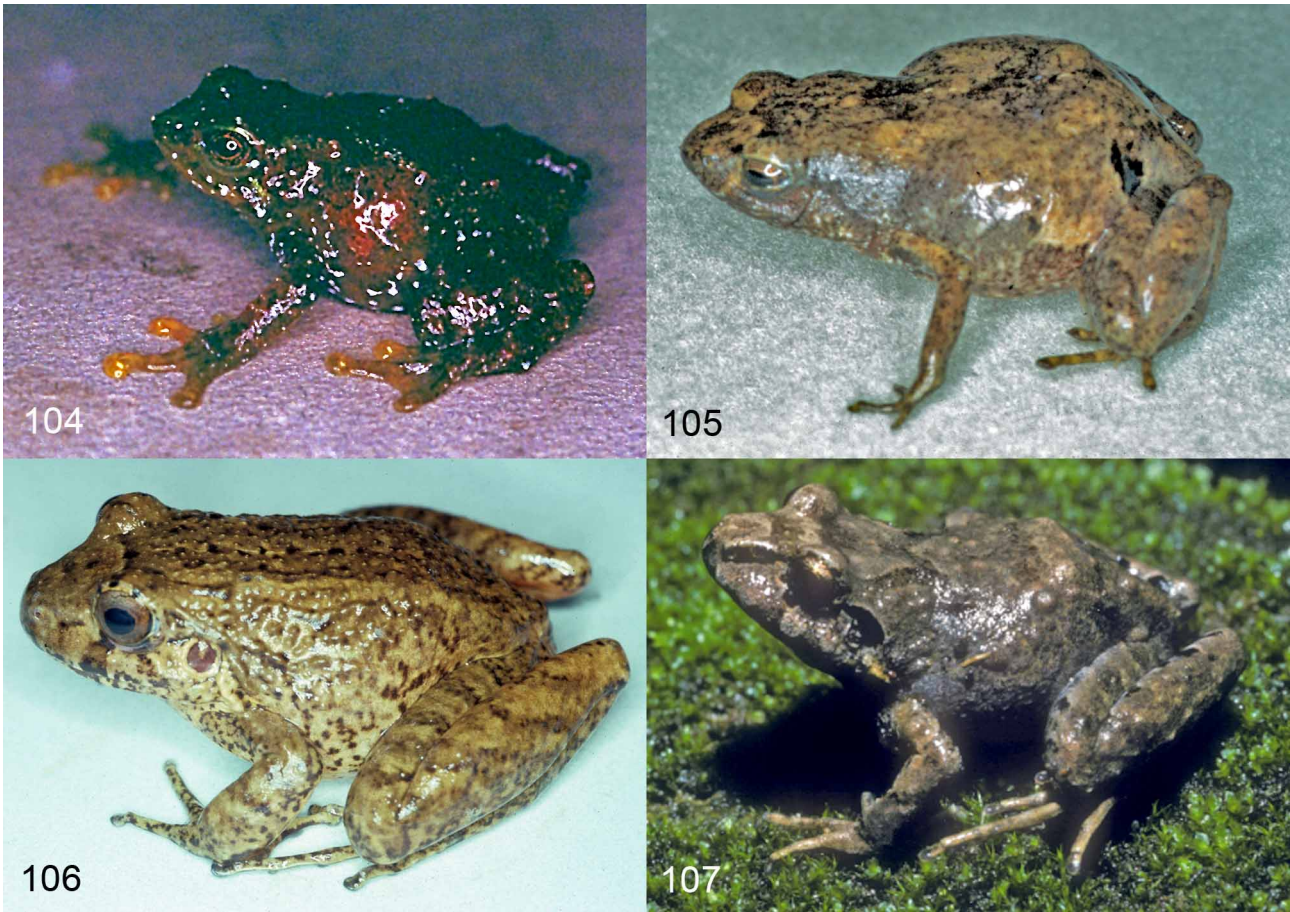


FIGURE 103. Distribution of the genera *Dischidodactylus*, *Pristimantis*, and *Strabomantis*, Subfamily Strabomantinae, Family Strabomantidae. The distribution of *Pristimantis* completely encompasses that of *Strabomantis*.



FIGURES 104–107. **104.** *Atopophrynus syntomopus* from 8 km E Sonsón, Antioquia, Colombia. Photo by J. D. Lynch. **105.** *Geobatrachus walkeri* from west slope of Cerro Kennedy, Magdalena, Colombia. Photo by W. E. Duellman. **106.** *Isodactylus dolops* from 10.3 km E El Pepino, Putumayo, Colombia. Photo by W. E. Duellman. **107.** *Lynchius parkeri* from the Cordillera de Huancabamba, Piura, Peru. Photo by T. H. Fritts.

Genus *Dischidodactylus* Lynch, 1979

Dischidodactylus Lynch, 1979:5. Type species: *Elosia duidensis* Rivero, 1968:1, by original designation.

Definition.—This genus is characterized by: (1) head not as wide as body; (2) tympanic membrane not differentiated; tympanic annulus visible below skin; (3) cranial crests absent; (4) dentigerous processes of vomers small, oblique; (5) “S” condition of adductor muscle; (6) terminal discs expanded, rounded, bifurcate; circumferential groove present; terminal phalanges T-shaped; (7) Finger I shorter than Finger II; (8) Toe III longer than Toe V; (9) subarticular tubercles not protruding; (10) dorsum granular; (11) venter areolate; (12) SVL to 43 mm in females.

Content.—Two species are known: *Dischidodactylus colonnelloi* and *duidensis*.

Distribution.—One species is confined to Cerro Duida and the other to Cerro Marahuaca in the Guiana Highlands of southeastern Venezuela (Fig. 103).

Etymology.—The generic name is derived from the Greek *dischidos*, meaning divided, and the Greek *dactylos*, meaning finger or toe, in reference to the divided ungual flap. The generic name is masculine.

Remarks.—Neither species of *Dischidodactylus* has been included in phylogenetic analyses; conse-

quently, the relationships of the genus are unknown. However, we tentatively place it in the Strabomantinae because of its possession of expanded terminal disks with circumferential grooves. *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). Possibly there is a radiation of cleft-digitated strabomantines on the tepuis in the Guiana Highlands like that in some other groups of anurans (e.g., *Stefania*: MacCulloch & Lathrop 2002; MacCulloch *et al.* 2006).

Genus *Geobatrachus* Ruthven, 1915

Geobatrachus Ruthven, 1915:1. Type species: *Geobatrachus walkeri* Ruthven, 1915:2, by original designation.

Definition.—This genus is characterized by: (1) head narrower than body; (2) tympanic membrane not differentiated; tympanic annulus visible beneath skin; (3) cranial crests absent; (4) dentigerous processes of vomers absent; (5) “S” condition of adductor muscle; (6) discs not expanded; tips of digits pointed; circumferential grooves absent; terminal phalanges narrowly T-shaped; (7) Finger I barely longer than Finger II; (8) Toe III slightly longer than Toes V; Toe I concealed externally and adherent to Toe II; (9) subarticular tubercles not projecting; (10) dorsum smooth with low longitudinal ridges; (11) venter smooth; (12) SVL to 24 mm in females.

Content.—The monotypic genus contains *Geobatrachus walkeri* (Fig. 105).

Distribution.—*Geobatrachus* is endemic to the Sierra Nevada de Santa Marta in northern Colombia (Fig. 102).

Etymology.—The generic name is derived from the Greek nouns *ge* and *batrachos*, meaning earth and frog, respectively. The generic name is masculine in gender.

Remarks.—The morphology, ecology, and life history of this small frog that originally was assigned to Dendrobatidae, were thoroughly examined by Ardila-Robayo (1979), who placed it in Leptodactylidae. The relationships of *Geobatrachus* are unknown, but it is worth noting that *Geobatrachus* and *Atopophrynus* from the Cordillera Central in northern Colombia are unique among strabomantids by having Toe I externally fused with Toe II. See comments under *Atopophrynus* concerning placement in Strabomantinae.

Genus *Isodactylus*, New Genus

Type species.—*Eleutherodactylus elassodiscus* Lynch, 1973:222.

Definition.—This genus is characterized by (1) head narrower than body; (2) tympanic membrane differentiated; only tympanic annulus visible under skin in *I. latens*, *manipus*, *nebulanastes*, and *peraccai*. (3) cranial crests absent; (4) dentigerous processes of vomers prominent; (5) “S” condition of adductor muscle; (6) terminal discs on digits not expanded, usually bearing weak circumferential grooves; terminal phalanges narrow, T-shaped; (7) Finger I equal to, or longer than Finger II; (8) Toes III and V about equal in length; (9) subarticular tubercles not projecting; (10) dorsum smooth to weakly tuberculate; (11) venter smooth; (12) range in snout–vent length 18.8 mm in males of *I. adercus* to 48.8 mm in females of *lundbergi*.

Content.—The genus contains 13 species, nine of which formerly were placed in *Eleutherodactylus*, whereas four species formerly were placed in *Phrynopus*: *Isodactylus adercus*, *araiodactylus*, *babax*, *brunneus*, *dolops* (Fig. 106), *elassodiscus*, *fallaciosus*, *latens*, *lucida*, *lundbergi*, *mantipus*, *nigrovittatus*, and *peraccai*.

Distribution.—The genus ranges from the northern parts of the Cordillera Occidental and Cordillera Ori-

ental in Colombia southward through Ecuador to the Cordillera Oriental in central Peru; most species occur at elevations of 1500–3710 m, but *I. nigrovittatus* inhabits the Amazon Basin in Ecuador and northern Peru (Fig. 101).

Etymology.—The masculine generic name is derived from the Greek *isos* meaning equal and the Greek *daktylos* meaning toe; the name applies to the equal, or nearly equal, lengths of Toes III and V.

Remarks.—Support for the genus in the molecular phylogeny (Fig. 4) was significant in the ML (98%) and Bayesian (100%) analyses. The relationship of this genus to other genera in the subfamily Strabomantinae is poorly resolved (Fig. 4) and will require additional gene sequences. As noted by Lynch (1994) and Lehr (2005), circumferential grooves in narrow-toed eleutherodactylids are difficult to distinguish and are not necessarily present on all digits. However, the presence of T-shaped terminal phalanges distinguishes species of *Isodactylus* from those of *Phrynopus*, *Noblella*, and most *Oreobates*.

Genus *Lynchius*, New Genus

Type Species.—*Phrynopus parkeri* Lynch, 1975a:21

Definition.—The small frogs of the genus *Lynchius* are characterized by (1) head narrow, not as wide as body; snout inclined anteroventrally in profile; (2) differentiated tympanic membrane and tympanic annulus present in *L. flavomaculatus*, membrane absent in other species; (3) cranial crests absent, except in *L. flavomaculatus*; (4) dentigerous processes of vomers prominent, oblique; (5) “S” condition of adductor muscle; (6) tips of digits narrow, rounded, or bulbous; circumferential grooves absent or weakly developed; terminal phalanges knob-shaped or weakly T-shaped; (7) Finger I longer than Finger II; (8) Toe V usually slightly longer than Toe III (toes equal in length in *L. parkeri*); (9) subarticular tubercles not projecting; (10) dorsum smooth; (11) venter smooth; (12) SVL to 43 mm in *L. flavomaculatus*.

Content.—Three species are placed in this genus: *Lynchius flavomaculatus*, *nebulanastes*, and *parkeri* (Fig. 107).

Distribution.—*Lynchius* is known from elevations of 2215–3100 m in the Cordillera Oriental in southern Ecuador and the Cordillera de Huancabamba in northern Peru (Fig. 101).

Etymology.—The masculine generic name is a patronym for John D. Lynch, who has devoted his professional life to the study of “eleutherodactylid” frogs and described the type species of this genus.

Remarks.—Support for the genus in the molecular phylogeny (Fig. 2) was significant (100%), and its position as a close relative of *Oreobates* received moderately strong support (80%) in the ML analysis and significant support (100%) in the Bayesian analysis (Fig. 4). The structure of the terminal phalanges is somewhat intermediate between the knob-shaped phalanges of *Phrynopus* and the T-shaped phalanges of *Pristimantis*. The similarities of the digital structure led Lehr (2005, 2006) to place *Lynchius flavomaculatus* and *L. nebulanastes* in “*Eleutherodactylus*.” Independent analyses of gene sequences by us (Figs. 2–4) and by E. Lehr (pers. comm.) revealed that the three species here assigned to *Lynchius* are in a clade well separated from true *Phrynopus*. A fourth (undescribed) species is represented in the tree by GenBank sequence AM039707 (Lehr *et al.* 2005).

Genus *Niceforonia* Goin & Cochran, 1963

Niceforonia Goin & Cochran, 1963:499. Type species: *Niceforonia nana* Goin & Cochran, 1963:499.
Phrynopus (in part)—Lynch, 1975a:8.

Definition.—The small frogs of the genus *Niceforonia* are characterized by (1) head narrow, not as wide as body; (2) differentiated tympanic membrane and tympanic annulus usually absent (present in *N. columbiana*);

(3) cranial crests absent; (4) dentigerous processes of vomers usually present and dentate; (5) “S” condition of adductor muscle; (6) tips of digits narrow, rounded; circumferential groves absent; terminal phalanges knob-shaped; (7) Finger I usually shorter than Finger II (equal in length in *N. colombiana*); (8) Toe V slightly longer than Toe III; (9) subarticular tubercles not projecting; (10) dorsum smooth; (11) venter smooth or areolate; (12) SVL to 20.9 mm in *N. nana*.

Content.—In addition to several undescribed species in Colombia (J. D. Lynch, pers. comm.) three species are recognized at this time: *Niceforonia adenobrachia*, *columbiana*, and *nana* (Fig. 108).

Distribution.—With the exception of the questionable locality of *Niceforonia columbiana* at an elevation of 1000–1300 m on the eastern slopes of the Cordillera Oriental, this genus is known only from paramos at elevations of 3000–3600 m in the Cordillera Central and Cordillera Oriental in Colombia (Fig. 102).

Etymology.—The feminine generic name is for the late Colombian herpetologist, Hermano Nicéforo María.

Remarks.—No species of Colombian *Niceforonia* has been included in molecular analyses, but as shown by our analyses (Figs. 2–4) and by E. Lehr (pers. comm.), the larger species described as *Phrynopus brunneus* and *P. peraccai* by Lynch (1975a) are in a clade containing members of the former “*Eleutherodactylus nigrovittatus*” group that herein is recognized as *Isodactylus*. Species of *Niceforonia* differ from *Lynchius* and most *Phrynopus* by lacking vomerine teeth. *Niceforonia* shares the distinction of having knobbed, rather than T-shaped, terminal phalanges with a well-supported clade (98% bootstrap support) that includes *Phrynopus*, *Oreobates*, and *Lynchius*. Because the other strabomantine genera have T-shaped phalanges, this may be considered a shared derived character uniting *Niceforonia* with these three genera.



108



109



110



111

FIGURES 108–111. 108. *Niceforonia nana* from 22 km SW Susacón, Boyacá, Colombia. Photo by W. E. Duellman. 109. *Oreobates discoidalis* from Km 26, Tafí del Valle, Tucumán, Argentina. Photo by D. C. Cannatella. 110. *Oreobates quixensis* from Santa Cecilia, Sucumbíos, Ecuador. Photo by W. E. Duellman. 111. *Phrynopus bracki* from 2.9 km N, 5.5 km E Oxapampa, Pasco, Peru. Photo by S. B. Hedges.

Genus *Oreobates* Jiménez de la Espada, 1872

Oreobates Jiménez de la Espada, 1872:87. Type species: *Oreobates quixensis* Jiménez de la Espada, 1872:87, by monotypy.

Teletrema Miranda-Ribeiro, 1937:67. Type species *Teletrema heterodactylum* Miranda-Ribeiro, 1937:67, by monotypy. Synonymy with *Eleutherodactylus* by Myers (1962:198). **New synonymy.**

Definition.—Frogs of the genus *Oreobates* can be defined as strabomantid frogs having (1) head about same width as body; (2) tympanic membrane differentiated; (3) cranial crests absent; (4) dentigerous processes of vomers prominent; (5) “S” condition of adductor muscle; (6) terminal segments of digits usually rounded with reduced, or absent, disc structure, when present only on Finger III and IV, and always with incomplete circumferential grooves and poorly defined unguis flap; terminal phalanges knob-shaped; (7) Finger I longer than, or equal to, Finger II; (8) Toe V equal in length to, or shorter than Toe III; (9) subarticular and supernumerary tubercles large, conical or subconical, projecting; (10) dorsum smooth to tuberculate; (11) venter smooth; (12) range in SVL 20 mm in males of *O. cruralis* to 63 mm in females of *O. quixensis*.

Content.—Fifteen species are recognized: *Oreobates choristolemma*, *cruralis*, *discoidalis* (Fig. 109), *granulosus*, *heterodactylus*, *ibischi*, *lehri*, *madidi*, *pereger*, *quixensis* (Fig. 110), *sanctaecrucis*, *sanderi*, *saxatilis*, *simmonsii*, and *zongoensis*. Most of these were recognized by Padial *et al.* (In press); we have added “*Phrynopus*” *pereger*, which shares morphological characters with species of *Oreobates* (E. Lehr, pers. comm.).

Distribution.—The genus occurs in western South America from southern Colombia to southwestern Brazil and northwestern Argentina. Most species occur in the Andes to elevations of 2830 m but two inhabit the upper Amazon Basin; one species inhabits the Brazilian Shield between Brazil and Bolivia (Fig. 102).

Etymology.—The generic name is derived from the Greek *oreos*, meaning mountain, and the Greek *bates*, meaning one that treads or haunts; the name refers to the mountainous region on the lower slopes of the Andes where the type species was found. The gender is masculine.

Remarks.—Support for the genus in the molecular phylogeny (Fig. 2) was significant (98%), and its position as a close relative of *Lynchius* received moderately strong support (80%) in the ML analysis and significant support (100%) in the Bayesian analysis (Fig. 4). Formerly, some of these species were assigned to the genus *Ischnocnema*, the type species of which, *Leiuperus verrucosus* Reinhardt and Lütken (1862), was shown to possess T-shaped terminal phalanges and was placed in the synonymy of “*Eleutherodactylus*” by Caramaschi and Canedo (2006); Heinicke *et al.* (2007) recognized *Ischnocnema* as a distinct genus, which herein is placed in the Brachycephalidae. Analyses of molecular and morphological data by Padial *et al.* (In press) provide a well-supported phylogenetic tree of *Oreobates*, a genus that also includes all species formerly placed in the “*Eleutherodactylus*” *discoidalis* Group sensu Lynch (Lynch 1989). The advertisement call of members of *Oreobates* is composed of a single pulsed note or a rapid series of pulse-like consecutive notes modulated in amplitude (Padial *et al.* 2007b). Call structure has been proposed as a putative shared derived character of the genus (Padial *et al.*, In press).

Genus *Phrynopus* Peters, 1873

Phrynopus Peters, 1873:416. Type species: *Phrynopus peruanus* Peters, 1873:416, by monotypy.

Definition.—Frogs of the genus *Phrynopus* are characterized by (1) head narrow, not as wide as body; (2) differentiated tympanic membrane and tympanic annulus usually absent (present in *P. auriculatus* and *P. peruanus*); (3) cranial crests absent; (4) dentigerous processes of vomers usually absent (present and dentate in *P. auriculatus*, *bracki*, *dagmarae*, *kauneorum*, and *peruanus*); (5) “S” condition of adductor muscle; (6) tips of

digits narrow, rounded, or bulbous; circumferential grooves absent; terminal phalanges knob-shaped; (7) Finger I usually shorter than Finger II (equal in length in *P. juninensis*, and *P. thompsoni*); (8) Toe V usually slightly longer than Toe III (toes equal in length in *P. thompsoni*; Toe V shorter than Toe III in *P. juninensis* and *P. peruanus*); (9) subarticular tubercles not projecting; (10) dorsum smooth to pustulate; (11) venter smooth or areolate; (12) SVL ranging from 14.5 in *P. auriculatus* to 54 mm in *P. kauneorum*.

Content.—Twenty-one species are recognized: *Phrynopus auriculatus*, *ayacucho*, *barthlenae*, *bracki* (Fig. 111), *bufoides*, *dagmarae*, *heimorum*, *horstpauli*, *juninensis*, *kauneorum*, *kotosh*, sp. 1 (Chaparro *et al.*, in press), *montium*, sp. 2 (Chaparro *et al.*, in press), *oblivius*, *paucari*, *peruanus*, *pesantesi*, *tautzorum*, *tribulosus*, and *thompsoni*.

Distribution.—The genus occurs mainly at elevations of 2200–4400 m in upper humid montane forests and supra-treeline grasslands in the Cordillera Oriental in central Peru and at one locality at an elevation of 3290 m in the Cordillera Occidental in Peru (Fig. 102).

Etymology.—The generic name is derived from the Greek *phrynos*, meaning toad, and the Latin *pusillus*, meaning small. The name is masculine in gender.

Remarks.—Support for the monophyly of the genus in the molecular phylogeny (Fig. 2) was significant (100%), and its position as a close relative of the clade composed of *Lynchius* and *Oreobates* was significant (98%) in the ML and Bayesian (100%) analyses (Fig. 4). The placement of several former species of *Phrynopus* in other genera (*Bryophryne*, *Lynchius*, *Isodactylus*, *Noblella*, *Niceforonia*, and *Psychrophrynella*) restricts *Phrynopus* to a clade of 21 described species in the high Andes of central Peru, the type species of which, *Phrynopus peruanus*, was recently rediscovered and described by Lehr (2007). In this region the genus does not overlap the distributions of other genera that formerly were placed in *Phrynopus*. Loss of a tympanic membrane and diminution and eventual loss of the tympanic annulus are derived character states in many groups of anurans. The only species of *Phrynopus* in our tree (Fig. 2) with a fully developed ear is the basal species, *P. auriculatus*. A molecular phylogeny including most of the species shown in Figure 2 (minus *P. auriculatus*, *bracki* and *tribulosus*) but including *P. peruanus*, which has a fully developed ear, has *P. peruanus* as the basal species (E. Lehr, pers. comm.). Thus, phylogenetic analyses of molecular data corroborate the existence of an ear as primitive.

Genus *Pristimantis* Jiménez de la Espada, 1871

Pristimantis Jiménez de la Espada, 1871:61. Type species: *Pristimantis galdi* Jiménez de la Espada, 1871:61, by monotypy.

Cyclocephalus Jiménez de la Espada, 1875:pl. 3. Type species: *Cyclocephalus lacrimosus* Jiménez de la Espada, 1875:pl. 3, by monotypy. Synonymy with *Eleutherodactylus* by Lynch and Schwartz (1971:109). **New synonymy.**

Pseudohyla Andersson, 1945:86. Type species *Pseudohyla nigrogrisea* Andersson, 1945:86, by monotypy. Synonymy with *Eleutherodactylus* by Lynch (1969:219). **New synonymy.**

Trachyphrynus Goin & Cochran, 1963:502. Type species: *Trachyphrynus myersi* Goin & Cochran, 1963:502, by original designation. Synonymy with *Eleutherodactylus* by Lynch (1968c:295). **New synonymy.**

Definition.—Members of the genus *Pristimantis* can be defined as strabomantid frogs having: (1) head about as wide as body; (2) tympanic membrane differentiated or not; (3) cranial crests usually absent; (4) dentigerous process of vomers usually present; (5) “S” condition of the adductor muscles, except in the *subgenus* *Yunguanastes*; (6) terminal discs on digits expanded (with apical papillae in members of the *P. chalceus* Group), bearing well-defined circumferential grooves, supported by T-shaped terminal phalanges; (7) comparative lengths of Fingers I and II variable; (8) Toe V as long as, or longer than, Toe III; (9) subarticular tubercles not protruding; (10) texture of skin on dorsum variable; (11) venter smooth or areolate; (12) range in SVL 13 mm in male *P. imitatrix* to 73 mm in female *P. lymani*.

Content.—As now recognized, the genus includes three subgenera and 427 species.

Distribution.—*Pristimantis* is most diverse in northwestern South America, where the distribution of the genus includes the lowlands to elevations of about 4000 m in the Andes in Colombia, Ecuador, and Peru (except for the arid coastal regions and semi-arid Pacific slopes of the Andes) (Fig. 103). The genus also occurs throughout much of Venezuela, except the arid coastal region and the llanos, as well as in Bolivia and south-central Brazil. *Pristimantis* occurs throughout the Amazon Basin, where it is most diverse in Ecuador; it also occurs in the Guianas, Trinidad, and Tobago. Ten species occur in lower Central America (*P. cerasinus* as far north as eastern Honduras); three of these (*P. altae*, *cerasinus*, and *pirrensis*) are endemic to Central America, and the others range principally into Chocoan South America. Two species exist on islands in the Lesser Antilles closest to the mainland of South America (*P. euphronides* on Grenada and *P. shrevei* on St. Vincent).

Etymology.—As stated by Jiménez de la Espada (1871 "1870"), the name *Pristimantis* is derived from two Greek words meaning sierra and treefrog. The earliest generic name ending with *mantis* is *Platymantis* coined by Günther (1859 "1858"-a), wherein he specifically stated that the name was derived from the Greek *platys* meaning flat and *mantis* meaning treefrog. The Greek word *mantis* normally is translated as meaning prophet and is masculine. But as pointed out by Kraus and Allison (2007), according to Liddell and Scott (1996), the masculine term was applied by ancient Greeks to treefrogs in reference to their calls prophesizing the advent of rains. Günther (1859 "1858"-a) did not state the gender of *Platymantis* and included two species, one with a masculine ending and the other with a feminine ending.

Inasmuch as Jiménez de la Espada (1871 "1870") described only one species as a genitive name, his determination of gender cannot be ascertained. However, Peters (1863) in his description of *Strabomantis* also referred to *mantis* as a frog and used the generic name as masculine, as did Laurent and Combaz (1950) for *Phlyctimantis*. Throughout most of the 20th Century, authors treated *Platymantis* as masculine, but Günther (1999) erroneously used *Platymantis* as a feminine name; this usage was followed by Frost (2007) and Global Amphibian Assessment (IUCN 2007) and has been forced upon some recent authors by editors of some journals. The gender of generic names ending in *mantis* definitely is masculine; as emphasized by Kraus and Allison (2007); recent usage of specific names of *Platymantis* as feminine are unjustified and should be rendered masculine.

Remarks.—Support for the monophyly of this genus in the taxon-dense molecular phylogeny (Fig. 2) was significant (97%) as was support for its monophyly (100%) in the character-dense molecular phylogeny (Fig. 4). In the latter tree, it appears as a close relative of the clade containing *Lynchius*, *Oreobates*, and *Phrynopus*, with moderate support (67%) in the ML analysis and significant support (100%) in the Bayesian analysis.

Heinicke *et al.* (2007) resurrected the generic name *Pristimantis* for this large "South American Clade" that they discovered, centered primarily in the Andes. Several well-supported groups within the genus are evident, but there is not complete agreement with the previously defined morphological species groups (Lynch & Duellman 1997). These discrepancies and the limited taxon-sampling (104 species) make it difficult to define subdivisions within *Pristimantis*. Nonetheless, the molecular phylogeny (Fig. 2) defines several strongly supported and large groups of species that show some, but not complete, agreement with previous groups defined by morphology (e.g., the former "*Eleutherodactylus*" *conspicillatus* and "*E.*" *unistrigatus* species groups, among others). Using this new perspective, we recognize three subgenera within *Pristimantis*. One includes species previously placed mostly in the "*Eleutherodactylus cruentus*" and "*E. cerasinus*" species groups, and one mostly includes species assigned to the "*E. fraudator*" Species Group. The other assemblage, the subgenus *Pristimantis*, contains the species placed previously in the enormous "*E.*" *unistrigatus* Species Group, as well as species placed in fifteen other species groups. Based on our molecular phylogenies (Figs. 2–4) many of the species groups retained here are demonstrably not monophyletic. Additional subgenera may be definable within the genus, especially those assigned herein to the subgenus *Pristimantis*, but we refrain from defining additional subgenera until DNA sequence data become available for a larger proportion of the subgenus.

The recognition of *Pristimantis* necessitates the removal of four nominal genera from the synonymy of *Eleutherodactylus* and their placement in the synonymy of *Pristimantis*, or as subgenera of *Pristimantis*. Furthermore, DNA sequence data show that some species were incorrectly placed in *Pristimantis* by Heinicke *et al.* (2007); several of the species placed in the “*Eleutherodactylus diastema*” Group by Lynch and Duellman (1997) and Lynch (2001) actually belong in the family Eleutherodactylidae as discussed above. One recently described species, *P. dendrobatoides* (Means & Savage 2007), appears basally among species in this genus in our tree (Fig. 2) and therefore we tentatively leave it unallocated to subgenus.

Subgenus *Hypodictyon* Cope (1885)

Hypodictyon Cope, 1885:383. Type species: *Phyllobates ridens* Cope, 1866a:131. Synonymy with *Eleutherodactylus* by Taylor (1952:690). **New synonymy.**

Definition.—Members of the subgenus *Hypodictyon* can be defined as strabomantid frogs having: (1) head moderately narrow; (2) tympanic membrane differentiated; (3) cranial crests usually absent; (4) dentigerous process of vomers well developed; (5) “S” condition of the adductor muscles; (6) terminal discs on digits expanded, bearing well-defined circumferential grooves, supported by T-shaped terminal phalanges; (7) Finger I slightly shorter or longer than Finger II; (8) Toe V longer than Toe III; (9) subarticular tubercles prominent; (10) texture of skin on dorsum variable; (11) texture of skin on venter variable; (12) range in SVL from 16 mm in males of *Pristimantis ridens* to 72 mm in females of *P. w-nigrum*.

Content.—The subgenus includes two species series (28 species): the *Pristimantis (Hypodictyon) ridens* and *P. (H.) rubicundus* species series.

Distribution.—Members of this subgenus range from Honduras through Central America onto the Pacific versant of Colombia and Ecuador, as well as on the eastern Andean slopes and in the upper Amazon Basin of Colombia, Ecuador, northern Peru, and extreme western Brazil Fig. 112).

Etymology.—The subgeneric name is derived from the Greek *hypo* meaning under or beneath and the Greek *diktyon* meaning net. Cope used the name in reference to the granulate skin on the belly.

Remarks.—Support for the monophyly of this subgenus in the taxon-dense molecular phylogeny (Fig. 2) was moderately strong (82%) and it was significant in the ML (97%) and Bayesian (100%) analyses of the character-dense data set (Fig. 4). However, the included species are variable with respect to most morphological features. There is no consistency in the presence or absence of tarsal folds or lateral fringes on the digits; furthermore, the venter may be smooth or areolate. However, within *Hypodictyon* there are two well-supported clades, recognized here as species series, that differ consistently in relative lengths of Toes III and V.

Pristimantis (Hypodictyon) ridens Species Series

Definition.—Frogs in this series are small to moderate in size with proportionately short limbs; the range in SVL is from 16 mm in male *Pristimantis ridens* to 45.2 mm in *P. jorgevelosai*. Head width is 35–43% SVL. Cranial crests are absent except in female *P. jorgevelosai*. The tympanic membrane and annulus are distinct, except in *P. pirrensis* and *cruentus*. The dorsum is smooth, shagreen, or tuberculate; the venter is coarsely areolate. The toes lack webbing, and Toe V is much longer than Toe III; an inner tarsal fold or elongate tubercle is usually present. Lateral fringes are usually present on the fingers and toes. Vocal slits and nuptial pads are present or absent. Species in this series usually are found on low vegetation at night.

Content.—The species series includes 16 species: *Pristimantis (Hypodictyon) altae*, *bicolor*, *caryophyllaceus*, *colomai*, *cremnobates*, *cruentus* (Fig. 113), *jorgevelosai*, *laticlavus*, *latidiscus*, *moro*, *museosus*, *pardalis*, *pirrensis*, *ridens*, *rosadoi*, and *sanguineus*.

Distribution.—Species in this series mostly occur at elevations less than 2000 m in lower Central America and on the Pacific versant of Colombia and Ecuador. *Pristimantis ridens* extends northward into Honduras. Two species (*P. cremnobates*, and *jorgevelasoi*) occur at elevations of 100–2050 m on the eastern slopes of the Andes in Colombia and Ecuador.

Remarks.—Several species in this series (e.g., *Pristimantis cruentus* and *ridens*) were among the most common eleutherodactylids in lower Central America prior to the amphibian declines of recent decades.

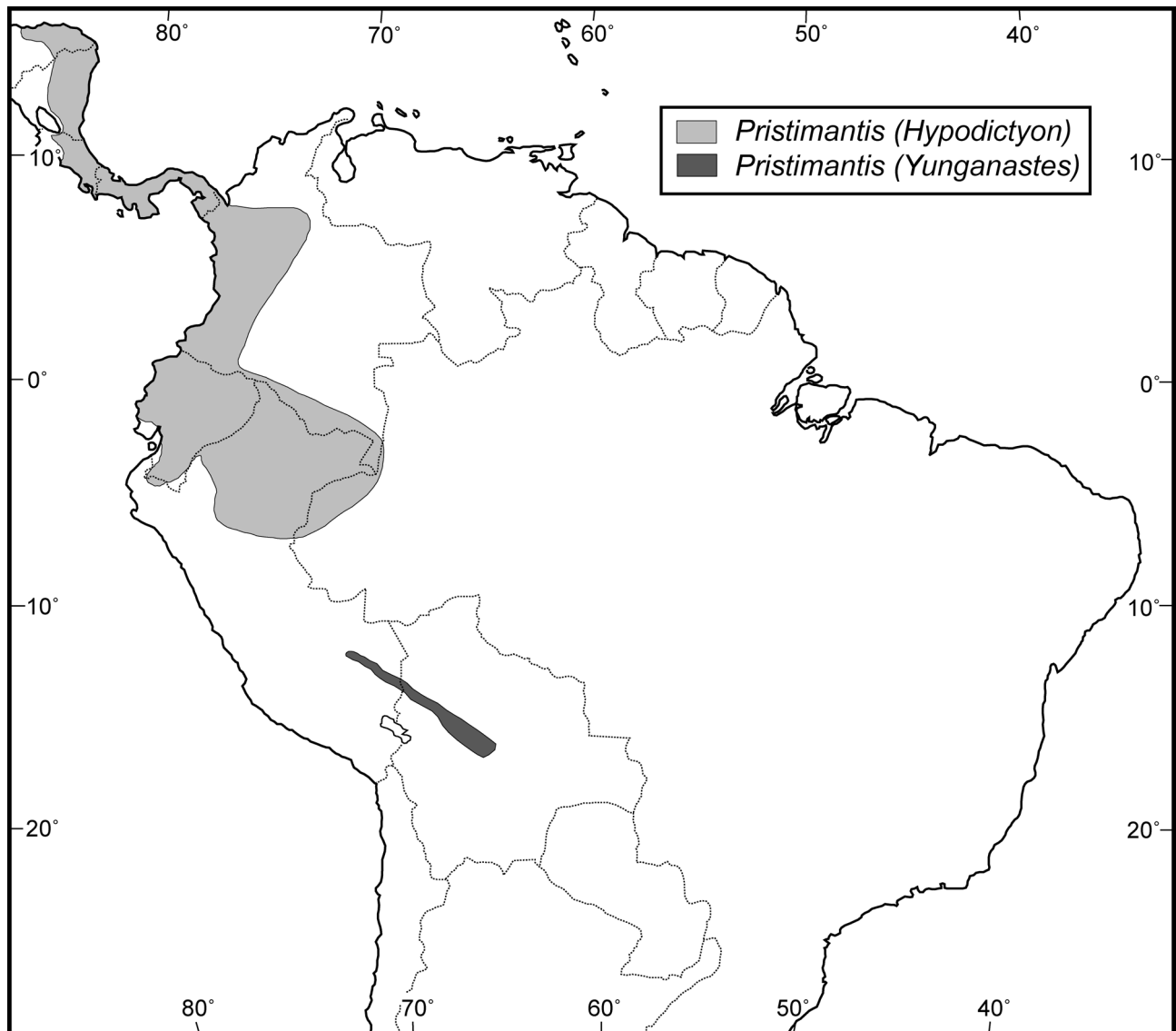


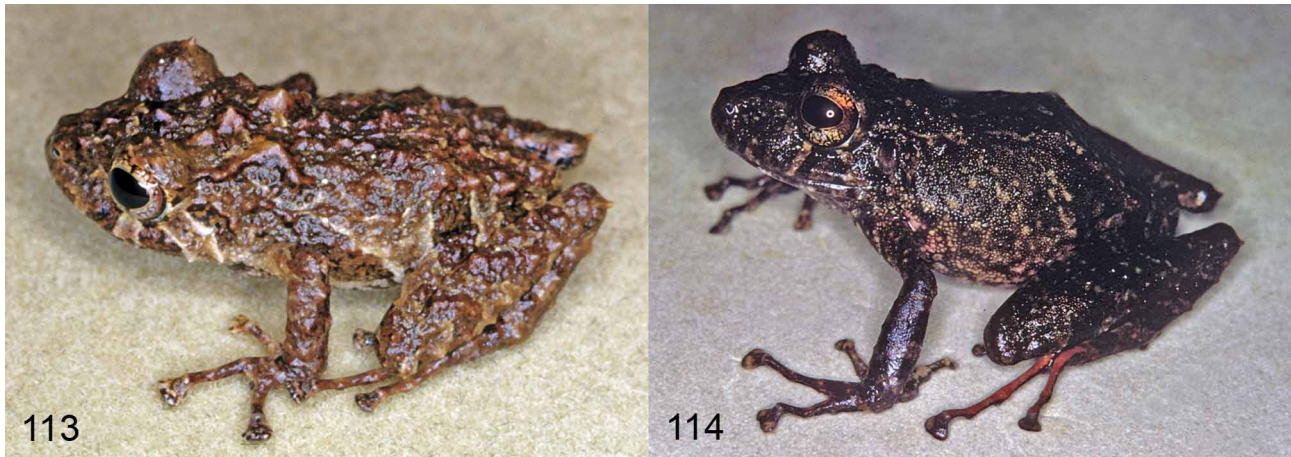
FIGURE 112. Distribution of the subgenera *Hypodictyon* and *Yunganastes*, Genus *Pristimantis*, Subfamily Strabomantinae, Family Strabomantidae.

Pristimantis (Hypodictyon) rubicundus Species Series

Definition.—Frogs in this series have moderately robust bodies and proportionately long limbs; the range in SVL is from 17 mm in male *Pristimantis cerasinus* to 72 mm in *P. w-nigrum*. Head width is 37–42% SVL. Cranial crests are absent except in female *P. orpacobates*. The tympanic membrane and annulus are distinct.

The dorsum is shagreen or tuberculate; the venter usually is smooth, but it is weakly areolate in *P. cerasinus*, *labiosus*, *orpacobates*, *rubicundus*, and *tenebrionis*. The toes lack webbing, and Toe V is only slightly longer than Toe III; an inner tarsal fold is absent, except in *P. actites* and *cerasinus*. Lateral fringes are absent on the fingers and toes, except in *P. achatinus*, *actites*, *ocellatus*, *w-nigrum*, and toes of *P. rubicundus*. Vocal slits are present, except in *P. orpacobates* and *rubicundus*; nuptial pads are present except in *P. crenunguis*, *labiosus*, and *tenebrionis*. Most species in this series are found on low vegetation at night; *P. actites* and *w-nigrum* are most common near streams.

Content.—The species series includes 12 species: *Pristimantis* (*Hypodictyon*) *actites*, *cerasinus*, *crenunguis*, *epacrus*, *ixalus*, *labiosus*, *lanthanites*, *ocellatus*, *orpacobates*, *rubicundus* (Fig. 114), *tenebrionis*, and *w-nigrum*.



FIGURES 113–114. 113. *Pristimantis* (*Hypodictyon*) *cruentus* of the *P. ridens* Species Series, from Lafuna Monte Alegre, Alajuela, Costa Rica. Photo by W. E. Duellman. 114. *Pristimantis* (*Hypodictyon*) *rubicundus* of the *P. rubicundus* Species Series, from Cordillera del Dué, Napo, Ecuador. Photo by W. E. Duellman.

Distribution.—Most species occur at elevations of 200–2700 m on the Pacific versant of the Andes in Colombia and Ecuador; three species occur at elevations of 1000–1700 m on the Amazonian slopes of the Andes in Colombia and Ecuador, and *Pristimantis w-nigrum* exists at elevations up to 3300 in the Andes of southern Colombia, Ecuador, and extreme northern Peru. One species, *P. cerasinus*, ranges from eastern Honduras to western Panama, and *P. achatinus*, although primarily distributed in Chococoan Colombia and Ecuador, also occurs in eastern Panama and in the Cauca and Magdalena valleys in Colombia.

Remarks.—Conceivably, other species (e.g., *Pristimantis fallax*) will be assigned to this series once molecular data become available.

Subgenus *Pristimantis* Jiménez de la Espada, 1871

Pristimantis Jiménez de la Espada, 1871:61. Type species: *Pristimantis galdi* Jiménez de la Espada (1871:61), by monotypy.

Mucubatrachus La Marca, 2007:68. Type species: *Hylodes briceni* Boulenger (1903:481), by original designation.

Paramophrynella La Marca, 2007:84. Type species: *Eusophus ginesi* Rivero (1964:299), by original designation.

Definition.—Members of the subgenus *Pristimantis* can be defined as strabomantid frogs having: (1) head about as wide as body; (2) tympanic membrane differentiated or not; (3) cranial crests present or absent; (4) dentigerous process of vomers usually present; (5) “S” condition of the adductor muscles; (6) terminal discs

on digits expanded (with apical papillae in *P. chaceus*), bearing well-defined circumferential grooves, supported by T-shaped terminal phalanges; (7) Finger I usually shorter than Finger II variable; (8) Toe V usually much longer than Toe III; (9) subarticular tubercles not protruding; (10) texture of skin on dorsum variable; (11) venter usually areolate; (12) range in SVL 13 mm in male *P. imitatrix* to 73 mm in female *P. lymani*.

Content.—The subgenus includes 16 species groups and 34 species unassigned to group (total, 385 species).

Distribution.—The distribution of the subgenus *Pristimantis* is essentially the same as that of the genus except that it barely enters Central America (Fig. 115).

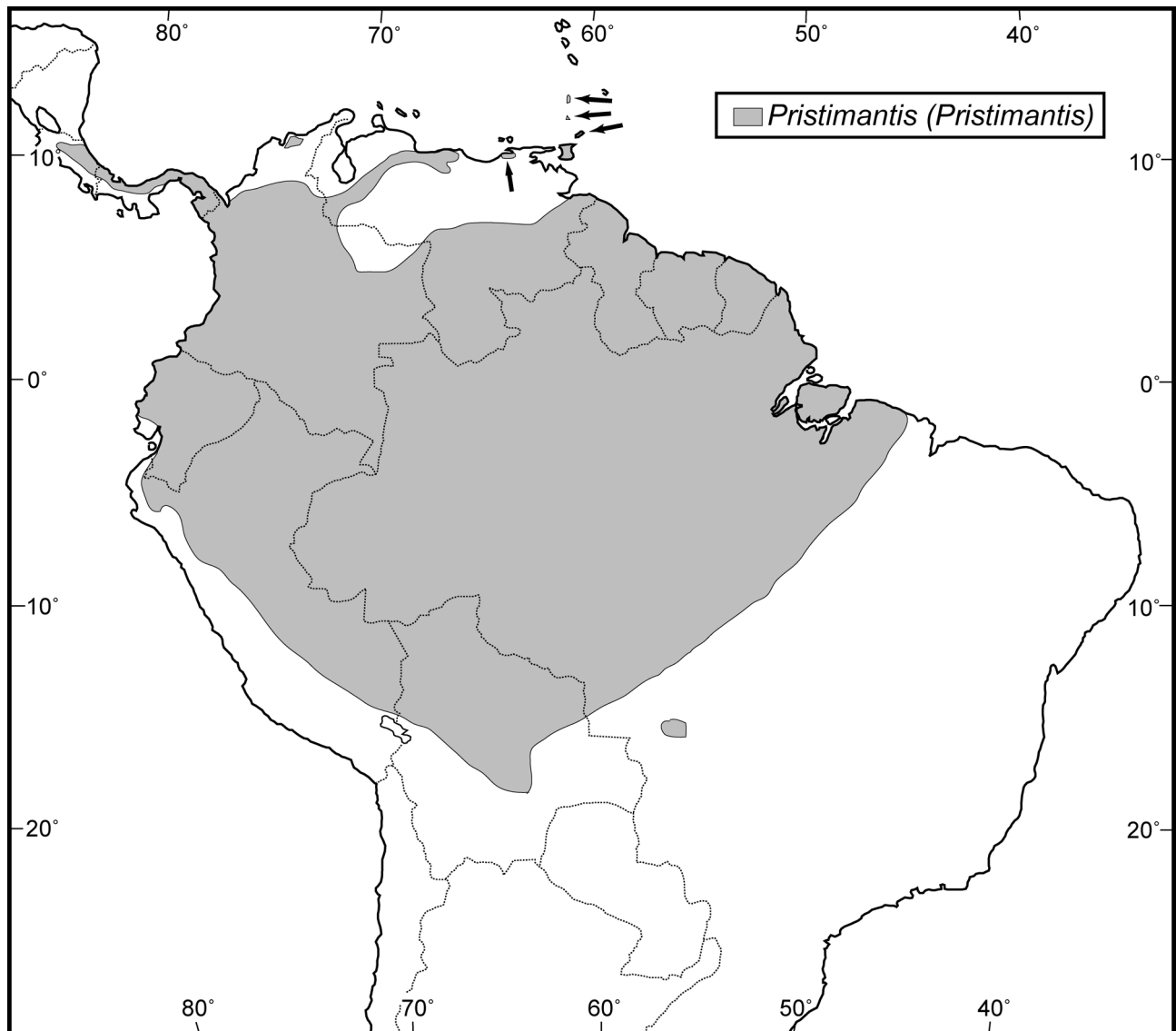


FIGURE 115. Distribution of the Subgenus *Pristimantis*, Genus *Pristimantis*, Subfamily Strabomantinae, Family Strabomantidae.

Etymology.—As for the genus.

Remarks.—There is no clear resolution of this subgenus in the taxon-dense molecular phylogeny (Fig. 2). Although it received moderately strong support (80%) in the ML analysis and significant support (100%) in the Bayesian analysis of the character-dense data set (Fig. 4), many species appearing basally within *Pristimantis* in the other phylogenies (Figs. 2–3) were not included in this analysis. Within what we now recognize as the subgenus *Pristimantis* several species groups were identified by Lynch and Duellman (1997) and others

have been proposed subsequently. None of these phenetic groups has been clearly distinguished in the various phylogenetic analyses (Figs. 2–4). In part, this presumed lack of distinction is because of insufficient taxon sampling. Many of these groups are moderately well defined by morphological characters, and some have restricted geographic ranges, principally in the Andes. However, in other cases, the phylogenetic trees clearly show instances of paraphyly and polyphyly. Because of this discordance between molecular and morphological definitions of groups, it would not be possible to allocate species lacking sequence data to groups defined only in the molecular phylogeny. For this reason we postpone the reclassification of the subgenus *Pristimantis* until a sufficient number of species is sampled with DNA sequences. Thus, except for two of the groups having strong support from the molecular phylogeny (*P. conspicillatus* and *P. peruvianus* species groups), the species groups listed below should not be assumed to be monophyletic.

Recently, La Marca (2007) described two new genera of terraranans from Venezuela, *Mucubatrachus* and *Paramophrynella*. He assigned seven species (*briceni*, *culatensis*, *flabellidiscus*, *lancinii*, *paramerus*, *rhigophilus*, and *thyllus*) to the former and three species (*boconoensis*, *ginesi*, and *jabonensis*) to the latter. Five of the species were newly described, three of the others (*briceni*, *paramerus*, and *boconoensis*) were previously placed in groups (*conspicillatus* and *unistrigatus*) assigned here to *Pristimantis* (*Pristimantis*), and the remaining two species (*lancinii* and *ginesi*) have characteristics that would also lead us to place them in the subgenus *Pristimantis*. Unfortunately, we have no sequence data for any of these species. Also, it is not clear from the description (La Marca 2007) that terraranans were surveyed broadly for the diagnostic morphological characteristics of those new genera. For both reasons we place *Mucubatrachus* and *Paramophrynella* in the synonymy of the subgenus *Pristimantis* and leave the ten species unassigned to species group. New morphological and/or molecular analyses will be needed to clarify the status of these taxa.

Because of incomplete descriptions or peculiar combinations of characters, we are unable to assign an additional 24 species to a species group within the subgenus *Pristimantis*. Thus, to summarize, the 34 species that have not been assigned to groups are *Pristimantis* (*Pristimantis*) *acutirostris*, *aemulatus*, *bicumulus*, *boconoensis*, *briceni*, *caliginosus*, *culatensis*, *factiosus*, *fallax*, *fetosus*, *flabellidiscus*, *ganonotus*, *ginesi*, *jabonensis*, *lancinii*, *lentiginosus*, *megalops*, *melanoproctus*, *paramerus*, *piceus*, *pleurostriatus*, *polychrus*, *pruniatus*, *pulvinatus*, *restrepoi*, *reticulatus*, *rhigophilus*, *ruedai*, *ruthveni*, *sanctaemartae*, *stenodiscus*, *thyllus*, *veletis*, and *viridis*.

Pristimantis (*Pristimantis*) *bellona* Species Group

Definition.—This is a small group of medium-sized frogs in which females attain a maximum SVL of 46 mm. The body is robust with a relatively broad head, short snout, and long limbs. Finger I is slightly shorter than Finger II; Toe V is much longer than Toe III and extends to the distal edge of the distal subarticular tubercle on Toe IV. The digital discs are expanded. A tympanic annulus and membrane are present. Cranial crests and cranial co-ossification are present in large females. Vocal slits and vomerine teeth are present.

Content.—Three species are included in this group—*Pristimantis* (*Pristimantis*) *bellona* (Fig. 116), *mars*, and *polemistes*.

Distribution.—These frogs inhabit humid montane forest on the Pacific versant of the Cordillera Occidental in Colombia.

Remarks.—This group is recognized by adult females having cranial crests and co-ossification of the dermis with underlying bones of the skull. This combination of characters is unknown elsewhere in the genus. No species were included in our molecular phylogenetic analyses.



FIGURE 116–119. **116.** *Pristimantis (Pristimantis) bellona* of the *Pristimantis bellona* Group from the Parque Nacional Las Orquidéas, Antioquia, Colombia. Photo by J. D. Lynch. **117.** *Pristimantis (Pristimantis) chalceus* of the *Pristimantis chalceus* Species Group from 4 km E Dos Rios, Pichincha, Ecuador. Photo by W. E. Duellman. **118.** *Pristimantis (Pristimantis) bipunctatus* of the *P. conspicillatus* Species Group, from 0.7 km S, 4.5 km E Oxapampa, Pasco, Peru. Photo by S. B. Hedges. **119.** *Pristimantis (Pristimantis) buckleyi* of the *Pristimantis curtipes* Species Group from 13 km W Santiago, Putumayo, Colombia. Photo by W. E. Duellman.

Pristimantis (Pristimantis) chalceus Species Group

Definition.—In these small frogs with SVLs to 31.2 mm in females, the bodies are moderately robust with short snouts, narrow heads, and short limbs. Finger I is shorter than Finger II; Toe V is much longer than Toe III and extends to the distal margin of the distal subarticular tubercle on Toe IV. The discs on the digits are expanded with terminal papillae (at least on Finger III). A tympanic membrane is not differentiated, but the tympanic annulus is visible beneath the skin. Cranial crests are absent. Vocal slits are present, and vomerine teeth are weak or absent.

Content.—Two species, *Pristimantis (Pristimantis) chalceus* (Fig. 117) and *P. (P.) scolodiscus*, are placed in this group.

Distribution.—Members of this group are arboreal in humid tropical forests on the Pacific lowlands and adjacent Andean slopes to 2000 m in Colombia and Ecuador.

Remarks.—These species formerly were placed in the “*Eleutherodactylus diastema*” Group by Lynch (2001) and Lynch and Duellman (1997). Our molecular data revealed *P. chalceus* to be imbedded in *Pristimantis*, whereas *Eleutherodactylus diastema* is a basal branch in the West Indian Clade. Morphological fea-

tures, such as the absence of)(-shaped gular folds and bifid palmar tubercle also distinguish members of the *Pristimantis (Pristimantis) chalceus* Species Group from the *E. diastema* and its relatives, now recognized as the genus *Diasporus*.

Pristimantis (Pristimantis) conspicillatus Species Group

Definition.—Frogs in this group are moderate to large in size with proportionately long hind limbs; the range in SVL is from 19 mm in male *Pristimantis skydmainos* to 72.9 mm in *P. lymani*. Head width is 30–43% SVL, and shank length is 45–64% SVL. Cranial crests are absent. The tympanic membrane and annulus are distinct, except in *P. carmelitae* and *P. johannesdei*. The dorsum is smooth or shagreen; a dorsolateral fold is present or absent. The venter usually is smooth, but it is weakly granular (areolate) in some species. The toes commonly have basal webbing, and Toe V is only slightly longer than Toe III; an inner tarsal fold is present or absent. Lateral fringes are present or absent on the fingers and toes. Vocal slits usually are present. A dark face mask is apparent in many species; the most common dorsal color pattern consists of two or three chevron-shaped marks on the back. Species in this group are primarily terrestrial, but they ascend low vegetation at night.

Content.—The species group includes 37 species: *Pristimantis (Pristimantis) achatinus*, *asiastolus*, *avicuporum*, *bipunctatus* (Fig. 118), *buccinator*, *caprifer*, *carlossanchezi*, *carmelitae*, *carranguerorum*, *charlottevillensis*, *chiastonotus*, *citriogaster*, *condor*, *conspicillatus*, *fenestratus*, *gaigeae*, *gutturalis*, *illotus*, *insignitus*, *johannesdei*, *lymani*, *malkini*, *medemi*, *meridionalis*, *metabates*, *padrekarlosi*, *pedimontanus*, *phalaroinguinis*, *samaipatae*, *savagei*, *skydmainos*, *stegolepis*, *terraebolivaris*, *thectopternus*, *vilersi*, *viridicans*, and *zeuctotylus*.

Distribution.—Members of this species group are principally distributed in northern South America from Colombia eastward to the Guianas and Isla Taboga. One species ranges northward into Costa Rica, and four species occur as far south as Bolivia.

Remarks.—Support for a monophyletic core of this species group in the taxon-dense molecular phylogeny (Fig. 2) was moderately strong (87%) and it received significant support (100%) in the ML and Bayesian analyses of the character-dense data set (Fig. 4). This group contains most of the species recognized in the “*Eleutherodactylus*” *conspicillatus* Group by Lynch and Duellman (1997). In the phylogenetic analyses of mitochondrial and nuclear gene sequences by Heinicke *et al.* (2007) as augmented herein by further analyses including more taxa, frogs formerly associated with the “*Eleutherodactylus*” *conspicillatus* Group were contained in two well-supported clades: the *Pristimantis (Pristimantis) conspicillatus* Species Group and the *P. (P.) peruvianus* Species Group. The two species groups are closest relatives in the ML phylogeny (Fig. 4), with weak support (23%), and are split apart in the Bayesian analysis. For this reason, we have chosen not to join these two groups into a higher taxon (series or subgenus) at this time. Nonetheless, individually they represent perhaps the two best-supported species groups within the subgenus *Pristimantis*. Two species assigned to the *conspicillatus* Group included in the molecular phylogeny (*P. zeuctotylus* and *P. caprifer*) are not part of this clade.

Pristimantis (Pristimantis) curtipes Species Group

Definition.—These are small to medium-sized frogs with a maximum SVL of 50 mm in females. These frogs have robust bodies, short snouts, relatively narrow heads, and proportionately short limbs. Finger I is shorter than Finger II; Toe V is only slightly longer than Toe III and does not extend to the proximal edge of the distal subarticular tubercle on Toe IV. The digital discs are narrow and rounded. A tympanic membrane and annu-

lus are absent (present in *P. buckleyi*). Cranial crests are present. Vocal slits are absent, and vomerine teeth are present.

Content.—There are six species in this group—*Pristimantis (Pristimantis) buckleyi* (Fig. 119), *cryophilus*, *curtipes*, *gentryi*, *satagi*, and *xestus*.

Distribution.—Members of this group occur in the Cordillera Occidental of the Andes from southern Colombia to central Ecuador, where they are terrestrial in paramos and humid upper montane forest.

Remarks.—The taxonomy of this group was summarized by Lynch (1995). This species group is not monophyletic in the molecular phylogeny (Fig. 2). However, there is a well-supported (95% bootstrap) clade that unites most members of the *curtipes*, *devillei*, and *surdus* species groups, as well as a member of the *unis-trigatus* group (*P. thymalopsoides*). The *curtipes*, *devillei*, and *surdus* groups (and *P. thymalopsoides*) share the presence of cranial crests, which is an otherwise rare trait within *Pristimantis*. These three groups are also distributed sympatrically and probably should be treated as a single species group (a more inclusive *devillei* Species Group).

Pristimantis (Pristimantis) devillei Species Group

Definition.—In these medium-sized frogs with SVLs to 52 mm in females; the bodies are slender to moderately robust with short snouts, narrow heads, and moderately short to relatively long limbs. Finger I is shorter than Finger II; Toe V is only slightly longer than Toe III and does not extend to the proximal edge of the distal subarticular tubercle on Toe IV. The discs on the digits are expanded. A tympanic membrane and annulus are present (absent in *P. siopelus*). Cranial crests are present (absent in *P. acatatelus* and *appendiculatus*). Vocal slits are absent (present in *P. acatatelus* and *appendiculatus*); vomerine teeth are present.

Content.—Thirteen species—*Pristimantis (Pristimantis) acatallelus*, *appendiculatus*, *cacao*, *chrysops*, *devillei* (Fig. 120), *quinquagesimus*, *silverstonei*, *siopelus*, *sulculus*, *susaguae*, *truebae*, *vertebralis*, and *xylochobates*—are recognized in this group.

Distribution.—Collectively, these species inhabit humid montane forests in the Andes in Colombia and Ecuador.

Remarks.—The relative lengths of the toes are like those of species in the *Pristimantis (Pristimantis) conspicillatus* and *P. (P.) peruvianus* species groups. One of the two species lacking cranial crests and having vocal slits (*P. appendiculatus*) was included in the molecular phylogeny (Fig. 2); it appears to be unrelated to the other species. The other species appear to be related to members of the *curtipes* and *surdus* Groups (see Remarks under *Pristimantis (Pristimantis) curtipes* Species Group).

Pristimantis (Pristimantis) frater Species Group

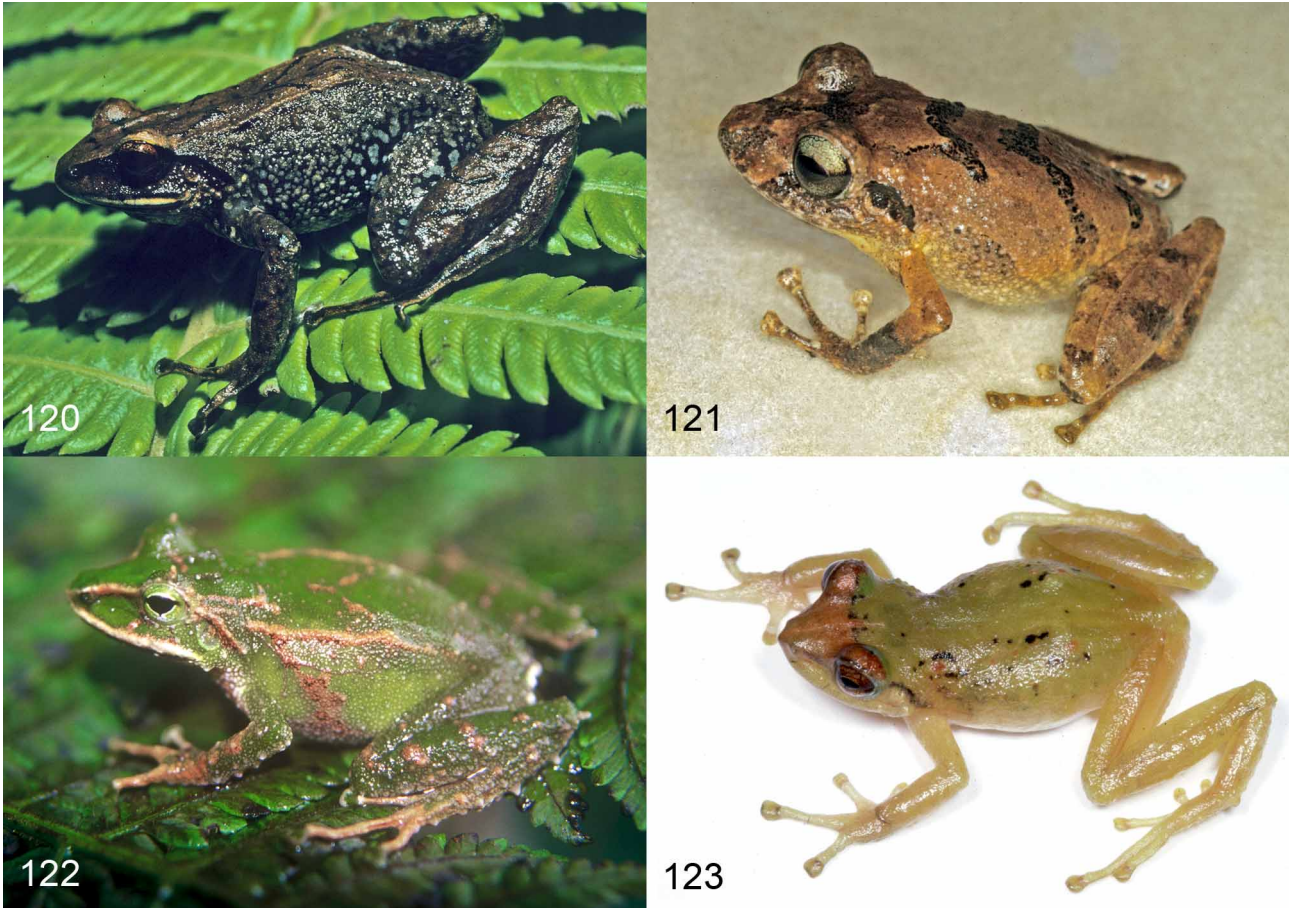
Definition.—These are small frogs with females attaining a SVL of 32.5 mm; they have moderately robust bodies with relatively narrow heads, short round to subacuminate snouts, and moderately long limbs. Finger I is shorter than Finger II; Toe V is much longer than Toe III and extends to the distal margin of the distal subarticular tubercle on Toe IV. The digital discs are expanded. The tympanic annulus and membrane are distinct. Cranial crests are absent. Vocal slits and vomerine teeth are present. Snout length is sexually dimorphic, being longer in males than in females.

Content.—Fourteen species—*Pristimantis (Pristimantis) frater*, *incomptus*, *librarius*, *martiae*, *miyatai*, *ockendeni*, *paisa*, *pecki*, *ptochus*, *quaquaversus*, *suetus*, *taeniatus* (Fig. 121), *viejaz*, *zophus*—are placed in this group.

Distribution.—Members of this group inhabit humid lowland and montane forests throughout the Pacific lowlands, Cauca and Magdalena valleys, and the Andes of Colombia, including the Sierra de Macarena but

not the Sierra Nevada de Santa Marta, and the eastern slopes of the Andes and Amazon Basin in Colombia, Ecuador, Peru, and Bolivia. One species, *Pristimantis taeniatus*, ranges from the Pacific lowlands of Colombia into central Panama.

Remarks.—This rather poorly defined group includes the “*Eleutherodactylus taeniatus* Complex” of Lynch and Ardila-Robayo (1999). The single species included in the molecular phylogeny, *P. ockendeni*, is embedded within a section of the *unistrigatus* Group (Fig. 2).



FIGURES 120–123. **120.** *Pristimantis (Pristimantis) devillei* of the *Pristimantis devillei* Species Group from 11 km E Papallacta, Napo, Ecuador. Photo by W. E. Duellman. **121.** *Pristimantis (Pristimantis) taeniatus* of the *Pristimantis frater* Group from Cerro Quia, Darién, Panama. Photo by W. E. Duellman. **122.** *Pristimantis (Pristimantis) galdi* of the *Pristimantis galdi* Species Group from Santuario Nacional Tabaconas-Namballe, Cajamarca, Peru. Photo by Y. Hooker. **123.** *Pristimantis (Pristimantis) bromeliaceus* of the *Pristimantis lacrimosus* Species Group from 2.9 km N, 5.5 km E Oxapampa, Pasco, Peru. Photo by S. B. Hedges.

Pristimantis (Pristimantis) galdi Species Group

Definition.—These are small to medium-sized frogs with SVLs to 34 mm in females; the bodies are rather robust with broad heads, long limbs, and long, acuminate snouts. Finger I is shorter than Finger II; Toe V is much longer than Toe III and extends to the distal edge of the distal subarticular tubercle on Toe IV. The digital discs are expanded. A tympanic annulus and differentiated tympanic membrane are present. Cranial crests are present, and the edges of the frontoparietals and squamosals are serrate. Vocal slits and vomerine teeth are present.

Content.—Four species—*Pristimantis (Pristimantis) delicatus*, *douglasi*, *galdi* (Fig. 122), and *tribulosus*—are placed in this group.

Distribution.—The distribution is disjunct—Sierra Nevada de Santa Marta, extreme northern part of the Cordillera Oriental in Colombia, Pacific slopes of the Cordillera Occidental in southwestern Colombia, and Amazonian slopes of the Andes in Ecuador and northern Peru.

Remarks.—The unusual condition of bony tubercles (serrations) along the lateral edges of the frontoparietals and dorsal edge of the squamosal are unique to this group (Lynch 1996a). In the molecular phylogeny, *Pristimantis galdi* appears to be unrelated to the clade containing other species with cranial crests (Fig. 2).

Pristimantis (Pristimantis) lacrimosus Species Group

Definition.—In these small to medium-sized frogs, females of the largest species attain a SVL of 34 mm. The body is moderately robust with a broad, flat head and acuminate, round, or truncate snout; the limbs are moderately long. Dorsal skin shagreen or smooth; belly areolate. Finger I is shorter than Finger II; Toe V is much longer than Toe III and extends to the distal edge of the distal subarticular tubercle on Toe IV. The digital discs are expanded. A tympanic annulus is present, and the tympanic membrane usually is differentiated. Cranial crests are absent; Vocal slits and vomerine teeth are present.

Content.—The group contains 18 species—*Pristimantis (Pristimantis) apiculatus*, *aureolineatus*, *boulengeri*, *brevifrons*, *bromeliaceus* (Fig. 123), *dorsopictus*, *eremitus*, *lacrimosus*, *mendax*, *olivaceus*, *pardalinus*, *petersorum*, *prolixodiscus*, *royi*, *schultei*, *tayrona*, *waoranii*, and *zimmermanae*.

Distribution.—Members of this group are arboreal and commonly inhabit bromeliads; the group is widespread in the upper Amazon Basin and adjacent slopes of the Andes from Colombia to Bolivia; other species inhabit humid forests on the Pacific versant of Ecuador and Colombia and the Sierra Nevada de Santa Marta in northern Colombia. At least two species, *Pristimantis aureolineata* and *P. waoranii*, are inhabitants of the canopy in lowland rainforest (Guayasamin *et al.* 2006; McCracken 2007).

Remarks.—The generic name *Cyclocephalus* (type species *C. lacrimosus*) Jiménez de la Espada (1875) is available for this group. In the molecular phylogeny, the included species form a monophyletic group (Fig. 2).

Pristimantis (Pristimantis) leptolophus Species Group

Definition.—The frogs in this group are small with females attaining a maximum SVL of less than 30 mm; they have robust bodies, narrow heads, short snouts, and moderately long legs. Finger I is shorter than Finger II, and Toe V is much longer than Toe III and extends to the distal edge of the distal subarticular tubercle on Toe IV. The discs on the digits are expanded. A tympanic membrane and annulus usually are present but weakly defined (absent in *P. peraticus*). Cranial crests are absent; vocal slits and vomerine teeth are present.

Content.—The group contains seven species—*Pristimantis (Pristimantis) lasallorum*, *leptolophus*, *maculosus*, *parectatus*, *peraticus*, *scoloblepharus*, and *uranobates* (Fig. 124).

Distribution.—These small terrestrial frogs inhabit paramo and subparamo throughout the length of the Cordillera Central in Colombia, but one species, *Pristimantis lasallorum*, is known only from a paramo in the northern part of the Cordillera Occidental in Colombia.

Remarks.—The resemblance of *Pristimantis lasallorum* to other members of the group is superficial; that species may not be related to the others. Species of this group were not included in the molecular phylogenies presented here.



FIGURES 124–127. **124.** *Pristimantis (Pristimantis) uranobates* of the *Pristimantis leptopus* Group from Hotel Termal del Ruis, Caldas, Colombia. Photo by J. D. Lynch. **125.** *Pristimantis (Pistimantis) hybotragus* of the *Pristimantis loustes* Species Group from Río Anchicayá, 8 km W Danubio, Valle, Colombia. Photo by W. E. Duellman. **126.** *Pristimantis (Pristimantis) myersi* of the *Pristimantis myersi* Species Group from 23 km E Puracé, Cauca, Colombia. Photo by W. E. Duellman. **127.** *Pristimantis (Pristimantis) melanogaster* of the *Pristimantis orestes* Species Group from Abra Barro Negro, Amazonas, Peru. Photo by W. E. Duellman.

Pristimantis (Pristimantis) loustes Species Group

Definition.—These are medium-sized frogs with SVLs to 56 mm in females; the bodies are slender with narrow heads and long snouts and limbs. Finger I is slightly shorter than Finger II, but slightly longer in *P. loustes*; Toe V is much longer than Toe III and extends to the distal edge of the distal subarticular tubercle on Toe IV. Cranial crests are present in females of *P. hybotragus* and *jaimiei*; vocal slits and vomerine teeth are present.

Content.—Only three species—*Pristimantis (Pristimantis) hybotragus* (Fig. 125), *jaimiei*, and *loustes*—are recognized in this group.

Distribution.—These frogs inhabit lowland and lower montane humid forest in southwestern Colombia and northwestern Ecuador, where they have been found on rocks and low vegetation in and near streams.

Remarks.—An apparently unique condition exists in members of this group; the ventral edge of the zygomatic ramus of the squamosal is expanded and evident externally as a knob immediately anterior to the tympanic annulus (Lynch & Duellman 1997). This species group is not present in our molecular phylogeny.

Pristimantis (Pristimantis) myersi Species Group

Definition.—Frogs in this group are small (females less than 28 mm) with short snouts, robust bodies, with short snouts and relative narrow heads; the limbs are short to moderately long. Finger I is shorter than Finger II, and Toe V is only slightly longer than Toe III and does not extend to the proximal edge of the distal subarticular tubercle of Toe IV the digital discs are narrow and rounded. The tympanic membrane is differentiated (except in *P. leoni* and *ocreatus*). Cranial crests are absent. Vocal slits are present (except in *P. floridus*); vomerine teeth are present.

Content.—Eleven species—*Pristimantis (Pristimantis) festae, floridus, gladiator, hectus, leoni, myersi* (Fig. 126), *ocreatus, pyrrhomerus, repens, scopaeus, and xeniolum*—are recognized in this group.

Distribution.—These terrestrial frogs inhabit paramos and upper humid montane forests in Ecuador and southern Colombia.

Remarks.—The generic name *Trachyphrynus* Goin and Cochran (1963) (type species *T. myersi*) is available for species in this group. The four species included in the molecular phylogeny form a monophyletic group which is part of a larger, strongly-supported assemblage (99% bootstrap) including the *curtipes, devillei*, and *surdus* groups, as well as some species in the *unistrigatus* Group (Fig. 2).

Pristimantis (Pristimantis) orcesi Species Group

Definition.—These small to medium-sized frogs (SVL in females to 36 mm) have robust bodies, narrow heads, short snouts, and moderately short limbs. Finger I is shorter than Finger II; Toe V is much longer than Toe III and extends to the distal edge of the distal subarticular tubercle on Toe IV. The digital discs are expanded. The tympanic annulus and membrane are differentiated (absent in *P. thymelensis*). Cranial crests are absent, except weakly developed in *P. thymelensis*. Vocal slits are present; vomerine teeth are present (absent in *P. orcesi*).

Content.—There are eight species—*Pristimantis (Pristimantis) huicundo, obmutescens, orcesi, ortizi, racemus, simoteriscus, simoterus, and thymelensis*—in this group.

Distribution.—Members of this group are terrestrial in paramos and subparamo in the Cordillera Occidental in Colombia and northern Ecuador.

Remarks.—This group was defined by Lynch (1981a) and revised by Guayasamin (2004). Two species are represented in the molecular phylogeny (*P. orcesi* and *P. thymelensis*). They appear to be unrelated (Fig. 2).

Pristimantis (Pristimantis) orestes Species Group

Definition.—Frogs in this group are small (females less than 34 mm) with short snouts, robust bodies, relative narrow heads, and proportionately short limbs. Finger I is shorter than Finger II, and Toe V is only slightly longer than Toe III inasmuch as it barely extends to the proximal edge of the distal subarticular tubercle of Toe IV; the digital discs are narrow and rounded. The tympanum is small with a differentiated tympanic membrane except in *P. orestes, pataikos, simonbolivari, and vidua*; both tympanic membrane and annulus absent in *P. simonsii*. Cranial crests are absent. Vocal slits usually are present (absent in *P. melanogaster* and *simonsii*); vomerine teeth are present or absent.

Content.—Fourteen species—*Pristimantis (Pristimantis) atrabracus, chimu, cordovae, corrugatus, melanogaster* (Fig. 127), *orestes, pataikos, pinguis, seorsus, simonbolivari, simonsii, stictoboubonus, ventriguttatus, and vidua*—currently are placed in this group.

Distribution.—These frogs are terrestrial in paramo and humid upper montane forest in the Andes of southern Ecuador and northern Peru.

Remarks.—Lynch and Duellman (1997) defined this group for three species in southern Ecuador, but within the last decade many new species in this group have been discovered in northern Peru (Duellman & Pramuk 1999; Duellman *et al.* 2006). Frogs in the *Pristimantis orestes* Group resemble those in the *Pristimantis myersi* Group in size, robustness, general proportions, relative lengths of Fingers I and II, and size of digital discs. Furthermore, the two groups are parapatric in the Andes of western Ecuador. Toe V is slightly longer in species in the *Pristimantis orestes* Group than it is in members of the *Pristimantis myersi* Group. Four species were included in the molecular phylogeny (Fig. 2). Whereas *P. orestes* and *P. simonbolivari* cluster together, the other species sampled (*P. simonsii* and *P. melanogaster*) do not. Nor do any of these species cluster with members of the *myersi* Group. Thus, the shared morphologies of these species may represent convergent evolution to cope with similar habitats.

Pristimantis (Pristimantis) peruvianus Species Group

Definition.—Frogs in this series are small to moderate in size with proportionately long hind limbs; the range in SVL is from 15.7 mm in male *Pristimantis peruvianus* to 45.8 mm in *P. danae*. Head width is 38–44% SVL, and shank length is 49–70% SVL. Cranial crests are absent. The tympanic membrane and annulus are distinct. The dorsum is smooth or shagreen; a dorsolateral fold is present or absent. The venter usually is smooth, but it is areolate in *P. danae*, *pharangobates*, *rhabdolaemus*, *sagittulus*, *stictogaster*, and *toftae*. The toes usually lack even basal webbing, and Toe V is only slightly longer than Toe III; an inner tarsal fold is present or absent. Lateral fringes are present or absent on the fingers and toes. Vocal slits are present. A dark face mask is present in some species, and the dorsal color pattern is highly variable, but two or three dark brown chevrons are present on the back of most species. Some of the frogs in this series are active on the ground by day, but all are found on low vegetation at night.

Content.—The species series includes 14 species: *Pristimantis (Pristimantis) albertus*, *aniptopalmatus* (Fig. 128), *crepitans*, *cuneirostris*, *danae*, *dundeei*, *ornatus*, *pharangobates*, *peruvianus*, *rhabdolaemus*, *sagittulus*, *stictogaster*, *tanyrhynchus*, and *toftae*.

Distribution.—Members of this species series occur in humid forests on the Amazonian slopes of the Andes and in the Amazon Basin in Ecuador, Peru, and Bolivia; two species (*P. crepitans* and *P. dundeei*) inhabit shrub and dry forest in Mato Grosso in southwestern Brazil.

Remarks.—Support for the monophyly of this species group is significant (100%) in all analyses (Figs. 2–4). See comments above in the account of the *Pristimantis (Pristimantis) conspicillatus* Species Group. Adults in the *P. (P.) peruvianus* Species Group generally are smaller than those in the *P. (P.) conspicillatus* Species Group. The former also has a more southern distribution than the latter, but the two groups broadly overlap in Peru and Bolivia. Recently, cryptic species have been discovered from among specimens identified as *P. peruvianus*, including those in lowland Amazonian Peru (Padial & De la Riva 2008). Sequence data are needed from topotypic *P. peruvianus* (our sample is not from the type locality) to resolve whether this group retains its current name or takes on another name. Additionally, two species placed here in the *P. peruvianus* group, *P. crepitans* and *P. dundeei*, may belong in the *P. conspicillatus* Group (J. M. Padial, pers. comm.).

Pristimantis (Pristimantis) surdus Species Group

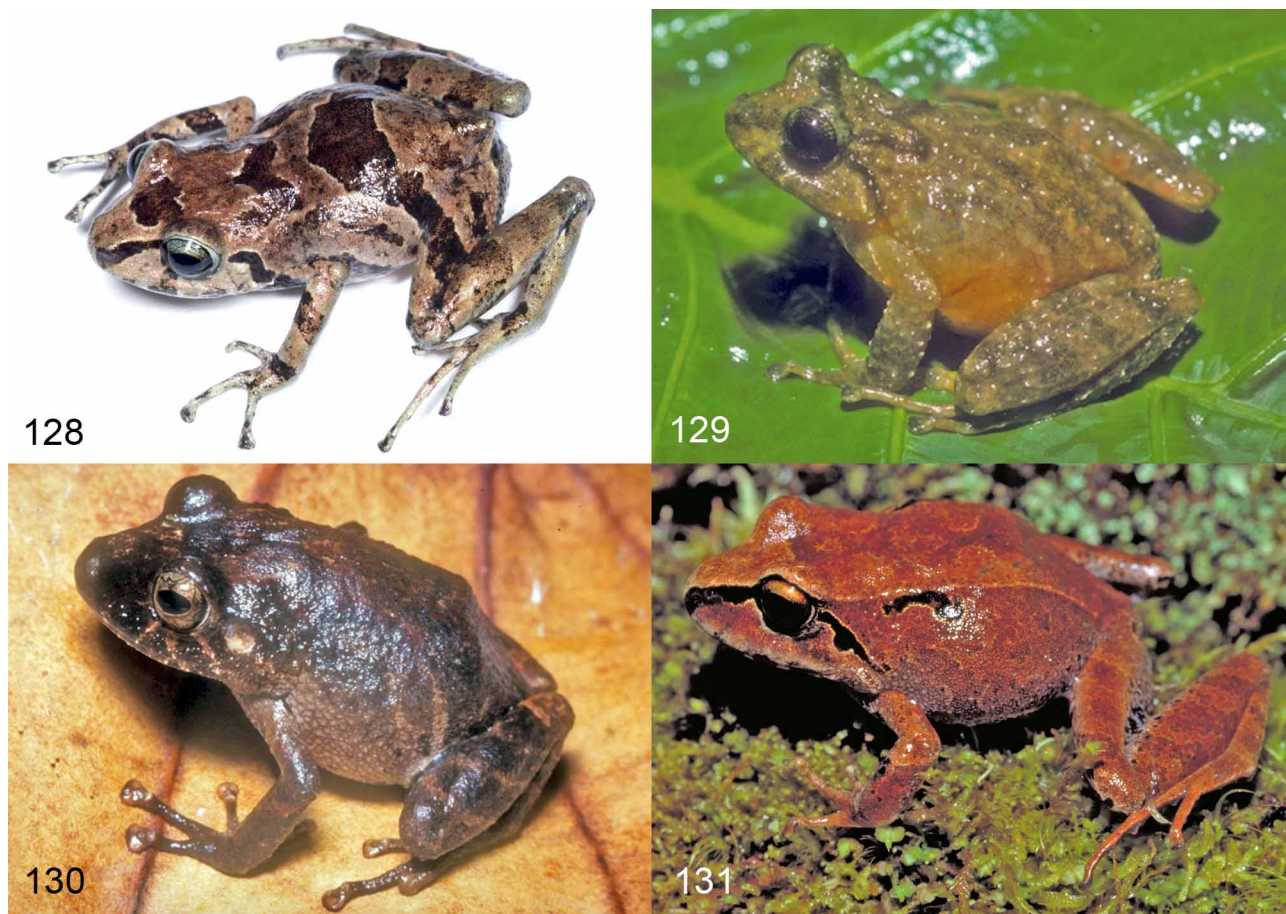
Definition.—In these medium-sized frogs with SVLs in females to 55 mm, the head is narrow, snout short, and limbs relatively long. Finger I is shorter than Finger II; Toe V is only slightly longer than Toe III and

extends to the proximal edge of the distal subarticular tubercle of Toe IV. The digital discs are expanded. The tympanic annulus and membrane are absent. Cranial crests are present. Vomerine teeth are present, and vocal slits are absent.

Content.—There are four species—*Pristimantis* (*Pristimantis*) *duellmani* (Fig. 129), *hamiotae*, *sobetes*, and *surdus*—in this putative group.

Distribution.—These frogs inhabit humid montane forest in the Cordillera Occidental in Ecuador, where individuals are primarily terrestrial and associated with streams.

Remarks.—For restriction of the content of this group, see Lynch and Duellman (1997). This group is not monophyletic, but part of a larger clade of crested species (Fig. 2). See Remarks under *Pristimantis* (*Pristimantis*) *curtipes* Species Group.



FIGURES 128–131. 128. *Pristimantis* (*Pristimantis*) *aniptopalmatum* of the *P. peruvianus* Species Group, from 2.9 km N, 5.5 km E Oxapampa, Pasco, Peru. Photo by S. B. Hedges. 129. *Pristimantis* (*Pristimantis*) *duellmani* of the *Pristimantis surdus* Species Group from 5 km E Chiriboga, Pichincha, Ecuador. Photo by W. E. Duellman. 130. *Pristimantis* (*Pristimantis*) *diadematus* of the *Pristimantis unistrigatus* Species Group from Quebada Vásquez, Loreto, Peru. Photo by W. W. Lamar. 131. *Pristimantis* (*Yunganastes*) *pluvicanorus* from La Yunga de Mairana, Departamento Santa Cruz, Bolivia; photo by J. Köhler.

Pristimantis (*Pristimantis*) *unistrigatus* Species Group

Definition.—In these small to medium sized frogs (SVL in females to 45 mm), the bodies are slender to robust with narrow heads, short snouts, and usually moderately long limbs (shorter in some high montane terrestrial species). Finger I is shorter than Finger II; toe V is much longer than Toe III and extends to the distal

edge of the distal subarticular tubercle on Toe IV. The digital discs are expanded. The tympanic annulus and tympanic membrane usually are present, but they are absent in a few species (e.g., *P. acuminatus*, *altamazonicus*, and *ventrimarmoratus*). Cranial crests usually are absent (present in a few species, such as *P. ruidus* and *thymalopsoides*). Vomerine teeth and vocal sacs usually are present.

Content.—There are 193 species assigned to this group—*Pristimantis* (*Pristimantis*) *aaptus*, *acerus*, *actinolaimus*, *acuminatus*, *affinis*, *alalocophus*, *alberico*, *altamazonicus*, *amydrotus*, *anemerus*, *angustilineatus*, *angustilineata*, *anolirex*, *anotis*, *aquilonaris*, *aracamuni*, *ardalonychus*, *atratus*, *aurantiguttatus*, *avius*, *bacchus*, *baiotis*, *balionotus*, *baryecuus*, *batrachites*, *bearsei*, *bellator*, *bernali*, *bogotensis*, *cabrerai*, *caeruleonotus*, *cajamaricensis*, *calcaratus*, *calcarulatus*, *cantitans*, *capitonis*, *carvalhoi*, *cavernibardus*, *celator*, *ceuthospilus*, *chloronotus*, *colodactylus*, *colonensis*, *colostichos*, *corniger*, *coronatus*, *cosnipatae*, *cristinae*, *croceoinguinus*, *crucifer*, *cruciocularis*, *cryptomelas*, *cuentasi*, *degener*, *deinops*, *delius*, *diadematus* (Fig. 130), *diaphonus*, *diogenes*, *dissimulatus*, *duende*, *elegans*, *eriphus*, *ernesti*, *erythropleura*, *esmeraldas*, *eugeniae*, *euphronides*, *eurydactylus*, *exoristus*, *flavobracatus*, *glandulosus*, *gracilis*, *grandiceps*, *helvolus*, *hernandezii*, *ignicolor*, *imitatrix*, *incanus*, *infraguttatus*, *inguinalis*, *inusitatus*, *jester*, *juanchoi*, *jubatus*, *karelinae*, *kaptoptroides*, *kelephas*, *lemur*, *leucopus*, *lichenoides*, *lindae*, *lirellus*, *lividus*, *llojsintuta*, *luscombei*, *luteolateralis*, *lutitus*, *lynchi*, *lythrodes*, *marahuaka*, *marmoratus*, *memorans*, *merostictus*, *minutulus*, *mnionaetes*, *modipeplus*, *molybrignus*, *mondolfi*, *muricatus*, *muscosus*, *myops*, *nephophilus*, *nervicus*, *nicefori*, *nigrogrieseus*, *nyctophylax*, *ornatissimus*, *orphnolaimus*, *palmeri*, *parvillus*, *pastazensis*, *paululus*, *penelopus*, *pernopterus*, *percultus*, *permixtus*, *petrobardus*, *phalarus*, *philipi*, *phoxocephalus*, *phragmipleuron*, *platychilus*, *platydactylus*, *prolatus*, *proserpens*, *pseudoacuminatus*, *pteridophilus*, *pugnax*, *pycnodermis*, *quaiquinimensis*, *quantus*, *reclusas*, *renjiformum*, *repens*, *rhabdocnemus*, *rhodoplichus*, *rhodostichus*, *riveroi*, *riveti*, *roseus*, *rozei*, *rufioculus*, *ruidus*, *salaputium*, *saltissimus*, *scitulus*, *serendipitus*, *shrevei*, *signifer*, *spilogaster*, *spinosus*, *sternothylax*, *subsigillatus*, *supernatis*, *taciturnus*, *tamsitti*, *tantanti*, *telefericus*, *tepuiensis*, *thymalopsoides*, *torrenticola*, *trachyblepharis*, *tubernasus*, *turpinorum*, *turumiquirensis*, *uisae*, *unistrigatus*, *urichi*, *vanadise*, *variabilis*, *ventrimarmoratus*, *verecundus*, *vermiculatus*, *versicolor*, *vicarius*, *vilcabambae*, *wagteri*, *walkeri*, *wiensi*, *yaviensis*, *yustizi*, *zoilae*.

Distribution.—This group is distributed throughout most of northwestern South America, where it occurs from lowland tropical rainforests to supra-treeline habitats in the Andes; it occurs southward to Bolivia and eastward into the Guianas, Trinidad, and Tobago; two species occur in the Lesser Antilles—*P. euphronides* on Grenada and *P. shrevei* on St. Vincent.

Remarks.—This is demonstrably not a natural group (Figs. 2–4), but rather an assemblage of species of *Pristimantis* that do not fit clearly in other groups. The phylogenetic trees, especially the tree constructed from complete 12S rRNA and 16S rRNA sequences (Fig. 3), show a well-supported structure among species in this group. For example, it is clear that the two Lesser Antillean members, *P. euphronides* and *P. shrevei*, form a clade distinct from other clades in the subgenus, and show affinity with the *conspicillatus* Group (Fig. 4). But without having a sufficient sampling of nearby Venezuelan taxa, it would be premature to erect a species group for that clade. The same logic applies for the many other well-supported clades (Fig. 3). Some of these species (e.g., *P. thymalopsoides*) have both morphological and molecular support for placement near or in other species groups. We have sequence data for less than a quarter of these species. As more data become available, it will be possible to divide this group into more manageable, named monophyletic units.

Subgenus *Yunganastes* Padial, Castroviejo-Fisher, Köhler, Domic & De la Riva 2007

Yunganastes Padial, Castroviejo-Fisher, Köhler, Domic & De la Riva, 2007: 219. Type species: *Eleutherodactylus pluviscanorus* De la Riva & Lynch (1997).

Definition.—Members of the subgenus *Yunganastes* can be defined as medium to large strabomantid frogs

with females attaining a SVL of 63 mm, having: (1) head wider or equal than long; (2) tympanic membrane and annulus differentiated; (3) cranial crests absent; (4) dentigerous processes of vomers present; (5) “E” condition of the adductor muscles (different from the standard “E” condition); (6) terminal discs on Finger III and IV and on toes broad, bearing poorly-defined and incomplete circumferential grooves, supported by T-shaped terminal phalanges; (7) Finger I slightly longer than, or equal to, Finger II; (8) Toe V equal or slightly shorter than Toe III, not reaching distal subarticular tubercle of Toe IV; (9) subarticular tubercles round, protruding; tarsal fold present in one species; (10) texture of skin on dorsum finely shagreen to smooth, with dorsolateral folds present or absent; (11) venter smooth to granular; (12) range in SVL 26 mm in male *P. bisignatus* to 63 mm in female *P. mercedesae*.

Content.—Five species—*Pristimantis (Yunganastes) ashkapara*, *bisignatus*, *fraudator*, *mercedesae*, and *pluvicanorus* (Fig. 131)—are placed in this subgenus.

Distribution.—Members of this subgenus inhabit humid montane forests on the Andean slopes from central Bolivia to southern Peru (Fig. 112).

Etymology.—According to Padial *et al.* (2007), the subgeneric name *Yunganastes* is derived from the Quechua word *yunga* applied to the humid forests in the Andean valleys and the Greek *nastes*, meaning dweller and refers to the habitat of these frogs.

Remarks.—Three members of this subgenus (*P. ashkapara*, *fraudator*, and *pluvicanorus*) were formerly assigned to the *Eleutherodactylus fraudator* group by Köhler (2000). Based on molecular and morphological characters, Padial *et al.* (2007a) proposed and described the subgenus *Yunganastes* to include these three species and two others (*P. bisignatus* and *mercedesae*); they described a new arrangement of the mandibular ramus of the adductor and the trigeminal nerve for *Yunganastes* and proposed it as a shared derived character for this taxon; they also rejected the hypothesis of relationship of *Craugastor* with members of the former *E. fraudator* Species Group. Only a short (~500 bp) sequence of a representative species of this subgenus (*Pristimantis pluvicanorus*) was available (I. de la Riva, pers. comm). In a separate analysis (not shown) it appeared as the most divergent (basal) subgenus within *Pristimantis*, although support levels were not significant. Additional sequence data will be needed to assess the relationships of this taxon and to confirm that it belongs in the genus *Pristimantis*.

Genus *Strabomantis* Peters, 1863

Strabomantis Peters, 1863:405. Type species: *Strabomantis biporcatus* Peters, 1863:405, by monotypy.

Limnophys Jiménez de la Espada, 1871:59. Type species: *Limnophys cornutus* Jiménez de la Espada, 1871:59, by subsequent designation (Myers, 1962:197). **New synonymy.**

Ctenocranius Melin, 1941:49. Type species: *Limnophys cornutus* Jiménez de la Espada, 1871:59, by original designation. Synonymy by Myers, 1962:198. **New synonymy.**

Amblyphrynus Cochran & Goin, 1961:543. Type species: *Amblyphrynus ingeri* Cochran & Goin, 1961:543, by original designation. Synonymy by Lynch (1981b:318). **New synonymy.**

Definition.—This genus of strabomantid frogs is characterized by (1) head much wider than body, up to 54% of SVL; (2) tympanic membrane and annulus distinct; (3) cranial crests usually present, except in *S. anapetes*, *anomalus*, *cheiroplethus*, and *zygodactylus*; (4) dentigerous processes of vomers prominent, triangular, or arched; (5) “E” or “S” condition of adductor muscle; (6) terminal discs on digits expanded, except in *S. biporcatus*, bearing circumferential grooves; terminal phalanges T-shaped; discs absent on fingers of *S. heleonotus*, *ingeri*, *ruizi*, and *sulcatus*, and absent on fingers and toes of *S. heleonotus* and *S. ingeri*; (7) Finger I longer than Finger II; (8) Toe III longer than Toe V; (9) subarticular tubercles projecting in *S. biporcatus*, not projecting in other species; (10) dorsum tuberculate with or without prominent longitudinal ridges (11) venter smooth in most species, areolate in *S. biporcatus*, *heleonotus*, *ingeri*, *ruizi*, and *sulcatus*; (12) SVL in adult females from 30 mm in *S. sulcatus* to 106 mm in *S. cheiroplethus*.

Content.—Two species series (16 species) are placed in the genus: the *Strabomantis biporcatus* and *bufoniformis* species series.

Distribution.—The genus occurs predominately on the Pacific lowlands and slopes of the Cordillera Occidental in Ecuador and Colombia, but also occurs in the Cordillera Central of Colombia and Cordillera Oriental of Colombia and Ecuador. One species (*S. biporcatus*) has a restricted range in the Cordillera de la Costa, Serranía del Interior, and Peninsula de Paria in northern Venezuela. Two species (*S. bufoniformis* and *S. laticorpus*) extend into Costa Rica and Panama, respectively; one species (*S. sulcatus*) occurs in the upper Amazon Basin of Ecuador, Peru, and western Brazil (Fig. 103).

Etymology.—The generic name is derived from the Greek *strabos*, meaning oblique, and the Greek *mantis*, meaning frog; the gender is masculine (see Etymology of *Pristimantis*).

Remarks.—Support for the monophyly of this genus is significant (100%) in all analyses (Figs. 2–4). Most of the species in this genus formerly were recognized as the “broad-headed eleutherodactyline frogs” (Lynch 1975b) or the “*Eleutherodactylus sulcatus* Group” (Lynch & Duellman 1997). In the various analyses of molecular data by Heinicke *et al.* (2007), four species (“*E.*” *anomalus*, *bufoniformis*, *necerus*, and *sulcatus*) formed a well-supported clade with support values of 99% in each analysis; Heinicke *et al.* (2007) resurrected the generic name *Limnophys* for this clade. In the more inclusive analyses reported herein, *Strabomantis biporcatus* is shown to be in the same clade. *Strabomantis* Peters, 1863, has priority over *Limnophys* Jiménez de la Espada, 1871, and therefore is used as the generic epithet for this clade.

Strabomantis biporcatus Peters (1863) is the correct name for the species known for more than half a century as *Eleutherodactylus maussi* Boettger (1893) (Savage & Myers 2002). This species was included in the *Eleutherodactylus (Craugastor) biporcatus* Group by Lynch and Duellman (1997) and Savage and Myers (2002), but the latter authors questioned the putative relationship of the species to the “*Eleutherodactylus biporcatus* Group.” By inference the species was included in the genus *Craugastor* by Crawford and Smith (2005). *Strabomantis biporcatus* differs from other members of the “*Eleutherodactylus biporcatus* Group” as defined by Savage and Myers (2002) by having coarsely areolate (instead of smooth) skin on the venter, distinct inner tarsal fold, accessory palmar and plantar tubercles, and vocal slits in adult males; furthermore, the karyotype of $2N = 36$ differs from the diploid number of $2N = 20$ known for other members of the group (DeWeese 1976; Schmid *et al.* 1992); in fact, the karyotype of $2N = 36$ is more like that of species of *Pristimantis* than species of *Craugastor*.

The phylogenetic analyses of molecular data reveal that those species of *Strabomantis* having the “E” condition of the adductor muscle are not closely related to *Craugastor*, all of which have the “E” condition. The placement of species having the “E” condition of the adductor muscle and formerly assigned to *Craugastor* (*Strabomantis anatipes*, *anomalus*, *biporcatus*, *bufoniformis*, *cheiroplethus*, *necerus*, and *zygodactylus*) together with other species having the “S” condition” of the adductor muscle (*S. cadenai*, *cerastes*, *cornutus*, *heleonotus*, *ingeri*, *laticorpus*, *necopinus*, *ruizi*, and *sulcatus*) is contradictory to the morphological assessment of Lynch (1986a). Savage and Myers (2002) postulated that the two conditions of the adductor musculature were derived independently from the plesiomorphic state in which both the *m. adductor subexternus posterior* and *m. adductor externus superficialis* are present, as in caecilians and most salamanders. Inasmuch as the “E” condition has evolved independently in disparate families of anurans (e.g., Rhinophrynidae, Bufonidae, Microhylidae) (Starrett 1968), the independent evolution of that state in different clades of eleutherodactylids is not unreasonable.

Strabomantis biporcatus Species Series

Definition.—Frogs in this series are moderately large with robust bodies and proportionately short limbs; the range in SVL is from 30 mm in female *Strabomantis sulcatus* to 74 mm in *S. biporcatus*. Head width is 45–

62% SVL. Cranial crests are present and are prominent in most species. The dorsum is tuberculate with longitudinal ridges in some species (*S. biporcatus*, *cerastes. ingeri*, *laticorpus*, *ruizi*, and *sulcatus*); the venter usually is smooth, but it is areolate in *S. biporcatus*, *heleonotus*, *ingeri*, *ruizi*, and *sulcatus*. The toes lack webbing. Lateral fringes are present on the fingers and toes, except in *S. cerastes* and *S. laticorpus*; discs are absent on the fingers of *S. heleonotus*, *ingeri*, *ruizi*, and *sulcatus*. Vocal slits and nuptial pads usually are absent. All species, except *S. biporcatus*, have the “S” condition of the adductor musculature. Frogs in this group are terrestrial and are found on the ground and amidst leaf litter on the forest floor.

Content.—Two species groups (10 species)—the *Strabomantis biporcatus* Group and the *Strabomantis cornutus* Group—are placed in this series.

Distribution.—With the exception of *Strabomantis biporcatus*, which is restricted to northern Venezuela, *S. sulcatus*, which occurs in the upper Amazon Basin, and *S. laticorpus* known only from the Cerro Tacarcuna area on the Colombian-Panamanian border, all species are confined to the Andes in Colombia and Ecuador.

Remarks.—Support for the monophyly of this species series was moderately strong (91%) in the analysis of complete 12S rRNA and 16SrRNA sequences (Fig. 3). This species series mostly represents the former “*Eleutherodactylus*” *sulcatus* Species Group as discussed above in the Remarks for this genus.

Strabomantis biporcatus Species Group

Definition.—This monotypic species group is characterized by a robust body attaining a maximum SVL of 74 mm in females and having a tuberculate dorsum and coarsely areolate venter. The terminal discs on the digits are barely expanded, and the lateral fringes on the toes are weak. Vocal slits are present. The species has the “E” condition of the adductor musculature.

Content.—The group consists of a single species, *Strabomantis biporcatus* (Fig. 132).

Distribution.—The species is restricted to the Cordillera de la Costa, Serranía del Interior, and the Peninsula de Paria in northern Venezuela.

Remarks.—In the present analyses (Figs. 2–4), *Strabomantis biporcatus* is in a clade with *S. sulcatus*, which differs by having the “S” condition of the adductor musculature; therefore we place *S. biporcatus* in a separate species group.

Strabomantis cornutus Species Group

Definition.—Frogs in this series are moderately large with robust bodies and proportionately short limbs; the range in SVL is from 30 mm in female *Strabomantis sulcatus* to 70 mm in *S. heleonotus*. The terminal digits are slightly to moderately expanded, and lateral fringes are present on the fingers and toes, except in *S. cerastes* and *S. laticorpus*. Vocal slits and nuptial pads are absent. These species have the “S” condition of the adductor musculature.

Content.—Nine species are placed in the species series: *Strabomantis cadenai*, *cerastes*, *cornutus*, *heleonotus*, *ingeri*, *laticorpus*, *necopinus*, *ruizi*, and *sulcatus* (Fig. 133).

Distribution.—With the exception of *Strabomantis sulcatus*, which occurs in the upper Amazon Basin, and *S. laticorpus* known only from the Cerro Tacarcuna area on the Colombian-Panamanian border, all species are confined to the Andes in Colombia and Ecuador.

Remarks.—This species group represents the former “*Eleutherodactylus*” *sulcatus* Species Group as discussed above in the Remarks for this genus. Only one species (*S. sulcatus*) of this species group was available for the molecular analyses.



132



133



134



135

FIGURES 132–135. **132.** *Strabomantis biporcatus* of the *S. biporcatus* Species Group, *S. biporcatus* Species Series, from Estación Biológica Rancho Grande, Aragua, Venezuela. Photo by W. E. Duellman. **133.** *Strabomantis sulcatus* of the *S. cornutus* Species Group, *S. biporcatus* Species Series, from Puerto Libre, Sucumbíos, Ecuador. Photo by W. E. Duellman. **134.** *Strabomantis anomalus* of the *S. bufoniformis* Species Series, from Estación Biológica Río Palenque, Los Rios, Ecuador. Photo by W. E. Duellman. **135.** *Strabomantis bufoniformis* of the *S. bufoniformis* Species Series, from Barro Colorado Island, Canal Zone, Panama. Photo by W. E. Duellman.

Strabomantis bufoniformis Species Series

Definition.—Frogs in this series are large with robust bodies and relatively short limbs; the range in SVL is from, 83 mm in females of *Strabomantis zygodactylus* to 106 mm in females of *S. cheiroplethus*. Head width is 37–58% of SVL. Cranial crests are low in *S. bufoniformis* and *S. necerus* and absent in the other species. The dorsum usually has distinct longitudinal dermal ridges (only low warts in *S. anatis* and *S. zygodactylus*); the venter is smooth. With the exception of *S. necerus*, the toes have various degrees of webbing—basal in *S. bufoniformis* to nearly entirely webbed in *S. anatis* and *S. zygodactylus*. Lateral fringes are absent on the fingers, except in *S. zygodactylus*; discs are present on all digits, and inner tarsal folds are absent. Vocal slits are present, except in *S. anomalus*, and nuptial pads are present in breeding males. All species have the “E” condition of the adductor musculature. These terrestrial frogs are usually in riparian situations; they are found at night on stones in streams and in the spray zones of waterfalls.

Content.—Six species are placed in the species series: *Strabomantis anatis*, *anomalus* (Fig. 134), *bufoniformis* (Fig. 135), *cheiroplethus*, *necerus*, and *zygodactylus*.

Distribution.—With the exception of *Strabomantis bufoniformis*, which ranges northward into Panama and Costa Rica, all members of this series are restricted to the Chocóan lowlands and adjacent slopes of the Cordillera Occidental on the Andes in Colombia and northwestern Ecuador.

Remarks.—Support for the monophyly of this species series was significant (96%) in the analysis of complete 12S rRNA and 16SrRNA sequences (Fig. 3). This species series combines the former “*E.*” *bufoniformis* and “*E.*” *anomalus* species groups as discussed above in the Remarks for this genus. The adductor musculature condition can be considered a derived character in this group.

Discussion

Classification

The new names and rearrangements that we introduce herein represent a major change in the classification of this large group of frogs. We have proposed these changes so that the classification better reflects phylogeny, as inferred from DNA sequence data (Figs. 2–4) and have increased the number of families so that it is more manageable for future research. We have also identified morphological characters that support the classification, where they are known, but further research will be needed to determine shared derived morphological characters for many of the taxa. Our definitions of the four families, while based on the molecular phylogeny, largely correspond to geography (Table 1; Fig. 136). Brachycephalidae now corresponds to the small Southeast Brazil Clade. Craugastoridae consists of the Middle American Clade (*Craugastor*) and its closest relatives in South America (*Haddadus*). Eleutherodactylidae consists of the Caribbean Clade (*Eleutherodactylus*) and its closest mainland relatives (*Diasporus*, *Adelophryne*, and *Phyzelaphryne*). Strabomantidae includes a Northwest South America Clade (*Pristimantis*) and 15 small genera that are distributed almost entirely in South America. Considering the average number of species in a family of anurans (~100), the allocation of 882 species to only four families is still conservative.

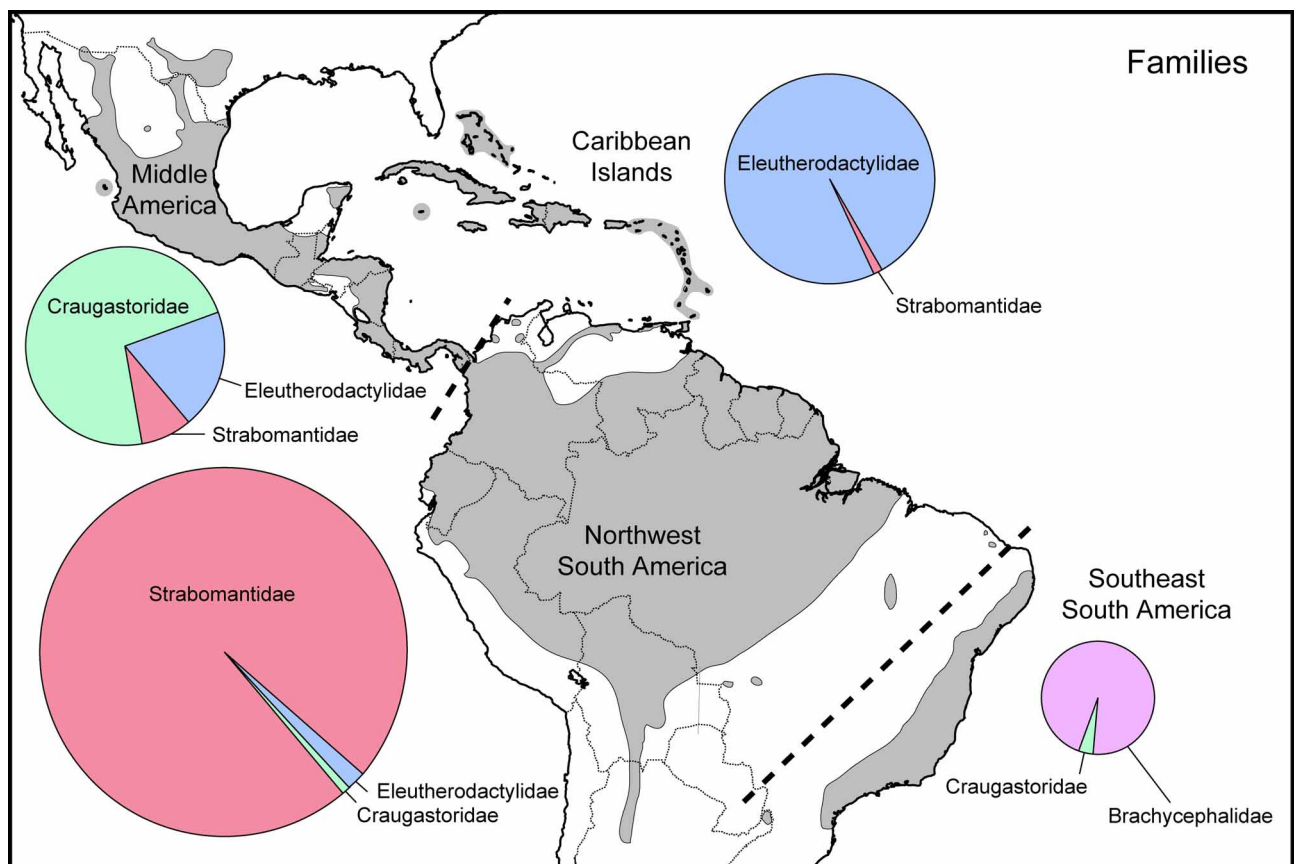


FIGURE 136. Proportion of species in each family of Terrarana, by geographic region. The area of each circle also is proportional to the total number of species in region. Data from Table 1.

TABLE 1. The number of species in each genus of Terrarana and within each geographic region. In some cases the sum of the number of species in the geographic regions is greater than the total because distributions of some species include more than one region.

Family	Genus	Species				
		Total	Caribbean	Middle America	NW South America	SE South America
Brachycephalidae	<i>Brachycephalus</i>	11	0	0	0	11
Brachycephalidae	<i>Ischnocnema</i>	29	0	0	0	29
Craugastoridae	<i>Craugastor</i>	111	0	111	4	0
Craugastoridae	<i>Haddadus</i>	2	0	0	0	2
Eleutherodactylidae	<i>Diasporus</i>	8	0	5	5	0
Eleutherodactylidae	<i>Eleutherodactylus</i>	185	161	24	0	0
Eleutherodactylidae	<i>Adelophryne</i>	5	0	0	5	1
Eleutherodactylidae	<i>Phyzelaphryne</i>	1	0	0	1	0
Strabomantidae	<i>Barycholos</i>	2	0	0	2	0
Strabomantidae	<i>Bryophryne</i>	2	0	0	2	0
Strabomantidae	<i>Euparkerella</i>	4	0	0	0	4
Strabomantidae	<i>Holoaden</i>	2	0	0	0	2
Strabomantidae	<i>Noblella</i>	8	0	0	8	0
Strabomantidae	<i>Psychrophrynella</i>	19	0	0	19	0
Strabomantidae	<i>Atopophrynus</i>	1	0	0	1	0
Strabomantidae	<i>Dischidodactylus</i>	2	0	0	2	0
Strabomantidae	<i>Geobatrachus</i>	1	0	0	1	0
Strabomantidae	<i>Isodactylus</i>	13	0	0	14	0
Strabomantidae	<i>Lynchius</i>	3	0	0	3	0
Strabomantidae	<i>Niceforonia</i>	3	0	0	3	0
Strabomantidae	<i>Oreobates</i>	15	0	0	15	0
Strabomantidae	<i>Phrynopus</i>	21	0	0	21	0
Strabomantidae	<i>Pristimantis</i>	406	2	10	412	0
Strabomantidae	<i>Strabomantis</i>	16	0	2	16	0
Totals		882	163	152	534	49

The allocation of generic names was guided by two criteria (1) phylogenetic relationships and (2) binomial stability. Because binomens are the most widely used components of the classification by non-systematists, it is important to minimize unnecessary generic changes, especially those based only on molecular evidence (field identification requires morphological or geographic evidence). We have accomplished this by making wide use of the category of subgenus and several informal categories (species series, species group, and species subgroup). As a result, all but two species occurring on Caribbean Islands are placed in a single genus, *Eleutherodactylus*, 73% of the species occurring in Middle America are placed in *Craugastor*, 77% of the species in northwestern South America are placed in *Pristimantis*, and 82% of species in southeastern South America are placed in either *Ischnocnema* or *Brachycephalus* (Fig. 137). In Middle America, the three additional terraranan genera occurring in that region can be distinguished based on morphological characters.

In South America, the chief difficulty for field identification (to genus) is among the non-*Pristimantis* species of the Andes, where a variety of morphologically similar genera (*Phrynopus*, *Noblella*, *Oreobates*, *Lynchius*, *Isodactylus*, *Niceforonia*, *Bryophryne*, and *Psychrophrynella*) occur, albeit in much smaller numbers than *Pristimantis*.

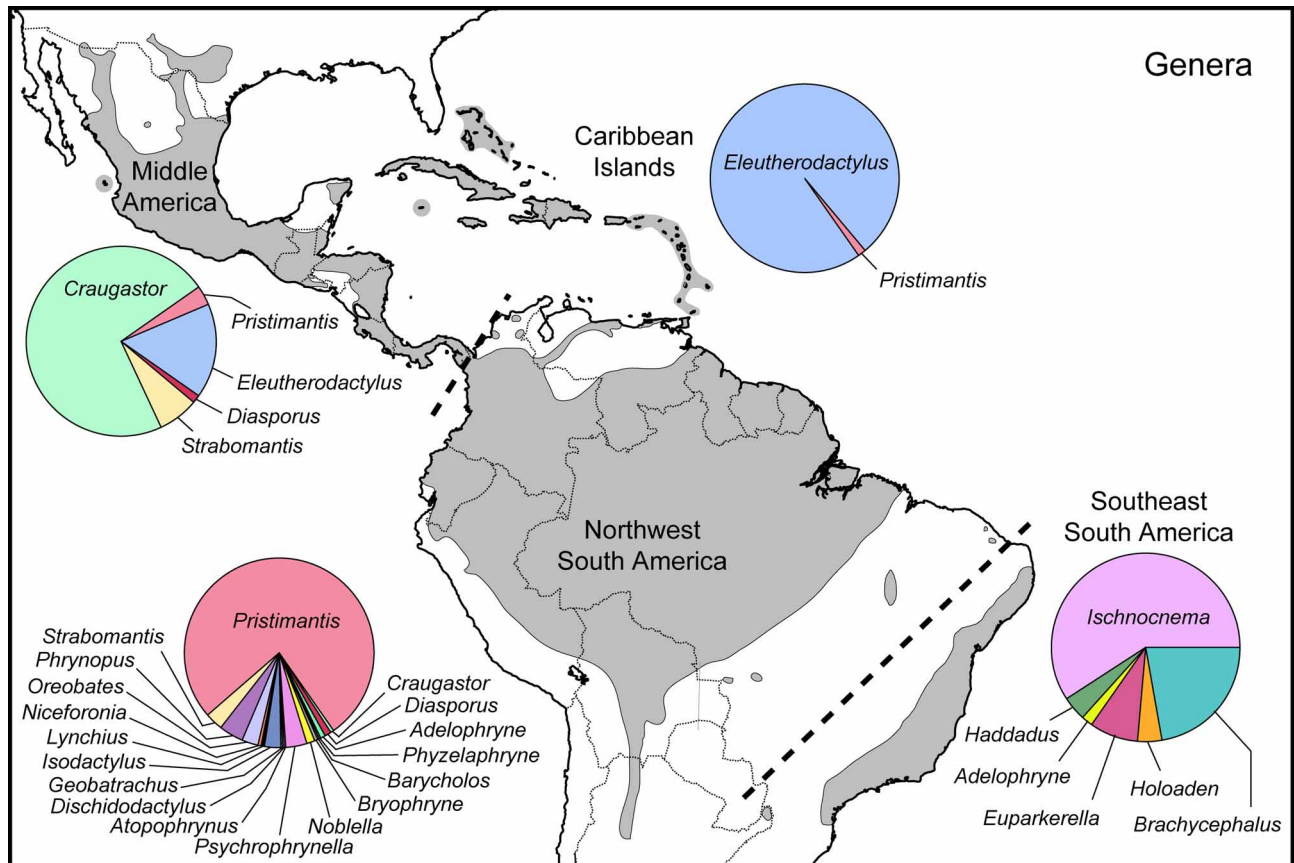


FIGURE 137. Proportion of species in each genus of Terrarana, by geographic region. Data from Table 1.

The relatively large number of taxa used for West Indian (Caribbean) species reflects the dense taxon-sampling for that region in our molecular phylogenies. Although longer sequences are needed and species will continue to be discovered, we do not anticipate major changes in the classification of West Indian eleutherodactylids. Our taxon sampling is sparser in Middle America. The subgenus *Syrrhophus* of *Eleutherodactylus* remains poorly sampled in that region and the species group definitions are based on morphology. More than one-third of the genus *Craugastor* has been sampled in molecular studies, and the phylogeny obtained here is well-supported at most nodes (Figs. 2–4). Nearly all of the species not sampled can be assigned to taxa based on their affinities with sampled species. Additional species will be discovered, but we do not anticipate major changes in classification of *Craugastor* in the future, except for the recognition of additional lower divisions (groups and subgroups). South America remains the most poorly sampled geographic region. Of the 23 genera occurring in South America, five have yet to be sampled in any molecular study. We have no doubt that some of the species and genera not yet sampled will require refinement of the generic classification when they become sampled. As we noted above in the account for *Pristimantis*, inclusion of more than 100 species in our molecular phylogeny was insufficient to revise the classification for most of the genus. Therefore, much more systematic work remains ahead in Terrarana.

As in most organisms, speciation in terraranans is not well-understood. However, their evolutionary history occurred almost entirely in the Cenozoic Era (65–0 million years ago, Ma) (Heinicke *et al.* 2007), thereby implying a relatively high rate of speciation. This evolutionary success probably can be attributed to the reproductive mode of these anurans. The innovation of direct development allowed them to disperse more widely over the land surface and exploit more terrestrial habitats, including some far from running or standing water. Thus rivers and other bodies of water have become barriers rather than conduits for gene flow. It has also been suggested that the small, terrestrial clutches of direct developing anurans are more susceptible to complete mortality (death of the entire clutch) compared with aquatic breeders, possibly increasing the rate of fixation of alleles (Dubois 2005a). This and other hypotheses to explain different rates of speciation among amphibians are reviewed elsewhere (Vences & Wake 2007).

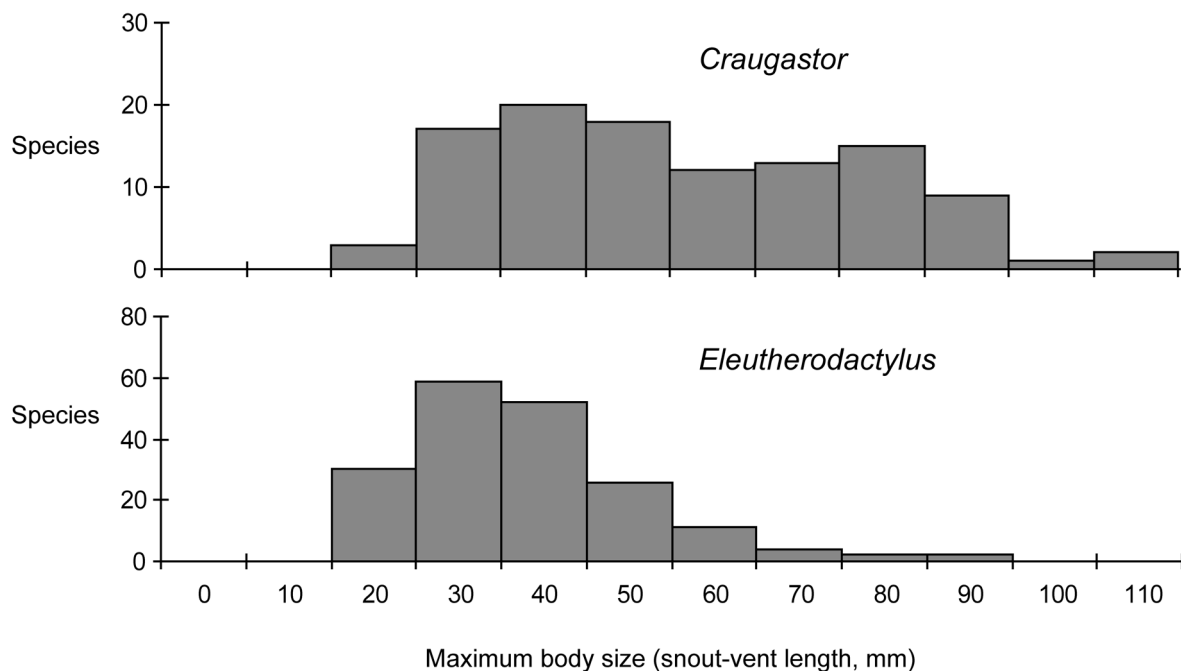
Terraranans have an unusually rapid rate of chromosome change (Bogart 1981; Kaiser *et al.* 1994; Bogart & Hedges 1995), but it is not yet clear how such change bears on the mechanism or rate of speciation in these frogs. They definitely are most diverse (species rich) in upland areas where their distributional and elevational ranges tend to be relatively small. The observation in molecular phylogenies (e.g., Fig. 2) that closely related species are often allopatric, especially on Caribbean islands where sampling is dense, suggests that allopatric speciation is the predominant mode of speciation in Terrarana. Geologic uplift and climate change during the Cenozoic would have frequently isolated populations of these forest-dwelling species, leading to speciation. However the details of this process and the subsequent changes leading to adaptive differences among species are unclear.

Terraranans have encountered and adapted to similar environments throughout the range of the group. In the process they have undergone evolutionary convergence in ecological habits and morphology. Several “ecomorphs” have been described for West Indian species of *Eleutherodactylus* (Hedges 1989a, 1989b); these probably are broadly applicable in Terrarana. For example, the aquatic (or stream) ecomorph includes species that occur in aquatic habitats, usually rocky streams, and have a streamlined body form, interdigital webbing, and large, round digital tips. The bromeliad ecomorph includes species adapted to bromeliads and have a dorsoventrally flattened body, large and rounded digital tips, and eyes oriented more forward on the head (Hedges *et al.* 1992). Other ecomorphs have been named, but a more comprehensive survey is needed to determine the occurrence of ecomorphs more generally among terraranans and whether or not they form discrete categories in adaptive space.

The new data here do not alter the major aspects of the biogeographic scenario that we presented recently elsewhere, based on the molecular phylogeny and estimated times of divergence (Heinicke *et al.* 2007). Terraranans arose in South America and dispersed, probably across marine waters, to colonize Middle America (*Craugastor*) and the Antilles (*Eleutherodactylus*) in the Mid-Cenozoic (47–29 Ma). However, the new data provide greater resolution of relationships and have allowed us to identify the closest relatives of the Middle American and Caribbean clades. *Haddadus* appears to be the closest relative of *Craugastor* whereas *Diasporus* is the closest relative of *Eleutherodactylus*. In the case of the Caribbean Clade, the phylogenetic tree (Fig. 4) shows that *Diasporus* breaks up what was previously a long branch leading to *Eleutherodactylus* (Heinicke *et al.* 2007) and indicates that the dispersal probably occurred late in the interval 47–29 Ma.

By including additional representatives of the subgenus *Syrrhophus* we found that the mainland and Cuban members are reciprocally monophyletic. This is consistent with the distribution of characters such as the presence of dentigerous processes of the vomers in the Cuban species and their absence in mainland *Syrrhophus*. It also further supports the origin of the mainland members of *Syrrhophus* by dispersal from Cuba. Nuptial pads in males are common in mainland terraranans but are absent in all species of *Eleutherodactylus* and the closely related genera *Diasporus*, *Adelophryne* and *Phyzelaphryne*, establishing this character as diagnostic for the family. Also in common among *Eleutherodactylus* and those three related genera is small body size. The average maximum SVL of species of *Eleutherodactylus* is only 33.6 mm and the smallest species of

tetrapod (tied with *Brachycephalus didactylus*) is a Cuban member of that genus (Estrada & Hedges 1996a). The average size of species in the three closely related genera is 18.1 mm. This contrasts with body size in *Craugastor* (Fig. 138), in which the average maximum SVL is 52.9 mm, or 57% larger. The two species of *Haddadus*, the closest relative of *Craugastor*, have maximum SVLs of 17 and 64 mm. Although this suggests an inheritance of ancestral body size in these large adaptive radiations, each genus contains species near the lower and upper limits of size for Terrarana indicating that size has been not been constrained. Nonetheless, miniaturization in vertebrates often is associated with loss of characters and fusion of bones (Trueb & Alberch 1985; Hanken & Wake 1993), and therefore some defining characteristics of *Eleutherodactylus* (e.g., absence of nuptial pads) may be the consequence of having a diminutive ancestor.



FIGURES 138. Body size distributions for species within two genera, *Craugastor* and *Eleutherodactylus*.

The relationships of the subgenera and species series of the Middle American Clade (*Craugastor*) (Figs. 2–3), considered along with their distributions, allow a reconstruction of the biogeographic history of that clade. As was also noted by Crawford and Smith (2005) the two most basal lineages (here designated as the subgenera *Campbellius* and *Hylactophryne*) are restricted to southern North America and northern Central America, indicating an initial colonization of the *Craugastor* lineage in that region. No species within those subgenera occurs further south than Honduras. In the mid-Cenozoic (31–42 Ma) when this initial colonization was estimated to have occurred (Heinicke *et al.* 2007), there may have been emergent land on the either the Chortis Block (now southern Guatemala, Honduras, El Salvador, and northern Nicaragua) or the southern portion of the North American continent (e.g., southern Mexico and Guatemala) or both (Pindell 1994; Iturralde-Vinent & MacPhee 1999; Hedges 2006b). Crawford and Smith (2005) found that the next most basal lineage was the “*C. gollmeri* group” (our *C. laticeps* Species Series), which includes taxa whose ranges extend southward into Panama. However, our molecular phylogeny (Figs. 2–3) differs in showing the next most basal lineage to be the *C. mexicanus* Species Series, which is restricted to Mexico and Guatemala. In our phylogeny, evidence of a migration south of Honduras is not seen until the next more derived node in the tree. All five of the remaining species series of the subgenus *Craugastor* form a monophyletic group that contains species that range at least as far south as Panama. Of that clade, two species series (*C. fitzingeri* and the *C. gulosus* species series) contain species that range further south, into South America. The southern portion of present-day Central America (Costa Rica and Panama) became emergent relatively late in the Cenozoic and therefore would

have been unavailable for initial colonization, explaining this stepwise southward migration. Only four species of *Craugastor* occur in South America, and the implication is that their distributions have extended southwards only recently, after the emergence of the Isthmus of Panama in the Pliocene.

In South America, the Southeast Brazil Clade (Brachycephalidae) has existed as long as the clade represented by the family Strabomantidae, approximately 30–50 million years, yet the former led to only 40 described species whereas the latter has led to more than ten times that number (518 species). Strabomantids are distributed over a wider area, but they are most diverse in the Andes of western South America. As has been noted elsewhere, mountain building (in addition to associated climatic change) probably resulted in habitat isolation and increased rates of speciation in these frogs (Lynch & Duellman 1997).

Within Strabomantidae the divergence of Holoadeninae and Strabomantinae occurred approximately 40–45 Ma (Heinicke *et al.* 2007). The greatly disjunct distributions of the two species of *Barycholos* in the relatively dry lowlands of Pacific Ecuador and Colombia and eastern Amazonian Brazil suggest a widespread distribution of an ancestor prior to the major uplift of the Andes in the Miocene and Pliocene and an earlier differentiation of *Noblilla*, which now inhabits Amazonian lowlands and the eastern cordilleras of the Andes. That part of the holoadenine ancestral stock that gave rise to *Bryophryne* and *Psychrophrynella* was associated later with the uplift of the Andes in Peru and Bolivia that occurred primarily since the early Miocene, 23 Ma (Gregory-Wodzicki 2002; MacFadden 2006).

Early evolution of strabomantine frogs involved the differentiation of at least four major clades approximately 30–40 Ma (Heinicke *et al.* 2007): *Isodactylus*, *Pristimantis*, *Strabomantis*, and the clade consisting of *Lynchius*, *Oreobates*, and *Phrynopus*. At least the differentiation of *Strabomantis* must have occurred before the major uplift of the northern Andes during the Pliocene (5.3–1.8 Ma), inasmuch as members of that genus are on both sides of the Andes. *Isodactylus* has one species in the Amazon Basin and several in the Andes, and apparently most of the speciation took place during the major Andean orogeny, since the early Miocene. Padial *et al.* (2007a) proposed that the early differentiation of the subgenus *Yunganastes* was coincident with the Andean orogeny.

Our molecular phylogeny identifies several previously recognized species groups of *Pristimantis* that were based solely on morphological features. These include the *Pristimantis myersi*, *orestes*, and *conspicillatus* species groups. Within the latter, as defined by Lynch and Duellman (1997), two groups are apparent—the *P. conspicillatus* group of larger and mostly Amazonian frogs and the *P. peruvianus* group of smaller and mostly Andean frogs. On the other hand, all members of the *P. curtipes*, *devillei*, and *surdus* species groups, as defined by Lynch and Duellman (1997) are nested together and intermixed in a clade that also contains one species in the *P. unistrigatus* Group (*P. thymalopsoides*). Members of the “catch-all” *P. unistrigatus* Species Group, as defined by Lynch and Duellman (1997) appear in 10 different clades in the species-rich tree (Fig. 2). Obviously molecular data are needed for many more species of *Pristimantis* before a reasonably clear picture of phylogenetic relationships will be visible. It also is apparent that careful re-examination of morphological characters is required to accurately define species groups within *Pristimantis*.

As we noted for some groups of *Eleutherodactylus* in the West Indies and some of *Craugastor* in Middle America, allopatric speciation also accounts for the great diversity of upland strabomantids in the Andes. Allopatric distributions within elevational belts were emphasized for groups of *Pristimantis* in Andean Colombia and Ecuador (Lynch 1997; Lynch & Duellman 1997). Such patterns are especially evident in the *Pristimantis* (*Pristimantis*) *curtipes*, *galdi*, and *orcesi* groups (Lynch *et al.* 1997), *myersi* group (Lynch & Duellman 1997), and *orestes* group (Duellman & Pramuk 1999). Lynch and Duellman (1997) also pointed out latitudinal displacement of closely related species of *Strabomantis* on the Pacific lowlands of Colombia and Ecuador and of *Pristimantis* on the Pacific slopes of the Andes in Colombia and Ecuador.

Several genera or groups of species include species in the lowlands and others in the Andes. An analysis of sequence data from six species of *Oreobates* by Padial *et al.* (In press) shows the Amazonian species to be basal to the five Andean species. In our analyses, the otherwise upland (Andean) *Pristimantis peruvianus*

group has the lowland *P. peruvianus* as the basal taxon. Based on morphology, Lynch (1997) postulated that *Strabomantis sulcatus* was basal to other members of the genus that occur in the Andes. All of these suggest that Andean taxa evolved from basal stocks in the lowlands, which existed before the uplift of the Andes. However, this apparent generalization may not hold true for all lineages. Based on morphological data, Lynch *et al.* (1997) postulated that in the “*Eleutherodactylus nigrovittatus*” Group a lowland species was imbedded in a clade of highland species; we are unable to refute this hypothesis because we lack molecular data for that lowland species that together with its Andean relatives is placed here in the genus *Isodactylus*.

In South America, the highlands of the great Andean mountain chain contain the greatest diversity of anurans on the continent (Duellman 1999), and a major component of that diversity is the family Strabomantidae. Of the 16 genera in Strabomantidae, only four (*Barycholos*, *Dischidodactylus*, *Euparkerella*, and *Holoaden*), with a total of 10 species, do not occur in the Andes. Eight genera (*Atopophrynus*, *Bryophryne*, *Geobatrachus*, *Lynchius*, *Niceforonia*, *Noblella*, *Phrynopus*, and *Psychrophrynella*), with a total of 58 species, are endemic to the Andes. The remaining genera (*Isodactylus*, *Oreobates*, *Pristimantis*, and *Strabomantis*) have representatives in the lowlands, but the vast majority of the 450 species inhabit the Andes, the northern, tropical part of which obviously is the center of strabomantid diversity (Fig. 137).

Conservation

The recent Global Amphibian Assessment (Stuart *et al.* 2004; IUCN 2007) found that 38% of terraranans are threatened and that 15% of terraranans are in the highest threat categories (critically endangered or extinct). Another 20% may also be threatened but there are insufficient data to determine their status. On Caribbean islands, the proportions are the highest of any region, for terraranans or for amphibians as a whole: 76% of the species are threatened and 40% are critically endangered. The threats are complex and still not well understood, although all potential causes involve the action of humans. Habitat loss is considered to be the overall major threat to amphibians in the Neotropics, affecting nearly 90% of the threatened species. Pollution and disease are the two other most commonly recorded threats (Stuart *et al.* 2004).

The fungal disease chytridiomycosis, caused by the species *Batrachochytrium dendrobatidis*, is central to many discussions of amphibian decline. Mass mortality of amphibians associated with the appearance of the fungus at localities in Panama provides compelling evidence that the fungus is the proximal cause of declines (Lips *et al.* 2006). On the other hand, the fungus is known to occur in other areas where it has not affected the resident amphibians (Daszak *et al.* 2005). Moreover, some frog populations have declined at the same time and to the same degree as co-occurring lizard populations suggesting that the proximal cause was not the fungus (Whitfield *et al.* 2007). In the latter case, those authors suggested that the declines were tied to a reduction in leaf litter as a result of global warming. Human-induced climate change already had been implicated in a previous study, although it was suggested in that case that warmer temperatures favored spread of the fungal disease (Pounds *et al.* 2006a).

Considering that lissamphibians and chytrid fungi probably have coexisted for at least 300 million years, it is unlikely that a disease would emerge naturally (without human influence), at this point in time, and potentially eradicate many species and clades of species that have evolved for tens of millions of years. Thus, if chytridiomycosis is the major proximal cause of amphibian decline, humans in some way must be affecting its distribution or enhancing conditions for its growth through climate change (Pounds *et al.* 2006a). In this respect, it is important to identify the place of origin of this disease, if possible (Morgan *et al.* 2007).

While the importance of fungal disease as a major cause of amphibian declines continues to be debated (Mendelson *et al.* 2006; Pounds *et al.* 2006b; Wake 2007), the importance of habitat destruction is well-established. Almost all species of terraranans are forest dwelling, and thus deforestation proportionately decreases numbers of individuals. Deforestation obviously can lead to species extinctions as well. As a rough guide, the species-area relationship (MacArthur & Wilson 1967) predicts that the destruction of 90% of forest habitat is expected to lead to a 50% reduction in the number of species. In the West Indies, where human population

density is at its highest in the New World, approximately 90% of original forests have been destroyed (Hedges & Woods 1993; Smith *et al.* 2005; Hedges 2006a). However, there is no evidence yet that 50% of the species have disappeared in the West Indies, and no expectation that they should do so immediately. Patches of forest often remain in the midst of broadly deforested areas, maintaining populations and species, if only temporarily. In Haiti, where forests have all but disappeared (Smith *et al.* 2005), much of the frog fauna—including 33 species of *Eleutherodactylus* endemic to Haiti and not found in the Dominican Republic—has survived in these precarious forest patches which also will soon disappear. For these Haitian frogs, habitat destruction is a more obvious threat than fungal disease. One of the better forested islands is Cuba, but even there only 15% of original forests remain intact (Smith *et al.* 2005).

Streamside species of terraranans seem to have suffered the most declines. In Central America, most of the species in *Craugastor* (*Campbellius*) and the *Craugastor* (*Craugastor*) *punctariolus* Species Group apparently have disappeared (Campbell 1999; McCranie & Wilson 2002; Savage 2002). In the West Indies, aquatic species on Jamaica (*Eleutherodactylus orcutti*), Hispaniola (*E. semipalmatus*), and Puerto Rico (*E. karlschmidti*) have not been seen in decades and may be extinct (Hedges 1993, 1999). In contrast, close relatives of those species, living in the same areas, appear to be unaffected. *Batrachochytrium dendrobatidis* is known to be in the West Indies, on at least Cuba (Díaz *et al.* 2007a) and Puerto Rico (Burrowes *et al.* 2004). However, the Cuban terraranan fauna—including aquatic species—has not shown any obvious declines at present (Hedges 1993, 1999; Hedges & Díaz 2008). Continued monitoring of these species will be important in the future (Díaz *et al.* 2007a).

Finally, the outcome of this reclassification has some important conservation implications. Saving the majority of the world's biodiversity would be prohibitively expensive, and therefore conservation practices invariably involve prioritization. The selection process of protected areas in individual countries is an example of prioritization at a local scale, whereas the concept of biodiversity “hot spots” (Myers *et al.* 2000) is an example of this on a global scale. Such systems of prioritization often rely on classifications and the maximizing of taxonomic diversity. We believe that this new classification better reflects the evolutionary history of these species, as well as their diversity, and therefore will better serve the conservation community as it faces difficult decisions ahead.

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Appendix I

Classification of species of Terrarana. Listed are the 882 recognized species as of 31 December 2007. Species used in the molecular phylogeny are shown in boldface; * = new taxonomic combinations; † = elevated from subspecific status; SG = species subgroup.

Genus (Subgenus) Species	Series	Group
BRACHYCEPHALIDAE		
<i>Brachycephalus alipioi</i> Pombal & Gasparini, 2006		
<i>Brachycephalus brunneus</i> Ribeiro, Alves, Haddad & Reis, 2005		
<i>Brachycephalus didactylus</i> (Izeckohn, 1871)		
<i>Brachycephalus ephippium</i> (Spix, 1824)		
<i>Brachycephalus ferruginus</i> Ribeiro, Alves, Haddad & Reis, 2005		
<i>Brachycephalus hermogenesi</i> (Giaretta & Sawaya, 1998)		
<i>Brachycephalus izecksohni</i> Ribeiro, Alves, Haddad & Reis, 2005		
<i>Brachycephalus nodoterga</i> Miranda-Ribeiro, 1920		
<i>Brachycephalus pernix</i> Pombal, Wistuba & Bornschein, 1998		
<i>Brachycephalus pombali</i> Ribeiro, Alves, Haddad & Reis, 2000		
<i>Brachycephalus vertebralis</i> Pombal, 2001		
<i>Ischnocnema epipeda</i> (Heyer, 1984)		<i>guentheri</i>
<i>Ischnocnema erythromera</i> (Heyer, 1984)		<i>guentheri</i>
<i>Ischnocnema gualteri</i> (Lutz, 1974)		<i>guentheri</i>
<i>Ischnocnema guentheri</i> (Steindachner, 1864)		<i>guentheri</i>
<i>Ischnocnema henselii</i> (Peters, 1870)		<i>guentheri</i>
<i>Ischnocnema hoehnei</i> (Lutz, 1958)		<i>guentheri</i>
<i>Ischnocnema izecksohni</i> (Caramaschi & Kisteumacher, 1969)		<i>guentheri</i>
<i>Ischnocnema nasuta</i> (Lutz, 1925)		<i>guentheri</i>
<i>Ischnocnema octavioi</i> (Bokermann, 1965)		<i>guentheri</i>
<i>Ischnocnema oea</i> (Heyer, 1984)		<i>guentheri</i>
<i>Ischnocnema vinhai</i> (Bokermann, 1975)		<i>guentheri</i>
<i>Ischnocnema bilineata</i> (Bokermann, 1975)		<i>lactea</i>
<i>Ischnocnema bolbodactyla</i> (Lutz, 1925)		<i>lactea</i>
<i>Ischnocnema gehrti</i> (Miranda-Ribeiro, 1926)		<i>lactea</i>
<i>Ischnocnema holti</i> (Cochran, 1948)		<i>lactea</i>
<i>Ischnocnema lactea</i> (Miranda-Ribeiro, 1923)		<i>lactea</i>
<i>Ischnocnema manezinho</i> (Garcia, 1996)		<i>lactea</i>
<i>Ischnocnema nigriventris</i> (Lutz, 1925)		<i>lactea</i>
<i>Ischnocnema paranaensis</i> (Langone & Segalla, 1996)		<i>lactea</i>
<i>Ischnocnema randorum</i> (Heyer, 1985)		<i>lactea</i>
<i>Ischnocnema sambaqui</i> (Castanho & Haddad, 2000)		<i>lactea</i>
<i>Ischnocnema spanios</i> (Heyer, 1985)		<i>lactea</i>
<i>Ischnocnema venancioi</i> (Lutz, 1958)		<i>lactea</i>
<i>Ischnocnema parva</i> (Girard, 1853)		<i>parva</i>
<i>Ischnocnema pusilla</i> (Bokermann, 1967)		<i>parva</i>

<i>Ischnocnema paulodutra</i> (Bokermann, 1975)	<i>ramagii</i>
<i>Ischnocnema ramagii</i> (Boulenger, 1888)	<i>ramagii</i>
<i>Ischnocnema juipoca</i> (Sazima & Cardoso, 1978)	<i>verrucosa</i>
<i>Ischnocnema verrucosa</i> Reinhardt & Lütken, 1862	<i>verrucosa</i>

CRAUGASTORIDAE

<i>Craugastor (Campbellius) adamastus</i> (Campbell, 1994)*		
<i>Craugastor (Campbellius) chrysozetetes</i> (McCranie, Savage & Wilson, 1989)*		
<i>Craugastor (Campbellius) cruzi</i> (McCranie, Savage & Wilson, 1989)*		
<i>Craugastor (Campbellius) daryi</i> (Ford & Savage, 1984)*		
<i>Craugastor (Campbellius) epochthidius</i> (McCranie & Wilson, 1997)*		
<i>Craugastor (Campbellius) fecundus</i> (McCranie & Wilson, 1997)*		
<i>Craugastor (Campbellius) matudai</i> (Taylor, 1941)*		
<i>Craugastor (Campbellius) milesi</i> (Schmidt, 1933)*		
<i>Craugastor (Campbellius) myllomyllon</i> (Savage, 2000)*		
<i>Craugastor (Campbellius) omoaensis</i> (McCranie & Wilson, 1997)*		
<i>Craugastor (Campbellius) saltuarius</i> (McCranie & Wilson, 1997)*		
<i>Craugastor (Campbellius) stadelmani</i> (Schmidt, 1936)*		
<i>Craugastor (Campbellius) trachydermus</i> (Campbell, 1994)*		
<i>Craugastor (Craugastor) crassidigitus</i> (Taylor, 1952)*	<i>fitzingeri</i>	<i>fitzingeri</i>
<i>Craugastor (Craugastor) fitzingeri</i> (Schmidt, 1857)*	<i>fitzingeri</i>	<i>fitzingeri</i>
<i>Craugastor (Craugastor) longirostris</i> (Boulenger, 1898)*	<i>fitzingeri</i>	<i>fitzingeri</i>
<i>Craugastor (Craugastor) raniformis</i> (Boulenger, 1896)*	<i>fitzingeri</i>	<i>fitzingeri</i>
<i>Craugastor (Craugastor) tabasarae</i> (Savage, Hollingsworth, Lips & Jaslow, 2004)*	<i>fitzingeri</i>	<i>fitzingeri</i>
<i>Craugastor (Craugastor) talamancae</i> (Dunn, 1931)*	<i>fitzingeri</i>	<i>fitzingeri</i>
<i>Craugastor (Craugastor) andi</i> (Savage, 1974)*	<i>fitzingeri</i>	<i>melanostictus</i>
<i>Craugastor (Craugastor) cuaquero</i> (Savage, 1980)*	<i>fitzingeri</i>	<i>melanostictus</i>
<i>Craugastor (Craugastor) emcelae</i> (Lynch, 1985)*	<i>fitzingeri</i>	<i>melanostictus</i>
<i>Craugastor (Craugastor) melanostictus</i> (Cope, 1875)*	<i>fitzingeri</i>	<i>melanostictus</i>
<i>Craugastor (Craugastor) monnichorum</i> (Dunn, 1940)*	<i>fitzingeri</i>	<i>melanostictus</i>
<i>Craugastor (Craugastor) phasma</i> (Lips & Savage, 1996)*	<i>fitzingeri</i>	<i>melanostictus</i>
<i>Craugastor (Craugastor) rayo</i> (Savage & DeWeese, 1979)*	<i>fitzingeri</i>	<i>melanostictus</i>
<i>Craugastor (Craugastor) aphanus</i> (Campbell, 1994)*	<i>gulosus</i>	
<i>Craugastor (Craugastor) gulosus</i> (Cope, 1875)*	<i>gulosus</i>	
<i>Craugastor (Craugastor) megacephalus</i> (Cope, 1875)*	<i>gulosus</i>	
<i>Craugastor (Craugastor) opimus</i> (Savage & Myers, 2002)*	<i>gulosus</i>	
<i>Craugastor (Craugastor) rugosus</i> (Peters, 1873)*	<i>gulosus</i>	
<i>Craugastor (Craugastor) chac</i> (Savage, 1987)*	<i>laticeps</i>	
<i>Craugastor (Craugastor) coffeus</i> (McCranie & Köhler, 1999)*	<i>laticeps</i>	
<i>Craugastor (Craugastor) gollmeri</i> (Peters, 1863)*	<i>laticeps</i>	
<i>Craugastor (Craugastor) greggi</i> (Bumzahem, 1955)*	<i>laticeps</i>	
<i>Craugastor (Craugastor) laticeps</i> (Duméril, 1853)*	<i>laticeps</i>	
<i>Craugastor (Craugastor) lineatus</i> (Brocchi, 1879)*	<i>laticeps</i>	
<i>Craugastor (Craugastor) mimus</i> (Taylor, 1955)*	<i>laticeps</i>	

<i>Craugastor (Craugastor) noblei</i> (Barbour & Dunn, 1921)*	<i>laticeps</i>	
<i>Craugastor (Craugastor) rostralis</i> (Werner, 1896)*	<i>laticeps</i>	
<i>Craugastor (Craugastor) hobartsmithi</i> (Taylor, 1937)*	<i>mexicanus</i>	
<i>Craugastor (Craugastor) mexicanus</i> (Brocchi, 1877)*	<i>mexicanus</i>	
<i>Craugastor (Craugastor) montanus</i> (Taylor, 1942)*	<i>mexicanus</i>	
<i>Craugastor (Craugastor) occidentalis</i> (Taylor, 1941)*	<i>mexicanus</i>	
<i>Craugastor (Craugastor) omiltemanus</i> (Günther, 1900)*	<i>mexicanus</i>	
<i>Craugastor (Craugastor) pygmaeus</i> (Taylor, 1937)*	<i>mexicanus</i>	
<i>Craugastor (Craugastor) saltator</i> (Taylor, 1941)*†	<i>mexicanus</i>	
<i>Craugastor (Craugastor) amniscola</i> (Campbell & Savage, 2000)*	<i>punctariolus</i>	
<i>Craugastor (Craugastor) anciano</i> (Savage, McCranie & Wilson, 1988)*	<i>punctariolus</i>	
<i>Craugastor (Craugastor) angelicus</i> (Savage, 1975)*	<i>punctariolus</i>	
<i>Craugastor (Craugastor) aurilegulis</i> (Savage, McCranie & Wilson, 1988)*	<i>punctariolus</i>	
<i>Craugastor (Craugastor) azueroensis</i> (Savage, 1975)*	<i>punctariolus</i>	
<i>Craugastor (Craugastor) berkenbuschii</i> (Peters, 1870)*	<i>punctariolus</i>	
<i>Craugastor (Craugastor) brocchi</i> (Boulenger, 1882)*	<i>punctariolus</i>	
<i>Craugastor (Craugastor) catalinae</i> (Campbell & Savage, 2000)*	<i>punctariolus</i>	
<i>Craugastor (Craugastor) charadra</i> (Campbell & Savage, 2000)*	<i>punctariolus</i>	
<i>Craugastor (Craugastor) emleni</i> (Dunn & Emlen, 1932)*	<i>punctariolus</i>	
<i>Craugastor (Craugastor) escoces</i> (Savage, 1975)*	<i>punctariolus</i>	
<i>Craugastor (Craugastor) fleischmanni</i> (Boettger, 1892)*	<i>punctariolus</i>	
<i>Craugastor (Craugastor) inachus</i> (Campbell & Savage, 2000)*	<i>punctariolus</i>	
<i>Craugastor (Craugastor) laevissimus</i> (Wermer, 1896)*	<i>punctariolus</i>	
<i>Craugastor (Craugastor) merendonensis</i> (Schmidt, 1933)*	<i>punctariolus</i>	
<i>Craugastor (Craugastor) obesus</i> (Barbour, 1928)*	<i>punctariolus</i>	
<i>Craugastor (Craugastor) olanchano</i> (McCranie & Wilson, 1999)*	<i>punctariolus</i>	
<i>Craugastor (Craugastor) palenque</i> (Campbell & Savage, 2000)*	<i>punctariolus</i>	
<i>Craugastor (Craugastor) pechorum</i> McCranie & Wilson, 1999)*	<i>punctariolus</i>	
<i>Craugastor (Craugastor) pelorus</i> (Campbell & Savage, 2000)*	<i>punctariolus</i>	
<i>Craugastor (Craugastor) pozo</i> (Johnson & Savage, 1995)*	<i>punctariolus</i>	
<i>Craugastor (Craugastor) psephosypharus</i> (Campbell, Savage & Meyer, 1994)*	<i>punctariolus</i>	
<i>Craugastor (Craugastor) punctariolus</i> (Peters, 1863)*	<i>punctariolus</i>	
<i>Craugastor (Craugastor) ranoides</i> (Cope, 1886)*	<i>punctariolus</i>	
<i>Craugastor (Craugastor) rhyacobatrachus</i> (Campbell & Savage, 2000)*	<i>punctariolus</i>	
<i>Craugastor (Craugastor) rivulus</i> (Campbell & Savage, 2000)*	<i>punctariolus</i>	
<i>Craugastor (Craugastor) rugulosus</i> (Cope, 1870)*	<i>punctariolus</i>	
<i>Craugastor (Craugastor) rupinius</i> (Campbell & Savage, 2000)*	<i>punctariolus</i>	
<i>Craugastor (Craugastor) sabrinus</i> (Campbell & Savage, 2000)*	<i>punctariolus</i>	
<i>Craugastor (Craugastor) sandersoni</i> (Schmidt, 1941)*	<i>punctariolus</i>	
<i>Craugastor (Craugastor) taurus</i> (Taylor, 1958)*	<i>punctariolus</i>	
<i>Craugastor (Craugastor) vocalis</i> (Taylor, 1940)*	<i>punctariolus</i>	
<i>Craugastor (Craugastor) vulcani</i> (Shannon & Werler, 1955)*	<i>punctariolus</i>	
<i>Craugastor (Craugastor) bransfordii</i> (Cope, 1886)*	<i>rhodopis</i>	<i>podiciferus</i>
<i>Craugastor (Craugastor) jota</i> (Lynch, 1980)*	<i>rhodopis</i>	<i>podiciferus</i>

<i>Craugastor (Craugastor) lauraster</i> (Savage, McCranie & Espinal, 1996)*	<i>rhodopis</i>	<i>podiciferus</i>
<i>Craugastor (Craugastor) persimilis</i> (Barbour, 1926)*	<i>rhodopis</i>	<i>podiciferus</i>
<i>Craugastor (Craugastor) podiciferus</i> (Cope, 1875)*	<i>rhodopis</i>	<i>podiciferus</i>
<i>Craugastor (Craugastor) polyptychus</i> (Cope, 1886)*	<i>rhodopis</i>	<i>podiciferus</i>
<i>Craugastor (Craugastor) stejnegerianus</i> (Cope, 1893)*	<i>rhodopis</i>	<i>podiciferus</i>
<i>Craugastor (Craugastor) underwoodi</i> (Boulenger, 1896)*	<i>rhodopis</i>	<i>podiciferus</i>
<i>Craugastor (Craugastor) loki</i> (Shannon & Werler, 1955)*	<i>rhodopis</i>	<i>rhodopis</i>
<i>Craugastor (Craugastor) rhodopis</i> (Cope, 1867)*	<i>rhodopis</i>	<i>rhodopis</i>
<i>Craugastor (Hylactophryne) augusti</i> (Dugès, 1879)*	<i>augusti</i>	
<i>Craugastor (Hylactophryne) tarahumaraensis</i> (Taylor, 1940)*	<i>augusti</i>	
<i>Craugastor (Hylactophryne) alfredi</i> (Boulenger, 1898)*	<i>bocourti</i>	
<i>Craugastor (Hylactophryne) batrachylus</i> (Taylor, 1940)*	<i>bocourti</i>	
<i>Craugastor (Hylactophryne) bocourti</i> (Brocchi, 1877)*	<i>bocourti</i>	
<i>Craugastor (Hylactophryne) campbelli</i> (Smith 2005)*	<i>bocourti</i>	
<i>Craugastor (Hylactophryne) cyanochthebius</i> McCranie & Smith, 2006*	<i>bocourti</i>	
<i>Craugastor (Hylactophryne) decoratus</i> (Taylor, 1942)*	<i>bocourti</i>	
<i>Craugastor (Hylactophryne) galacticorhinus</i> (Canseco-Márquez & Smith, 2004)*	<i>bocourti</i>	
<i>Craugastor (Hylactophryne) glaucus</i> (Lynch, 1967)*	<i>bocourti</i>	
<i>Craugastor (Hylactophryne) guerreroensis</i> (Lynch, 1967)*	<i>bocourti</i>	
<i>Craugastor (Hylactophryne) megalotympanum</i> (Shannon & Werler, 1955)*	<i>bocourti</i>	
<i>Craugastor (Hylactophryne) nefrens</i> (Smith, 2005)*	<i>bocourti</i>	
<i>Craugastor (Hylactophryne) polymniae</i> (Campbell, Lamar & Hillis, 1989)*	<i>bocourti</i>	
<i>Craugastor (Hylactophryne) silvicola</i> (Lynch, 1967)*	<i>bocourti</i>	
<i>Craugastor (Hylactophryne) spatulatus</i> (Smith, 1939)*	<i>bocourti</i>	
<i>Craugastor (Hylactophryne) stuarti</i> (Lynch, 1967)*	<i>bocourti</i>	
<i>Craugastor (Hylactophryne) taylora</i> (Lynch, 1966)*	<i>bocourti</i>	
<i>Craugastor (Hylactophryne) uno</i> (Savage, 1984)*	<i>bocourti</i>	
<i>Craugastor (Hylactophryne) xucanebi</i> (Stuart, 1941)*	<i>bocourti</i>	
<i>Craugastor (Hylactophryne) yucatanenensis</i> (Lynch, 1965)*	<i>bocourti</i>	
<i>Haddadus binotatus</i> (Spix, 1824)*		
<i>Haddadus plicifer</i> (Boulenger, 1888)*		

ELEUTHERODACTYLIDAE, Eleutherodactylinae

<i>Diasporus anthrax</i> (Lynch, 2001)*		
<i>Diasporus diastema</i> (Cope, 1875)*		
<i>Diasporus gularis</i> (Boulenger, 1898)*		
<i>Diasporus hylaeformis</i> (Cope, 1875)*		
<i>Diasporus quidditus</i> (Lynch, 2001)*		
<i>Diasporus tigrillo</i> (Savage, 1997)*		
<i>Diasporus tinker</i> (Lynch, 2001)*		
<i>Diasporus vocator</i> (Taylor, 1955)*		
<i>Eleutherodactylus (Eleutherodactylus) abbotti</i> Cochran , 1923	<i>auriculatus</i>	<i>abbotti</i>
<i>Eleutherodactylus (Eleutherodactylus) audanti</i> Cochran, 1934	<i>auriculatus</i>	<i>abbotti</i>
<i>Eleutherodactylus (Eleutherodactylus) haitianus</i> Barbour, 1942	<i>auriculatus</i>	<i>abbotti</i>

<i>Eleutherodactylus (Eleutherodactylus) melatrigonum</i> Schwartz, 1966*†	<i>auriculatus</i>	<i>abbotti</i>
<i>Eleutherodactylus (Eleutherodactylus) notidodes</i> Schwartz, 1966*†	<i>auriculatus</i>	<i>abbotti</i>
<i>Eleutherodactylus (Eleutherodactylus) parabates</i> Schwartz, 1964	<i>auriculatus</i>	<i>abbotti</i>
<i>Eleutherodactylus (Eleutherodactylus) pituinus</i> Schwartz, 1965	<i>auriculatus</i>	<i>abbotti</i>
<i>Eleutherodactylus (Eleutherodactylus) auriculatus</i> (Cope, 1862)	<i>auriculatus</i>	<i>auriculatus</i>
<i>Eleutherodactylus (Eleutherodactylus) bartonsmithi</i> Schwartz, 1960	<i>auriculatus</i>	<i>auriculatus</i>
<i>Eleutherodactylus (Eleutherodactylus) eileenae</i> Dunn, 1926	<i>auriculatus</i>	<i>auriculatus</i>
<i>Eleutherodactylus (Eleutherodactylus) glamyrus</i> Estrada & Hedges 1997	<i>auriculatus</i>	<i>auriculatus</i>
<i>Eleutherodactylus (Eleutherodactylus) mariposa</i> Hedges, Estrada & Thomas, 1992	<i>auriculatus</i>	<i>auriculatus</i>
<i>Eleutherodactylus (Eleutherodactylus) principalis</i> Estrada & Hedges, 1997	<i>auriculatus</i>	<i>auriculatus</i>
<i>Eleutherodactylus (Eleutherodactylus) ronaldi</i> Schwartz, 1960	<i>auriculatus</i>	<i>auriculatus</i>
<i>Eleutherodactylus (Eleutherodactylus) minutus</i> Noble 1923	<i>auriculatus</i>	<i>minutus</i>
<i>Eleutherodactylus (Eleutherodactylus) poolei</i> Cochran, 1938	<i>auriculatus</i>	<i>minutus</i>
<i>Eleutherodactylus (Eleutherodactylus) antillensis</i> (Reinhardt & Lütken, 1863)	<i>martinicensis</i>	<i>antillensis</i> (<i>antillensis</i> SG)
<i>Eleutherodactylus (Eleutherodactylus) brittoni</i> Schmidt, 1920	<i>martinicensis</i>	<i>antillensis</i> (<i>antillensis</i> SG)
<i>Eleutherodactylus (Eleutherodactylus) cochranae</i> Grant, 1932	<i>martinicensis</i>	<i>antillensis</i> (<i>antillensis</i> SG)
<i>Eleutherodactylus (Eleutherodactylus) hedricki</i> Rivero, 1963	<i>martinicensis</i>	<i>antillensis</i> (<i>antillensis</i> SG)
<i>Eleutherodactylus (Eleutherodactylus) gryllus</i> Schmidt, 1920	<i>martinicensis</i>	<i>antillensis</i> (<i>gryllus</i> SG)
<i>Eleutherodactylus (Eleutherodactylus) jasperi</i> Drewry & Jones, 1976	<i>martinicensis</i>	<i>antillensis</i> (<i>gryllus</i> SG)
<i>Eleutherodactylus (Eleutherodactylus) juanriveroi</i> Rios-López & Thomas, 2007	<i>martinicensis</i>	<i>antillensis</i> (<i>gryllus</i> SG)
<i>Eleutherodactylus (Eleutherodactylus) cooki</i> (Grant, 1932)	<i>martinicensis</i>	<i>antillensis</i> (<i>locustus</i> SG)
<i>Eleutherodactylus (Eleutherodactylus) eneidae</i> Rivero, 1959	<i>martinicensis</i>	<i>antillensis</i> (<i>locustus</i> SG)
<i>Eleutherodactylus (Eleutherodactylus) locustus</i> Schmidt, 1920	<i>martinicensis</i>	<i>antillensis</i> (<i>locustus</i> SG)
<i>Eleutherodactylus (Eleutherodactylus) coqui</i> Thomas, 1966	<i>martinicensis</i>	<i>antillensis</i> (<i>wightmanae</i> SG)
<i>Eleutherodactylus (Eleutherodactylus) portoricensis</i> Schmidt, 1927	<i>martinicensis</i>	<i>antillensis</i> (<i>wightmanae</i> SG)
<i>Eleutherodactylus (Eleutherodactylus) schwartzi</i> Thomas, 1966	<i>martinicensis</i>	<i>antillensis</i> (<i>wightmanae</i> SG)
<i>Eleutherodactylus (Eleutherodactylus) wightmanae</i> Schmidt, 1920	<i>martinicensis</i>	<i>antillensis</i> (<i>wightmanae</i> SG)
<i>Eleutherodactylus (Eleutherodactylus) flavescens</i> Noble, 1923	<i>martinicensis</i>	<i>flavescens</i>
<i>Eleutherodactylus (Eleutherodactylus) amplinympha</i> Kaiser, Green & Schmid, 1994	<i>martinicensis</i>	<i>martinicensis</i>
<i>Eleutherodactylus (Eleutherodactylus) barlagnei</i> Lynch, 1965	<i>martinicensis</i>	<i>martinicensis</i>
<i>Eleutherodactylus (Eleutherodactylus) johnstonei</i> Barbour, 1914	<i>martinicensis</i>	<i>martinicensis</i>
<i>Eleutherodactylus (Eleutherodactylus) martinicensis</i> (Tschudi, 1838)	<i>martinicensis</i>	<i>martinicensis</i>
<i>Eleutherodactylus (Eleutherodactylus) pinchoni</i> Schwartz, 1967	<i>martinicensis</i>	<i>martinicensis</i>

<i>Eleutherodactylus (Eleutherodactylus) karlschmidti</i> Grant, 1931	<i>richmondi</i>	<i>richmondi</i>
<i>Eleutherodactylus (Eleutherodactylus) richmondi</i> Stejneger, 1904	<i>richmondi</i>	<i>richmondi</i>
<i>Eleutherodactylus (Eleutherodactylus) unicolor</i> Stejneger, 1904	<i>richmondi</i>	<i>richmondi</i>
<i>Eleutherodactylus (Eleutherodactylus) fowleri</i> Schwartz, 1973	<i>varians</i>	<i>lamprotes</i>
<i>Eleutherodactylus (Eleutherodactylus) lamprotes</i> Schwartz, 1973	<i>varians</i>	<i>lamprotes</i>
<i>Eleutherodactylus (Eleutherodactylus) auriculatoides</i> Noble, 1923	<i>varians</i>	<i>montanus</i>
<i>Eleutherodactylus (Eleutherodactylus) montanus</i> Schmidt, 1919	<i>varians</i>	<i>montanus</i>
<i>Eleutherodactylus (Eleutherodactylus) patriciae</i> Schwartz, 1965	<i>varians</i>	<i>montanus</i>
<i>Eleutherodactylus (Eleutherodactylus) leberi</i> Schwartz, 1965	<i>varians</i>	<i>varians (leberi SG)</i>
<i>Eleutherodactylus (Eleutherodactylus) melacara</i> Hedges, Estrada & Thomas, 1992	<i>varians</i>	<i>varians (leberi SG)</i>
<i>Eleutherodactylus (Eleutherodactylus) guantanamera</i> Hedges, Estrada & Thomas, 1992	<i>varians</i>	<i>varians (varians SG)</i>
<i>Eleutherodactylus (Eleutherodactylus) ionthus</i> Schwartz, 1960	<i>varians</i>	<i>varians (varians SG)</i>
<i>Eleutherodactylus (Eleutherodactylus) olibrus</i> Schwartz, 1958*†	<i>varians</i>	<i>varians (varians SG)</i>
<i>Eleutherodactylus (Eleutherodactylus) staurometopon</i> Schwartz, 1960*†	<i>varians</i>	<i>varians (varians SG)</i>
<i>Eleutherodactylus (Eleutherodactylus) varians</i> Gundlach & Peters, 1864	<i>varians</i>	<i>varians (varians SG)</i>
<i>Eleutherodactylus (Eleutherodactylus) diplasius</i> Schwartz, 1973*†	<i>varians</i>	<i>wetmorei</i>
<i>Eleutherodactylus (Eleutherodactylus) sommeri</i> Schwartz, 1977*†	<i>varians</i>	<i>wetmorei</i>
<i>Eleutherodactylus (Eleutherodactylus) wetmorei</i> Cochran, 1932	<i>varians</i>	<i>wetmorei</i>
<i>Eleutherodactylus (Euhyas) alcoae</i> Schwartz, 1971	<i>armstrongi</i>	
<i>Eleutherodactylus (Euhyas) armstrongi</i> Noble & Hassler, 1933	<i>armstrongi</i>	
<i>Eleutherodactylus (Euhyas) darlingtoni</i> Cochran, 1935	<i>armstrongi</i>	
<i>Eleutherodactylus (Euhyas) leonci</i> Shreve & Williams, 1963	<i>armstrongi</i>	
<i>Eleutherodactylus (Euhyas) albipes</i> Barbour & Shreve, 1937	<i>dimidiatus</i>	<i>dimidiatus</i>
<i>Eleutherodactylus (Euhyas) dimidiatus</i> (Cope, 1862)	<i>dimidiatus</i>	<i>dimidiatus</i>
<i>Eleutherodactylus (Euhyas) emiliae</i> Dunn, 1926	<i>dimidiatus</i>	<i>dimidiatus</i>
<i>Eleutherodactylus (Euhyas) maestrensis</i> Díaz, Cádiz & Navarro, 2005	<i>dimidiatus</i>	<i>dimidiatus</i>
<i>Eleutherodactylus (Euhyas) limbensis</i> Lynn, 1958*†	<i>dimidiatus</i>	<i>schmidti</i>
<i>Eleutherodactylus (Euhyas) rucillensis</i> Cochran, 1939*†	<i>dimidiatus</i>	<i>schmidti</i>
<i>Eleutherodactylus (Euhyas) schmidti</i> Noble, 1923	<i>dimidiatus</i>	<i>schmidti</i>
<i>Eleutherodactylus (Euhyas) greyi</i> Dunn, 1926	<i>greyi</i>	
<i>Eleutherodactylus (Euhyas) cuneatus</i> (Cope, 1862)	<i>luteolus</i>	<i>cuneatus</i>
<i>Eleutherodactylus (Euhyas) turquinensis</i> Barbour & Shreve, 1937	<i>luteolus</i>	<i>cuneatus</i>
<i>Eleutherodactylus (Euhyas) cavernicola</i> Lynn, 1954	<i>luteolus</i>	<i>luteolus (cundalli SG)</i>
<i>Eleutherodactylus (Euhyas) cundalli</i> Dunn, 1926	<i>luteolus</i>	<i>luteolus (cundalli SG)</i>
<i>Eleutherodactylus (Euhyas) glaucoreius</i> Schwartz & Fowler, 1973	<i>luteolus</i>	<i>luteolus (cundalli SG)</i>
<i>Eleutherodactylus (Euhyas) fuscus</i> Lynn & Dent, 1943	<i>luteolus</i>	<i>luteolus (gossei SG)</i>
<i>Eleutherodactylus (Euhyas) gossei</i> Dunn, 1926	<i>luteolus</i>	<i>luteolus (gossei SG)</i>
<i>Eleutherodactylus (Euhyas) junori</i> Dunn, 1926	<i>luteolus</i>	<i>luteolus (gossei SG)</i>
<i>Eleutherodactylus (Euhyas) pantoni</i> Dunn, 1926	<i>luteolus</i>	<i>luteolus (gossei SG)</i>
<i>Eleutherodactylus (Euhyas) pentasyringos</i> Schwartz & Fowler, 1973	<i>luteolus</i>	<i>luteolus (gossei SG)</i>
<i>Eleutherodactylus (Euhyas) jamaicensis</i> Barbour 1910	<i>luteolus</i>	<i>luteolus (jamaicensis SG)</i>
<i>Eleutherodactylus (Euhyas) grabhami</i> Dunn, 1926	<i>luteolus</i>	<i>luteolus (luteolus SG)</i>
<i>Eleutherodactylus (Euhyas) luteolus</i> (Gosse, 1851)	<i>luteolus</i>	<i>luteolus (luteolus SG)</i>

<i>Eleutherodactylus (Euhyas) sisypodemus</i> Crombie, 1977	<i>luteolus</i>	<i>luteolus (luteolus SG)</i>
<i>Eleutherodactylus (Euhyas) alticola</i> Lynn, 1937	<i>luteolus</i>	<i>luteolus (nubicola SG)</i>
<i>Eleutherodactylus (Euhyas) andrewsi</i> Lynn, 1937	<i>luteolus</i>	<i>luteolus (nubicola SG)</i>
<i>Eleutherodactylus (Euhyas) griphus</i> Crombie, 1986	<i>luteolus</i>	<i>luteolus (nubicola SG)</i>
<i>Eleutherodactylus (Euhyas) nubicola</i> Dunn, 1926	<i>luteolus</i>	<i>luteolus (nubicola SG)</i>
<i>Eleutherodactylus (Euhyas) orcutti</i> Dunn, 1926	<i>luteolus</i>	<i>luteolus (nubicola SG)</i>
<i>Eleutherodactylus (Euhyas) riparius</i> Estrada & Hedges, 1998	<i>luteolus</i>	<i>riparius</i>
<i>Eleutherodactylus (Euhyas) rivularis</i> Diaz, Estrada & Hedges, 2001	<i>luteolus</i>	<i>riparius</i>
<i>Eleutherodactylus (Euhyas) toa</i> Estrada & Hedges, 1991	<i>luteolus</i>	<i>toa</i>
<i>Eleutherodactylus (Euhyas) amadeus</i> Hedges, Thomas & Franz, 1987	<i>oxyrhyncus</i>	<i>bakeri</i>
<i>Eleutherodactylus (Euhyas) bakeri</i> Cochran, 1935	<i>oxyrhyncus</i>	<i>bakeri</i>
<i>Eleutherodactylus (Euhyas) caribe</i> Hedges & Thomas, 1992	<i>oxyrhyncus</i>	<i>bakeri</i>
<i>Eleutherodactylus (Euhyas) corona</i> Hedges & Thomas, 1992	<i>oxyrhyncus</i>	<i>bakeri</i>
<i>Eleutherodactylus (Euhyas) dolomedes</i> Hedges & Thomas, 1992	<i>oxyrhyncus</i>	<i>bakeri</i>
<i>Eleutherodactylus (Euhyas) eunaster</i> Schwartz, 1973	<i>oxyrhyncus</i>	<i>bakeri</i>
<i>Eleutherodactylus (Euhyas) glanduliferoides</i> Shreve, 1936	<i>oxyrhyncus</i>	<i>bakeri</i>
<i>Eleutherodactylus (Euhyas) glaphycompus</i> Schwartz, 1973	<i>oxyrhyncus</i>	<i>bakeri</i>
<i>Eleutherodactylus (Euhyas) heminota</i> Shreve & Williams, 1963	<i>oxyrhyncus</i>	<i>bakeri</i>
<i>Eleutherodactylus (Euhyas) semipalmatus</i> Shreve, 1936	<i>oxyrhyncus</i>	<i>bakeri</i>
<i>Eleutherodactylus (Euhyas) thorectes</i> Hedges, 1988	<i>oxyrhyncus</i>	<i>bakeri</i>
<i>Eleutherodactylus (Euhyas) brevirostris</i> Shreve, 1936	<i>oxyrhyncus</i>	<i>glandulifer</i>
<i>Eleutherodactylus (Euhyas) glandulifer</i> Cochran, 1935	<i>oxyrhyncus</i>	<i>glandulifer</i>
<i>Eleutherodactylus (Euhyas) sciagraphus</i> Schwartz, 1973	<i>oxyrhyncus</i>	<i>glandulifer</i>
<i>Eleutherodactylus (Euhyas) ventrilineatus</i> Shreve, 1936	<i>oxyrhyncus</i>	<i>glandulifer</i>
<i>Eleutherodactylus (Euhyas) jugans</i> Cochran, 1937	<i>oxyrhyncus</i>	<i>jugans</i>
<i>Eleutherodactylus (Euhyas) apostates</i> Schwartz 1973	<i>oxyrhyncus</i>	<i>oxyrhyncus</i>
<i>Eleutherodactylus (Euhyas) oxyrhyncus</i> Duméril & Bibron, 1841	<i>oxyrhyncus</i>	<i>oxyrhyncus</i>
<i>Eleutherodactylus (Euhyas) paulsoni</i> Schwartz, 1964	<i>oxyrhyncus</i>	<i>paulsoni</i>
<i>Eleutherodactylus (Euhyas) furcyensis</i> Shreve & Williams, 1963	<i>oxyrhyncus</i>	<i>rufifemoralis</i>
<i>Eleutherodactylus (Euhyas) rufifemoralis</i> Noble & Hassler, 1933	<i>oxyrhyncus</i>	<i>rufifemoralis</i>
<i>Eleutherodactylus (Euhyas) atkinsi</i> Dunn, 1925	<i>planirostris</i>	<i>atkinsi</i>
<i>Eleutherodactylus (Euhyas) adelus</i> Díaz, Cádiz & Hedges, 2003	<i>planirostris</i>	<i>gundlachi</i>
<i>Eleutherodactylus (Euhyas) gundlachi</i> Schmidt, 1920	<i>planirostris</i>	<i>gundlachi</i>
<i>Eleutherodactylus (Euhyas) intermedius</i> Barbour & Shreve, 1937	<i>planirostris</i>	<i>gundlachi</i>
<i>Eleutherodactylus (Euhyas) tetajulia</i> Estrada & Hedges, 1996	<i>planirostris</i>	<i>gundlachi</i>
<i>Eleutherodactylus (Euhyas) varleyi</i> Dunn, 1925	<i>planirostris</i>	<i>gundlachi</i>
<i>Eleutherodactylus (Euhyas) cubanus</i> Barbour, 1942	<i>planirostris</i>	<i>limbatus</i>
<i>Eleutherodactylus (Euhyas) etheridgei</i> Schwartz, 1958	<i>planirostris</i>	<i>limbatus</i>
<i>Eleutherodactylus (Euhyas) iberia</i> Estrada & Hedges, 1996	<i>planirostris</i>	<i>limbatus</i>
<i>Eleutherodactylus (Euhyas) jaumei</i> Estrada & Alonso, 1997	<i>planirostris</i>	<i>limbatus</i>
<i>Eleutherodactylus (Euhyas) limbatus</i> (Cope, 1862)	<i>planirostris</i>	<i>limbatus</i>
<i>Eleutherodactylus (Euhyas) orientalis</i> Barbour & Shreve, 1937	<i>planirostris</i>	<i>limbatus</i>
<i>Eleutherodactylus (Euhyas) pezopetrus</i> Schwartz, 1960	<i>planirostris</i>	<i>pezopetrus</i>
<i>Eleutherodactylus (Euhyas) blairhedgesi</i> Estrada, Díaz & Rodriguez, 1998	<i>planirostris</i>	<i>pinarensis</i>

<i>Eleutherodactylus (Euhyas) pinarensis</i> Dunn, 1926	<i>planirostris</i>	<i>pinarensis</i>
<i>Eleutherodactylus (Euhyas) thomasi</i> Schwartz, 1969	<i>planirostris</i>	<i>pinarensis</i>
<i>Eleutherodactylus (Euhyas) casparii</i> Dunn, 1926	<i>planirostris</i>	<i>planirostris</i>
<i>Eleutherodactylus (Euhyas) goini</i> Schwartz, 1960	<i>planirostris</i>	<i>planirostris</i>
<i>Eleutherodactylus (Euhyas) guanahacabibes</i> Estrada & Rodriguez, 1985	<i>planirostris</i>	<i>planirostris</i>
<i>Eleutherodactylus (Euhyas) planirostris</i> (Cope, 1862)	<i>planirostris</i>	<i>planirostris</i>
<i>Eleutherodactylus (Euhyas) rogersi</i> Goin, 1955	<i>planirostris</i>	<i>planirostris</i>
<i>Eleutherodactylus (Euhyas) simulans</i> Diaz & Fong, 2001	<i>planirostris</i>	<i>planirostris</i>
<i>Eleutherodactylus (Euhyas) tonyi</i> Estrada & Hedges, 1997	<i>planirostris</i>	<i>planirostris</i>
<i>Eleutherodactylus (Euhyas) grahami</i> Schwartz, 1979	<i>ricordii</i>	<i>lentus</i>
<i>Eleutherodactylus (Euhyas) lentus</i> (Cope, 1862)	<i>ricordii</i>	<i>lentus</i>
<i>Eleutherodactylus (Euhyas) lucioi</i> Schwartz, 1980	<i>ricordii</i>	<i>lentus</i>
<i>Eleutherodactylus (Euhyas) monensis</i> Meerwarth, 1901	<i>ricordii</i>	<i>lentus</i>
<i>Eleutherodactylus (Euhyas) paralius</i> Schwartz, 1976*†	<i>ricordii</i>	<i>lentus</i>
<i>Eleutherodactylus (Euhyas) pictissimus</i> Cochran, 1935	<i>ricordii</i>	<i>lentus</i>
<i>Eleutherodactylus (Euhyas) probolaeus</i> Schwartz, 1965	<i>ricordii</i>	<i>lentus</i>
<i>Eleutherodactylus (Euhyas) rhodesi</i> Schwartz, 1980	<i>ricordii</i>	<i>lentus</i>
<i>Eleutherodactylus (Euhyas) warreni</i> Schwartz, 1976	<i>ricordii</i>	<i>lentus</i>
<i>Eleutherodactylus (Euhyas) weinlandi</i> Barbour, 1914	<i>ricordii</i>	<i>lentus</i>
<i>Eleutherodactylus (Euhyas) acmonis</i> Schwartz, 1960	<i>ricordii</i>	<i>ricordii</i>
<i>Eleutherodactylus (Euhyas) bresslerae</i> Schwartz, 1960	<i>ricordii</i>	<i>ricordii</i>
<i>Eleutherodactylus (Euhyas) michaelsschmidi</i> Días, Cádiz & Navarro, 2007	<i>ricordii</i>	<i>ricordii</i>
<i>Eleutherodactylus (Euhyas) ricordii</i> (Duméril & Bibron, 1841)	<i>ricordii</i>	<i>ricordii</i>
<i>Eleutherodactylus (Euhyas) erythroproctus</i> Schwartz, 1960*†	<i>zugii</i>	
<i>Eleutherodactylus (Euhyas) klinikowskii</i> Schwartz, 1959	<i>zugii</i>	
<i>Eleutherodactylus (Euhyas) zugii</i> Schwartz, 1958	<i>zugii</i>	
<i>Eleutherodactylus (Pelorius) chlorophenax</i> Schwartz, 1976	<i>inoptatus</i>	
<i>Eleutherodactylus (Pelorius) inoptatus</i> Barbour, 1914	<i>inoptatus</i>	
<i>Eleutherodactylus (Pelorius) nortoni</i> Schwartz, 1976	<i>inoptatus</i>	
<i>Eleutherodactylus (Pelorius) aporostegus</i> Schwartz, 1965*†	<i>ruthae</i>	
<i>Eleutherodactylus (Pelorius) bothroboans</i> Schwartz, 1965*†	<i>ruthae</i>	
<i>Eleutherodactylus (Pelorius) hypostenor</i> Schwartz, 1965	<i>ruthae</i>	
<i>Eleutherodactylus (Pelorius) parapelates</i> Hedges & Thomas, 1987	<i>ruthae</i>	
<i>Eleutherodactylus (Pelorius) ruthae</i> Noble, 1923	<i>ruthae</i>	
<i>Eleutherodactylus (Pelorius) tychathrous</i> Schwartz, 1965*†	<i>ruthae</i>	
<i>Eleutherodactylus (Schwartzius) counouspeus</i> Schwartz, 1964*		
<i>Eleutherodactylus (Syrrhophus) cystignathoides</i> (Cope, 1877)	<i>longipes</i>	<i>leprus</i>
<i>Eleutherodactylus (Syrrhophus) leprus</i> (Cope, 1879)	<i>longipes</i>	<i>leprus</i>
<i>Eleutherodactylus (Syrrhophus) rubrimaculatus</i> (Taylor & Smith, 1945)	<i>longipes</i>	<i>leprus</i>
<i>Eleutherodactylus (Syrrhophus) dennisi</i> (Lynch, 1970)	<i>longipes</i>	<i>longipes</i>
<i>Eleutherodactylus (Syrrhophus) longipes</i> (Baird, 1859)	<i>longipes</i>	<i>longipes</i>
<i>Eleutherodactylus (Syrrhophus) guttilatus</i> (Cope, 1879)	<i>longipes</i>	<i>marnockii</i>
<i>Eleutherodactylus (Syrrhophus) marnockii</i> (Cope, 1878)	<i>longipes</i>	<i>marnockii</i>
<i>Eleutherodactylus (Syrrhophus) verrucipes</i> (Cope, 1885)	<i>longipes</i>	<i>marnockii</i>

<i>Eleutherodactylus (Syrrhophus) verruculatus</i> (Peters, 1870)	<i>longipes</i>	<i>marnockii</i>
<i>Eleutherodactylus (Syrrhophus) interorbitalis</i> (Langebartel & Shannon, 1956)	<i>longipes</i>	<i>modestus</i>
<i>Eleutherodactylus (Syrrhophus) modestus</i> (Taylor, 1942)	<i>longipes</i>	<i>modestus</i>
<i>Eleutherodactylus (Syrrhophus) nivicolimae</i> (Dixon & Webb, 1966)	<i>longipes</i>	<i>modestus</i>
<i>Eleutherodactylus (Syrrhophus) pallidus</i> (Duellman, 1958)	<i>longipes</i>	<i>modestus</i>
<i>Eleutherodactylus (Syrrhophus) teretistes</i> (Duellman, 1958)	<i>longipes</i>	<i>modestus</i>
<i>Eleutherodactylus (Syrrhophus) pipilans</i> (Taylor, 1940)	<i>longipes</i>	<i>pipilans</i>
<i>Eleutherodactylus (Syrrhophus) albolabris</i> (Taylor, 1943)	<i>longipes</i>	<i>nitidus</i>
<i>Eleutherodactylus (Syrrhophus) angustidigitorum</i> (Taylor, 1940)	<i>longipes</i>	<i>nitidus</i>
<i>Eleutherodactylus (Syrrhophus) dilatus</i> (Davis & Dixon, 1955)	<i>longipes</i>	<i>nitidus</i>
<i>Eleutherodactylus (Syrrhophus) grandis</i> (Dixon, 1957)	<i>longipes</i>	<i>nitidus</i>
<i>Eleutherodactylus (Syrrhophus) maurus</i> (Hedges, 1989)	<i>longipes</i>	<i>nitidus</i>
<i>Eleutherodactylus (Syrrhophus) nitidus</i> (Peters, 1870)	<i>longipes</i>	<i>nitidus</i>
<i>Eleutherodactylus (Syrrhophus) rufescens</i> (Duellman & Dixon, 1959)	<i>longipes</i>	<i>nitidus</i>
<i>Eleutherodactylus (Syrrhophus) saxatilis</i> Webb, 1962)	<i>longipes</i>	<i>nitidus</i>
<i>Eleutherodactylus (Syrrhophus) syristes</i> (Hoyt, 1965)	<i>longipes</i>	<i>nitidus</i>
<i>Eleutherodactylus (Syrrhophus) symingtoni</i> Schwartz, 1957	<i>symingtoni</i>	
<i>Eleutherodactylus (Syrrhophus) zeus</i> Schwartz, 1958	<i>symingtoni</i>	

ELEUTHERODACTYLIDAE, Phyzelaphryninae

- Adelophryne adiaastola* Hoogmoed & Lescure, 1984
Adelophryne baturitensis Hoogmoed, Borges & Cascon, 1994
***Adelophryne gutturosa* Hoogmoed & Lescure, 1984**
Adelophryne maranguapensis Hoogmoed, Borges & Cascon, 1994
Adelophryne pachydactyla Hoogmoed, Borges & Cascon, 1994
***Phyzelaphryne miriamae* Heyer, 1977**

STRABOMANTIDAE, Holoadeninae

- Barycholos pulcher* Boulenger, 1898**
***Barycholos ternetzi* Miranda Ribeiro, 1937**
Bryophryne bustamantei (Chaparro, De la Riva, Padial, Ochoa, & Lehr, 2007)*
Bryophryne cophites* (Lynch, 1975)
Euparkerella brasiliensis (Parker, 1926)
Euparkerella cochranae Izecksohn, 1988
Euparkerella robusta Izecksohn, 1988
Euparkerella tridactyla Izecksohn, 1988
***Holoaden bradei* Lutz, 1958**
***Holoaden luederwaldti* Miranda-Ribeiro, 1920**
Noblella peruviana (Noble, 1921)
Noblella carrascoicola (De la Riva & Köhler, 1998)
Noblella duellmani (Lehr, Aguilar & Lundberg, 2004)
Noblella heyeri (Lynch, 1986)
***Noblella lochites* (Lynch, 1976)**
Noblella lynchi (Duellman, 1991)

Noblella myrmecoides (Lynch, 1976)
Noblella ritarasquinae (Köhler, 2000)
Psychrophrynella adenopleurus (Aguayo-Vedia & Harvey, 2001)*
Psychrophrynella ancohuma (Padial and De la Riva, 2007)*
Psychrophrynella bagrecito (Lynch, 1986)*
Psychrophrynella boettgeri (Lehr, 2006)*
Psychrophrynella chacaltaya (De la Riva, Padial, & Cortéz, 2007)*
Psychrophrynella condoriri (De la Riva, Aguayo, & Padial, 2007)*
Psychrophrynella guillei (De la Riva, 2007)*
Psychrophrynella harveyi (Muñoz, Aguayo, & De la Riva, 2007)*
Psychrophrynella iani (De la Riva, Reichle, & Cortéz, 2007)*
Psychrophrynella iatamasi* (Aguayo-Vedia & Harvey, 2001)
Psychrophrynella illampu (De la Riva, Reichle, & Padial, 2007)*
Psychrophrynella illimani (De la Riva & Padial, 2007)*
Psychrophrynella kallawaya (De la Riva & Martínez-Solano, 2007)*
Psychrophrynella katantika (De la Riva & Martínez-Solano, 2007)*
Psychrophrynella kempffi (De la Riva, 1992)*
Psychrophrynella pinguis (Harvey & Ergueta-Sandoval, 1998)*
Psychrophrynella quimsacruzis (De la Riva, Reichle, & Bosch, 2007)*
Psychrophrynella wettsteini* (Parker, 1932)

STRABOMANTIDAE, Strabomantinae

Atopophrynus syntomopus Lynch & Ruiz-Carranza, 1982
Dischidodactylus colomelloi Ayarzagüina, 1985
Dischidodactylus duidensis (Rivero, 1968)
Geobatrachus walkeri Ruthven, 1915
Isodactylus adercus (Lynch, 2003)*
Isodactylus araiodactylus (Duellman & Pramuk, 1999)*
Isodactylus babax (Lynch, 1989)*
Isodactylus brunneus* (Lynch, 1975)
Isodactylus dolops* (Lynch & Duellman, 1980)
Isodactylus elassodiscus* (Lynch, 1973)
Isodactylus fallaciosus (Duellman, 2000)*
Isodactylus latens (Lynch, 1989)*
Isodactylus lucida (Cannatella, 1984)*
Isodactylus lundbergi (Lehr, 2005)*
Isodactylus mantipus (Boulenger, 1908)*
Isodactylus nigrovittatus (Andersson, 1945)*
Isodactylus peraccai* (Lynch, 1975)
Lynchius flavomaculatus* (Parker, 1938)
Lynchius nebulanastes* (Cannatella, 1984)
Lynchius parkeri* (Lynch, 1975)
Niceforonia adenobrachia (Ardila-Robayo, Ruiz-Carranza & Barrera-Rodriguez, 1996)*
Niceforonia columbiana (Werner, 1899)

Niceforonia nana Goin & Cochran, 1963
Oreobates choristolemma (Harvey & Sheehy, 2005)
Oreobates cruralis* (Boulenger, 1902)
Oreobates discoidalis (Peracca, 1895)*
Oreobates granulatus (Boulenger, 1903)*†
Oreobates heterodactylus (Miranda-Ribeiro, 1937)*
Oreobates ibischi (Reichle, Lötters & Se la Riva, 2001)*
Oreobates lehri (Padial, Chaparro & De la Riva, 2007)*
Oreobates madidi (Padial, González & De la Riva, 2005)*
Oreobates pereger (Lynch, 1975)*
***Oreobates quixensis* Jiménez de la Espada, 1872**
Oreobates sanctaerucis (Harvey & Keck, 1995)
Oreobates sanderi (Padial, Reichle & De la Riva, 2005)
***Oreobates saxatilis* (Duellman, 1990)**
Oreobates simmonsii (Lynch, 1974)
Oreobates zongoensis (Reichle & Köhler, 1997)*
***Phrynopus auriculatus* Duellman & Hedges, 2008**
Phrynopus ayacucho Lehr, 2007
***Phrynopus barthlenae* Lehr & Aguilar, 2002**
***Phrynopus bracki* Hedges, 1990**
***Phrynopus bufoides* Lehr, Lundberg & Aguilar, 2005**
Phrynopus dagmarae Lehr, Aguilar & Köhler, 2002
***Phrynopus heimorum* Lehr, 2001**
***Phrynopus horstpauli* Lehr, Köhler & Ponce, 2000**
***Phrynopus juninensis* (Shreve, 1938)**
***Phrynopus kauneorum* Lehr, Aguilar & Köhler, 2002**
Phrynopus kotosh Lehr, 2007
Phrynopus sp. 1 Chaparro, Padial, & De la Riva, 2008
Phrynopus montium (Shreve, 1938)
Phrynopus sp. 2 Chaparro, Padial, & De la Riva, 2008
Phrynopus oblivius Lehr, 2007
Phrynopus paucari Lehr, Lundberg & Aguilar, 2005
Phrynopus peruanus Peters, 1873
***Phrynopus pesantesi* Lehr, Lundberg & Aguilar, 2005**
***Phrynopus tautzorum* Lehr & Aguilar, 2003**
Phrynopus thompsoni Duellman, 2000
***Phrynopus tribulosus* Duellman & Hedges, 2008**
***Pristimantis dendrobatoides* Means & Savage, 2007**
Pristimantis (Hypodictyon) altae (Dunn, 1942)* *ridens*
Pristimantis (Hypodictyon) bicolor (Rueda-Almonacid & Lynch, 1983)* *ridens*
Pristimantis (Hypodictyon) colomai* (Lynch & Duellman, 1997) *ridens*
Pristimantis (Hypodictyon) cremnobates* (Lynch & Duellman, 1980) *ridens*
Pristimantis (Hypodictyon) cruentus* (Peters, 1873) *ridens*
Pristimantis (Hypodictyon) jorgevelosai (Lynch, 1994)* *ridens*

<i>Pristimantis (Hypodictyon) laticlavus</i> (Lynch & Burrowes, 1990)*	<i>ridens</i>
<i>Pristimantis (Hypodictyon) latidiscus</i> (Boulenger, 1899)*	<i>ridens</i>
<i>Pristimantis (Hypodictyon) moro</i> (Savage, 1965)*	<i>ridens</i>
<i>Pristimantis (Hypodictyon) museosus</i> (Ibáñez, Jaramillo & Arosemena, 1994)*	<i>ridens</i>
<i>Pristimantis (Hypodictyon) pardalis</i> (Barbour, 1928)*	<i>ridens</i>
<i>Pristimantis (Hypodictyon) pirrensis</i> (Ibáñez & Crawford, 2004)*	<i>ridens</i>
<i>Pristimantis (Hypodictyon) ridens</i> (Cope, 1888)*	<i>ridens</i>
<i>Pristimantis (Hypodictyon) rosadoi</i> (Flores, 1988)*	<i>ridens</i>
<i>Pristimantis (Hypodictyon) sanguineus</i> (Lynch, 1998)*	<i>ridens</i>
<i>Pristimantis (Hypodictyon) achatinus</i> (Boulenger, 1898)*	<i>rubicundus</i>
<i>Pristimantis (Hypodictyon) actites</i> (Lynch, 1979)*	<i>rubicundus</i>
<i>Pristimantis (Hypodictyon) cerasinus</i> (Cope, 1875)*	<i>rubicundus</i>
<i>Pristimantis (Hypodictyon) crenunguis</i> (Lynch, 1976)*	<i>rubicundus</i>
<i>Pristimantis (Hypodictyon) epacrus</i> (Lynch & Suárez-Mayorga, 2000)*	<i>rubicundus</i>
<i>Pristimantis (Hypodictyon) ixalus</i> (Lynch, 2003)*	<i>rubicundus</i>
<i>Pristimantis (Hypodictyon) labiosus</i> (Lynch, Ruiz-Carranza & Ardila-Robayo, 1994)*	<i>rubicundus</i>
<i>Pristimantis (Hypodictyon) lanthanites</i> (Lynch, 1975)*	<i>rubicundus</i>
<i>Pristimantis (Hypodictyon) ocellatus</i> (Lynch & Burrows, 1990)*	<i>rubicundus</i>
<i>Pristimantis (Hypodictyon) orpacobates</i> (Lynch, Ruiz-Carranza & Ardila-Robayo, 1994)*	<i>rubicundus</i>
<i>Pristimantis (Hypodictyon) rubicundus</i> (Jiménez de la Espada, 1875)*	<i>rubicundus</i>
<i>Pristimantis (Hypodictyon) tenebrionis</i> (Lynch & Miyata, 1980)*	<i>rubicundus</i>
<i>Pristimantis (Hypodictyon) w-nigrum</i> (Boettger, 1892)*	<i>rubicundus</i>
<i>Pristimantis (Pristimantis) adiaxolus</i> Duellman & Hedges, 2007*	<i>conspicillatus</i>
<i>Pristimantis (Pristimantis) avicuporum</i> (Duellman & Pramuk, 1999)*	<i>conspicillatus</i>
<i>Pristimantis (Pristimantis) bipunctatus</i> (Duellman & Hedges, 2005)*	<i>conspicillatus</i>
<i>Pristimantis (Pristimantis) buccinator</i> (Rodríguez, 1994)*	<i>conspicillatus</i>
<i>Pristimantis (Pristimantis) caprifer</i> (Lynch, 1977)*	<i>conspicillatus</i>
<i>Pristimantis (Pristimantis) carlossanchezi</i> (Arroyo, 2007)*	<i>conspicillatus</i>
<i>Pristimantis (Pristimantis) carmelitae</i> (Ruthven, 1912)*	<i>conspicillatus</i>
<i>Pristimantis (Pristimantis) carrangerorum</i> (Lynch, 1994)*	<i>conspicillatus</i>
<i>Pristimantis (Pristimantis) charlottevillensis</i> (Kaiser, Dwyer, Feichtinger & Schmid, 1995)*	<i>conspicillatus</i>
<i>Pristimantis (Pristimantis) chiastonotus</i> (Lynch & Hoogmoed, 1977)*	<i>conspicillatus</i>
<i>Pristimantis (Pristimantis) citriogaster</i> (Duellman, 1992)*	<i>conspicillatus</i>
<i>Pristimantis (Pristimantis) condor</i> (Lynch & Duellman, 1980)*	<i>conspicillatus</i>
<i>Pristimantis (Pristimantis) conspicillatus</i> (Günther, 1858)*	<i>conspicillatus</i>
<i>Pristimantis (Pristimantis) fenestratus</i> (Steindachner, 1864)*	<i>conspicillatus</i>
<i>Pristimantis (Pristimantis) gaigeae</i> (Dunn, 1931)*	<i>conspicillatus</i>
<i>Pristimantis (Pristimantis) gutturalis</i> (Hoogmoed, Lynch & Lescure, 1977)*	<i>conspicillatus</i>
<i>Pristimantis (Pristimantis) illotus</i> (Lynch & Duellman, 1997)*	<i>conspicillatus</i>
<i>Pristimantis (Pristimantis) insignitus</i> (Ruthven, 1917)*	<i>conspicillatus</i>
<i>Pristimantis (Pristimantis) johannesdei</i> (Rivero & Serna, 1988)*	<i>conspicillatus</i>
<i>Pristimantis (Pristimantis) lymani</i> (Barbour & Noble, 1920)*	<i>conspicillatus</i>
<i>Pristimantis (Pristimantis) malkini</i> (Lynch, 1980)*	<i>conspicillatus</i>
<i>Pristimantis (Pristimantis) medemi</i> (Lynch, 1984)*	<i>conspicillatus</i>

<i>Pristimantis (Pristimantis) meridionalis</i> (Lehr & Duellman, 2007)*	<i>conspicillatus</i>
<i>Pristimantis (Pristimantis) metabates</i> (Duellman & Pramuk, 1999)*	<i>conspicillatus</i>
<i>Pristimantis (Pristimantis) padrecarlosi</i> (Mueses-Cisneros, 2006)*	<i>conspicillatus</i>
<i>Pristimantis (Pristimantis) pedimontanus</i> (La Marca, 2004)*	<i>conspicillatus</i>
<i>Pristimantis (Pristimantis) phalaroinguinis</i> (Duellman & Lehr, 2007)*	<i>conspicillatus</i>
<i>Pristimantis (Pristimantis) samaipatae</i> (Köhler & Jungfer, 1995)*	<i>conspicillatus</i>
<i>Pristimantis (Pristimantis) savagei</i> (Pyburn & Lynch, 1981)*	<i>conspicillatus</i>
<i>Pristimantis (Pristimantis) skydmainos</i> (Flores & Rodríguez, 1997)*	<i>conspicillatus</i>
<i>Pristimantis (Pristimantis) stegolepis</i> (Schlüter & Rödder, 2007)*	<i>conspicillatus</i>
<i>Pristimantis (Pristimantis) terraebolivaris</i> (Rivero, 1961)*	<i>conspicillatus</i>
<i>Pristimantis (Pristimantis) thectopternus</i> (Lynch, 1975)*	<i>conspicillatus</i>
<i>Pristimantis (Pristimantis) vilarsi</i> (Melin, 1941)*	<i>conspicillatus</i>
<i>Pristimantis (Pristimantis) viridicans</i> (Lynch, 1977)*	<i>conspicillatus</i>
<i>Pristimantis (Pristimantis) zeuctotylus</i> (Lynch & Hoogmoed, 1977)*	<i>conspicillatus</i>
<i>Pristimantis (Pristimantis) bellona</i> (Lynch, 1992)*	<i>bellona</i>
<i>Pristimantis (Pristimantis) mars</i> (Lynch & Ruiz-Carranca, 1996)*	<i>bellona</i>
<i>Pristimantis (Pristimantis) polemistes</i> (Lynch & Ardila-Robayo, 2004)*	<i>bellona</i>
<i>Pristimantis (Pristimantis) chalceus</i> (Peters, 1873)*	<i>chalceus</i>
<i>Pristimantis (Pristimantis) scolodiscus</i> (Lynch & Burrowes, 1990)*	<i>chalceus</i>
<i>Pristimantis (Pristimantis) buckleyi</i> (Boulenger, 1882)*	<i>curtipes</i>
<i>Pristimantis (Pristimantis) cryophilus</i> (Lynch, 1979)*	<i>curtipes</i>
<i>Pristimantis (Pristimantis) curtipes</i> (Boulenger, 1882)*	<i>curtipes</i>
<i>Pristimantis (Pristimantis) gentryi</i> (Lynch & Duellman, 1997)*	<i>curtipes</i>
<i>Pristimantis (Pristimantis) satagius</i> (Lynch, 1995)*	<i>curtipes</i>
<i>Pristimantis (Pristimantis) xestus</i> (Lynch, 1995)*	<i>curtipes</i>
<i>Pristimantis (Pristimantis) acatallelus</i> (Lynch & Ruiz-Carranza, 1983)*	<i>devillei</i>
<i>Pristimantis (Pristimantis) appendiculatus</i> (Werner, 1894)*	<i>devillei</i>
<i>Pristimantis (Pristimantis) cacao</i> (Lynch, 1992)*	<i>devillei</i>
<i>Pristimantis (Pristimantis) chrysops</i> (Lynch & Ruiz-Carranza, 1996)*	<i>devillei</i>
<i>Pristimantis (Pristimantis) devillei</i> (Boulenger, 1880)*	<i>devillei</i>
<i>Pristimantis (Pristimantis) quinquagesimus</i> (Lynch & Trueb, 1980)*	<i>devillei</i>
<i>Pristimantis (Pristimantis) silverstonei</i> (Lynch & Ruiz-Carranza, 1996)*	<i>devillei</i>
<i>Pristimantis (Pristimantis) siopelus</i> (Lynch & Burrowes, 1990)*	<i>devillei</i>
<i>Pristimantis (Pristimantis) sulculus</i> (Lynch & Burrowes, 1990)*	<i>devillei</i>
<i>Pristimantis (Pristimantis) susaguae</i> (Rueda-Almonacid, Lynch & Galvis, 2003)*	<i>devillei</i>
<i>Pristimantis (Pristimantis) truebae</i> (Lynch & Duellman, 1997)*	<i>devillei</i>
<i>Pristimantis (Pristimantis) vertebralis</i> (Boulenger, 1886)*	<i>devillei</i>
<i>Pristimantis (Pristimantis) xylochobates</i> (Lynch & Ruiz-Carranza, 1996)*	<i>devillei</i>
<i>Pristimantis (Pristimantis) frater</i> (Werner, 1899)*	<i>frater</i>
<i>Pristimantis (Pristimantis) incomptus</i> (Lynch & Duellman, 1980)*	<i>frater</i>
<i>Pristimantis (Pristimantis) librarius</i> (Flores & Vigle, 1994)*	<i>frater</i>
<i>Pristimantis (Pristimantis) martiae</i> (Lynch, 1974)*	<i>frater</i>
<i>Pristimantis (Pristimantis) miyatai</i> (Lynch, 1984)*	<i>frater</i>
<i>Pristimantis (Pristimantis) ockendeni</i> (Boulenger, 1912)*	<i>frater</i>

<i>Pristimantis (Pristimantis) paisa</i> (Lynch & Ardila-Robalo, 1999)*	<i>frater</i>
<i>Pristimantis (Pristimantis) pecki</i> (Duellman & Lynch, 1988)*	<i>frater</i>
<i>Pristimantis (Pristimantis) ptochus</i> (Lynch, 1998)*	<i>frater</i>
<i>Pristimantis (Pristimantis) quaquaversus</i> (Lynch, 1974)*	<i>frater</i>
<i>Pristimantis (Pristimantis) suetus</i> (Lynch & Rueda-Almonacid, 1998)*	<i>frater</i>
<i>Pristimantis (Pristimantis) taeniatus</i> (Boulenger, 1912)*	<i>frater</i>
<i>Pristimantis (Pristimantis) viejas</i> (Lynch & Rueda-Almonacid, 1999)*	<i>frater</i>
<i>Pristimantis (Pristimantis) zophus</i> (Lynch & Ardila-Robalo, 1999)*	<i>frater</i>
<i>Pristimantis (Pristimantis) delicatus</i> (Ruthven, 1917)*	<i>galdi</i>
<i>Pristimantis (Pristimantis) douglasi</i> (Lynch, 1996)*	<i>galdi</i>
<i>Pristimantis (Pristimantis) galdi</i> Jiménez de la Espada, 1871*	<i>galdi</i>
<i>Pristimantis (Pristimantis) tribulosus</i> (Lynch & Rueda-Almonacid, 1997)*	<i>galdi</i>
<i>Pristimantis (Pristimantis) apiculatus</i> (Lynch & Burrowes, 1990)*	<i>lacrimosus</i>
<i>Pristimantis (Pristimantis) aureolineatus</i> (Guayasamin, Ron, Cisneros-Heredia, Lamar & McCracken, 2006)*	<i>lacrimosus</i>
<i>Pristimantis (Pristimantis) boulengeri</i> (Lynch, 1981)*	<i>lacrimosus</i>
<i>Pristimantis (Pristimantis) brevifrons</i> (Lynch, 1981)*	<i>lacrimosus</i>
<i>Pristimantis (Pristimantis) bromeliaceus</i> (Lynch, 1979)*	<i>lacrimosus</i>
<i>Pristimantis (Pristimantis) dorsopictus</i> (Rivero & Serna, 1988)*	<i>lacrimosus</i>
<i>Pristimantis (Pristimantis) eremitus</i> (Lynch, 1980)*	<i>lacrimosus</i>
<i>Pristimantis (Pristimantis) lacrimosus</i> (Jiménez de la Espada, 1875)*	<i>lacrimosus</i>
<i>Pristimantis (Pristimantis) mendax</i> (Duellman, 1978)*	<i>lacrimosus</i>
<i>Pristimantis (Pristimantis) olivaceus</i> (Köhler, Morales, Lötters, Reichle & Apaico, 1994)*	<i>lacrimosus</i>
<i>Pristimantis (Pristimantis) pardalinus</i> (Lehr, Lundberg, Aguila & von May, 2006)*	<i>lacrimosus</i>
<i>Pristimantis (Pristimantis) petersorum</i> (Lynch, 1991)*	<i>lacrimosus</i>
<i>Pristimantis (Pristimantis) prolixodiscus</i> (Lynch, 1978)*	<i>lacrimosus</i>
<i>Pristimantis (Pristimantis) royi</i> (Morales, 2007)*	<i>lacrimosus</i>
<i>Pristimantis (Pristimantis) schultei</i> (Duellman, 1990)*	<i>lacrimosus</i>
<i>Pristimantis (Pristimantis) tayrona</i> (Lynch & Ruiz-Carranza, 1985)*	<i>lacrimosus</i>
<i>Pristimantis (Pristimantis) waoranii</i> (McCracken, Forstner & Dixon, 2007)*	<i>lacrimosus</i>
<i>Pristimantis (Pristimantis) zimmermanae</i> (Heyer & Hardy, 1991)*	<i>lacrimosus</i>
<i>Pristimantis (Pristimantis) lasalleorum</i> (Lynch, 1995)*	<i>leptolophus</i>
<i>Pristimantis (Pristimantis) leptolophus</i> (Lynch 1980)*	<i>leptolophus</i>
<i>Pristimantis (Pristimantis) maculosus</i> (Lynch, 1991)*	<i>leptolophus</i>
<i>Pristimantis (Pristimantis) parectatus</i> (Lynch & Rueda-Almonacid, 1998)*	<i>leptolophus</i>
<i>Pristimantis (Pristimantis) peraticus</i> (Lynch, 1980)*	<i>leptolophus</i>
<i>Pristimantis (Pristimantis) scoloblepharus</i> (Lynch, 1991)*	<i>leptolophus</i>
<i>Pristimantis (Pristimantis) uranobates</i> (Lynch, 1991)*	<i>leptolophus</i>
<i>Pristimantis (Pristimantis) hybotragus</i> (Lynch, 1992)*	<i>loustes</i>
<i>Pristimantis (Pristimantis) jaimiei</i> (Lynch, 1992)*	<i>loustes</i>
<i>Pristimantis (Pristimantis) loustes</i> (Lynch, 1979)*	<i>loustes</i>
<i>Pristimantis (Pristimantis) festae</i> (Peracca, 1904)*	<i>myersi</i>
<i>Pristimantis (Pristimantis) floridus</i> (Lynch & Duellman, 1997)*	<i>myersi</i>
<i>Pristimantis (Pristimantis) gladiator</i> (Lynch, 1976)*	<i>myersi</i>

<i>Pristimantis (Pristimantis) hectus</i> (Lynch & Burrowes, 1990)*	<i>myersi</i>
<i>Pristimantis (Pristimantis) leoni</i> (Lynch, 1976)*	<i>myersi</i>
<i>Pristimantis (Pristimantis) myersi</i> (Goin & Cochran, 1963)*	<i>myersi</i>
<i>Pristimantis (Pristimantis) ocreatus</i> (Lynch, 1981)*	<i>myersi</i>
<i>Pristimantis (Pristimantis) pyrrhomerus</i> (Lynch, 1976)*	<i>myersi</i>
<i>Pristimantis (Pristimantis) repens</i> (Lynch, 1984)*	<i>myersi</i>
<i>Pristimantis (Pristimantis) scopaeus</i> (Lynch, Ruiz-Carranza * Ardila-Robayo, 1996)*	<i>myersi</i>
<i>Pristimantis (Pristimantis) xeniolum</i> (Lynch, 2001)*	<i>myersi</i>
<i>Pristimantis (Pristimantis) obmutescens</i> (Lynch, 1980)*	<i>orcesi</i>
<i>Pristimantis (Pristimantis) orcesi</i> (Lynch, 1972)*	<i>orcesi</i>
<i>Pristimantis (Pristimantis) racemus</i> (Lynch, 1980)*	<i>orcesi</i>
<i>Pristimantis (Pristimantis) simoteriscus</i> (Lynch, Ruiz-Carranza * Ardila-Robayo, 1997)*	<i>orcesi</i>
<i>Pristimantis (Pristimantis) simoterus</i> (Lynch, 1980)*	<i>orcesi</i>
<i>Pristimantis (Pristimantis) thymelensis</i> (Lynch, 1972)*	<i>orcesi</i>
<i>Pristimantis (Pristimantis) atrabracus</i> (Duellman & Pramuk, 1999)*	<i>orestes</i>
<i>Pristimantis (Pristimantis) chimu</i> Lehr, 2007*	<i>orestes</i>
<i>Pristimantis (Pristimantis) cordovae</i> (Lehr & Duellman, 2007)*	<i>orestes</i>
<i>Pristimantis (Pristimantis) corrugatus</i> (Duellman, Lehr & Venegas, 2006)*	<i>orestes</i>
<i>Pristimantis (Pristimantis) melanogaster</i> (Duellman & Pramuk, 1999)*	<i>orestes</i>
<i>Pristimantis (Pristimantis) orestes</i> (Lynch, 1979)*	<i>orestes</i>
<i>Pristimantis (Pristimantis) pataikos</i> (Duellman & Pramuk, 1999)*	<i>orestes</i>
<i>Pristimantis (Pristimantis) pinguis</i> (Duellman & Pramuk, 1999)*	<i>orestes</i>
<i>Pristimantis (Pristimantis) seorsus</i> Lehr, 2007*	<i>orestes</i>
<i>Pristimantis (Pristimantis) simonbolivari</i> (Wiens & Coloma, 1992)*	<i>orestes</i>
<i>Pristimantis (Pristimantis) simonsii</i> (Boulenger, 1900)*	<i>orestes</i>
<i>Pristimantis (Pristimantis) stictoboubonus</i> (Duellman, Lehr & Venegas, 2006)*	<i>orestes</i>
<i>Pristimantis (Pristimantis) ventriguttatus</i> (Lehr & Köhler, 2007)*	<i>orestes</i>
<i>Pristimantis (Pristimantis) vidua</i> (Lynch, 1979)*	<i>orestes</i>
<i>Pristimantis (Pristimantis) albertus</i> Duellman & Hedges, 2007*	<i>peruvianus</i>
<i>Pristimantis (Pristimantis) aniptopalmatus</i> (Duellman & Hedges, 2005)*	<i>peruvianus</i>
<i>Pristimantis (Pristimantis) crepitans</i> (Bokermann, 1965)*	<i>peruvianus</i>
<i>Pristimantis (Pristimantis) cuneirostris</i> (Duellman & Pramuk, 1999)*	<i>peruvianus</i>
<i>Pristimantis (Pristimantis) danae</i> (Duellman, 1978)*	<i>peruvianus</i>
<i>Pristimantis (Pristimantis) dundeei</i> (Heyer & Muñoz, 1999)*	<i>peruvianus</i>
<i>Pristimantis (Pristimantis) ornatus</i> (Lehr, Lundberg, Aguilar & von May, 2006)*	<i>peruvianus</i>
<i>Pristimantis (Pristimantis) peruvianus</i> (Melin, 1941)*	<i>peruvianus</i>
<i>Pristimantis (Pristimantis) pharangobates</i> (Duellman, 1978)*†	<i>peruvianus</i>
<i>Pristimantis (Pristimantis) rhabdolaemus</i> (Duellman, 1978)*	<i>peruvianus</i>
<i>Pristimantis (Pristimantis) sagittulus</i> (Lehr, Aguilar & Duellman, 2004)*	<i>peruvianus</i>
<i>Pristimantis (Pristimantis) stictogaster</i> (Duellman & Hedges, 2005)*	<i>peruvianus</i>
<i>Pristimantis (Pristimantis) tanyrhynchus</i> Lehr, 2007*	<i>peruvianus</i>
<i>Pristimantis (Pristimantis) toftae</i> (Duellman, 1978)*	<i>peruvianus</i>
<i>Pristimantis (Pristimantis) vilcabambae</i> Lehr, 2007*	<i>peruvianus</i>
<i>Pristimantis (Pristimantis) duellmani</i> (Lynch, 1980)*	<i>surdus</i>

<i>Pristimantis (Pristimantis) hamiotae</i> (Flores, 1994)*	<i>surdus</i>
<i>Pristimantis (Pristimantis) sobetes</i> (Lynch, 1980)*	<i>surdus</i>
<i>Pristimantis (Pristimantis) surdus</i> (Boulenger, 1882)*	<i>surdus</i>
<i>Pristimantis (Pristimantis) aaptus</i> (Lynch & Lescure, 1980)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) acerus</i> (Lynch & Duellman, 1980)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) actinolaimus</i> (Lynch & Rueda-Almonacid, 1998)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) acuminatus</i> (Shreve, 1935)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) affinis</i> (Werner, 1899)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) alalocophus</i> (Roa-Trujillo & Ruiz-Carranza, 1991)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) albericoi</i> (Lynch & Ruiz-Carranza, 1996)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) altamazonicus</i> (Barbour & Dunn, 1921)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) amydrotus</i> (Duellman & Lehr, 2007)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) anemerus</i> (Duellman & Pramuk, 1999)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) angustilineata</i> (Lynch, 1998)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) anolirex</i> (Lynch, 1983)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) anotis</i> (Walker & Test, 1955)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) aquilonaris</i> (Lehr, Aguilar, Siu-Ting & Jordán, 2007)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) aracamuni</i> (Barrio-Amorós & Molina, 2006)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) ardalonychus</i> (Duellman & Pramuk, 1999)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) atratus</i> (Lynch, 1979)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) aurantiguttatus</i> (Ruiz-Carranza, Lynch & Ardila-Robayo, 1997)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) avius</i> (Myers & Donnelly, 1997)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) bacchus</i> (Lynch, 1984)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) baiotis</i> (Lynch, 1998)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) balionotus</i> (Lynch, 1979)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) baryecucus</i> (Lynch, 1979)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) batrachites</i> (Lynch, 2003)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) barsei</i> (Duellman, 1992)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) bellator</i> (Lehr, Aguilar, Siu-Ting & Jordán, 2007)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) bernali</i> (Lynch, 1986)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) bogotensis</i> (Peters, 1863)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) cabrerai</i> (Cochran & Goin, 1970)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) caeruleonotus</i> (Lehr, Aguilar, Siu-Ting & Jordán, 2007)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) cajamarcensis</i> (Barbour & Noble, 1920)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) calcaratus</i> (Boulenger, 1908)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) calcarulatus</i> (Lynch, 1976)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) cantitans</i> (Myers & Donnelly, 1996)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) capitonis</i> (Lynch, 1998)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) carvalhoi</i> (Lutz, 1952)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) caryophyllaceus</i> (Barbour, 1928)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) cavernibardus</i> (Myers & Donnelly, 1997)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) celator</i> (Lynch, 1976)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) ceuthospilus</i> (Duellman & Wild, 1993)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) chloronotus</i> (Lynch, 1969)*	<i>unistrigatus</i>

<i>Pristimantis (Pristimantis) colodactylus</i> (Lynch, 1979)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) colonensis</i> (Mueses-Cisneros, 2007)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) colostichos</i> (La Marca & Smith, 1982)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) corniger</i> (Lynch & Suárez-Mayorga, 2003)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) coronatus</i> Lehr & Duellman, 2007*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) cosnipatae</i> (Duellman, 1978)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) cristinae</i> (Lynch & Ruiz-Carranza, 1985)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) croceinguinis</i> (Lynch, 1968)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) crucifer</i> (Boulenger, 1899)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) cruciocularis</i> (Lehr, Lundberg, Aguilar & von May, 2006)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) cryptomelas</i> (Lynch, 1979)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) cuentasi</i> (Lynch, 2003)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) degener</i> (Lynch & Duellman, 1997)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) deinops</i> (Lynch, 1996)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) delius</i> (Duellman & Mendelson, 1995)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) diadematus</i> (Jiménez de la Espada, 1875)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) diaphonus</i> (Lynch, 1986)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) diogenes</i> (Lynch & Ruiz-Carranza, 1996)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) dissimulatus</i> (Lynch & Duellman, 1997)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) duende</i> (Lynch, 2001)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) elegans</i> (Peters, 1863)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) eriphus</i> (Lynch & Duellman, 1980)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) ernesti</i> (Flores, 1987)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) erythropleura</i> (Boulenger, 1898)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) esmeraldas</i> (Guayasamin, 1994)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) eugeniae</i> (Lynch & Duellman, 1997)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) euphronides</i> (Schwartz, 1967)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) eurydactylus</i> (Hedges & Schlüter, 1992)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) exoristus</i> (Duellman & Pramuk, 1999)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) flavobracatus</i> (Lehr, Lundberg, Aguilar & von May, 2006)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) glandulosus</i> Boulenger, 1880)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) gracilis</i> (Lynch, 1986)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) grandiceps</i> (Lynch, 1984)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) helvolus</i> (Lynch & Rueda-Almonacid, 1998)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) hernandezi</i> (Lynch & Ruiz-Carranza, 1983)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) huicundo</i> (Guayasamin, Almeida-Reinoso & Nogales-Sornosa, 2004)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) ignicolor</i> (Lynch & Duellman, 1980)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) imitatrix</i> (Duellman, 1978)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) incanus</i> (Lynch & Duellman, 1980)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) infraguttatus</i> (Duellman & Pramuk, 1999)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) inguinalis</i> (Parker, 1940)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) inusitatus</i> (Lynch & Duellman, 1980)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) jester</i> Means & Savage, 2007*	<i>unistrigatus</i>

<i>Pristimantis (Pristimantis) juanchoi</i> (Lynch, 1996)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) jubatus</i> (Garcia & Lynch, 2006)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) kareliae</i> (La Marca, 2005)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) katoptroides</i> (Flores, 1988)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) kelephas</i> (Lynch, 1998)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) lemur</i> (Lynch & Rueda-Almonacid, 1998)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) leucopus</i> (Lynch, 1976)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) lichenoides</i> (Lynch & Rueda-Almonacid, 1997)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) lindae</i> (Duellman, 1978)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) lirellus</i> (Dwyer, 1995)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) lividus</i> (Lynch & Duellman, 1980)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) llojsintuta</i> (Köhler & Lötters, 1999)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) luscombei</i> (Duellman & Mendelson, 1995)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) luteolateralis</i> (Lynch, 1976)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) lutitus</i> (Lynch, 1984)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) lynchi</i> (Duellman & Simmons, 1977)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) lythrodes</i> (Lynch & Lescure, 1980)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) marahuaka</i> (Fuentes-Ramos & Barrio-Amorós, 2004)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) marmoratus</i> (Boulenger, 1900)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) memorans</i> (Myers & Donnelly, 1997)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) merostictus</i> (Lynch, 1984)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) minutulus</i> Duellman & Hedges, 2007*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) mnionaetes</i> (Lynch, 1998)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) modipeplus</i> (Lynch, 1981)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) molybrignus</i> (Lynch, 1986)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) mondolfi</i> (Rivero, 1984)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) muricatus</i> (Lynch & Miyata, 1980)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) muscosus</i> (Duellman & Pramuk, 1999)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) myops</i> (Lynch, 1988)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) nephophilus</i> (Duellman & Pramuk, 1999)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) nervicus</i> (Lynch, 1994)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) nicefori</i> (Cochran & Goin, 1970)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) nigrogriseus</i> (Andersson, 1945)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) nyctophylax</i> (Lynch, 1976)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) ornatissimus</i> (Despax, 1911)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) orphnolaimus</i> (Lynch, 1970)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) ortizi</i> (Guayasamin, Almeida-Reinoso & Nogales-Sornosa, 2004)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) palmeri</i> (Boulenger, 1912)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) parvillus</i> (Lynch, 1976)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) pastazensis</i> (Andersson, 1945)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) paululus</i> (Lynch, 1974)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) penelopus</i> (Lynch & Rueda-Almonacid, 1999)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) percnopterus</i> (Duellman & Pramuk, 1999)*	<i>unistrigatus</i>

<i>Pristimantis (Pristimantis) percultus</i> (Lynch, 1979)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) permixtus</i> (Lynch, Ruiz-Carranza & Ardila-Robayo, 1994)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) petrobardus</i> (Duellman, 1991)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) phalarus</i> (Lynch, 1998)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) philipi</i> (Lynch & Duellman, 1995)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) phoxocephalus</i> (Lynch, 1979)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) phragmipleuron</i> (Rivero & Serna, 1988)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) platychilus</i> (Lynch, 1996)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) platydactylus</i> (Boulenger, 1903)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) prolatus</i> (Lynch & Duellman, 1980)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) proserpens</i> (Lynch, 1979)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) pseudoacuminatus</i> (Shreve, 1935)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) pteridophilus</i> (Lynch & Duellman, 1997)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) pugnax</i> (Lynch, 1973)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) pycnodermis</i> (Lynch, 1979)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) quaiquinimensis</i> (Schlüter & Rödder, 2007)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) quantus</i> (Lynch, 1998)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) reclusas</i> (Lynch, 2003)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) renjiforum</i> (Lynch, 2000)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) rhabdocnemus</i> (Duellman & Hedges, 2005)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) rhodoplichus</i> (Duellman & Wild, 1993)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) rhodostichus</i> (Duellman & Pramuk, 1999)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) riveroi</i> (Lynch & La Marca, 1993)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) riveti</i> (Despax, 1911)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) roseus</i> (Boulenger, 1918)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) rozei</i> (Riveroi, 1961)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) rufioculis</i> (Duellman & Pramuk, 1999)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) ruidus</i> (Lynch, 1979)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) salapatium</i> (Duellman, 1978)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) saltissimus</i> Means & Savage, 2007*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) scitulus</i> (Duellman, 1978)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) serendipitus</i> (Duellman & Pramuk, 1999)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) shrevei</i> (Schwartz, 1967)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) signifer</i> (Ruiz-Carranza, Lynch & Ardila-Robayo, 1997)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) spilogaster</i> (Lynch, 1984)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) spinosus</i> (Lynch, 1979)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) tepuiensis</i> (Schlüter & Rödder, 2007)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) sternothylax</i> (Duellman & Wild, 1993)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) subsigillatus</i> (Boulenger, 1902)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) supernatis</i> (Lynch, 1979)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) taciturnus</i> (Lynch & Suárez-Mayorga, 2003)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) tamsitti</i> (Cochran & Goin, 1970)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) tantanti</i> (Lehr, Torres & Suárez, 2007)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) telefericus</i> (La Marca, 2005)*	<i>unistrigatus</i>

<i>Pristimantis (Pristimantis) thymalopsoides</i> (Lynch, 1976)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) torrenticola</i> (Lynch & Rueda-Almanacid, 1998)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) trachyblepharis</i> (Boulenger, 1918)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) tubernasus</i> (Rivero, 1984)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) turpinorum</i> (Hardy, 2001)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) turuniquirensis</i> (Rivero, 1961)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) uisae</i> (Lynch, 2003)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) unistrigatus</i> (Günther, 1859)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) urichi</i> (Boettger, 1894)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) vanadise</i> (La Marca, 1984)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) variabilis</i> (Lynch, 1968)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) ventrimarmoratus</i> (Boulenger, 1912)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) verecundus</i> (Lynch & Burrowes, 1990)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) vermiculatus</i> (Duellman & Lehr, 2007)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) versicolor</i> (Lynch, 1979)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) vicarius</i> (Lynch & Ruiz-Carranza, 1983)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) wagteri</i> (Venegas, 2007)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) walkeri</i> (Lynch, 1974)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) wiensi</i> (Duellman & Wild, 1993)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) yaviensis</i> (Myers & Donnelly, 1996)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) yustizi</i> (Barrio-Amorós & Chacón, 2004)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) zolae</i> (Mueses-Cisneros, 2007)*	<i>unistrigatus</i>
<i>Pristimantis (Pristimantis) acutirostris</i> (Lynch, 1984)*	
<i>Pristimantis (Pristimantis) aemulatus</i> (Ruiz-Carranza, Lynch & Ardila-Robayo, 1997)*	
<i>Pristimantis (Pristimantis) bicumulus</i> (Peters, 1863)*	
<i>Pristimantis (Pristimantis) boconoensis</i> (Rivero & Mayorga, 1973)*	
<i>Pristimantis (Pristimantis) briceni</i> (Boulenger, 1903)*	
<i>Pristimantis (Pristimantis) caliginosus</i> (Lynch, 1996)*	
<i>Pristimantis (Pristimantis) culatensis</i> (La Marca, 2007)*	
<i>Pristimantis (Pristimantis) factiosus</i> (Lynch & Rueda-Almonacid, 1998)*	
<i>Pristimantis (Pristimantis) fallax</i> (Lynch & Rueda-Almonacid, 1999)*	
<i>Pristimantis (Pristimantis) fetusus</i> (Lynch & Rueda-Almonacid, 1998)*	
<i>Pristimantis (Pristimantis) flabellidiscus</i> (La Marca, 2007)*	
<i>Pristimantis (Pristimantis) ganonotus</i> (Duellman & Lynch, 1988)*	
<i>Pristimantis (Pristimantis) ginesi</i> (Rivero, 1964)*	
<i>Pristimantis (Pristimantis) jabonensis</i> (La Marca, 2007)*	
<i>Pristimantis (Pristimantis) lancinii</i> (Donoso-Barros, 1965)*	
<i>Pristimantis (Pristimantis) lentiginosus</i> (Rivero, 1984)*	
<i>Pristimantis (Pristimantis) megalops</i> (Ruthven, 1917)*	
<i>Pristimantis (Pristimantis) melanoproctus</i> (Rivero, 1984)*	
<i>Pristimantis (Pristimantis) paramerus</i> (Rivero, 1984)*	
<i>Pristimantis (Pristimantis) piceus</i> (Lynch, Ruiz-Carranza & Ardila-Robayo, 1996)*	
<i>Pristimantis (Pristimantis) pleurostriatus</i> (Rivero, 1984)*	
<i>Pristimantis (Pristimantis) polychrus</i> (Ruiz-Carranza, Lynch & Ardila-Robayo, 1997)*	

<i>Pristimantis (Pristimantis) pruinatus</i> (Myers & Donnelly, 1996)*		
<i>Pristimantis (Pristimantis) pulvinatus</i> (Rivero, 1968)*		
<i>Pristimantis (Pristimantis) restrepoi</i> (Lynch, 1996)*		
<i>Pristimantis (Pristimantis) reticulatus</i> (Walker & Test, 1955)*		
<i>Pristimantis (Pristimantis) rhigophilus</i> (La Marca, 2007)*		
<i>Pristimantis (Pristimantis) ruedai</i> (Ruiz-Carranza, Lynch & Ardila-Robayo, 1997)*		
<i>Pristimantis (Pristimantis) ruthveni</i> (Lynch & Ruiz-Carranza, 1985)*		
<i>Pristimantis (Pristimantis) sanctaemartae</i> (Ruthven, 1917)*		
<i>Pristimantis (Pristimantis) stenodiscus</i> (Walker & Test, 1955)*		
<i>Pristimantis (Pristimantis) thyellus</i> (La Marca, 2007)*		
<i>Pristimantis (Pristimantis) veletis</i> (Lynch & Rueda-Almonacid, 1997)*		
<i>Pristimantis (Pristimantis) viridis</i> (Ruiz-Carranza, Lynch & Ardila-Robayo, 1997)*		
<i>Pristimantis (Yunganastes) ashkapara</i> (Köhler, 2000)*		
<i>Pristimantis (Yunganastes) bisignatus</i> (Werner, 1899)*		
<i>Pristimantis (Yunganastes) fraudator</i> (Lynch & McDiarmid, 1987)*		
<i>Pristimantis (Yunganastes) mercedesae</i> (Lynch & McDiarmid, 1987)*		
<i>Pristimantis (Yunganastes) pluvicanorus</i> (De la Riva & Lynch, 1997)*		
<i>Strabomantis biporcatus</i> Peters, 1863	<i>biporcatus</i>	<i>biporcatus</i>
<i>Strabomantis cadenai</i> (Lynch, 1986)*	<i>biporcatus</i>	<i>cornutus</i>
<i>Strabomantis cerastes</i> (Lynch, 1975)*	<i>biporcatus</i>	<i>cornutus</i>
<i>Strabomantis cornutus</i> (Jiménez de la Espada, 1871)	<i>biporcatus</i>	<i>cornutus</i>
<i>Strabomantis helonotus</i> (Lynch, 1975)*	<i>biporcatus</i>	<i>cornutus</i>
<i>Strabomantis ingeri</i> (Cochran & Goin, 1961)*	<i>biporcatus</i>	<i>cornutus</i>
<i>Strabomantis laticorpus</i> (Myers & Lynch, 1997)*	<i>biporcatus</i>	<i>cornutus</i>
<i>Strabomantis necopinus</i> (Lynch, 1997)*	<i>biporcatus</i>	<i>cornutus</i>
<i>Strabomantis ruizi</i> (Lynch, 1981)*	<i>biporcatus</i>	<i>cornutus</i>
<i>Strabomantis sulcatus</i> (Cope, 1874)*	<i>biporcatus</i>	<i>cornutus</i>
<i>Strabomantis anatypes</i> (Lynch & Myers, 1983)*	<i>bufoniformis</i>	
<i>Strabomantis anomalus</i> (Boulenger, 1898)*	<i>bufoniformis</i>	
<i>Strabomantis bufoniformis</i> (Boulenger, 1896)*	<i>bufoniformis</i>	
<i>Strabomantis cheioplethus</i> (Lynch, 1990)*	<i>bufoniformis</i>	
<i>Strabomantis necerus</i> (Lynch, 1975)*	<i>bufoniformis</i>	
<i>Strabomantis zygodactylus</i> (Lynch & Myers, 1983)*	<i>bufoniformis</i>	

Appendix II

Specimens and sequences used in this study. The laboratory tissue catalog number refers to the frozen tissue collection of the senior author (SBH). Locality information for all samples is associated, and retrievable, with the GenBank accession numbers. Museum vouchers and tissue catalog numbers are given for all specimens sequenced for this study and for Heinicke *et al.* (2007). New sequences for this study have GenBank accession numbers EU186650–780; species with newly-generated sequences are denoted with an asterisk; n/a = not applicable. Museum abbreviations are AMNH (American Museum of Natural History), BWMC (Bobby Witcher Memorial Collection, Avila University), CVULA (Collection of Vertebrates, University of the Andes, Mérida, Venezuela), KU (University of Kansas Natural History Museum), LSUMZ (Louisiana State University, Museum of Zoology), MNHNCu (National Museum of Natural History, Havana, Cuba), MHNSM (Universidad Nacional Mayor de San Marcos, Lima, Peru), MVZ (Museum of Vertebrate Zoology, University of California, Berkeley), MZUSP (Museum of Zoology, University of São Paulo), QCAZ (Catholic University of Ecuador, Museum of Zoology), ROM (Royal Ontario Museum, Toronto, Canada), UPRRP (University of Puerto Rico, at Rio Piedras, Museum of Natural History), USNM (United States National Museum of Natural History, Smithsonian Institution), UTA (University of Texas at Arlington, Museum of Natural History).

Species	Museum Voucher	Tissue Number	GenBank Accession Number			
			12S	16S	Rag1	Tyr
<i>Brachycephalus ephippium</i> *	n/a	n/a	AY326008		n/a	n/a
	n/a	n/a	DQ283091		n/a	DQ282917
	USNM207716	268117	n/a	n/a	EU186761	n/a
<i>Ischnocnema guentheri</i> *	No voucher	267345	EF493533		EF493407	EF493510
<i>Ischnocnema hoehnei</i>	No voucher	267886	EF493359		n/a	n/a
<i>Ischnocnema holti</i> *	USNM 318165	268112	EU186740	EU186722	n/a	n/a
<i>Ischnocnema parva</i>	No voucher	267328	EF493532		EF493400	EF493509
<i>Ischnocnema juipoca</i>	n/a	n/a	DQ283093		n/a	n/a
<i>Craugastor daryi</i>	UTA 57940	267858	EF493531		EF493452	EF493480
<i>Craugastor crassidigitus</i> *	MVZ 207248	268033	EU186733	EU186715	n/a	n/a
<i>Craugastor fitzingeri</i>	n/a	n/a	AY326001		n/a	n/a
<i>Craugastor longirostris</i>	KU177803	267853	EF493395		EF493454	EF493482
<i>Craugastor andi</i> *	MVZ 207254	268030	EU186687		n/a	n/a
<i>Craugastor emcelae</i> *	AMNH 124468	268109	EU186738	EU186720	n/a	n/a
<i>Craugastor melanostictus</i> *	MVZ 203856	268026	EU186683		n/a	n/a
<i>Craugastor megacephalus</i> *	MVZ 207243	268031	EU186688		n/a	n/a
<i>Craugastor laticeps</i> *	MVZ 143299	268024	EU186731	EU186713	n/a	n/a
<i>Craugastor lineatus</i> *	MVZ 143301	268032	EU186732	EU186714	n/a	n/a
<i>Craugastor sp.</i> *	UTA 51036	268102	EU186697		n/a	n/a
<i>Craugastor montanus</i>	UTA 51105	267888	EF493530		EF493453	EF493478
<i>Craugastor pygmaeus</i>	UTA 55241	267855	EF493711		EF493451	EF493479
<i>Craugastor angelicus</i> *	MVZ 149762	268023	EU186681		n/a	n/a
<i>Craugastor obesus</i> *	AMNH 124540	268108	EU186737	EU186719	n/a	n/a
<i>Craugastor punctariolus</i>	n/a	n/a	DQ283168		n/a	n/a
<i>Craugastor rugulosus</i> *	MVZ 207279	268022	EU186680		n/a	n/a
<i>Craugastor rupinius</i> *	KU 289861	267970	EU186669		n/a	n/a
<i>Craugastor sandersoni</i>	UTA-A49803	267854	EF493712		n/a	n/a
<i>Craugastor bransfordii</i>	AMNH 124398	267852	EF493822	EF493661	n/a	n/a
<i>Craugastor podiciferus</i>	MVZ12020	266082	EF493360		EF493450	EF493481

<i>Craugastor loki</i> *	MVZ 137064	268028	EU186685	n/a	n/a
<i>Craugastor rhodopis</i>	n/a	n/a	DQ283317	n/a	n/a
<i>Craugastor sp.</i> *	UTA 56684	268007	EU186675	n/a	n/a
<i>Craugastor augusti</i>	n/a	n/a	DQ283271	n/a	n/a
<i>Craugastor tarahumarensis</i> *	No voucher	268111	EU186702	n/a	n/a
<i>Craugastor alfredi</i>	n/a	n/a	DQ283318	n/a	n/a
<i>Craugastor bocourti</i>	UTA-A55235	267856	EF493713	n/a	n/a
<i>Craugastor sp.</i> *	No voucher	268103	EU186698	n/a	n/a
<i>Craugastor sp.</i> *	No voucher	268113	EU186703	n/a	n/a
<i>Craugastor spatulatus</i> *	AMCC 118375	268006	EU186674	EU186749	EU186770
<i>Craugastor stuarti</i> *	MVZ 143310	268027	EU186684	n/a	n/a
<i>Craugastor uno</i> *	AMCC 118080	268005	EU186673	EU186748	EU186769
<i>Haddadus binotatus</i>	n/a	n/a	n/a	n/a	DQ282918
	USNM303077	267339	EF493361	EF493397	n/a
<i>Diasporus diastema</i> *	MVZ 203844	268025	EU186682	EU186752	EU186773
<i>Eleutherodactylus abbotti</i>	USNM564974	267594	EF493540	EF493412	EF493457
<i>Eleutherodactylus audanti</i> *	No voucher	267577	EU186662	n/a	n/a
<i>Eleutherodactylus haitianus</i>	No voucher	103103	EF493743	EF493583	n/a
<i>Eleutherodactylus notidodes</i>	USNM331514	161405	EF493744	EF493584	n/a
<i>Eleutherodactylus parabates</i>	USNM332136	161393	EF493746	EF493581	n/a
<i>Eleutherodactylus pituinus</i>	USNM332229	161658	EF493747	EF493582	n/a
<i>Eleutherodactylus sp.</i>	USNM337773	161469	EF493745	EF493580	n/a
<i>Eleutherodactylus auriculatus</i>	USNM564980	192808	EF493344	EF493417	EF493458
<i>Eleutherodactylus bartonsmithi</i>	USNM309753	190019	EF493736	EF493576	n/a
<i>Eleutherodactylus eileenae</i>	No voucher	172823	EF493740	EF493577	n/a
<i>Eleutherodactylus glamyrus</i>	USNM564987	190453	EF493737	EF493575	n/a
<i>Eleutherodactylus mariposa</i>	MNHNCu591	190919	EF493738	EF493573	n/a
<i>Eleutherodactylus ronaldi</i>	USNM309760	190023	EF493739	EF493574	n/a
<i>Eleutherodactylus minutus</i>	USNM331987	101305	EF493741	EF493578	n/a
<i>Eleutherodactylus poolei</i>	USNM332236	160779	EF493742	EF493579	n/a
<i>Eleutherodactylus antillensis</i>	USNM326747	172065	EF493728	EF493556	n/a
<i>Eleutherodactylus brittoni</i>	USNM326765	172078	EF493727	EF493554	n/a
<i>Eleutherodactylus cochranae</i>	USNM326775	172062	EF493725	EF493555	n/a
<i>Eleutherodactylus hedricki</i>	USNM564995	191587	EF493726	EF493553	n/a
<i>Eleutherodactylus gryllus</i>	USNM269304	101684	EF493724	EF493552	n/a
<i>Eleutherodactylus juanariveroi</i>	UPRRP6361	267815	EF493538	EF493365	n/a
<i>Eleutherodactylus cooki</i>	USNM326784	160048	EF493539	EF493413	EF493455
<i>Eleutherodactylus eneidae</i>	USNM326857	101754	EF493729	EF493557	n/a
<i>Eleutherodactylus locustus</i>	USNM326861	172085	EF493730	EF493558	n/a
<i>Eleutherodactylus coqui</i>	USNM305421	172037	EF493722	EF493550	n/a
<i>Eleutherodactylus portoricensis</i>	USNM326885	101784	EF493720	EF493548	n/a
<i>Eleutherodactylus schwartzi</i>	No voucher	266012	EF493723	EF493551	n/a
<i>Eleutherodactylus wightmanae</i> *	USNM 326915	101680	EU186651	n/a	n/a
<i>Eleutherodactylus flavescens</i>	USNM331662	102358	EF493731	EF493559	n/a

<i>Eleutherodactylus amplinympha</i>	USNM564978	194183	EF493732	EF493560	n/a	n/a
<i>Eleutherodactylus barlagnei</i>	USNM564982	102110	EF493735	EF493563	n/a	n/a
<i>Eleutherodactylus johnstonei</i>	USNM336018	172650	EF493733	EF493561	n/a	n/a
<i>Eleutherodactylus martinicensis</i>	USNM565001	102092	EF493343	EF493419	EF493456	
<i>Eleutherodactylus pinchoni</i>	USNM565006	101896	EF493734	EF493562	n/a	n/a
<i>Eleutherodactylus richmondi*</i>	USNM326894	172042	EF493541	EU186758	EF493461	
<i>Eleutherodactylus unicolor</i>	USNM326897	160038	EF493542	EF493398	EF493462	
<i>Eleutherodactylus fowleri</i>	USNM269266	160239	EF493752	EF493568	n/a	n/a
<i>Eleutherodactylus lamprotes*</i>	USNM564997	192242	EF493379	EU186759	EF493460	
<i>Eleutherodactylus auriculatoides</i>	USNM331627	161584	EF493754	EF493572	n/a	n/a
<i>Eleutherodactylus montanus</i>	USNM332069	161648	EF493756	EF493571	n/a	n/a
<i>Eleutherodactylus patriciae</i>	No voucher	161628	EF493755	EF493570	n/a	n/a
<i>Eleutherodactylus leberi</i>	USNM309758	190598	EF493342	EF493403	EF493459	
<i>Eleutherodactylus melacara</i>	USNM309733	190442	EF493751	EF493567	n/a	n/a
<i>Eleutherodactylus guantanamera</i>	MNHNCu590	191061	EF493749	EF493565	n/a	n/a
<i>Eleutherodactylus ionthus</i>	USNM309757	190915	EF493748	EF493564	n/a	n/a
<i>Eleutherodactylus olibrus</i>	USNM309763	172526	EF493750	EF493566	n/a	n/a
<i>Eleutherodactylus diplasius</i>	USNM332369	104639	EF493753	EF493569	n/a	n/a
<i>Eleutherodactylus sommeri*</i>	USNM 332341	161592	EU186654	n/a	n/a	
<i>Eleutherodactylus wetmorei*</i>	No voucher	103845	EU186652	n/a	n/a	
<i>Eleutherodactylus alcoae</i>	USNM564977	194867	EF493382	EF493406	EF493469	
<i>Eleutherodactylus armstrongi</i>	USNM329962	160557	EF493778	EF493611	n/a	n/a
<i>Eleutherodactylus darlingtoni</i>	USNM307236	104190	EF493777	EF493610	n/a	n/a
<i>Eleutherodactylus leoncei</i>	USNM564999	267599	EF493375	EF493715	EF493404	EF493468
<i>Eleutherodactylus albipes</i>	USNM564976	190449	EF493386	EF493409	EF493475	
<i>Eleutherodactylus dimidiatus</i>	USNM564986	190049	EF493802	EF493640	n/a	n/a
<i>Eleutherodactylus emiliae</i>	No voucher	266680	EF493368	EF493638	n/a	n/a
<i>Eleutherodactylus maestrensis</i>	MNHNCu1003	266593	EF493369	EF493639	n/a	n/a
<i>Eleutherodactylus rucillensis</i>	USNM332313	161668	EF493803	EF493641	n/a	n/a
<i>Eleutherodactylus schmidti*</i>	No voucher	161545	EU186653	n/a	n/a	
<i>Eleutherodactylus greyi</i>	USNM564991	172799	EF493801	EF493628	n/a	n/a
<i>Eleutherodactylus cuneatus</i>	USNM564985	191146	EF493775	EF493608	n/a	n/a
<i>Eleutherodactylus turquinensis</i>	USNM348803	193530	EF493776	EF493609	n/a	n/a
<i>Eleutherodactylus cavernicola</i>	USNM266357	103261	EF493763	EF493614	n/a	n/a
<i>Eleutherodactylus cundalli</i>	USNM266364	103511	EF493761	EF493612	n/a	n/a
<i>Eleutherodactylus glaucoreius</i>	USNM305366	103568	EF493762	EF493613	n/a	n/a
<i>Eleutherodactylus fuscus</i>	USNM266380	103205	EF493769	EF493618	n/a	n/a
<i>Eleutherodactylus gossei</i>	USNM327419	103312	EF493716	EF493410	EF493466	
<i>Eleutherodactylus junori</i>	USNM269239	161028	EF493764	EF493617	n/a	n/a
<i>Eleutherodactylus pantoni</i>	USNM327822	103514	EF493766	EF493616	n/a	n/a
<i>Eleutherodactylus pentasyringos</i>	USNM266455	103477	EF493765	EF493615	n/a	n/a
<i>Eleutherodactylus jamaicensis</i>	USNM327594	161119	EF493770	EF493621	n/a	n/a
<i>Eleutherodactylus grabhami</i>	USNM327565	161260	EF493772	EF493624	n/a	n/a
<i>Eleutherodactylus luteolus*</i>	USNM327744	101469	EF493545	EU186757	EF493464	

<i>Eleutherodactylus sisymphodemus</i>	USNM266467	103219	EF493773	EF493625	n/a	n/a
<i>Eleutherodactylus alticola</i>	USNM266340	103583	EF493768	EF493620	n/a	n/a
<i>Eleutherodactylus andrewsi</i>	USNM327267	171593	EF493544	n/a	n/a	n/a
	USNM327274	103275	n/a	EF493623	n/a	n/a
<i>Eleutherodactylus griphus</i>	USNM564992	103185		EF493381	EF493415	EF493465
<i>Eleutherodactylus nubicola</i>	USNM327777	103272	EF493771	EF493622	n/a	n/a
<i>Eleutherodactylus orcutti</i>	USNM327808	103499	EF493767	EF493619	n/a	n/a
<i>Eleutherodactylus riparius</i>	n/a	n/a		Y10944	n/a	n/a
<i>Eleutherodactylus rivularis</i>	USNM565009	193690	EF493376	EF493626	n/a	n/a
<i>Eleutherodactylus toa</i>	USNM306544	191333	EF493774	EF493627	n/a	n/a
<i>Eleutherodactylus amadeus</i>	USNM329866	267898	EF493805	EF493644	n/a	n/a
<i>Eleutherodactylus bakeri</i>	USNM564981	104652	EF493808	EF493647	n/a	n/a
<i>Eleutherodactylus caribe</i>	USNM314179	191962		EF493385	EF493411	EF493472
<i>Eleutherodactylus corona</i>	KU218431	192197	EF493807	EF493645	n/a	n/a
<i>Eleutherodactylus dolomedes</i>	KU218434	192109	EF493809	EF493648	n/a	n/a
<i>Eleutherodactylus eunaster</i>	No voucher	267897	EF493804	EF493646	n/a	n/a
<i>Eleutherodactylus glanduliferoides</i>	USNM564989	160571	EF493546	EF493364	n/a	n/a
<i>Eleutherodactylus glaphycompus</i>	USNM292259	103958		EF493383	n/a	n/a
<i>Eleutherodactylus heminota</i>	USNM331829	267899	EF493806	EF493649	n/a	n/a
<i>Eleutherodactylus thorectes</i>	USNM565011	192230		EF493384	EF493416	EF493473
<i>Eleutherodactylus brevirostris</i>	USNM329968	267905	EF493819	EF493657	n/a	n/a
<i>Eleutherodactylus glandulifer</i>	USNM564988	192074	EF493816	EF493655	n/a	n/a
<i>Eleutherodactylus sciagraphus</i>	USNM332316	103943	EF493817	EF493656	n/a	n/a
<i>Eleutherodactylus ventrilineatus</i>	USNM332320	267904	EF493818	EF493658	n/a	n/a
<i>Eleutherodactylus jugans</i>	USNM331952	267901	EF493810	EF493652	n/a	n/a
<i>Eleutherodactylus apostates</i>	USNM564979	192240	EF493811	EF493650	n/a	n/a
<i>Eleutherodactylus oxyrhynchus</i>	USNM332073	267902	EF493812	EF493651	n/a	n/a
<i>Eleutherodactylus paulsoni</i>	USNM310833	191998	EF493815	EF493659	n/a	n/a
<i>Eleutherodactylus furcyensis</i>	USNM331673	267903	EF493814	EF493654	n/a	n/a
<i>Eleutherodactylus ruffifemoralis</i>	No voucher	160226	EF493813	EF493653	n/a	n/a
<i>Eleutherodactylus atkinsi</i>	USNM335686	172520	EF493797	EF493598	n/a	n/a
<i>Eleutherodactylus gundlachi</i>	USNM564994	190260	EF493798	EF493597	n/a	n/a
<i>Eleutherodactylus intermedius</i>	USNM564996	190245	EF493799	EF493595	n/a	n/a
<i>Eleutherodactylus varleyi</i>	USNM335732	172529	EF493800	EF493596	n/a	n/a
<i>Eleutherodactylus cf. varleyi</i>	MNHNCu1002	266765		EF493345	EF493408	EF493467
<i>Eleutherodactylus cubanus</i>	No voucher	193693	EF493796	EF493594	n/a	n/a
<i>Eleutherodactylus etheridgei</i>	USNM335715	161908	EF493794	EF493593	n/a	n/a
<i>Eleutherodactylus iberia</i>	MNHNCu1001	266768	EF493374	EF493591	n/a	n/a
<i>Eleutherodactylus jaumei*</i>	MNHNCu 1002	267998		EU186672	n/a	n/a
<i>Eleutherodactylus limbatus</i>	USNM565000	172513	EF493795	EF493590	n/a	n/a
<i>Eleutherodactylus orientalis</i>	USNM565003	190034	EF493373	EF493592	n/a	n/a
<i>Eleutherodactylus pezopetrus</i>	USNM565004	190536	EF493793	EF493601	n/a	n/a
<i>Eleutherodactylus blairhedgesi</i>	No voucher	266679	EF493371	EF493606	n/a	n/a
<i>Eleutherodactylus pinarensis</i>	USNM565005	191490	EF493792	EF493607	n/a	n/a

<i>Eleutherodactylus thomasi</i>	No voucher	266681	EF493370	EF493605	n/a	n/a
<i>Eleutherodactylus casparii</i>	USNM564984	172843	EF493788	EF493599	n/a	n/a
<i>Eleutherodactylus goini</i>	USNM335725	172589	EF493791	EF493604	n/a	n/a
<i>Eleutherodactylus guanahacabibes</i>	USNM564993	192798	EF493789	EF493600	n/a	n/a
<i>Eleutherodactylus planirostris</i>	USNM565007	192884		EF493346	EF493396	EF493470
<i>Eleutherodactylus rogersi</i>	USNM565010	192891	EF493372	EF493603	n/a	n/a
<i>Eleutherodactylus tonyi</i>	No voucher	193932	EF493790	EF493602	n/a	n/a
<i>Eleutherodactylus grahami</i>	USNM564990	192409	EF493781	EF493632	n/a	n/a
<i>Eleutherodactylus lentus</i>	USNM564998	266089		EF493717	EF493418	EF493471
<i>Eleutherodactylus monensis</i>	USNM565002	192871	EF493783	EF493633	n/a	n/a
<i>Eleutherodactylus pictissimus</i>	USNM266310	101354	EF493782	EF493631	n/a	n/a
<i>Eleutherodactylus probolaeus</i>	USNM322252	160303	EF493784	EF493634	n/a	n/a
<i>Eleutherodactylus rhodesi</i>	USNM332259	267890	EF493779	EF493629	n/a	n/a
<i>Eleutherodactylus weinlandi</i>	USNM332332	160385	EF493780	EF493630	n/a	n/a
<i>Eleutherodactylus acmonis</i>	USNM564975	190024	EF493787	EF493637	n/a	n/a
<i>Eleutherodactylus bresslerae</i>	USNM564983	190021	EF493785	EF493635	n/a	n/a
<i>Eleutherodactylus ricordii</i>	USNM565008	190351	EF493786	EF493636	n/a	n/a
<i>Eleutherodactylus klinikowskii</i>	MNHNCu1004	266592	EF493547	EF493363	n/a	n/a
<i>Eleutherodactylus zugi</i>	USNM335744	172578		EF493347	EF493401	EF493474
<i>Eleutherodactylus chlorophenax</i>	USNM257730	160673	EF493543	EF493589	n/a	n/a
<i>Eleutherodactylus inoptatus</i>	USNM331931	101237		EF493380	EF493405	EF493463
<i>Eleutherodactylus nortoni</i>	USNM257744	160630	EF493760	EF493588	n/a	n/a
<i>Eleutherodactylus aporostegus</i>	USNM257752	160686	EF493759	EF493586	n/a	n/a
<i>Eleutherodactylus bothroboans</i> *	USNM 332278	161634		EU186655	n/a	n/a
<i>Eleutherodactylus hypostenor</i>	USNM257731	101336	EF493757	EF493585	n/a	n/a
<i>Eleutherodactylus parapelates</i>	USNM257726	104622	EF493758	EF493587	n/a	n/a
<i>Eleutherodactylus counouspeus</i> *	USNM329989	103848		EF493719	EU186760	n/a
<i>Eleutherodactylus marnockii</i>	n/a	n/a	DQ283102	DQ283101	n/a	n/a
	No voucher	194156	EF493820	EF493642	EF493399	EF493476
<i>Eleutherodactylus pipilans</i> *	AMCC 118110	268008	EU186729	EU186711	n/a	n/a
<i>Eleutherodactylus nitidus</i> *	AMCC 118239	268009	EU186730	EU186712	n/a	n/a
<i>Eleutherodactylus symingtoni</i>	No voucher	172583	EF493821	EF493643	n/a	n/a
<i>Eleutherodactylus zeus</i>	USNM335740	172582		EF493718	EF493402	EF493477
<i>Adelophryne gutturosa</i> *	ROM 39578	268015		EU186679	EU186751	EU186772
<i>Phyzelaphryne miriamae</i> *	LSUMZ 16935	268034		EU186689	EU186753	EU186774
<i>Barycholos pulcher</i> *	KU 217781	267963	EU186727	EU186709	EU186744	EU186765
<i>Barycholos ternetzi</i>	n/a	n/a	n/a	DQ283094	n/a	DQ284144
<i>Bryophryne cophites</i>	KU173497	267882		EF493537	EF493423	EF493508
<i>Holoaden bradei</i> *	USNM207945	267883	EF493378	EF493366	EF493449	EU186779
<i>Holoaden luederwaldi</i> *	MZUSP 131872	268004	EU186728	EU186710	EU186747	EU186768
<i>Noblella lochites</i> *	KU 177356	268104		EU186699	EU186756	EU186777
<i>Noblella sp.</i>	n/a	n/a	AM039714	AM039646	n/a	n/a
<i>Psychrophrynella iatamasi</i>	n/a	n/a	AM039712	AM039644	n/a	n/a
<i>Psychrophrynella sp.</i> *	KU173495	267889		EF493714	EU186762	EU186780

<i>Psychrophrynella</i> sp.	n/a	n/a	AM039710	AM039642	n/a	n/a
<i>Psychrophrynella</i> sp.	n/a	n/a	AY843720		n/a	n/a
<i>Psychrophrynella wettsteini</i> *	KU 183049	268101	EU186696		EU186755	EU186776
<i>Isodactylus brunneus</i>	KU178258	267860	EF493357		EF493422	EF493484
<i>Isodactylus dolops</i>	No voucher	267862	EF493394		EF493414	EF493483
<i>Isodactylus elassodiscus</i>	KU177282	267861	EF493358		n/a	n/a
<i>Isodactylus peraccai</i>	KU178266	267859	EF493710		EF493420	EF493485
<i>Lynchiuss flavomaculatus</i> *	KU 218210	267966	EU186667		EU186745	EU186766
<i>Lynchiuss nebulanastes</i> *	KU 181408	268115	EU186704		n/a	n/a
<i>Lynchiuss parkeri</i> *	KU 181307	268116	EU186705		n/a	n/a
<i>Lynchiuss</i> sp.	n/a	n/a	AM039707	AM039639	n/a	n/a
<i>Oreobates cruralis</i> *	KU 215462	267962	EU186666		EU186743	EU186764
<i>Oreobates quixensis</i>	KU178249-250	267881	EF493828	EF493662	n/a	n/a
	n/a	n/a	AY819344	AY819474	n/a	n/a
<i>Oreobates saxatilis</i> *	KU 212327	267960	EU186726	EU186708	EU186742	EU186763
<i>Oreobates</i> sp.	n/a	n/a	DQ283060	DQ283061	n/a	n/a
<i>Phrynopus auriculatus</i>	KU291634	171082	EF493708		n/a	n/a
<i>Phrynopus barthlenae</i>	n/a	n/a	AM039717	AM039649	n/a	n/a
<i>Phrynopus bracki</i>	USNM286919	171045	EF493709		EF493421	EF493507
<i>Phrynopus bufoides</i>	n/a	n/a	AM039713	AM039645	n/a	n/a
<i>Phrynopus heimorum</i>	n/a	n/a	AM039703	AM039635	n/a	n/a
<i>Phrynopus horstpauli</i>	n/a	n/a	AM039715	AM039647	n/a	n/a
<i>Phrynopus juninensis</i>	n/a	n/a	AM039725	AM039657	n/a	n/a
<i>Phrynopus kauneorum</i>	n/a	n/a	AM039718	AM039650	n/a	n/a
<i>Phrynopus pesantesi</i>	n/a	n/a	AM039724	AM039656	n/a	n/a
<i>Phrynopus tautzorum</i>	n/a	n/a	AM039720	AM039652	n/a	n/a
<i>Phrynopus tribulosus</i> *	KU 291630	171083	EU186725	EU186707	n/a	n/a
<i>Pristimantis dendrobatoides</i> *	ROM 43318	268093	EU186735	EU186717	n/a	n/a
<i>Pristimantis colomai</i>	QCAZ17101	267635	EF493354		EF493440	EF493502
<i>Pristimantis cremnobates</i>	KU177252	267878	EF493528		EF493424	EF493486
<i>Pristimantis cruentus</i>	AMNH12444-448	267876	EF493697		n/a	n/a
<i>Pristimantis latidiscus</i>	KU218016	267219	EF493698		n/a	n/a
<i>Pristimantis ridens</i>	AMNH-A124551	267877	EF493355		n/a	n/a
<i>Pristimantis achatinus</i>	KU217809	267208	EF493827	EF493660	n/a	n/a
<i>Pristimantis actites</i>	KU217830	267209	EF493696		EF493432	EF493494
<i>Pristimantis crenunguis</i>	KU177730	267879	EF493693	EF493666	n/a	n/a
<i>Pristimantis labiosus</i>	QCAZ19771	267640	EF493694		n/a	n/a
<i>Pristimantis lanthanites</i>	KU222001	267252	EF493695		n/a	n/a
<i>Pristimantis w-nigrum</i>	n/a	n/a	AY326004		n/a	n/a
<i>Pristimantis bipunctatus</i>	KU291638	171021	EF493702		EF493430	EF493492
<i>Pristimantis caprifer</i>	KU177680	267880	EF493391		n/a	n/a
<i>Pristimantis citriogaster</i>	KU212278	267201	EF493700		n/a	n/a
<i>Pristimantis condor</i>	KU217857	267212	EF493701		EF493443	EF493504
<i>Pristimantis conspicillatus</i>	QCAZ28448	267636	EF493529		EF493437	EF493499

<i>Pristimantis fenestratus</i>	MHNSM9298	266046	EF493703	n/a	n/a
<i>Pristimantis lymani</i>	KU218019	267220	EF493392	n/a	n/a
<i>Pristimantis malkini*</i>	QCAZ 28296	267642	EU186663	n/a	n/a
<i>Pristimantis skydmainos</i>	MHNSM10071	266052	EF493393	n/a	n/a
<i>Pristimantis sp.</i>	MHNSM-LR4341	266049	EF493356	n/a	n/a
<i>Pristimantis terraebolivaris*</i>	No voucher	102301	EU186650	n/a	n/a
<i>Pristimantis zeuctotylus*</i>	ROM 43978	268013	EU186678	n/a	n/a
<i>Pristimantis chalceus</i>	KU177638	267865	EF493675	n/a	n/a
<i>Pristimantis buckleyi</i>	KU217836	267210	EF493350	n/a	n/a
<i>Pristimantis cryophilus</i>	KU217863	267214	EF493672	n/a	n/a
<i>Pristimantis curtipes</i>	KU217871	267215	EF493513	EF493435	EF493497
<i>Pristimantis gentryi</i>	KU218109	267230	EF493511	n/a	n/a
<i>Pristimantis appendiculatus</i>	KU177637	267866	EF493524	n/a	n/a
<i>Pristimantis devillei</i>	KU217991	267216	EF493688	n/a	n/a
<i>Pristimantis quinquagesimus</i>	KU179374	267872	EF493690	n/a	n/a
<i>Pristimantis truebae</i>	KU218013	267229	EF493512	n/a	n/a
<i>Pristimantis vertebralis</i>	KU177972	267870	EF493689	n/a	n/a
<i>Pristimantis ockendeni</i>	KU222023	267253	EF493519	EF493434	EF493496
<i>Pristimantis galdi*</i>	QCAZ 32368	267975	EU186670	EU186746	EU186767
<i>Pristimantis bromeliaceus</i>	KU291702	171051	EF493351	n/a	n/a
<i>Pristimantis cf mendax*</i>	MTD 45080	267140	EU186659	n/a	n/a
<i>Pristimantis schultei</i>	KU212220	267199	EF493681	n/a	n/a
<i>Pristimantis festae</i>	KU218234	267247	EF493515	n/a	n/a
<i>Pristimantis leoni</i>	KU218227	267437	EF493684	EF493433	EF493495
<i>Pristimantis ocreatus</i>	KU208508	267439	EF493682	n/a	n/a
<i>Pristimantis pyrrhomerus</i>	KU218030	267441	EF493683	n/a	n/a
<i>Pristimantis orcesi</i>	KU218021	267221	EF493679	n/a	n/a
<i>Pristimantis thymelensis</i>	QCAZ16428	267644	EF493516	EF493442	EF493503
<i>Pristimantis melanogaster</i>	MHNSM- WED56846	267438	EF493826	EF493664	n/a
<i>Pristimantis orestes</i>	KU218257	267249	EF493388	n/a	n/a
<i>Pristimantis simonsii*</i>	KU 212350	267961	EU186665	n/a	n/a
<i>Pristimantis simonbolivari</i>	KU218254	267248	EF493671	n/a	n/a
<i>Pristimantis albertus*</i>	KU 291675	171100	EU186695	n/a	n/a
<i>Pristimantis aniptopalmatius</i>	KU291627	171070	EF493390	n/a	n/a
<i>Pristimantis peruvianus</i>	MHNSM9267	266050	EF493707	EF493436	EF493498
<i>Pristimantis "pluvicanorus"</i>	n/a	n/a	AY843586	n/a	n/a
<i>Pristimantis rhabdolaemus</i>	KU173492	267875	EF493706	n/a	n/a
<i>Pristimantis cf rhabdolaemus*</i>	MTD 45073	267143	EU186660	n/a	n/a
<i>Pristimantis sagittulus</i>	KU291635	171098	EF493705	EF493439	EF493501
<i>Pristimantis stictogaster</i>	KU291659	171080	EF493704	EF493445	EF493506
<i>Pristimantis toftae</i>	KU215493	267206	EF493353	n/a	n/a
<i>Pristimantis duellmani</i>	KU217998	267444	n/a	n/a	EF493438
	n/a	n/a	AY326003	n/a	n/a

<i>Pristimantis surdus</i>	KU177847	267871	EF493687	n/a	n/a
<i>Pristimantis sp.*</i>	KU 179221	268106	EU186700	n/a	n/a
<i>Pristimantis sp.*</i>	KU 218140	267442	EU186661	n/a	n/a
<i>Pristimantis acerus</i>	KU217786	267207	EF493678	n/a	n/a
<i>Pristimantis altamazonicus*</i>	KU215460	267204	EF493670	EF493441	EU186778
<i>Pristimantis ardalonychus*</i>	KU 212301	267959	EU186664	n/a	n/a
<i>Pristimantis cajamarcensis</i>	KU217845	267211	EF493823 EF493663	n/a	n/a
<i>Pristimantis calcarulatus</i>	KU177658	267868	EF493523	n/a	n/a
<i>Pristimantis caryophyllaceus*</i>	MVZ 203810	268029	EU186686	n/a	n/a
<i>Pristimantis celator</i>	KU177684	267874	EF493685	n/a	n/a
<i>Pristimantis ceuthospilus</i>	KU 212216	267198	EF493520	n/a	n/a
<i>Pristimantis chloronotus</i>	n/a	n/a	AY326007	n/a	n/a
<i>Pristimantis croceoinguinis</i>	KU217862	267213	EF493669 EF493665	n/a	n/a
<i>Pristimantis crucifer*</i>	KU 177733	268105	EU186736 EU186718	n/a	n/a
<i>Pristimantis cruciocularis*</i>	KU 291673	171097	EU186656	n/a	n/a
<i>Pristimantis diadematus*</i>	KU 221999	267967	EU186668	n/a	n/a
<i>Pristimantis dissimulatus</i>	KU179090	267867	EF493522	n/a	n/a
<i>Pristimantis eriphus*</i>	QCAZ 32705	267976	EU186671	n/a	n/a
<i>Pristimantis euphronides</i>	BWMC6918	266624	EF493527	EF493427	EF493489
<i>Pristimantis glandulosus</i>	KU218002	267217	EF493676	n/a	n/a
<i>Pristimantis imitatrix</i>	KU215476	267205	EF493824 EF493667	n/a	n/a
<i>Pristimantis inguinalis*</i>	ROM 40164	268010	EU186676	n/a	n/a
<i>Pristimantis inusitatus</i>	KU218015	267218	EF493677	n/a	n/a
<i>Pristimantis jester*</i>	ROM 43302	268091	EU186734 EU186716	n/a	n/a
<i>Pristimantis lirellus</i>	KU212226	267200	EF493521	n/a	n/a
<i>Pristimantis luteolateralis</i>	KU177807	267863	EF493517	n/a	n/a
<i>Pristimantis marmoratus*</i>	ROM 43913	268090	EU186692	n/a	n/a
<i>Pristimantis minutulus*</i>	KU 291677	171117	EU186657	n/a	n/a
<i>Pristimantis nyctophylax</i>	KU177812	267869	EF493526	EF493425	EF493487
<i>Pristimantis parvillus</i>	KU177821	267864	EF493351	n/a	n/a
<i>Pristimantis petrobarbus</i>	KU212293	267202	EF493825 EF493367	n/a	n/a
<i>Pristimantis phoxocephalus</i>	KU218025	267222	EF493349	n/a	n/a
<i>Pristimantis prolatus*</i>	KU 177433	268107	EU186701	n/a	n/a
<i>Pristimantis pycnodermis</i>	KU218028	267223	EF493680	n/a	n/a
<i>Pristimantis rhabdocnemus*</i>	KU 291651	171063	EU186724 EU186706	n/a	n/a
<i>Pristimantis rhodoplichus</i>	KU219788	267250	EF493674	n/a	n/a
<i>Pristimantis riveti</i>	KU218035	267224	EF493348	n/a	n/a
<i>Pristimantis rozei</i>	No voucher	102308	EF493691	EF493429	EF493491
<i>Pristimantis saltissimus*</i>	ROM 43310	268092	EU186693	n/a	n/a
<i>Pristimantis shrevei</i>	No voucher	266036	EF493692	n/a	n/a
<i>Pristimantis sp.*</i>	No voucher	266045	EU186658	n/a	n/a
<i>Pristimantis sp.*</i>	LSUMZ 16898	268035	EU186690	n/a	n/a
<i>Pristimantis sp.*</i>	No voucher	268110	EU186739 EU186721	n/a	n/a
<i>Pristimantis sp.</i>	n/a	n/a	AY326002	n/a	n/a

<i>Pristimantis spinosus</i>	KU218052	267225	EF493673	n/a	n/a
<i>Pristimantis subsigillatus</i>	KU218147	267246	EF493525	n/a	n/a
<i>Pristimantis supernatis</i>	n/a	n/a	AY326005	n/a	n/a
<i>Pristimantis thymalopsoides</i>	KU177861	267873	EF493514	n/a	n/a
<i>Pristimantis unistrigatus</i>	KU218057	267227	EF493387	EF493444	EF493505
<i>Pristimantis urichi</i>	USNM336098	101646	EF493699	EF493426	EF493488
<i>Pristimantis verecundus</i>	QCAZ12410	267646	EF493686	n/a	n/a
<i>Pristimantis versicolor</i>	KU218096	267228	EF493389	EF493431	EF493493
<i>Pristimantis walkeri</i>	KU218116	267231	EF493518	EF493428	EF493490
<i>Pristimantis wiensi</i>	KU219796	267251	EF493377	EF493668	n/a
<i>Pristimantis pulvinatus*</i>	KU 181015	268114	EU186741	EU186723	n/a
<i>Strabomantis biporcatus*</i>	CVULA 7073	268087	EU186691	EU186754	EU186775
<i>Strabomantis sulcatus</i>	KU218055	267226	EF493536	n/a	n/a
<i>Strabomantis anomalus</i>	KU177627	267884	EF493534	EF493447	n/a
<i>Strabomantis bufoniformis</i>	n/a	n/a	DQ283165	n/a	DQ282942
<i>Strabomantis necerus</i>	KU179076	267885	EF493535	n/a	n/a
<i>Agalychnis callidryas</i>	n/a	n/a	DQ283423	n/a	DQ283018
	n/a	n/a	n/a	n/a	EF493362
<i>Bufo melanostictus</i>	n/a	n/a	AY458592	n/a	n/a
<i>Caudiverbera caudiverbera</i>	n/a	n/a	DQ283439	n/a	n/a
<i>Centrolene prosoblepon</i>	n/a	n/a	AY843574	n/a	n/a
<i>Ceratophrys cornuta</i>	n/a	n/a	AY326014	n/a	n/a
<i>Cryptobatrachus sp.</i>	n/a	n/a	AY326050	n/a	n/a
<i>Dendrobates sylvaticus</i>	n/a	n/a	AY364569	n/a	n/a
<i>Hyla chinensis</i>	n/a	n/a	AY458593	n/a	n/a
<i>Leptodactylus pentadactylus</i>	n/a	n/a	AY326017	n/a	n/a
<i>Litoria caerulea</i>	n/a	n/a	AY843692	n/a	AY844131
	No voucher	267887	n/a	n/a	EF493446
<i>Melanophryniscus klappenbachi</i>	n/a	n/a	AY843699	n/a	n/a
<i>Odontophrynus achalensis</i>	n/a	n/a	DQ283248	n/a	n/a
<i>Pseudis paradoxa</i>	n/a	n/a	AY843740	n/a	n/a
<i>Pseudophryne bibroni</i>	n/a	n/a	AY843742	n/a	n/a
<i>Rhinoderma darwinii</i>	n/a	n/a	DQ283324	n/a	n/a
<i>Telmatobius verrucosus</i>	n/a	n/a	DQ283040	n/a	n/a
<i>Unidentified hyloid sp.*</i>	ROM 40161	268011	EU186677	EU186750	EU186771
<i>Rana catesbeiana</i>	n/a	n/a	M57527	n/a	n/a
	n/a	n/a	DQ283257	n/a	DQ282959
	No voucher	266591	n/a	n/a	EF493448

Appendix III

Primers used in this study, written 5-prime to 3-prime. Location refers to nucleotide sites of reference sequences: AY458592 (12S/16S), L19324 (RAG-1), AY333967 (Tyr). All primers are from Heinicke *et al.* (2007), except Tyr1C/Tyr1G (Bossuyt and Milinkovitch 2000), and R182/R270 (D. Cannatella, pers. comm.).

Primer	Sequence	Direction	Location
12s/tRNA-Val/16s			
12L9	AAAGCAHRRCACTGAARATGYDAGA	F	229-254
12L29E	AAAGCRTAGCACTGAAAATGCTAAGA	F	229-254
12.1L4E	TACACATGCAAGTYTCCGC	F	322-340
12L12E	CAAACCTGGGATTAGATACCCCACTATG	F	697-723
12L15	CAAACCTGGGATTAGATACCCCACTAT	F	697-722
12.2L4E	GCTTAAAACCYAARGGAYTTGACG	F	775-798
12H42	GCTGCACCTTGACCTGACGTATTG	R	939-961
12L27	ACGTCAGGTCAARGTGACG	F	943-962
12H46E	GCTGCACYTTGACCTGACGT	R	943-962
12L30E	GTACAMACCGCCCGTCACCCTC	F	1097-1118
12.2H1E	TCCGGTATACTTACCATGTTAC	R	1175-1196
12L34	GTAACATGGTAAGYRTACCGGA	F	1175-1196
12H10	CACYTTCCRGTRCRYTTACCRTGTTACGACTT	R	1170-1201
16L43E	CTYGTACCTTTTGCATCATGGTTTA	F	1462-1486
16H50	TARACCATRATGCAAAAGGTAC	R	1465-1486
16L19	AATACCTAACGAACCTTAGCGATAGCTGGTT	F	1614-1644
16H49E	AACCAGCTATMRCTAAGTTCGSTAGG	R	1618-1644
16L33E	AAGTWGGCCTAARAGCAGCCAYCTTT	F	1792-1817
16H48E	AAAGRTGGCTGCTYTYAGGCC	R	1797-1817
16L28E	AAGTRGGCCTAARAGCAGCCA	F	1792-1812
16L42	GGCCTRATAGCAGCCAYCT	F	1797-1815
16H46	TCWTGTTACTAGTTYTARCAT	R	1919-1939
16L37	GATTAYAAGAAAAAGAAGGAACCTCGGCA	F	2082-2109
16H41	GAGGCGATGTTTTTGGTAAACAGGC	R	2122-2144
16L34	TTTAACGGCCGCGGTATCCTAACCG	F	2186-2210
16H24	TACCTTCGCACGGTTAGKRTACCGCGGCCGTT	R	2190-2220
16L29E	TATCCTAACCGTGCRAAGCTAGC	F	2200-2222
16L1	CTGACCGTGCAAAGGTAGCGTAATCACT	F	2204-2231
16H36E	AAGCTCCAWAGGGTCTTCTCGTC	R	2341-2363
16H37	TTACTCCGGTCTGAACTCAGATC	R	2710-2732
16H25	GACCTGGATTACTCCGGTCTGAACTCAGAT	R	2711-2740
16H1	CTCCGGTCTGAACTCAGATCACGTAGG	R	2703-2729
16H47	AAAGRGCTTAGRTCTTTYGCA	R	2903-2923
RAG-1			
R182	GCCATAACTGCTGGAGCATYAT	F	1391-1412
Rag1FF2	ATGCATCRAAAATTCARCAAT	F	1411-1431
Rag1FR2	CCYCCTTTRTTGATAKGGWCATA	R	2029-2051

R270	AGYAGATGTTGCCTGGGTCTTC	R	2051-2072
	Tyr		
Tyr1C	GGCAGAGGAWCRTGCCAAGATGT	F	101-123
TyrFE	GTTGYGTATCTACCTCRCC	F	122-141
TyrRE	GMAGGGAATGGTGAARTTCTC	R	635-655
Tyr1G	TGCTGGGCRTCTCTCCARTCCCA	R	656-678