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PHYLOGENETIC SYSTEMATICS OF DART-POISON FROGS AND THEIR RELATIVES (AMPHIBIA: ATHESPHATANURA: DENDROBATIDAE)

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Frontispiece. *Adelphobates castaneoticus* (Caldwell and Myers, 1990), the type species of *Adelphobates* **n.gen.**, named for Charles W. Myers and John W. Daly in recognition of the enormity of their contribution to the scientific knowledge of dart-poison frogs.

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ABSTRACT

The known diversity of dart-poison frog species has grown from 70 in the 1960s to 247 at present, with no sign that the discovery of new species will wane in the foreseeable future. Although this growth in knowledge of the diversity of this group has been accompanied by detailed investigations of many aspects of the biology of dendrobatids, their phylogenetic relationships remain poorly understood. This study was designed to test hypotheses of dendrobatid diversification by combining new and prior genotypic and phenotypic evidence in a total evidence analysis. DNA sequences were sampled for five mitochondrial and six nuclear loci (approximately 6,100 base pairs [bp]; $\bar{x}$=3,740 bp per terminal; total dataset composed of approximately 1.55 million bp), and 174 phenotypic characters were scored from adult and larval morphology, alkaloid profiles, and behavior. These data were combined with relevant published DNA sequences. Ingroup sampling targeted several previously unsampled species, including *Aromobates nocturnus*, which was hypothesized previously to be the sister of all other dendrobatids. Undescribed and problematic species were sampled from multiple localities when possible. The final dataset consisted of 414 terminals: 367 ingroup terminals of 156 species and 47 outgroup terminals of 46 species.

Direct optimization parsimony analysis of the equally weighted evidence resulted in 25,872 optimal trees. Forty nodes collapse in the strict consensus, with all conflict restricted to conspecific terminals. Dendrobatids were recovered as monophyletic, and their sister group consisted of *Crossodactylus*, *Hylodes*, and *Megaelosia*, recognized herein as Hylodidae. Among outgroup taxa, Centrolenidae was found to be the sister group of all athesphatanurans except Hylidae, Leptodactyidae was polyphyletic, *Thoropa* was nested within Cycloramphidae, and Ceratophryinae was paraphyletic with respect to Telmatobiinae. Among dendrobatids, the monophyly and content of *Mannophryne* and *Phyllobates* were corroborated. *Aromobates nocturnus* and *Colostethus saltuensis* were found to be nested within *Nephelobates*, and *Minyobates* was paraphyletic and nested within *Dendrobates*. *Colostethus* was shown to be rampantly nonmonophyletic, with most species falling into two unrelated *cis*- and *trans*-Andean clades. A morphologically and behaviorally diverse clade of median lingual process-possessing species was discovered.

In light of these findings and the growth in knowledge of the diversity of this large clade over the past 40 years, we propose a new, monophyletic taxonomy for dendrobatids, recognizing the inclusive clade as a superfamily (Dendrobatoidea) composed of two families (one of which is new), six subfamilies (three new), and 16 genera (four new). Although poisonous frogs did not form a monophyletic group, the three poisonous lineages are all confined to the revised family Dendrobatidae, in keeping with the traditional application of this name. We also propose changes to achieve a monophyletic higher-level taxonomy for the athesphatanuran outgroup taxa.

Analysis of character evolution revealed multiple origins of phytotelm-breeding, parental provisioning of nutritive oocytes for larval consumption (larval oophagy), and endotrophy. Available evidence indicates that transport of tadpoles on the dorsum of parent nurse frogs—a dendrobatid synapomorphy—is carried out primitively by male nurse frogs, with three independent origins of female transport and five independent origins of biparental transport. Reproductive amplexus is optimally explained as having been lost in the most recent common ancestor of Dendrobatoidea, with cephalic amplexus arising independently three times.

INTRODUCTION

The past four decades have witnessed a dramatic increase in scientific knowledge of dendrobatid frogs, known commonly as dart-poison frogs. Extensive field and collection studies have more than tripled the number of recognized species from 70 in 1960 to 247 at the time of manuscript completion. Dendrobatid species occupy streams, dense forests, open fields, lowland rainforests, cloud forests, páramos, and aquatic, terrestrial, and arboreal habitats from Nicaragua to Bolivia and the Atlantic forest of Brazil and from the Pacific coast of South America to Martinique in the French

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Antilles. All species but one are diurnal. Insfar as is known, all dendrobatids lay terrestrial eggs, either on the ground or in phytotelmata, and many are characterized by elaborate reproductive behaviors, including transport of tadpoles on the dorsum of parent frogs and provisioning of nutritive oocytes for larval consumption.

Approximately one-third of the known species of dendrobatids secrete powerful toxins from dermal granular (poison) glands. Three of these poisonous species were used traditionally by the Emberá people of the Chocó region of western Colombia to poison their blow-gun darts for hunting (Myers et al., 1978), earning the group its common name. The pioneering work initiated by John W. Daly and Charles W. Myers more than 30 years ago has led to the discovery in dendrobatids of over 450 lipophilic alkaloids of at least 24 major structural classes (Daly et al., 1999), with novel alkaloids being discovered continuously. Many of these so-called dendrobatid alkaloids have proven to be invaluable research tools outside systematics. For example, batrachotoxins are used extensively in research on sodium channels, epibatidine is a powerful tool in the study of nicotinic receptors and functions, and histrionicotoxins are important for studying the neuromuscular subtype of nicotinic receptors (Daly et al., 1997, 2000; Daly, 1998). It has become clear that some kind of sequestration mechanism is responsible for obtaining alkaloids from the diet and incorporating them into the skin (Daly et al., 1994a), but the details of the mechanism are unknown, as are the dietary sources of the vast majority of dendrobatid alkaloids. Formicine ants, a siphonotid millipede, melyrid beetles, and scheloribatid mites have been identified as likely dietary sources for certain alkaloids (Saporito et al., 2003; Dumbacher et al., 2004; Saporito et al., 2004; Takada et al., 2005), but the remaining alkaloids are still unknown elsewhere in nature. The hydrophilic alkaloid tetrodotoxin has also been detected in one species of dendrobatid (Daly et al., 1994b), and it is unknown if its occurrence is of symbiotic or dietary origin. Dendrobatid toxicology continues to be a highly active area of investigation.

In addition to studies of dendrobatid toxins, the conspicuous, diurnal activity of many species of dendrobatids has given rise to a large and growing literature in many areas of evolutionary biology. Among the diverse studies are many investigations of breeding biology and territoriality (e.g., Silverstone, 1973; Wells, 1978, 1980a, 1980b, 1980c; Weygoldt, 1987; Zimmermann and Zimmermann, 1988; Summers, 1989; Aichinger, 1991; Caldwell, 1997; Fandiño et al., 1997; Juncá, 1998; Caldwell and de Oliveira, 1999; Summers et al., 1999a, 1999b; Lüddecke, 2000 ''1999''; Bourne et al., 2001; Pröhl and Berke, 2001; Pröhl, 2003; Narins et al., 2003, 2005; Summers and McKeon, 2004), diet specialization (Silverstone, 1975a, 1976; Toft, 1980,1995; Donnelly, 1991; Caldwell, 1996; Parmelee, 1999; Darst et al., 2005), predation (Test et al., 1966), resource use and partitioning (Crump, 1971; Donnelly, 1989b; Caldwell, 1993; Lima and Moreira, 1993; Lima and Magnusson, 1998; Wild, 1996), learning (Lüddecke, 2003), population dynamics (e.g., Toft et al., 1982; Aichinger, 1987; Donnelly, 1989a, 1989c; Duellman, 1995), phonotaxis (Gerhardt and Rheinlaender, 1980), energetics (Navas, 1996a, 1996b), and correlates of ecology and physiology (Pough and Taigen, 1990). Similarly, investigations in comparative and developmental morphology have revealed bizarre and fascinating structures (Haas, 1995; Grant et al., 1997; de Sá, 1998; Myers and Donnelly, 2001). Ongoing research in these and related fields continues to generate novel discoveries with far-reaching implications in evolutionary biology.

In contrast to the major advances achieved in many aspects of their biology, the phylogeny of dendrobatid frogs remains poorly understood. Detailed knowledge of phylogeny is necessary to explain the evolutionary origins of the behaviors and other features that have been studied and provides an essential predictive framework to guide future research. Some progress has been made in recent years, as several workers have incorporated phylogenetic analysis into their research programs (e.g., Summers et al., 1999b; Santos et al., 2003; Vences et al., 2003a; Graham et al., 2004; Darst et al., 2005), but they have looked at only a small

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portion of the diversity of dendrobatids and have not incorporated all available evidence. Many questions remain unaddressed or unsatisfactorily answered because of a lack of understanding of dendrobatid phylogeny.

Dendrobatid monophyly has been upheld consistently (e.g., Myers and Ford, 1986; Ford and Cannatella, 1993; Haas, 2003; Vences et al., 2003a) since it was first proposed by Noble (1926; see Grant et al., 1997), but the relationships among dendrobatids remain largely unresolved. Recently, studies of DNA sequences (e.g., Clough and Summers, 2000; Vences et al., 2000, 2003a; Santos et al., 2003) have provided some insights, but limitations in both taxon and character sampling have restricted their impact on the understanding of dendrobatid phylogeny, and few taxonomic changes have resulted. Generally, dendrobatid systematics has been based on few characters, few rigorous tests, and no comprehensive analysis of available evidence.

Difficulties in understanding the phylogeny of dendrobatid frogs are compounded by the taxonomic problems that surround many nominal species and lack of appreciation of species diversity (Grant and Rodríguez, 2001). Sixty-six recognized species were named over the decade 1996–2005, 51 of which are currently referred to *Colostethus*. Many nominal species throughout Dendrobatidae are likely composed of multiple cryptic species awaiting diagnosis (e.g., Caldwell and Myers, 1990; Grant and Ardila-Robayo, 2002), but the rapid increase in recognized diversity is not unaccompanied by error, and critical evaluation of the limits of nominal taxa will undoubtedly result in some number of these being placed in synonymy (e.g., Coloma, 1995; Grant, 2004).

The most generally accepted view of dendrobatid systematics is based primarily on the work of Savage (1968), Silverstone (1975a, 1976), and Myers and colleagues (e.g., Myers and Daly, 1976b; Myers et al., 1978, 1991; Myers, 1982, 1987; Myers and Ford, 1986), with additional taxonomic contributions by Zimmermann and Zimmermann (1988), La Marca (1992, 1994), and Kaplan (1997). Approximately two-thirds of the species of dendrobatids are assigned to a ''basal'' grade of brown, nontoxic frogs (including *Aromobates*, *Colostethus*, *Mannophryne*, and *Nephelobates*), whereas the remaining third is hypothesized to form a clade of putatively aposematic frogs (including *Allobates*, *Ameerega*, *Dendrobates*, *Epipedobates*, *Minyobates*, *Oophaga*, *Phobobates*, *Phyllobates*, and *Ranitomeya*). Compelling evidence for that split is lacking, however, as some of the putatively aposematic taxa have been shown experimentally to be unable to sequester significant amounts of alkaloids (e.g., Daly, 1998), alkaloid profiles for most dendrobatids remain unexamined, and several of the species assigned to the ''basal'' grade are no less brightly colored than several of the species assigned to the aposematic clade (e.g., *Colostethus abditaurantius* and *C. imbricolus*). Furthermore, recent molecular studies (e.g., Clough and Summers, 2000; Vences et al., 2000, 2003a; Santos et al., 2003) have found several putatively aposematic taxa to be more closely related to species of *Colostethus* than to other toxic species.

Compelling evidence for the monophyly of most genera, especially the ''basal'' taxa, is also lacking. The nonmonophyly of *Colostethus* has been recognized for decades (Lynch, 1982), and the naming of *Ameerega*, *Aromobates*, *Epipedobates*, *Mannophryne*, and *Nephelobates* has merely exacerbated the problem (Kaiser et al., 1994; Coloma, 1995; Meinhardt and Parmelee, 1996; Grant et al., 1997; Grant and Castro-Herrera, 1998). *Colostethus* is also the most diverse genus of dendrobatids, with 138 named species recognized currently. Generally, *Colostethus* is regarded as a group of convenience for all dendrobatids that cannot be referred to one of the other genera (e.g., Grant and Rodríguez, 2001). Detailed investigations of several new species of *Colostethus* have led to the discovery of novel morphological characters that help elucidate phylogeny (Coloma, 1995; Grant et al., 1997; Grant and Castro-Herrera, 1998; Grant and Rodríguez, 2001; Myers and Donnelly, 2001; Caldwell et al., 2002a), and molecular studies are accumulating data rapidly (e.g., Santos et al., 2003; Vences et al., 2003a), but to date progress has been limited. Molecular evidence for the monophyly of *Mannophryne* and *Nephelobates* was presented by La Marca et al. (2002) and Vences et al. (2003a), but the

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relationship of those genera to other dendrobatids is unclear. *Aromobates* has been hypothesized to be the monotypic sister group of all other dendrobatids (Myers et al., 1991), but synapomorphies shared with *Mannophryne* and *Nephelobates*, also from the northern Andes of Venezuela, cast doubt on that claim; no molecular evidence has been presented for this taxon.

Among the "aposematic" taxa, only *Phyllobates* is strongly corroborated (Myers et al., 1978; Myers, 1987; Clough and Summers, 2000; Vences et al., 2000; Widmer et al., 2000). No synapomorphy is known for *Ameerega* or *Epipedobates*, and they are likely para- or polyphyletic with respect to each other and/or *Allobates*, *Colostethus*, *Cryptophyllobates*, and *Phobobates*. Schulte (1989) and Myers et al. (1991) rejected *Allobates* and *Phobobates* on the basis of errors in the analysis of behavior, lack of evidence, unaccounted character conflict, incorrect character coding, and creation of paraphyly in *Epipedobates* (as also found by Clough and Summers, 2000; Vences et al., 2000, 2003; Santos et al., 2003), but many authors continue to recognize those genera. Conflicting results have been obtained for some genera. *Phobobates* was found to be monophyletic by Vences et al. (2000), but paraphyletic by Clough and Summers (2000). *Minyobates* may or may not be nested within *Dendrobates* (Silverstone, 1975a; Myers, 1982, 1987; Jungfer et al., 1996a, 2000; Clough and Summers, 2000). Likewise, although neither study recognized *Minyobates*, it was found to be monophyletic by Santos et al. (2003) but polyphyletic by Vences et al. (2003a). *Cryptophyllobates* is the most recently named genus, but it contains only two species and its relationship to other dendrobatids is unclear.

Although the recent studies have demonstrated unambiguously the inadequacies of the current state of dendrobatid systematics, they have generated many more questions than decisive answers. To a certain extent, this means that this is an exciting time in dendrobatid systematics. New light is being shed on old problems, which is causing scientists to reconsider their prior beliefs (e.g., regarding the single origin of aposematism; Santos et al., 2003; Vences et al., 2003a). However, much of the current confusion is due to unreconciled conflict among datasets analyzed in isolation (e.g., regarding the monophyly of *Minyobates*), limited taxon sampling, and failure to include prior evidence (e.g., morphology) in the new analyses. This is not surprising, as most studies to date have been designed to address particular questions in evolutionary biology rather than to resolve dendrobatid phylogeny per se (e.g., Santos et al., 2003). The two kinds of problems are inextricably linked, and more thorough phylogenetic studies may have important consequences for the proposed evolutionary scenarios, but their empirical and analytical requirements differ.

The present study was designed to test current hypotheses of dendrobatid diversification as severely as possible by combining new and prior genotypic and phenotypic evidence in a total evidence analysis. We included as many species of dendrobatids as possible through our own fieldwork, colleagues' ongoing fieldwork, and existing natural history collections. In light of the many outstanding problems in species taxonomy, we included numerous undescribed species and samples of taxonomically problematic species from multiple localities. The primary aim of this paper is to address dendrobatid systematics, and to that end we used the optimal phylogenetic hypothesis to construct a monophyletic taxonomy. Finally, we analyzed the evolution of several character systems given the new hypothesis of relationships.

HISTORY OF DENDROBATID SYSTEMATICS

Scientific knowledge of dendrobatid frogs began in 1797 when the first species was named by Cuvier as *Rana tinctoria* (see Savage et al., in press). Over the next two centuries the number of available species-group names associated with the family swelled to 304, of which 247 are currently recognized and included in Dendrobatidae (fig. 1; for data see appendix 1). New species continue to be described at a rapid rate, especially in the taxonomically challenging genus *Colostethus*.

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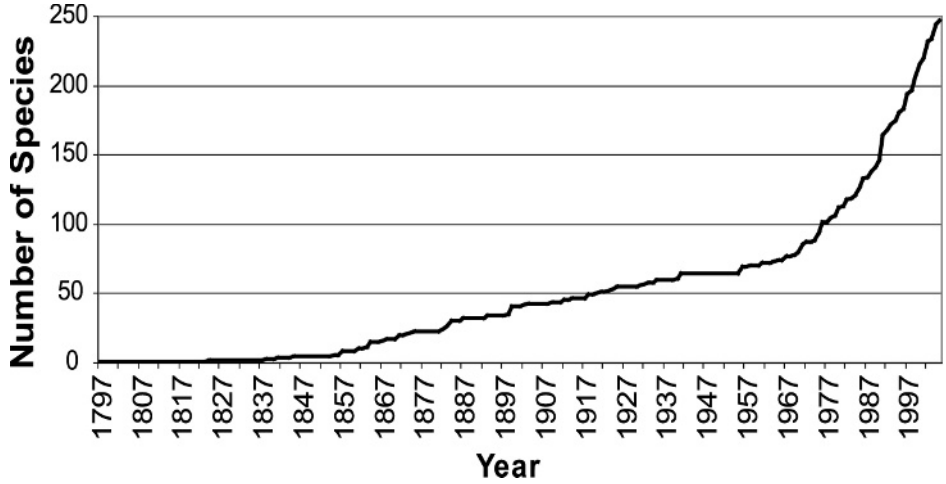

Fig. 1. Accumulation of dendrobatid species, 1797–2005. Only named species currently recognized and included in Dendrobatidae are counted. For data see appendix 1.

In this section we review the development of knowledge of the systematics of dendrobatids as background for the present study. Rather than present a strict chronology, this review is divided into three parts. The first part looks at the early history, ending in 1926 when Noble provided the modern content of the group. The second and third parts begin in 1926 with a monophyletic Dendrobatidae and continue to the present, examining the relationships among dendrobatids and between Dendrobatidae and other frogs, respectively. Ford (1993) and Grant et al. (1997) summarized many aspects of the early history and the relationships of Dendrobatidae to other groups, but we also cover some details here.

This review does not treat every paper published on dendrobatids. First, we include only systematics papers (and only the most relevant of these; i.e., species descriptions and synonymies are not detailed), and second, we include only papers published for a scientific audience. Because of the elaborate behaviors, brilliant coloration, diurnal activity, and occurrence of skin toxins in some species, large ecological, ethological, biochemical, and hobbyist literatures exist, and reviewing them all lies beyond the scope and purpose of the present paper. Also, we include only authorship and date of publication of scientific names where relevant; authorship and date of species-, genus-, and family-group names (including new taxa proposed below) are included in appendices 1–3, respectively. We do not address nomenclatural problems. Grant et al. (2006; see also Grant, 2004) and Savage et al. (in press) have pending petitions to the Commission on Zoological Nomenclature regarding the use of the species-group name *panamensis* and family-group name Dendrobatidae, respectively, and we direct the reader to those papers (especially the latter) for nomenclatural discussion. Throughout, ''dendrobatid frogs'' and ''dendrobatids'' refer to species contained in the modern Dendrobatidae, and formal taxonomic names are used as by the author in question.

The most thorough study of amphibian relationships to appear in recent years is that of Frost et al. (2006). Owing to the disproportionate importance of that paper in designing the present study (e.g., in sampling outgroup species), we address it in a separate section (Phylogenetic Placement of Dendrobatidae and Outgroup Sampling).

Part I: 1797–1926, Early History

Although scientific study of dendrobatids had begun roughly 40 years earlier (Cuvier, 1797), little progress was achieved until Duméril and Bibron's (1841) publication.

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They delimited major groups of frogs based on the occurrence of teeth (vomerine [''palate''] and jaw) and the tongue, but they also employed characters from the tympanum and middle ear, parotoid glands, number of digits, webbing, hand and foot tubercles, vertebrae, and vocal sac to distinguish and group species. Additionally, they employed the relative length of the first finger as a character to arrange the three recognized species of *Dendrobates* (Duméril and Bibron, 1841: 651). All dendrobatids were placed in Phaneroglossa, but they were allocated to different families based on the presence and absence of maxillary teeth. Duméril and Bibron named *Phyllobates bicolor* as a new genus and species, and they considered it to be the last hylaeform genus, grouped with either *Crossodactylus* and *Elosia* (p. 637) or *Hylodes* and *Phyllomedusa* (p. 502). *Dendrobates* was the first bufoniform genus, grouped with *Hylaedactylus* (= *Hyladactylus*, currently a junior synonym of the microhylid *Kaloula*; p. 645). Although the dendrobatid genera were placed in different families, Duméril and Bibron (p. 638; translated freely from the French) actually saw them as being much closer to each other than many subsequent workers would appreciate:

> This genus [*Phyllobates*], by the whole of its structure, makes obvious the passage of the last Hylaeformes to the first species [those of *Dendrobates*] of the following family, that of Bufoniformes, in which there are no longer teeth on the whole of the upper jaw and which almost always lack them on the palate.

That is, in the transitional, ''grade-thinking'' of the time (as opposed to the ''clade-thinking'' of the present), *Dendrobates* and *Phyllobates* were adjacent genera.

Fitzinger (1843: 32; see also Fitzinger, 1860) also recognized the resemblance of dendrobatid species. He grouped *Dendrobates* and *Phyllobates* in his family Phyllobatae, but he included *Crossodactylus* and *Scinacodes* (= *Hylodes*) as well.

Günther (1858) placed all dendrobatids in Opisthoglossa Platydactyla, but *Phyllobates* was in Hylodidae with *Crossodactylus*, *Hylodes*, and *Platymantis* (now in Ceratobatrachidae; Frost et al., 2006), while *Hylaplesia* (= *Hysaplesia* = *Dendrobates*) was in its own family, Hylaplesidae.

Cope (1865) named the family Dendrobatidae for *Dendrobates* and placed it in Bufoniformia. The remaining dendrobatids were placed in Arcifera in the heterogeneous family Cystignathidae. As discussed in detail by Grant et al. (1997: 30), within two years, Cope (1867; see also Cope, 1871) had begun to see the problems with separating dendrobatids solely on the basis of teeth, but he still refused to group them together. All dendrobatids were placed in Raniformia, but Colostethidae (containing *Colostethus*) was in Ranoid Raniformia, whereas Dendrobatidae (containing *Dendrobates*) was in Bufonoid Raniformia (he did not address *Phyllobates*). In his description of *Prostherapis*, Cope (1868: 137) argued that, although *Prostherapis* was closest in general appearance to *Phyllobates*, it was most closely related to *Colostethus*, and he placed both in his Colostethidae. He also stated that *Limnocharis* (now a synonym of *Crossodactylus*) was most closely related to *Phyllobates*. Subsequently, Cope (1875) restricted Raniformia to the ranoids and applied the name Firmisternia to the bufonoid taxa. This arrangement was based on novel characters of the pectoral girdle and the number of lobes of the liver, as well as the traditional ones dating to Duméril and Bibron (1841).

Boulenger (1882) simplified Cope's scheme somewhat, grouping all dendrobatids in Firmisternia, but he placed *Hyloxalus* (misspelled *Hylixalus*), *Prostherapis*, *Phyllodromus*, and *Colostethus* in Ranidae, *Dendrobates* and *Mantella* in the separate family Dendrobatidae, and *Phyllobates* in Cystignathidae. Gadow (1901) divided Ranidae into three subfamilies (Ceratobatrachinae, Dendrobatinae, and Raninae), with the toothed dendrobatids (including *Phyllobates*) in Raninae, and *Dendrobates*, *Mantella*, and *Cardioglossa* in Dendrobatinae. Gadow was uncomfortable with this arrangement, however, noting (1901: 272):

> This mere loss of teeth, and the geographical distribution suggest that these frogs do not form a natural group, but have been developed independently from other Ranidae, the Neotropical *Dendrobates* from some likewise Neotropical genus like *Prostherapis*, the Malagasy

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Mantella from an African form like *Megalixalus*.

Boulenger (1910) eliminated Dendrobatinae altogether and placed all dendrobatids in Ranidae. However, although he did not formally recant, it seems that he was not entirely convinced that Dendrobatidae was not a valid group, given that Ruthven (1915: 3) acknowledged Boulenger "for assistance in diagnosing the form" *Geobatrachus walkeri* as a new species and genus of Dendrobatidae, and further specified that "the form falls under Boulenger's definition of the family Dendrobatidae" (Ruthven, 1915: 1). Given that Ruthven only collected the specimens in 1913, his interactions with Boulenger must have occurred after the publication of *Les Batraciens* in 1910.

Nicholls (1916) did away with Arcifera and Firmisternia and proposed instead to divide Phaneroglossa into four groups based on the structure of the vertebral column, particularly the centra, the groups being descriptively named Opisthocoela (sacral vertebra biconvex, free from coccyx; presacral vertebrae convex anteriorly and concave posteriorly [=opisthocoelous]); Anomocoela (sacral vertebra ankylosed to coccyx or articulating with single condyle; presacral vertebrae concave anteriorly and convex posteriorly [=procoelous] or rarely opisthocoelous); Procoela (sacral vertebra free and articulating with double condyle; presacral vertebrae procoelous); and Diplasiocoela (sacral vertebra biconvex; eighth presacral vertebra biconcave, other seven presacrals procoelous). Insofar as he believed the diplasiocoelous condition to occur in all firmisternal taxa, this new arrangement did not affect the placement of dendrobatids.

In a series of four papers, G. K. Noble synthesized published information with his own research on the development and structure of vertebrae, pectoral girdles, thigh musculature, and external morphology to provide the framework for the modern understanding of Dendrobatidae. First, Barbour and Noble (1920) carried out a major taxonomic revision. They followed Peracca (1904: 17) in referring *Phyllodromus* to *Prostherapis*, but they went on to include both *Prostherapis* and *Colostethus* (the latter based largely on a letter from Boulenger to Barbour) as junior synonyms of *Phyllobates*. Next, Noble (1922) argued against the close relationship of *Dendrobates* and *Mantella* and explicitly endorsed Boulenger's (1910) elimination of Dendrobatidae (p. 8), disputed Nicholls's (1916) claim that all firmisternal species are diplasiocoelous (describing a numberof dendrobatid species as procoelous and transferring them to Procoela [pp. 14–15]), and gathered together *Brachycephalus*, *Atelopus*, *Rhinoderma*, *Sminthillus* (now a synonym of the brachycephalid *Eleutherodactylus*), *Geobatrachus*, *Oreophrynella*, *Phyllobates*, *Hyloxalus*, *Chilixalus* (now a synonym of *Rana*), and *Dendrobates* in Brachycephalidae (pp. 68–69). Noble (1923) subsequently diagnosed *Hyloxalus* from *Phyllobates* by the presence of webbing (contra Savage, 1968, who attributed the definition of *Hyloxalus* as toothed dendrobatids with webbed toes to Dunn, 1931). Finally, on the basis of the occurrence of "leathery scutes on the upper surface of each digit tip", Noble (1926: 7) united *Phyllobates*, *Hyloxalus*, and the toothless *Dendrobates* in a single, exclusive group, the first time such an arrangement had been proposed (Grant et al., 1997).

Noble (1926) was not only the first to unite the dendrobatids into an exclusive group, but he also provided the hypothesis of family-level phylogeny that has guided thinking ever since by proposing that (p. 9)

> *Crossodactylus* gave rise to *Hyloxalus* by merely a fusion of the coracoid cartilages. … *Hyloxalus* gave rise to *Phyllobates* by a reduction in its digital webs. The latter genus evolved and is evolving directly into *Dendrobates* by a loss of its maxillary teeth.

That is, although most of the theoretical views Noble held are no longer embraced, such as the notion of group or stock evolution and nonmonophyletic yet natural groups (see below and Grant et al., 1997: 31, footnote 18), the scheme of the webbed, more aquatic species being primitive to the unwebbed, more terrestrial species, and these being primitive to the terrestrial, toothless species has yet to be seriously questioned—or tested.

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Part II: 1926–Present, Relationships among Dendrobatids

Having grouped dendrobatids together wholly on the basis of anatomical characters, Noble (1927: 103) noted that his conclusion "receives an eloquent support from life history data" as well. He pointed out that males of species of *Dendrobates* and *Phyllobates* transport tadpoles to pools, and, further, that "[n]o other Salientia have breeding habits exactly like *Dendrobates* and *Phyllobates*" (p. 104).

Noble (1931: 507) formally recognized the group of *Phyllobates*, *Hyloxalus*, and *Dendrobates* as Dendrobatinae, a subfamily of the procoelan Brachycephalidae, and he reiterated that the group evolved from *Crossodactylus*.

The same year, Dunn (1931) named *Phyllobates flotator*, a new species with a swollen third finger in males and an umbelliform oral disc, reduced rows of keratodonts, and scattered median papillae in tadpoles. Dunn (1924) had previously observed the same third finger morphology in *P. nubicola*, also from Panama, and he postulated that these two species formed a group within *Phyllobates*. In error, Dunn (1924) had attributed these characteristics to *P. talamancae*, and he later stated (Dunn, 1931) that in his 1924 paper he had mistakenly referred specimens of his new *P. flotator* to *P. talamancae*. (However, his [Dunn, 1924: 7] description that "[t]he throat of the male is black" indicates that the specimens mistakenly identified as *P. talamancae* were *P. nubicola*, not *P. flotator*; but see also Savage, 1968.)

Dunn (1931: 389) explicitly followed Noble's (1926) evolutionary scenario but further partitioned *Phyllobates* into groups, stating:

> The *Phyllobates* from Panama, Costa Rica, and Nicaragua that I have seen fall into three groups; typical *Phyllobates*, without specialized tadpoles, or modified male third finger (these apparently stem from *Hyloxalus*, which has webbed toes); *Phyllobates* which have specialized tadpoles and modified third finger (*flotator* and *nubicola*); and *Phyllobates* which have markings black and yellow instead of black and white, and ventral light markings. (These are close to *Dendrobates*.)

Dunn (1933: 69) reviewed *Hyloxalus* and modified it slightly to include species with both webbed *and* fringed toes. He concluded that six species were attributable to *Hyloxalus* thus diagnosed, including *Hyloxalus fuliginosus*, *H. bocagei*, *H. chocoensis*, *Hylixalus collaris*, *H. granuliventris* (now a synonym of *Phyllobates palmatus*), and *H. panamansis* (name subsequently emended to *H. panamensis* by Dunn, 1940; see Grant, 2004; Grant et al., 2006). Dunn (1933) excluded *H. huigrae* (now a junior synonym of the brachycephalid "*Eleutherodactylus*" *diastema*) and *H. beebei*—the latter exclusion being the only practical consequence of Dunn's (1933) redelimitation of *Hyloxalus*. Dunn did not apply his new diagnosis consistently over subsequent years, however; on occasion he returned to Noble's (1923) diagnosis, that is, without reference to fringes (e.g., Dunn, 1941: 89, 1944: 519), but he also applied his own diagnosis of having both webbing and fringes (e.g., Dunn, 1957: 77 [as *Prostherapis*, see below]). Dunn (1933) noted that males of his new species *H. panamensis* possessed a swollen third finger, which he had previously observed in *Phyllobates nubicola* and *P. flotator* and had used to group them phylogenetically, but he did not attribute any phylogenetic significance to the present observation.

In his discussion of the relationships of *Dendrobates auratus*, Dunn (1941: 88–89) recognized a group of species with rounded light markings, formed by *D. auratus*, a species from "the western part of Colombia … [in which] the light color is red or yellow" (presumably *D. histrionicus*), *D. pumilio*, and *D. speciosus*. He also recognized a second group of "typical *Dendrobates*" with "dorsolateral light lines like *Phyllobates* … [but] lacking maxillary teeth" for "*tinctorius*, *trivittatus*, etc.", as well as "*lugubris*, *minutus*, and *shrevei*." In total, Dunn (1941) now recognized 18 species of *Dendrobates*, 26 *Phyllobates*, and 8 *Hyloxalus*.

Prostherapis remained in the synonymy of *Phyllobates*, where it had been placed by Barbour and Noble (1920), for over 35 years. The sole exception was Breder (1946: 405) who reported *Prostherapis inguinalis* from Panama without commenting on the status of the genus. It was Test (1956: 6), acting on the

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advice of Dunn, who resurrected the genus as a senior synonym of *Hyloxalus*. A more detailed account of this synonymy was published after Dunn's death (Dunn, 1957: 77), where Dunn clarified that "the presence of webs and fringes on the toes distinguishes *Prostherapis* from *Phyllobates* which hasn't got them."

Bhaduri (1953) studied the urinogenital systems of diverse amphibians, including *Dendrobates auratus*, *D. tinctorius*, and *Colostethus flotator* (as *Phyllobates nubicola flotator*). He noted several differences among these species, such as the greater posterior extension of the kidneys in *Dendrobates* than in *Phyllobates* (p. 56), but he nonetheless concluded that "[t]he structural similarities of the urinogenital organs which I have observed in these two genera lend further support to Noble's view [that *Dendrobates* and *Phyllobates* are closely related]" (p. 72).

Rivero (1961) provided accounts for Venezuelan species. In his description of *Prostherapis shrevei*, he postulated that it was "perhaps a race" of *Prostherapis bocagei*, but he concluded that the two were distinct, but presumably closely related, species. Rivero (1961) suggested that *Phyllobates brunneus* and *Phyllobates marchesianus* might prove to be conspecific, but he did not propose phylogenetic relationships for the other species.

Dunn's arrangement was followed until 1966, by which time Cochran (1966) had become skeptical of the usefulness of toe webbing in diagnosing these groups of frogs. This change was foreshadowed by Cochran and Goin's (1964) description of a new webbed dendrobatid with teeth as *Phyllobates mertensi*. Cochran (1966) accepted the recognition of *Phyllobates* and *Dendrobates* on the basis of maxillary teeth, but she (p. 61; see also p. 64) argued against the further division of toothed species because "[t]he variation in degree of webbing of the species [of *Prostherapis*] is so great … that no valid reliance can be placed on it to justify such a separation on that characteristic." Cochran and Goin (1970) employed this taxonomy, even though it had already become outdated by the time their monograph was published.

Although Cochran (1966) treated only the Colombian species, she proposed a number of novel groups. These included a group for *D. trivittatus* and an as yet undescribed species (*D. ingeri*), and a second group for *D. hahneli* and *D. lugubris*. A third group was further divided into subgroups for *D. opisthomelas* and *D. minutus ventrimaculatus*, and for the subspecies of *D. tinctorius*: *D. t. histrionicus*, *D. t. wittei*, *D. t. chocoensis*, and *D. t. confluens*. Among Colombian species of *Phyllobates*, Cochran (1966) recognized a group for *P. bicolor*, *P. mertensi*, *P. boulengeri*, and *P. femoralis*, with the latter two species more closely related. Another group included *P. subpunctatus*, *P. vergeli*, *P. chocoensis*, and another as yet unnamed species (presumably *P. thorntoni*, named by Cochran and Goin, 1970). Curiously, a soon-to-be-named subspecies of *P. subpunctatus* (*P. s. walesi*) was placed in a different group with *P. palmatus*. Finally, a group containing *P. brunneus*, *P. pratti*, *P. latinasus*, and *P. inguinalis* was also proposed.

Savage (1968) ushered in the modern era of dendrobatid research. Although his study focused on the Central American taxa, it was highly influential and arguably the most important paper since Noble's (1926) in establishing a framework for much of the dendrobatid systematics research of the following decades. In addition to addressing a number of species-level taxonomic problems in Central America, Savage divided the Central American species into three groups, and to each of these groups he assigned the oldest available name. He also referred species outside of Central America to each genus, as far as he could, though subsequent authors would have to provide complete assignments. New characters Savage employed to diagnose his three groups included pigmentation of the flesh, size of digital discs, and in larvae the oral disc morphology, rows of keratodonts, and position of the anus.

Savage (1968: 746–747) resurrected *Colostethus* for his Group I, which included five Central American species and "most species called *Phyllobates* in South America". Savage (1968: 765) clarified that *Dendrobates lugubris* was a toothed species and that recent workers had mistakenly applied that name to *Dendrobates truncatus*. Consequently, he assigned *Phyllobates* to his Group II, composed of *P. lugubris* in Central America, and *P.*

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bicolor and *P. aurotaenia* "among others" in South America. *Dendrobates* was assigned to his remaining Group III, still composed of toothless dendrobatids, as it always had been.

In the late 1960s, two graduate students undertook studies of the systematics of Dendrobatidae. Stephen R. Edwards wrote his Ph.D. dissertation (Edwards, 1974a) on *Colostethus* (sensu Savage, 1968, with minor modification). He studied 63 species in his dissertation, including many undescribed species, but only two small papers on dendrobatids were published as a result of this work (Edwards, 1971, 1974b); the bulk of Edwards's dissertation research—including descriptions for the unnamed species in his dissertation and the quantitative phenetic analysis—were never published (which prompted the naming of *Colostethus exasperatus*; see Duellman and Lynch, 1988) and will therefore not be discussed here (but see discussion below of Rivero, 1990 "1988" and Rivero and Serna, 1989 "1988"). In the first of his papers, Edwards (1971) referred 43 nominal species to *Colostethus* and described two more species as new; he did not discuss the relationships among the species. In his second publication, Edwards (1974b) named a new species and clarified the identities of another three. More importantly, he also arranged the nominal species into seven groups. Although Edwards (1974b: 1) was explicit that these groups "do not reflect evolutionary or taxonomic units" and that their sole purpose was to facilitate comparisons (e.g., *C. vertebralis*, shown below in bold, was listed in each appropriate group), this was the first arrangement ever provided for most of these species. The groups were as follows:

1. *C. elachyhistus*, *C. fraterdanieli*, *C. kingsburyi*, *C. subpunctatus*, *C. variabilis*.
2. *C. alagoanus*, *C. brunneus*, *C. capixaba*, *C. carioca*, *C marchesianus*.
3. *C. collaris*, *C. dunni*, *C. herminae*, *C. meridensis*, *C. riveroi*, *C. trinitatus* [= *trinitatis*].
4. *C. beebei*, *C. chocoensis*, *C. fuliginosus*, *C. granuliventris*, *C. mandelorum*, *C. mertensi*, *C. palmatus*, *C. shrevei*, *C. talamancae*, *C. vergeli*.
5. *C. intermedius*, *C. latinasus*.
6. *C. nubicola*, *C. pratti*.
7. *C. alboguttatus*, *C. bromelicola*, *C. infraguttatus*, *C. olfersioides*, *C. pratti*, *C. ranoides*, ***C. vertebralis***.
8. *C. anthracinus*, *C. infraguttatus*, *C. lehmanni*, *C. ramosi*, *C. taeniatus*, ***C. vertebralis***, *C. whymperi*.

Because Edwards's dissertation was a quantitative phenetic analysis, he focused largely on meristic data and reported few novel characters. His most lasting contribution in terms of character delimitation was to focus on and demarcate explicitly the different pale lateral stripes found in most species.

Philip A. Silverstone carried out his Ph.D. research on the systematics of *Dendrobates* (Silverstone, 1970). He published two small papers (Silverstone, 1971, 1975b) on dendrobatid systematics, but most of Silverstone's findings were published in two comprehensive monographs; the first (Silverstone, 1975a) summarized his dissertation on *Dendrobates* and included accounts for 16 species; the second (Silverstone, 1976) reported his research on *Phyllobates* and included 20 species.

Silverstone (1975a: 3) did not put much credence in the generic taxonomy he employed (which was largely that of Savage, 1968). He noted that there were species with morphology intermediate between the genera, and that "any rigidly applied definition of more than one genus for dendrobatid frogs could result in unnatural (= polyphyletic) groups." But rather than place all dendrobatids into a single genus, Silverstone (1975a: 3) continued "to recognize the three currently accepted genera as categories of convenience, that is, as taxonomic units convenient to study, but not necessarily natural." Although he thought the three genera may grade into each other, Silverstone (1975a: 4) implicitly followed Noble's (1926) evolutionary scenario, stating that he was "concerned more with the relationship of *Phyllobates* to *Dendrobates* than with that of *Phyllobates* to *Colostethus*."

The generic diagnoses Silverstone used were very similar to Savage's (1968), although he did incorporate new characters (occurrence of the palatine, omosternum, vertebral fusion; he also used fusion and sculpturing of the cranium to diagnose

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species groups). In terms of content, there were two major differences. First, *Phyllobates* sensu Savage was, explicitly at least, a group of only three, very similar species, whereas *Phyllobates* sensu Silverstone included 20 species, most of which had been implicitly referred to *Colostethus* by Savage. Second, Silverstone went against all previous workers by transferring two toothless species from *Dendrobates* to *Phyllobates*. Although all specimens of *P. trivittatus* and most of *P. pictus* lacked teeth, Silverstone (1975a) was overwhelmed by evidence from chromosomes and finger morphology that indicated these species should be placed in *Phyllobates*. Thus, dendrobatid systematics was finally rid of the a priori weighting applied to teeth that had hindered progress since Duméril and Bibron (1841).

In his two monographs, Silverstone (1975a, 1976) proposed numerous species groups, many of which he thought were natural. Within *Dendrobates*, he proposed the *histrionicus* group for *D. histrionicus* and *D. leucomelas*. Significantly, Silverstone (1975a: 25) clarified that *D. histrionicus* was not a subspecies of "the large, striped, Guianan species to which *D. tinctorius* is restricted", but he remained ambivalent with regard to the putative subspecies of *D. histrionicus*; he did not separate them formally, but he did attribute diagnostic color patterns to several of them. His reasons for treating all the color patterns as a single species were that they all "lack an omosternum and have the same breeding call" (Silverstone, 1975a: 23). Based on larval morphology, Silverstone (1975a: 23) surmised that "the *histrionicus* group is more closely related to the *pumilio* group than to the other two groups of *Dendrobates*."

Silverstone's *minutus* group contained six species: *D. altobueyensis*, *D. fulguritus*, *D. minutus*, and *D. opisthomelas* from Central America and northwestern South America and *D. quinquevittatus* and *D. steyermarki* from the Amazon basin (the former from lowlands, the latter from 1,200 m on the summit of the tepui Cerro Yapacana). Within this group, Silverstone (1975a: 29) hypothesized a close relationship between *D. fulguritus* and *D. minutus* on the basis of size and dorsal striping; his decision to treat them as distinct species was due to his having collected them in sympatry. He also conjectured that *D. minutus* and *D. opisthomelas* were closely related, as tadpoles of these species were the only ones in the genus with an indented oral disc and dextral anus; Silverstone was not completely convinced of the identity of the tadpoles he assigned to *D. altobueyensis* and *D. fulguritus*, but they also had an indented oral disc and dextral anus. Tadpoles of *D. quinquevittatus* and *D. steyermarki* were unknown to Silverstone, and he assigned those species to the *minutus* group on the basis of other characters. He also hypothesized that *D. steyermarki* was "more closely related to [the western Andean *D. opisthomelas*] than to any other species of *Dendrobates*" (Silverstone, 1975a: 36).

Silverstone (1975a) proposed the *pumilio* group for *D. granuliferus*, *D. pumilio*, and *D. speciosus*. Silverstone (1975a: 38) argued that *D. granuliferus* and *D. pumilio* were very closely related, perhaps even conspecific, and that they were "probably geographically and genetically continuous before the onset of orogeny and aridity in Costa Rica." This would leave *D. speciosus* as their sister group. As mentioned above, Silverstone hypothesized that the *pumilio* and *histrionicus* groups were sister groups.

The *tinctorius* group included *D. auratus*, *D. azureus*, *D. galactonotus*, *D. tinctorius*, and *D. truncatus*. Within this group, Silverstone (1975a) proposed that *D. auratus* was most closely related to *D. truncatus*. He also hypothesized that *D. azureus* had "arisen by isolation of a population of *D. tinctorius* in forest islands surrounded by unsuitable habitat" (Silverstone, 1975a: 44).

The 20 species of *Phyllobates* Silverstone (1976) recognized were arranged into four groups, but the relationships among these four groups were not addressed. The *bicolor* group was the same as *Phyllobates* sensu Savage (1968) with the addition of two more species. That is, he placed *P. aurotaenia*, *P. bicolor*, and *P. lugubris* in a single group (as had Savage) together with an as yet unnamed taxon (later named *Dendrobates silverstonei*; Silverstone doubted the inclusion of this species in this group but placed it there due to its superficial resemblance with *P. bicolor*) and *P. vittatus* (which Savage considered to be conspecific with *P. lugubris*). Silverstone

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did not further resolve the relationships of this group.

The *femoralis* group included *P. anthonyi*, *P. boulengeri*, *P. espinosai*, *P. femoralis*, *P. tricolor*, and *P. zaparo*. Within this group, Silverstone (1976) proposed the following relationships: (*P. tricolor* (*P. femoralis P. zaparo*) (*P. anthonyi P. boulengeri P. espinosai*)).

The *pictus* group contained *P. bolivianus*, *P. ingeri*, *P. parvulus*, *P. petersi*, *P. pictus*, *P. pulchripectus*, and *P. smaragdinus*. Silverstone (1976) was doubtful that this group was monophyletic, but he did think parts of it were. He grouped *P. pictus* and *P. parvulus* together based on the shared presence of a calf spot. He also grouped *P. petersi* and *P. pulchripectus* on the basis of similar color patterns, and united them with *P. bolivianus* (although he was more ambivalent about the latter's relationship). Silverstone did not place *P. smaragdinus*, and he did not propose a scheme of relationships among these groups.

Silverstone (1976) was more certain about the naturalness of the *trivittatus* group, which contained only the similarly colored *P. bassleri* and *P. trivittatus*. Silverstone did not publish further studies on dendrobatid frogs, as he discontinued working in herpetology to pursue a scientific career in botany.

In 1976, Charles W. Myers and John W. Daly began publishing on the systematics implications of their work initiated a decade earlier (Daly and Myers, 1967). They added three new sources of evidence: alkaloid profiles, vocalizations, and behavior. Modern research in dendrobatid alkaloids was initiated by Märki and Witkop (1963), and the accumulated data appeared to have clear systematics implications. Similarly, audiospectrographic analysis of vocalizations had been carried out for several groups of frogs (e.g., Bogert, 1960; Martin, 1972), but not for dendrobatids. Numerous workers had published observations on dendrobatid parental care and other behaviors (Wyman, 1859a, 1859b [reported as *Hylodes lineatus*; *Dendrobates trivittatus* fide Boulenger, 1888], Ruthven and Gaige, 1915; Senfft, 1936; Dunn, 1944; Test, 1954; Stebbins and Hendrickson, 1959; Duellman, 1966; Goodman, 1971; Crump, 1972; Bunnell, 1973; Silverstone, 1973, 1975a, 1976; Dole and Durant, 1974), and to these were added the extensive field and laboratory observations of Myers and Daly, who analyzed the phylogenetic implications of these advances.

Based on these and traditional data, Myers and Daly (1976b) named three new species and redescribed *D. histrionicus*. They also added support to Silverstone's (1975a) *pumilio* group, and they proposed a group consisting of *D. histrionicus*, *D. lehmanni*, and *D. occultator* (they did not mention *D. leucomelas*, which Silverstone had grouped with *D. histrionicus*). That same year, Myers and Daly (1976a) named *D. abditus* and added it and *D. viridis* to Silverstone's (1975a) *minutus* group.

Myers et al. (1978) proposed a restricted application of *Phyllobates* as an explicitly monophyletic genus (the first in the family). They argued that *Phyllobates* sensu Silverstone (1976) had been diagnosed on the basis of symplesiomorphy, whereas the occurrence of batrachotoxins was a synapomorphy for a group containing *P. aurotaenia*, *P. bicolor*, *P. lugubris*, *P. terribilis*, and *P. vittatus*, and thus resembling *Phyllobates* sensu Savage (1968). In order to avoid coining new names without evidence of monophyly, Myers et al. (1978) referred the rest of *Phyllobates* sensu Silverstone (1976) to *Dendrobates*, pending a comprehensive phylogenetic analysis.

Rivero (1978 "1976") named three species of *Colostethus* and proposed that *C. haydeeae* and *C. orostoma* were closest relatives (later dubbed the *haydeeae* group by Rivero, 1980 "1978": 99). This conjecture was based largely on the supposed occurrence of four anterior and five posterior rows of keratodonts in larvae, although Rivero did note the possibility that the larvae were not of these species. Rivero (1978 "1976") speculated that *C. leopardalis* was most closely related to *C. alboguttatus*, *C. collaris*, and *C. meridensis* and concluded that "in spite of the presence of a collar in *C. leopardalis* and its absence in *C. alboguttatus*, these two species are more closely related to each other than either is to *C. collaris* [which has a collar]" (p. 334; translated from the Spanish).

Rivero (1979) suggested that the presence of a dark chest collar delimited a monophyletic group of species confined to the

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Venezuelan Cordillera de la Costa. Rivero (1979) mentioned the occurrence of similar dark spotting on each side of the chest in several species from southern Colombia to northern Peru, and he (Rivero, 1979: 172) proposed that the collared species were derived from the species with chest spotting. Curiously, Rivero (1984 "1982") later included *C. mandelorum*, a species that lacks a dark collar, in this group, and, following Rivero (1979: 173), went on to hypothesize that the "ancestral stock of *C. trinitatis* … gave origin to the other collared forms of Venezuela and *C. mandelorum*" (p. 12). The inclusion of this uncollared species in this group was based on the species's "affinity with collared species, its limited altitudinal distribution, and the absence currently of any uncollared species similar to it" (Rivero, 1984 "1982": 12).

Myers and Daly (1979) further characterized the *trivittatus* group based on vocalizations, and they added to it *D. silverstonei*. The following year, Myers and Daly (1980) named a new species (*D. bombetes*), resurrected *D. reticulatus*, and assigned both to the *minutus* group. (They also included an unnamed species, finally described 20 years later as *D. claudiae* by Jungfer et al., 2000.) Furthermore, they hypothesized that *D. abditus*, *D. bombetes*, and *D. opisthomelas*, all from the western Andes of Colombia and Ecuador, formed a monophyletic group delimited by a "median gap that interrupts the papillate fringe on the posterior (lower) edge of the oral disc" (Myers and Daly, 1980: 20).

Based on finger length and color pattern, Rivero (1980 "1978") proposed that *C. inflexus* was part of the *haydeeae* group (sensu Rivero 1978 "1976"), and that their closest relative was *C. alboguttatus*. *Colostethus inflexus* was later placed in the synonymy of *C. alboguttatus* by Rivero (1984 "1982"), but he did not address the phylogenetic implications of this change. Although he did not retract his previous claim that *C. haydeeae* and *C. orostoma* had a larval keratodont row formula of 4/5, Rivero (1980 "1978") did seriously question its veracity, given that no other *Colostethus* was known to possess this morphology. La Marca (1985) subsequently identified Rivero's *C. haydeeae* tadpole as *Hyla platydactyla*.

Myers (1982) resurrected and redescribed *D. maculatus* but clarified that he was "unable at this time to demonstrate a close relationship with any other known dendrobatid" (p. 2). Myers (1982: 2) also resurrected *D. fantasticus* from synonymy with *D. quinquevittatus* and placed *D. vanzolinii*, *D. fantasticus*, *D. quinquevittatus*, and *D. reticulatus* in a monophyletic *quinquevittatus* group delimited by "distinctively reticulate limbs". Myers (1982) speculated that *D. captivus* and *D. mysteriosus* were sister species, but he was unable to present any synapomorphies to corroborate this hypothesis.

In 1982, Lynch published two papers on Colombian dendrobatids. Lynch (1982) named *C. edwardsi* and *C. ruizi* and hypothesized that they formed a distinct group within Dendrobatidae, based on the occurrence of an "anal sheath" and putatively derived absence of a tarsal fold or tubercle (also known in dendrobatid literature as "tarsal keel"). He refrained from naming this group formally to avoid encumbering future research; he also observed that no synapomorphies were known for *Colostethus* and declared that the genus was paraphyletic (although he did not present evidence to that effect).

Lynch and Ruiz-Carranza (1982) described the new genus and species *Atopophrynus syntomopus* as a dendrobatid. They reported a number of features unknown in other dendrobatids, but they were unable to elucidate the relationships of this taxon with respect to other dendrobatids. They (Lynch and Ruiz-Carranza, 1982: 561) explicitly rejected the absence of teeth as a synapomorphy "because it postulates loss of an attribute."

Rivero (1984) clarified that *C. dunni* did not have a throat collar (contra Edwards, 1974a, 1974b) and provided a name, *C. oblitteratus*, for the MCZ material Edwards had seen.

Myers et al. (1984) combined what had been the *pumilio* and *histrionicus* groups into a new, expressly monophyletic *histrionicus* group delimited by the synapomorphic occurrence of a "chirp call". This group contained *D. arboreus*, *D. granuliferus*, *D.*

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histrionicus, *D. lehmanni*, *D. occultator*, *D. pumilio*, *D. speciosus*, and an unnamed species.

Maxson and Myers (1985) employed microcomplement fixation to compare the serum albumin of several dendrobatids. They concluded that recognition of *Phyllobates* as a separate group was warranted, and that the "[s]peciation events leading to the living species of true dart-poison frogs (*Phyllobates*) appear to have occurred within the last five million years" (Maxson and Myers, 1985: 50). They also found that the species of *Dendrobates* they studied were much more divergent than the species of *Phyllobates*, and that this was "consistent with accumulating evidence that *Dendrobates* is a polyphyletic assemblage" (Maxson and Myers, 1985: 50). They suggested that at least four major lineages were represented, and that initial divergence dated back some 60 million years.

Péfaur (1985) described two new species of *Colostethus* from Venezuela, but he did not discuss their phylogenetic relationships. La Marca (1985: 4) claimed that his new species *C. molinarii* was "a member of the *C. alboguttatus* group, a monophyletic assemblage" comprised additionally of *C. alboguttatus*, *C. dunni*, *C. haydeeae*, *C. leopardalis*, *C. mayorgai*, *C. meridensis*, and *C. orostoma*. However, La Marca (1985) did not offer any evidence in support of this conjecture.

Dixon and Rivero-Blanco (1985) named *Colostethus guatopoensis* (placed in the synonymy of *Colostethus oblitterata* by Rivero, 1990 "1988") and grouped it with *C. riveroi* on the basis of the shared absence of the outer metatarsal tubercle. This synapomorphy was disputed by La Marca (1996 "1994"), who reported the occurrence of the outer metatarsal tubercle in both species (and considered both species to be valid).

In a series of privately published but nomenclaturally valid (according to ICZN, 1999) papers, Bauer (1986, 1988, 1994) named several genera and speculated on their relationships. Bauer's proposals were based on reinterpretations of Silverstone (1975a, 1976) and Myers and colleagues (mainly Myers et al., 1978, 1984; Myers and Burrowes, 1987) augmented with limited observations of a few species in captivity. Bauer's publications were overlooked by all workers except Wells (1994), and as a result the literature is now quite confusing; for that reason we break from chronological order to summarize Bauer's contributions. Bauer (1986) named *Ameerega* (type specie: *Hyla trivittata*) for the species of *Phyllobates* sensu Silverstone (1976) that were not placed in *Phyllobates* sensu Myers et al. (1978). Bauer (1988) named *Ranitomeya* (type species: *Dendrobates reticulatus*) for *Dendrobates captivus*, *D. fantasticus*, *D. imitator*, *D. mysteriosus*, *D. quinquevittatus*, *D. reticulatus*, and *D. vanzolinii*. Bauer (1988) attributed the name to "Bauer, 1985", and it was also employed by Bauer (1986); however, those prior uses do not constitute nomenclatural actions because (1) the 1985 use was in a publication that did not specify authorship (Anonymous, 1985) and (2) the 1986 use did not specify a type species. Only Bauer's 1988 use was sufficient to make *Ranitomeya* an available name. In that paper, Bauer also named *Pseudendrobates*, but that is an objective synonym of *Phobobates* Zimmermann and Zimmermann, 1988 (see below) because it was published later and specified the same type species (*Dendrobates silverstonei*). Bauer (1994: 1) stated that "*Phobobates* should be considered a synonym", but of what he did not say, and he did not provide evidence to substantiate his view. Bauer (1994) proposed the name *Oophaga* (type species: *Dendrobates pumilio*) for the *histrionicus* group of Myers et al. (1984), namely, *Dendrobates arboreus*, *D. granuliferus*, *D. histrionicus*, *D. lehmanni*, *D. occultator*, *D. pumilio*, *D. speciosus*, and *D. sylvaticus*. Although *Oophaga* was never placed in the synonymy of *Dendrobates*, it was also never used again. Finally, Bauer (1994) named *Paruwrobates* as a monotypic genus to accommodate *D. andinus*; Bauer did not address the placement of *D. erythromos*, although Myers and Burrowes (1987) had grouped them together (and Bauer claimed to be basing his new taxonomy on their paper). In that paper, Bauer also resurrected *Prostherapis*, but he did not list the content of the genus and the evidence he cited for distinguishing *Prostherapis inguinalis* from *Colostethus latinasus* was his erroneous claim that they differ in the occurrence of swelling in the third finger in adult males (see Grant, 2004).

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Bauer (1986, 1988, 1994) was the only recent worker to recognize subfamilies within Dendrobatidae. In the most recent proposal (Bauer, 1994), he recognized Dendrobatinae for *Dendrobates*, *Oophaga*, *Ranitomeya*, and *Minyobates*; Phyllobatinae for *Phyllobates* and *Ameerega*; and Colostethinae for *Aromobates*, *Colostethus*, and *Epipedobates*. (Note that Bauer's use of *Epipedobates* was restricted to Silverstone's *femoralis* group, and he applied *Ameerega* to the bulk of *Phyllobates* sensu Silverstone.) Bauer was apparently unaware of *Mannophryne* La Marca, 1992. Subfamily diagnoses employed differences in chromosome number, coloration, occurrence of maxillary teeth, skin toxins, webbing, length of first finger, muscle coloration, clutch size, breeding biology, and tadpole specialization. He believed Dendrobatinae and Phyllobatinae to be monophyletic, but thought that Colostethinae was paraphyletic (though he did not say with respect to what); he did not otherwise propose relationships among the subfamilies.

Meanwhile, Myers and Ford (1986) examined Lynch and Ruiz-Carranza's (1982) assertion that *Atopophrynus* was a dendrobatid. They could find no support for Lynch and Ruiz-Carranza's claim, given that specimens they examined showed major differences from dendrobatids in external morphology, jaw musculature, thigh musculature, skull, finger structure, and hyoid structure, and shared no particular synapomorphy. Consequently, they removed the genus from Dendrobatidae and placed it in Leptodactylidae (transferred with other eleutherodactylines to Brachycephalidae by Frost et al., 2006).

Myers (1987) proposed a major taxonomic rearrangement aimed to better reflect hypotheses of monophyly, whereby "[d]endrobatids that produce lipophilic alkaloids are a monophyletic group that is now partitioned among four genera" (p. 304). *Epipedobates* (type species: *Prostherapis tricolor*) was named to accommodate most species of *Phyllobates* sensu Silverstone (1976) minus the species Myers et al. (1978) had placed in their restricted *Phyllobates*. Although Myers's intention was the same as Bauer's (discussed above), his designation of a different type species means that the two names may be applied to different groups. *Dendrobates* was redefined as a monophyletic group delimited by a suite of synapomorphies from larval, adult, behavioral, and alkaloid characters. *Dendrobates* included the *quinquevittatus* group of Myers (1982), which had been part of the *minutus* group (Silverstone, 1975a; Myers and Daly, 1976a, 1980; Myers, 1982). The remainder of the *minutus* group was transferred to *Minyobates*, which retained the plesiomorphic states not found in *Dendrobates*. *Dendrobates* and *Phyllobates* were claimed to be sister groups based on "the loss of cephalic amplexus (cephalic embrace sometimes retained in an aggressive context), loss of the primitive oblique lateral line, and first appearance of 3,5-disubstituted indolizidine alkaloids" (Myers, 1987: 305).

Myers and Burrowes (1987) named *Epipedobates andinus* and postulated that its nearest relative was *E. erythromos* based on "a few similarities of the color patterns" and "an overall morphological similarity" (Myers and Burrowes, 1987: 16). They followed Vigle and Miyata (1980) in tentatively placing these species in Silverstone's (1976) *pictus* group. Given their placement in this group, indirect evidence for the close relationship of *E. andinus* and *E. erythromos* not cited by Myers and Burrowes is given by their occurrence on the Pacific slopes in contrast to the *cis*-Andean distribution of the remainder of the *pictus* group. Myers and Burrowes (1987) also transferred *Phyllobates azureiventris* to *Epipedobates*, also in the *pictus* group.

Zimmermann and Zimmermann (1988) performed a phenetic analysis of 62 characteristics (mostly behavioral, but also including vocalizations and larval morphology) for 32 species. Their analysis resulted in nine groups of decreasing similarity:

- *Colostethus* group: *C. inguinalis*, *C. collaris*, *C. trinitatis*, *C. palmatus*
- *Epipedobates pictus* group: *E. pulchripectus*, *E. pictus*, *E. parvulus*
- *Epipedobates tricolor* group: *E. anthonyi*, *E. boulengeri*, *E. espinosai*, *E. tricolor*
- *Epipedobates silverstonei* group: *E. bassleri*, *E. silvestonei*, *E. trivittatus*
- *Epipedobates femoralis* group: *E. femoralis*
- *Phyllobates terribilis* group: *P. lugubris*, *P. terribilis*, *P. vittatus*

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- *Dendrobates leucomelas* group: *D. auratus*, *D. azureus*, *D. leucomelas*, *D. tinctorius*, *D. truncatus*
- *Dendrobates quinquevittatus* group: *D. fantasticus*, *D. imitator*, *D. quinquevittatus*, *D. reticulatus*, *D. variabilis*
- *Dendrobates histrionicus* group: *D. granuliferus*, *D. histrionicus*, *D. lehmanni*, *D. pumilio*, *D. speciosus*

Furthermore, Zimmermann and Zimmermann (1988) proposed *Phobobates* for their *silverstonei* group (viz., *Dendrobates bassleri*, *D. silverstonei*, and *Hyla trivittata*) and *Allobates* for the monotypic *femoralis* group. However, Schulte (1989: 41) and Myers et al. (1991: 18) rejected those genera, citing errors in the analysis of behavior, lack of evidence, unaccounted character conflict, incorrect character coding, and creation of paraphyly.

In 1989, the *Colostethus collaris* group, delimited by "a dark band present on the posterior part of the throat and anterior part of the chest in all members", was proposed by La Marca (1989: 175) for *C. collaris*, *C. oblitteratus* (as *C. guatopoensis*), *C. herminae*, *C. neblina*, *C. olmonae*, *C. riveroi*, *C. trinitatis*, and *C. yustizi*.

Over 60 years after the only previous specimen had been collected, Schulte (1990) rediscovered *Dendrobates mysteriosus* from Amazonian Peru. Despite some similarities, Schulte (1990: 66) determined that it was necessary to exclude *D. mysteriosus* from the *quinquevittatus* group (sensu Silverstone, 1975a, presumably), and he further stipulated that it was not closely related to *D. captivus* as proposed by Myers (1982). Rather, Schulte (1990: 67) believed *D. mysteriosus* to be most closely related to *D. histrionicus* from the lowlands of Pacific Ecuador and Colombia. He based this on shared size, absence of omosternum, occurrence of round spots on a dark background, reproductive behavior, an elevated number of small ova, and a similar fundamental frequency of the call, although no audiospectrographic analysis was performed. None of these characters is unique to the *histrionicus* group, and several other reported character states conflict with this relationship (e.g., larval mouth parts).

Rivero (1990 "1988") selectively extracted data from Edwards's unpublished dissertation (1974a) and arranged the species of *Colostethus* into eight groups, which were soon expanded to nine by Rivero and Serna (1989 "1988"). Numerous species were not placed in any group because of apparent character conflict and other concerns. Although these groups were putatively based on derived characters and were hypothesized to be monophyletic, "characteristics shared by the majority of members" and geographic distribution were attributed evidential significance (Rivero, 1990 "1988": 4). The content of the groups (as modified by Rivero and Serna, 1989 "1988" and augmented by Rivero and Granados-Díaz, 1990 "1989"; Rivero, 1991a ,1991b; Rivero and Almendáriz, 1991; Rivero and Serna, 1991, 2000 "1995"; La Marca, 1998 "1996") was as follows:

- Group I (*vertebralis* group): *C. elachyhistus*, *C. exasperatus*, *C. idiomelus*, *C. infraguttatus*, *C. mittermeieri*, *C. peculiaris*, *C. shuar*, *C. sylvaticus*, *C. vertebralis*
- Group II (*brunneus* group): *C. brunneus*, *C. intermedius* [= *C. kingsburyi* fide Coloma, 1995], *C. kingsburyi*, *C. marchesianus*, *C. olfersioides*, *C. peruvianus*, *C. talamancae*, *C. trilineatus*
- Group III (*alagoanus* group): *C. alagoanus*, *C. capixaba*, *C. carioca*
- Group IV (*inguinalis* group): *C. agilis*, *C. alacris*, *C. brachistriatus* [as *C. brachystriatus*], *C. cacerensis* [= *inguinalis* fide Grant, 2004], *C. dysprosium*, *C. erasmios*, *C. fallax*, *C. fraterdanieli*, *C. inguinalis*, *C. latinasus*, *C. mertensi*, *C. nubicola*, *C. paradoxus* [= *Epipedobates tricolor* fide Coloma, 1995], *C. pratti*
- Group V (*edwardsi* group): *C. edwardsi*, *C. ruizi*
- Group VI (*fuliginosus* group sensu stricto; i.e., sensu Rivero and Serna, 1989 "1988"): *C. abditaurantius*, *C. betancuri*, *C. chocoensis*, *C. excisus*, *C. faciopunctulatus*, *C. fuliginosus*, *C. furviventris*, *C. maculosus* [= *C. bocagei* fide Coloma, 1995], *C. nexipus*, *C. palmatus*, *C. pseudopalmatus*, *C. ramirezi* (?), *C. shrevei*, *C. thorntoni*, *C. vergeli*
- Group VII (*trinitatis* group): *C. collaris*, *C. neblina*, *C. oblitteratus*, *C. olmonae*, *C. riveroi*, *C. trinitatis*
- Group VIII (*alboguttatus* group): *C. alboguttatus*, *C. duranti*, *C. haydeeae*, *C. mayorgai*, *C. molinarii*, *C. orostoma*, *C. saltuensis*, *C. serranus*
- Group IX (*subpunctatus* group): *C. anthracinus*, *C. borjai*, *C. cevallosi*, *C. citreicola* [= *C.*

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nexipus fide Coloma, 1995], *C. degranvillei*, *C. festae*, *C. jacobuspetersi*, *C. lehmanni*, *C. marmoreoventris*, *C. mystax*, *C. parcus* [= *C. exasperatus* fide Coloma, 1995], *C. pinguis*, *C. poecilonotus*, *C. pumilus*, *C. ramirezi* (?), *C. ramosi*, *C. ranoides*, *C. sauli*, *C. subpunctatus*, *C. taeniatus* [= *C. pulchellus* fide Coloma, 1995], *C. tergogranularis* [= *C. pulchellus* fide Coloma, 1995], *C. torrenticola* [= *C. jacobuspetersi* fide Coloma, 1995], *C. whymperi*, *C. yaguara*

Among these groups, Rivero (1990 "1988": 26) hypothesized that the *brunneus* group formed (or was close to) the "ancestral stock" from which the other *Colostethus* were derived. On the same page, he also hypothesized that the *brunneus* group gave rise to the *inguinalis* group (see also Rivero, 1991a: 23). He postulated that the *fuliginosus* group (sensu lato; *fuliginosus* + *subpunctatus* groups of Rivero and Serna, 1989 "1988") was derived from the *inguinalis* group, and that the members of the *fuliginosus* group that lack toe webbing "could be close to the ancestral stock that gave rise to [the *vertebralis* group]." The *edwardsi* group was conjectured to have arisen from the *fuliginosus* group (sensu lato), and the *alboguttatus* group was believed to have arisen from the same ancestral stock as the *edwardsi* group. However, Rivero (1990 "1988") also speculated that the *trinitatis* group (which was identical to La Marca's, 1989, *collaris* group) may have given rise to the *alboguttatus* group (which differed only slightly from La Marca's, 1985, *alboguttatus* group), citing putative intermediate forms as evidence. Rivero (1990 "1988") was more ambivalent with regard to the relationships of the *trinitatis* group than he had been previously (Rivero, 1979). He now concluded that the *trinitatis* group may have arisen from the *vertebralis* group (as he had argued in 1979), or that both the *trinitatis* and *vertebralis* groups may have arisen from the *fuliginosus* group (sensu lato). Besides Rivero and his colleagues, few authors have recognized these groups (see Coloma, 1995).

Caldwell and Myers (1990) further elucidated the systematics of the *Dendrobates quinquevittatus* group, which had been revised previously by Myers (1982). In the process, they proposed that *D. quinquevittatus* sensu stricto was sister to *D. castaneoticus*, united by the synapomorphic absence of the inner metacarpal tubercle, as well as a number of character states of more ambiguous polarity. As a working hypothesis, they further proposed that this group was sister to a clade united by the synapomorphy of pale limb reticulation (i.e., *D. fantasticus*, *D. quinquevittatus*, *D. reticulatus*, *D. vanzolinii*), but they were unable to propose any synapomorphies to support this arrangement.

Myers et al. (1991) named a new genus and species, *Aromobates nocturnus*. They argued that this was the sister of all other dendrobatids on the basis of (1) nocturnal and (2) aquatic behavior, (3) large size, and (4) presence of m. adductor mandibulae externus superficialis in many specimens. They also proposed an informal redefinition of *Colostethus* based on the occurrence of the swollen third finger in adult males; they were explicit that they were not proposing formal nomenclatural changes. Their *Colostethus* sensu stricto corresponded with Rivero's (1990 "1988") and Rivero and Serna's (1989 "1988") *inguinalis* group with the addition of *Phyllobates flotator* and *Colostethus imbricolus*. The remaining species of *Colostethus* sensu lato were assigned to *Hyloxalus* (within which was included *Phyllodromus*), although no synapomorphies or diagnostic characters (besides the lack of the swollen third finger) were proposed. Almost immediately, Myers (1991; see also Myers and Donnelly, 1997: 25) retreated from this arrangement, given that the swollen third finger also occurs in some species of *Epipedobates*. Myers et al. (1991) provided a cladogram summarizing their views on the relationships of the dendrobatid frogs, reproduced here as figure 2.

In comparing *Aromobates nocturnus* to other dendrobatids, Myers et al. (1991) speculated that it may be most closely related to the collared species of Venezuelan *Colostethus*. They listed 10 species (1 undescribed) as definitely possessing a collar and 2 more as possibly having one. They did not define a group for these species, and their list of collared species differed from La Marca's (1989) *collaris* group (= *trinitatis* group of Rivero, 1990 "1988" and Rivero and Serna,

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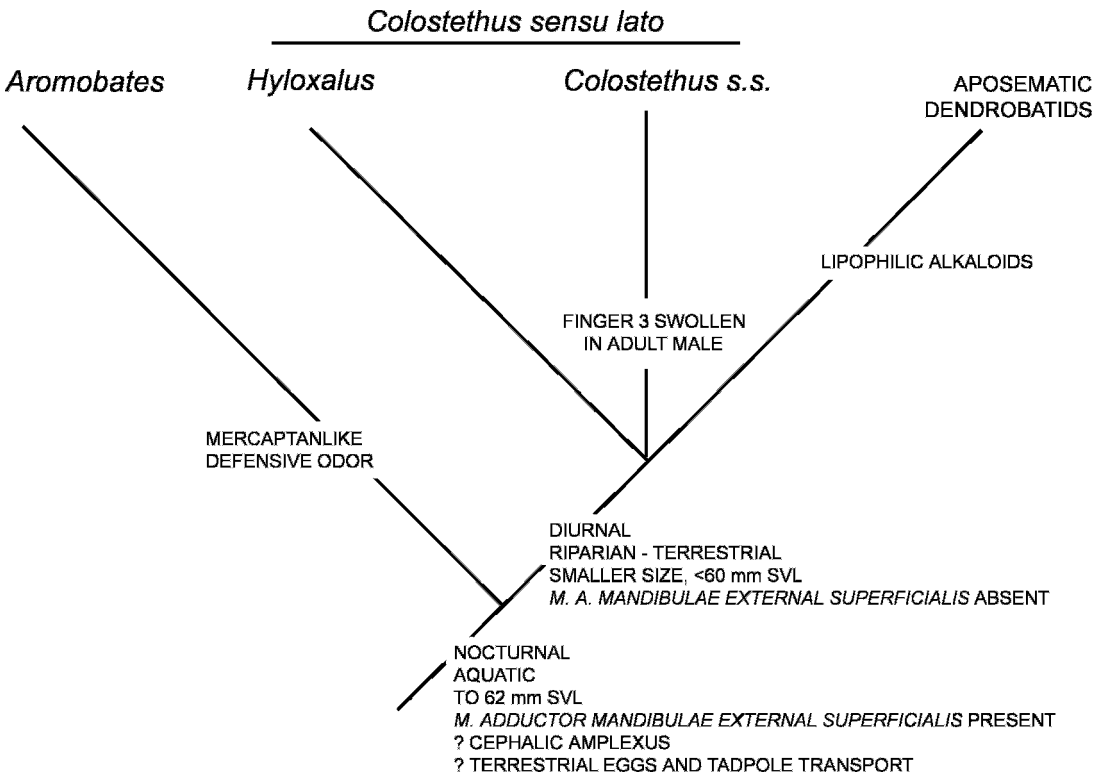

Fig. 2. Hypothesized phylogeny of dendrobatids, redrawn from Myers et al. (1991: 29, fig. 20). All evidence is shown on the cladogram. In this scenario, *Aromobates nocturnus* is postulated to be the sister species of all other dendrobatids. All of the unquestioned synapomorphies listed for Dendrobatidae apply only to *A. nocturnus* and are unknown in any other dendrobatid.

1989 "1988") by including species of La Marca's *alboguttatus* group.

Also in 1991, Myers named *Colostethus lacrimosus* and, based on several similarities (but no clear synapomorphies), speculated that it may be closely related to *C. chocoensis*. He also suggested that they, in turn, were related to *C. fuliginosus*.

In a series of papers in the 1990s, La Marca proposed a number of novel relationships and taxonomic changes. In 1992 he formally named the *collaris* group as *Mannophryne* and later (La Marca, 1995) presented a hypothesis of relationships based on five characters from morphology and behavior, shown here as figure 3.

Although this study purported to be a quantitative cladistic analysis, few characters were used and some characters discussed by the author were ignored, not all characters were scored based on observations (i.e., some states were merely assumed), and monophyly and character polarity were assumed (i.e., no outgroup species were included). In addition to the species originally placed in *Mannophryne*, the genus currently includes *M. caquetio*, *M. cordilleriana*, *M. larandina*, and *M. lamarcai* (Mijares-Urrutia and Arends R., 1999).

In discussing the systematics of *Colostethus mandelorum* (about which he only concluded that the species is not closely related to either *Mannophryne* or the *C. alboguttatus* group), La Marca (1993) considered *Aromobates nocturnus* to be most closely related to the *C. alboguttatus* group of La Marca (1985). Regardless, instead of transferring the *alboguttatus* group into *Aromobates*, La Marca (1994) named it *Nephelobates*. The group was delimited by the occurrence of elongate teeth (also reported for *Aromobates*; see Myers et al., 1991; La Marca, 1993) and a dermal

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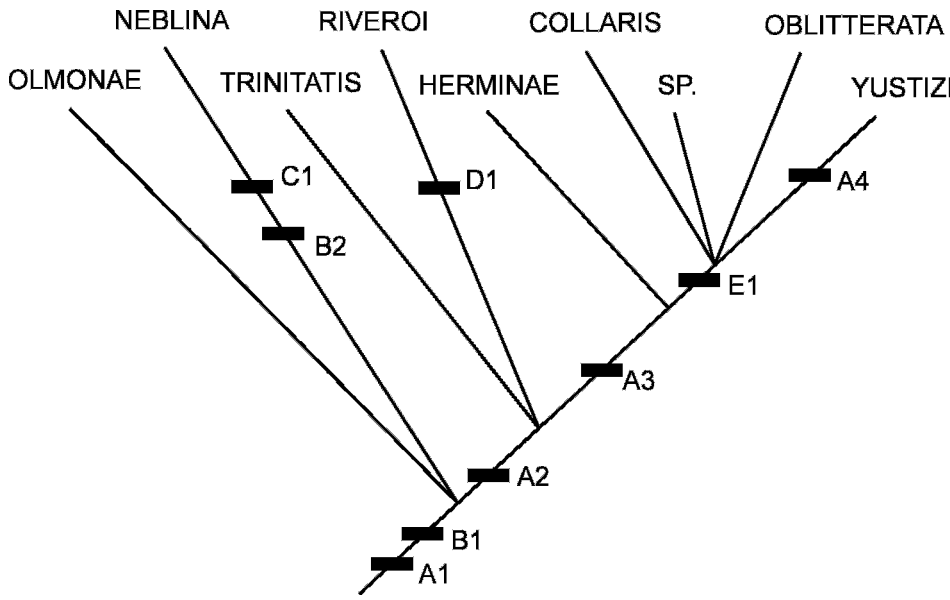

Fig. 3. Hypothesized phylogeny of *Mannophryne*, redrawn from La Marca (1995: 70, fig. 11). Synapomorphies are: A1, narrow collar, uniformly colored; B1, tadpoles with small papillae (presumably B1 on the cladogram is B0 from the text on p. 53); B2, tadpoles with large papillae (B2 is undefined in the text on p. 53; presumably it refers to B1); C1, uniformly colored dorsum; A2, wide collar without conspicuous pale markings; D1, posteroventral dark band present; A3, wide collar with pale flecks or spots; E1, bright throat coloration reduced, melanophores on anterior part of throat; A4, wide collar with large pale dots.

covering of the cloaca (also reported for the *edwardsi* group; Lynch, 1982), and it included *N. alboguttatus*, *N. haydeeae*, *N. leopardalis*, *N. mayorgai*, *N. meridensis*, *N. molinarii*, and *N. orostoma*; Mijares-Urrutia and La Marca (1997) subsequently included *N. duranti* and *N. serranus*. La Marca (1994) did not include *C. saltuensis*, which had been included in Rivero's *alboguttatus* group (Rivero, 1990 "1988"), but he did not state his reasons for its exclusion. No explicit hypothesis of relationships has been proposed for the species of *Nephelobates*, but Mijares-Urrutia and La Marca (1997) reported several larval character-states of unclear polarity, as well as the occurrence of "reduced nasal bones" (p. 134) as a synapomorphy for the genus.

Kaiser et al. (1994) described *Colostethus chalcopis* from Martinique in the French Antilles. Although they were skeptical of the monophyly of *Mannophryne*, they conjectured that *C. chalcopis* could be the sister species to that assemblage on the basis of the shared occurrence of a dark throat collar.

Although Coloma (1995) did not intend to provide a phylogenetic hypothesis for *Colostethus*, the taxonomic changes he made had numerous phylogenetic implications. For example, some of the species he considered to be synonymous had been placed in different and presumably distantly related groups by Rivero (e.g., Rivero and Almendáriz, 1991, placed *C. nexipus* in the *fuliginosus* group, whereas its junior synonym *C. citreicola* was placed in the *subpunctatus* group), which called into question the phylogenetic validity (or even taxonomic utility) of those groups. Coloma (1995: 58) also summarized the recognized species groups of *Colostethus*, arguing that "most of the character states given by Rivero [1990 "1988"] and Rivero and Serna [1989 "1988"] seem to be plesiomorphic at the level used." Although he concluded that "the phylogenetic relationships within '*Colostethus*' (sensu lato) constitute an enormous polytomy" (Coloma, 1995: 60), Coloma tentatively supported the following relationships:

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- Some species of *Colostethus* may be more closely related to some species of *Epipedobates* (based on the shared occurrence of a swollen third finger in adult males) than to other species of *Colostethus*.
- Species in *Aromobates*, *Mannophryne*, and the *vertebralis* and *fuliginosus* groups may be basal within *Colostethus*.
- The *edwardsi* group is monophyletic.
- A novel group composed of *Aromobates nocturnus*, *Colostethus awa*, *C. bocagei*, *C. nexipus*, and *C. riveroi* may be monophyletic on the basis of shared (albeit facultative) nocturnal behavior. Myers et al.'s (1991) claim that nocturnal activity is plesiomorphic was not addressed.

Grant et al. (1997) reviewed the distribution of the median lingual process in dendrobatids and other frogs. The occurrence of the median lingual process in a putative sister group (see Interfamilial Relationships, below) led them to interpret it tentatively as symplesiomorphic and, consequently, they did not use it to delimit a group within Dendrobatidae.

Kaplan (1997) followed Silverstone (1975a) in studying the distribution of the palatine (neopalatine of Trueb, 1993), and he used these data to further resolve Myers et al.'s (1991) hypothesis of relationships (and he explicitly incorporated *Mannophryne* and *Nephelobates*). He concluded that the absence of the palatine delimits a clade composed of part of *Hyloxalus* sensu Myers et al. (1991), *Colostethus* sensu stricto, and the aposematic dendrobatids. Kaplan (1997) presented a cladogram, shown here as figure 4. The separate treatment of *Epipedobates* was due to the presence of a swollen third finger in some species of that genus (Myers, 1991).

La Marca (1998 "1996") reviewed the species of Guayanan *Colostethus* and assigned *C. ayarzaguenai*, *C. guanayensis*, *C. murisipanensis*, *C. parimae*, *C. parkerae*, *C. praderioi*, *C. roraima*, *C. sanmartini*, *C. shrevei*, and *C. tepuyensis* to the *fuliginosus* group sensu lato (i.e., sensu Rivero, 1990 "1988"). He did not note the occurrence of the median lingual process, although it is present in several of these species.

Grant and Castro (1998) proposed the *Colostethus ramosi* group based on the occurrence of a patch of black, apparently glandular tissue on the ventral and medial surfaces of the distal extreme of the upper arm, just proximal to the elbow (referred to by Grant and Castro as the black arm band). This group presently includes *C. cevallosi*, *C. exasperatus*, *C. fascianiger*, *C. lehmanni*, *C. ramosi*, and *C. saltuarius* (Grant and Ardila-Robayo, 2002), but this character-state also occurs in *C. anthracinus* and an undescribed species from the slopes of the Magdalena valley, Colombia (T. Grant, personal obs.).

Schulte's (1999) book on Peruvian *Dendrobates* and *Epipedobates* included a number of novel phylogenetic arrangements, many of which involved non-Peruvian species as well. Lötters and Vences (2000) strongly criticized many of Schulte's (1999) taxonomic conclusions, and below we exclude the nomina nuda and taxa they placed in synonymy. Schulte (1999) proposed eight groups of *Dendrobates* and six groups of *Epipedobates*, and he provided branching diagrams depicting the relationships of each (Schulte, 1999: 24–25, 160–161). The groups he proposed are as follows:

Dendrobates:

- Group 1 (*amazonicus*): *D. amazonicus*, *D. duellmani*, *D. fantasticus*, *D. variabilis*
- Group 2 (*quinquevittatus*): *D. quinquevittatus*, *D. castaneoticus*, *D. flavovittatus*
- Group 3 (*imitator*): *D. imitator*
- Group 4 (*vanzolinii*): *D. biolat*, *D. lamasi*, *D. vanzolinii*
- Group 5 (*ventrimaculatus*): *D. ventrimaculatus*
- Group 6: *D. reticulatus*, *D. rubrocephalus*, *D. sirensis*, *D. steyermarki*, *D.* (*M.*) *virolinensis* [sic]
- Group 7: *D. captivus*
- Group 8 (*histrionicus*): *D. histrionicus*, *D. lehmanni*, *D. mysteriosus*

Epipedobates:

- Group 1 (giant types ["Riesenarten"]): *E. bassleri*, *E. planipaleae*, *E. silverstonei*, *E. trivittatus*
- Group 2 (*petersi/pictus*): *petersi* subgroup: *E. cainarachi*, *E. labialis*, *E. macero*, *E. petersi*, *E. pongoensis*, *E. smaragdinus*, *E. zaparo*; *pictus* subgroup: *E. bolivianus*, *E. hahneli*, *E. pictus*, *E. rubriventris*
- Group 3 (*azureiventris*): *E. azureiventris*, *Phyllobates* [i.e., *Phyllobates* sensu Myers et al., 1978]

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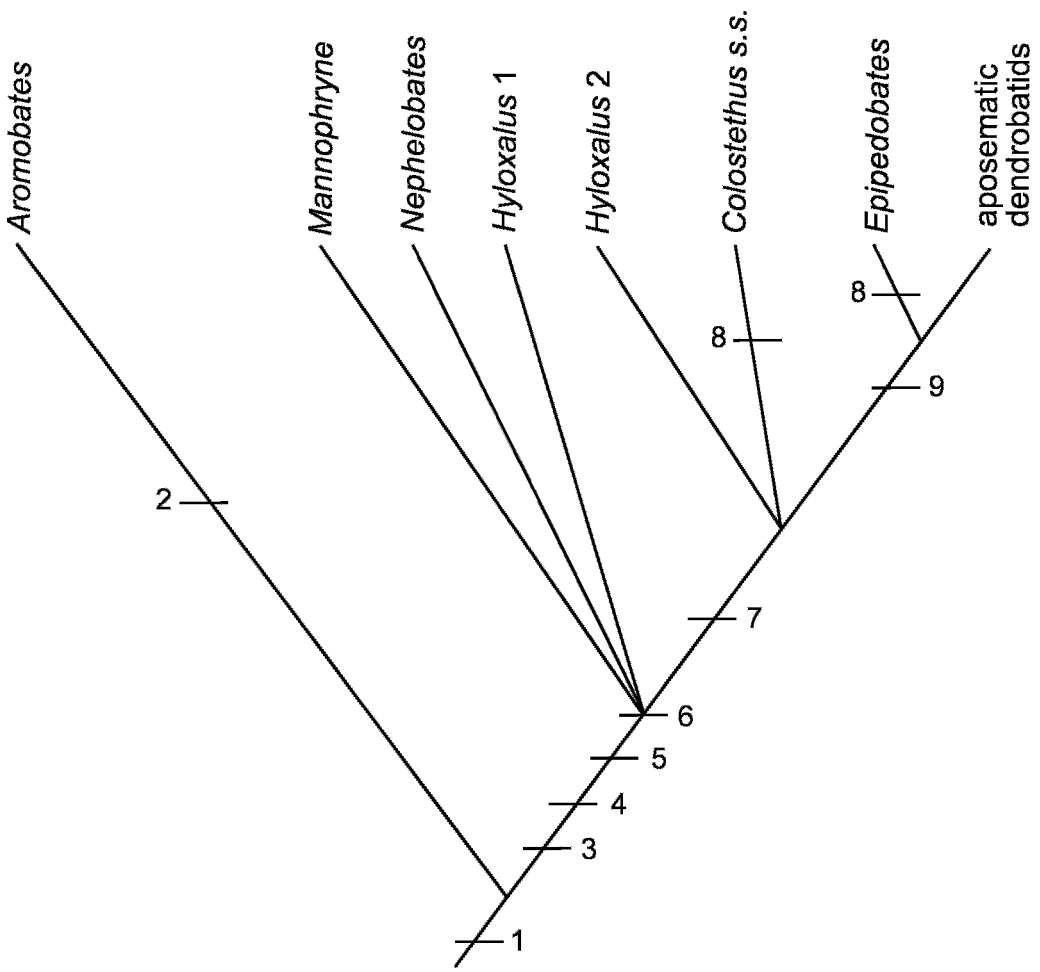

Fig. 4. Hypothesized phylogeny of dendrobatids, redrawn from Kaplan (1997: 373, fig. 3). Numbered synapomorphies are: (1) tympanum posterodorsally tilted under anterior edge of massive superficial slip of m. depressor mandibulae, (2) mercaptanlike defensive odor, (3) diurnal activity, (4) riparian–terrestrial habitat preference, (5) smaller size (<50 mm SVL), (6) m. adductor mandibulae externus superficialis absent ("s" pattern), (7) neopalatines absent, (8) finger three of males swollen, and (9) lipophilic alkaloids present.

- Group 4 (*femoralis*): *E. femoralis*, *E. ingeri*, *E. labialis*, *E. myersi*, *E. zaparo*
- Group 5 (*parvulus*): *E. espinosai*, *E. parvulus*
- Group 6 (*tricolor*): *E. anthonyi*, *E. espinosai*, *E. parvulus*, *E. subpunctatus*, *E. tricolor*

Rather than detail exhaustively the relationships Schulte (1999) proposed, we limit ourselves to pointing out a few of his more heterodox hypotheses. Without comment he transferred *Prostherapis subpunctatus* from *Colostethus* (where it had been placed by Edwards, 1971) to *Epipedobates* as sister species to *E. anthonyi* and *E. tricolor*. Also without comment, he referred *Dendrobates steyermarki* and *Minyobates virolinensis*—both of which had been in *Minyobates* (Myers, 1987; Ruiz-Carranza and Ramírez-Pinilla, 1992)—to *Dendrobates*, but he did not discuss the relationships of the remaining species of *Minyobates*. Further, according to his own diagrams he rendered *Epipedobates* paraphyletic by grouping *E. azureiventris* with species of *Phyllobates*. Schulte redefined the *histrionicus* group to include *D. mysteriosus*, but he excluded most of the species

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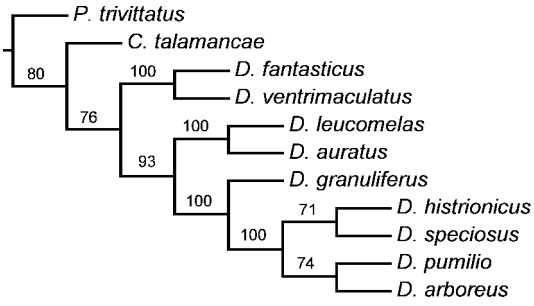

Fig. 5. Hypothesized phylogeny of *Dendrobates*, redrawn from Summers et al. (1999b: 261, fig. 1), based on parsimony analysis of cytochrome oxidase I, cytochrome *b*, and 16S DNA sequences aligned with Clustal W (Thompson et al., 1994) (parameters not specified) and modified manually, excluding ambiguously aligned regions. Numbers are bootstrap frequencies (unlabeled nodes present in fewer than 50% of replicates).

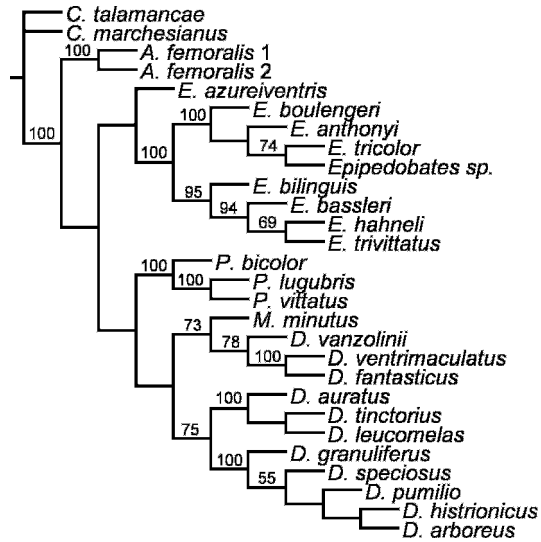

Fig. 6. Hypothesized phylogeny of dendrobatids, redrawn from Clough and Summers (2000: 342, fig. 1), based on parsimony analysis of 12S, 16S, and cytochrome *b* DNA sequences aligned with Clustal W (Thompson et al., 1994) (parameters not specified) and modified by eye and excluding ambiguously aligned regions. Numbers are bootstrap frequencies (unlabeled nodes present in fewer than 50% of replicates).

Myers et al. (1984)—and even Silverstone (1975a) and Myers and Daly (1976b)—had referred to that group, and he once again placed *D. leucomelas* in that group (as had Silverstone, 1975a). Relationships among most groups were not specified, but some groups (e.g., Groups 1 and 7) were paraphyletic in Schulte's own diagrams, and some species (e.g., *D. labialis* and *D. zaparo*; *E. parvulus* and *E. espinosai*) were included in multiple groups, with their relationships to each other being different in each group. No new character systems were added in this study, and, although Schulte provided limited group diagnoses and details on natural history, behavior, coloration and color patterns, and external morphology, no explicit synapomorphies were provided for any of his groups.

Grant (1998) named *Colostethus lynchi* and argued that it was part of the *C. edwardsi* group on the basis of the occurrence of a cloacal tube (he did not address the occurrence of this character in *Nephelobates*). More specifically, he argued that *C. lynchi* was the sister species to the group of *C. edwardsi* + *C. ruizi*.

The first attempt to address phylogenetic relationships among dendrobatids with DNA sequence data was published by Summers et al. (1997), although that paper only included the distantly related *Dendrobates pumilio*, *Dendrobates claudiae* (as *Minyobates* sp.), and *Phyllobates lugubris* (plus *C. talamancae*, used as the root). Since 1999, nearly a dozen phylogenetic studies of differing scales, scopes, and datasets have appeared (Summers et al., 1999b; Clough and Summers, 2000; Vences et al., 2000, 2003a; Widmer et al., 2000; Symula et al., 2001, 2003; La Marca et al., 2002; Santos et al., 2003). The cladograms that resulted from those studies are redrawn in figures 5–13. Interpretation of these studies is complicated by their use of different methods, nonoverlapping taxon samples, and heterogeneous datasets, but their findings can be summarized as follows:

- *Colostethus*: Found to be either para- or polyphyletic by all authors who tested its monophyly.
- *Epipedobates*: Found to be monophyletic by Clough and Summers (2000) (with *femoralis* placed outside in *Allobates*) but polyphyletic by Vences et al. (2000, 2003a; see also Santos et al., 2003).

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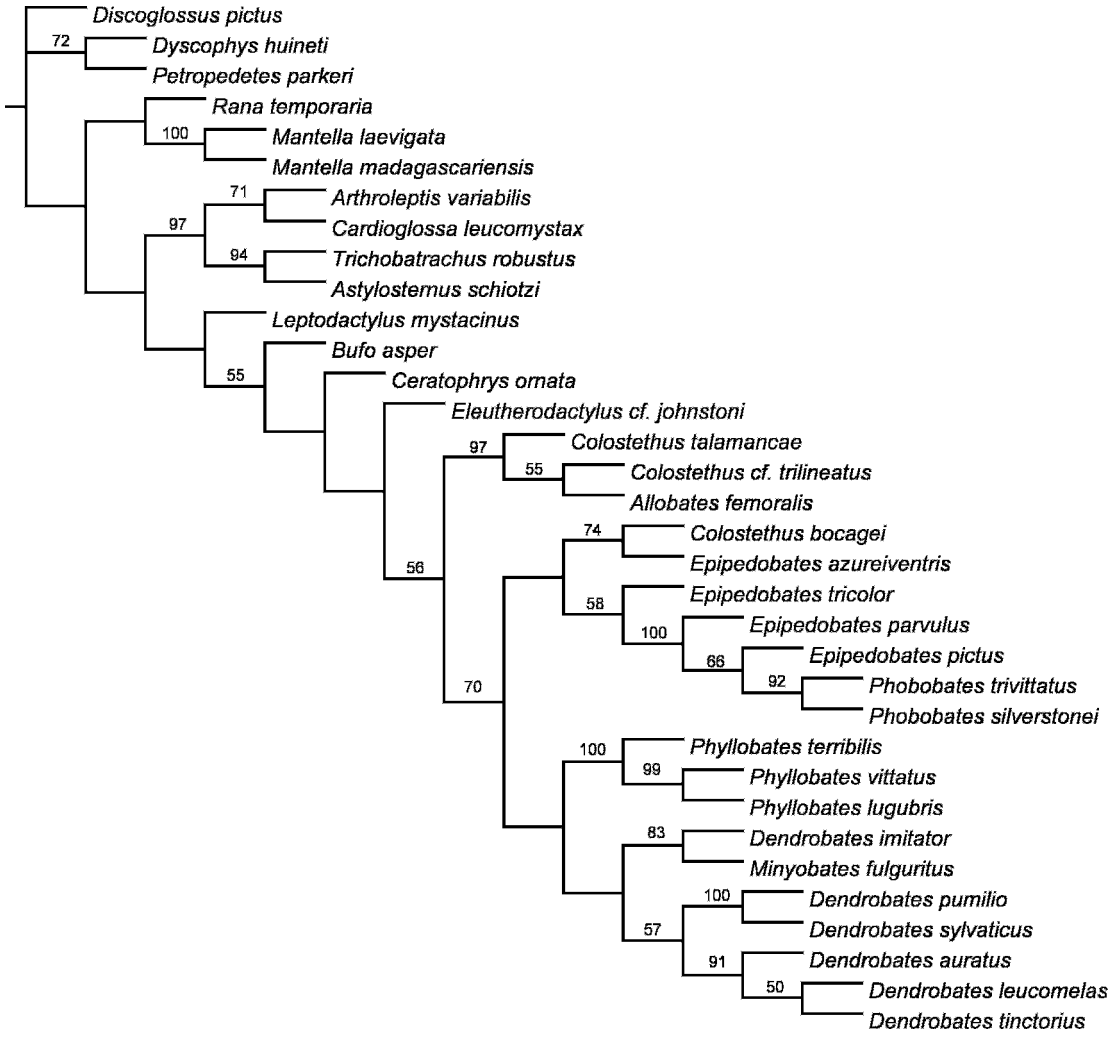

Fig. 7. Hypothesized phylogeny of dendrobatids, redrawn from Vences et al. (2000: 37, fig. 1), based on neighbor-joining analysis of 16S DNA sequences aligned manually and excluding highly variable regions. Numbers are bootstrap frequencies (unlabeled nodes present in fewer than 50% of replicates).

- *Phobobates*: Found to be monophyletic by Vences et al. (2000) but paraphyletic by Clough and Summers (2000), Santos et al. (2003), and Vences et al. (2003a).
- *Allobates*: This small genus fell out in a clade with species of *Colostethus* in Vences et al. (2000, 2003a) and Santos (2003). (Jungfer and Böhme, 2004 added the enigmatic *Dendrobates rufulus* to *Allobates*, but that species has not been included in any analysis.)
- *Phyllobates*: Without exception, this genus was found to be monophyletic. The optimal topology found by Widmer et al. (2000) was ((*vittatus lugubris*) (*aurotaenia* (*bicolor terribilis*))) (outgroup taxa were *Epipedobates azureiventris* and *Dendrobates sylvaticus*, and the tree was rooted on *E. azureiventris*). In their more inclusive study, Vences et al. (2003a) found *P. aurotaenia* to be the sister of the remainder, and *P. bicolor* to be sister to the Central American species, giving the topology (*aurotaenia* (*terribilis* (*bicolor* (*lugubris vittatus*)))).
- *Minyobates*: Both Clough and Summers (2000) and Vences et al. (2000) found *Minyobates* to be nested within *Dendrobates*. Because each analysis used only one species of *Minyobates*, they did not test the monophyly

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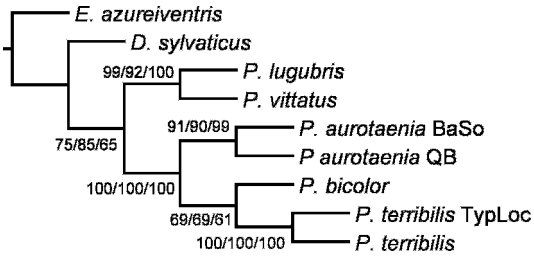

Fig. 8. Hypothesized phylogeny of dendrobatids, redrawn from Widmer et al. (2000: 561, fig. 2), based on parsimony analysis of cytochrome *b* sequences aligned with Clustal W (Thompson et al., 1994) (parameters not specified). Numbers are parsimony/maximum likelihood/neighbor-joining bootstrap frequencies.

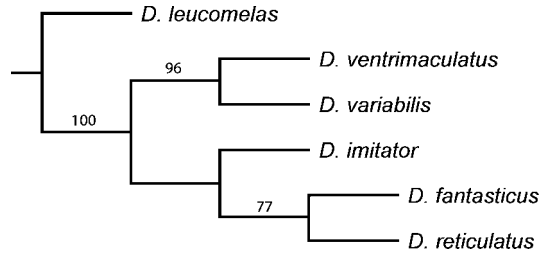

Fig. 9. Cladogram summarizing species level phylogeny of *Dendrobates* (reduced from 30 terminals) proposed by Symula et al. (2001: 2419, fig. 3), based on maximum likelihood analysis (under the GTR + Γ + I model) of cytochrome *b*, cytochrome oxidase I, 12S, and 16S DNA sequences aligned with ClustalX (Thompson et al., 1997) (parameters not specified) and "a few regions of ambiguous alignment … removed from the analysis". Numbers are parsimony bootstrap frequencies.

of *Minyobates* itself. Vences et al. (2003a) included *M. steyermarki* (type species), *M. minutus*, and *M. fulguritus* and found *Minyobates* to be paraphyletic with respect to all other *Dendrobates*. Santos et al. (2003) included *M. minutus* and *M. fulguritus* and found them to be the monophyletic sister to the *D. quinquevittatus* group (i.e., they recovered a monophyletic *minutus* group sensu Silverstone, 1975b).

- The *Dendrobates histrionicus* group is monophyletic in all studies that test its monophyly.
- The *Dendrobates quinquevittatus* group is potentially monophyletic. Although the tree presented by Clough and Summers (2000: 524) indicates that *Minyobates minutus* is the sister species of a monophyletic *D. quinquevittatus* group, there is in fact no evidence to support this assertion, given that these nodes collapse in the strict consensus. Symula et al. (2003) found *Dendrobates leucomelas* to be sister to part of the *D. quinquevittatus* group, with a *D. quinquevittatus* + *D. castaneoticus* clade in a basal trichotomy (they rooted the network with *D. histrionicus*, so it is unknown from their results if *D. quinquevittatus* + *D. castaneoticus* or *D. histrionicus* is more closely related to the *D. leucomelas* + other *D. quinquevittatus* group clade).
- *Nephelobates* and *Mannophryne* were both found to be monophyletic by La Marca et al. (2002) and Vences et al. (2003a).

Lötters et al. (2000) erected the new genus *Cryptophyllobates* for *Phyllobates azureiventris* (which was placed in *Epipedobates* by Myers and Burrowes, 1987). The justification for this monotypic genus is somewhat convoluted. On pp. 235–236, the authors stated that "from the genetic point of view, it is apparent that *azureiventris* is more closely related to *Epipedobates* than to *Phyllobates*", but that "the species is not a member of *Epipedobates*, from which it differs by at least one apomorphy." However, they also asserted that "[i]t shares more—but not all—characters with *Phyllobates* from which it appears genetically well separated." Similarly, although Vences et al. (2000) found this species to be the sister of *Colostethus bocagei*, Lötters et al. (2000) stated that they "negate that both species are representatives of the same genus for *C. bocagei* is cryptically coloured, lacking dorsal stripes at all, and possesses webbed feet." Insofar as this change did not fix the nonmonophyly of *Epipedobates*, the creation of this monotypic genus did little to improve matters. Recently, Caldwell (2005) described a new species and referred it to this genus based on the sister-species relationship between the new species and *azureiventris* recovered in an independent phylogenetic study, despite noting that these species "were nested in a clade of Ecuadorian and Peruvian *Colostethus*."

Morales (2002 "2000") combined Rivero's Groups II (*brunneus*) and III (*alagoanus*) into a newly defined *trilineatus* group (which excluded *C. kingsburyi* and *C. peruvianus*)

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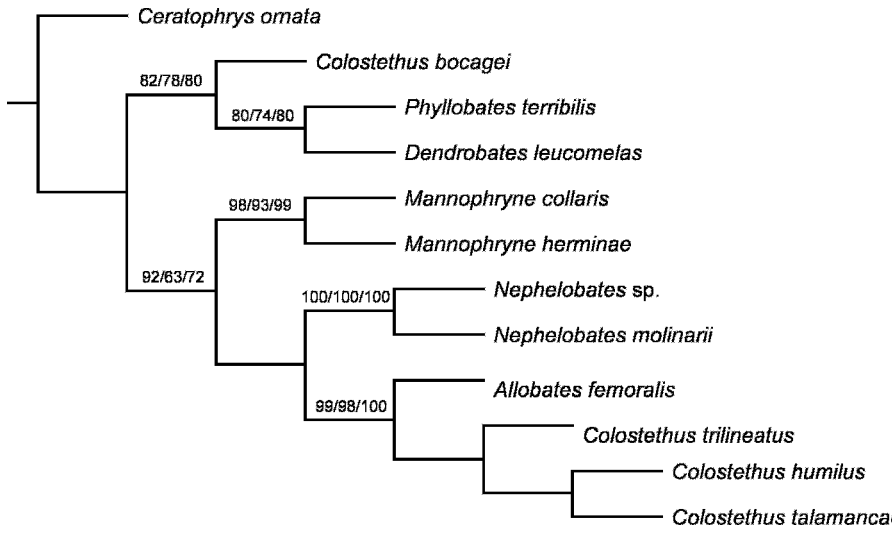

Fig. 10. Hypothesized phylogeny of dendrobatids, redrawn from La Marca et al. (2002: 239, fig. 4), based on maximum likelihood analysis (model not specified) of 16S DNA sequences (alignment method not stated), excluding hypervariable regions. Numbers are maximum likelihood/parsimony/neighbor-joining bootstrap frequencies.

on the basis of an analysis of 12 characters. However, in addition to problems of character individuation (e.g., characters 6, "línea lateral oblicua", and 10, "lista oblicua anteroinguinal", are logically dependent; see Grant and Rodríguez, 2001), the monophyly of the group was assumed (the cladogram was rooted on an unspecified "*Hylodes*" and no other dendrobatids were included), and the putatively derived states of all 12 characters are well known to occur in many dendrobatids.

In the most recent contribution to dendrobatid phylogenetics, Graham et al. (2004) added 12S, $tRNA^{val}$, and 16S mtDNA sequences from a specimen collected near the type locality of *Epipedobates tricolor* and analyzed them with the data from Santos et al. (2003). Graham et al. reported that the *E. tricolor* sample from southern Ecuador was more closely related to *Colostethus machalilla* than to true *E. tricolor*, and, as such, they resurrected *E. anthonyi* from synonymy with *E. tricolor*. However, the Bremer support value[1] reported for the critical node is 0, meaning that this relationship is not recovered in other, equally parsimonious solutions.

Part III: 1926–Present, Relationships between Dendrobatidae and Other Frogs

Noble (1931) summarized his research on the evolutionary relationships of anurans. He considered the three genera of dendrobatids, which he had grouped together in his earlier paper (Noble, 1926), to be a subfamily of Brachycephalidae. The other subfamilies were Rhinodermatinae (*Geobatrachus*, *Sminthillus*, and *Rhinoderma*) and Brachycephalinae (*Atelopus*, *Brachycephalus*, *Dendrophryniscus*, and *Oreophrynella*). Noble (1931: 505; see Grant et al., 1997: 31, footnote 18) maintained his curious view that independently derived groups may constitute natural assemblages:

> Each subfamily has arisen from a different stock of bufonids, but as all the ancestral stocks were bufonids residing in the same general region, Brachycephalidae may be considered natural, even though a composite, family.

[1]Graham et al. (2004) did not define the numbers on the nodes in their cladogram, but C. H. Graham (personal commun.) informed us that they are bootstrap frequencies (above) and Bremer values (below).

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Particularly, Noble (1931; see also Noble, 1926) reiterated that Dendrobatinae evolved from the elosiine bufonid genus *Crossodactylus*. Brachycephalidae was included in the suborder Procoela, which also contained Bufonidae and Hylidae, as well as the extinct Palaeobatrachidae.

Noble was aware that his placement of Brachycephalidae in Procoela instead of Diplasiocoela could be viewed as problematic. He (Noble, 1931: 514) pointed out that the frogs he referred to Diplasiocoela "differ strikingly from most other Salientia except Brachycephalidae", but he reasoned that "[t]he latter are purely neotropical, and as the genera of Brachycephalidae are well defined, they should not be confused with the Diplasiocoela." He also observed that both Dendrobatinae and the African ranid Petropedetinae (nested well within Diplasiocoela) had "apparently identical" (Noble, 1931: 520) dermal scutes on the upper surface of each digit, but he explained away this similarity as adding "one more to the many cases of parallel evolution in the Salientia".

Although Noble's general scheme was widely accepted as the standard for decades (e.g., Dunlap, 1960), it attracted extensive criticism almost immediately. For example, Trewavas (1933: 517) concluded that the hyolaryngeal apparatus provided "little support for the inclusion of *Dendrobates* in the family [Brachycephalidae]" and recommended that the relationships of the family be reconsidered. Davis (1935: 91) criticized Noble's belief that independently derived taxa could be grouped naturally, and he raised each of Noble's (1931) brachycephalid subfamilies (i.e., Brachycephalinae, Dendrobatinae, and Rhinodermatinae) to family rank. Laurent (1942: 18; translated, italics as in original) concluded that the similarities in the initial phases of parental care of larvae in dendrobatids (tadpoles are transported on the male's back) and rhinodermatids (tadpoles are transported in the male's mouth) "constituted a weighty argument in favor of the common ancestry of the *Rhinodermatinae* and the *Dendrobatinae*", and he included both in Dendrobatidae. Orton (1957; see also Orton, 1953) was highly critical of Noble's system because it conflicted with larval morphology; but, beyond her rejection of suborder rank within Salientia, dendrobatids were unaffected. Likewise, Reig (1958) incorporated evidence from a variety of previous studies (e.g., Trewavas, 1933; Davis, 1935; Walker, 1938; Taylor, 1951; Griffiths, 1954) and his own fossil work to provide an extensively modified higher taxonomy, but the placement of Dendrobatidae was unaffected (i.e., Reig's neobatrachian "Superfamily A" [now Hyloidea, = Bufonoidea *auctorum*] was identical to Noble's Procoela with the exclusion of Palaeobatrachidae).

Griffiths (1959, 1963) provided the first major challenge to Noble's placement of Dendrobatidae. Griffiths (1959) reviewed Noble's (1922, 1926, 1931) evidence that dendrobatids were part of Procoela and related to *Crossodactylus*, and, arguing that (1) "vertebral pattern has not the exact taxonomic validity vested in it by Noble" (p. 481); (2) path of insertion of the m. semitendinosus is ranoid in *Hyloxalus*; (3) "Noble's claim that *Phyllobates* has an arciferal stage cannot be held" (p. 482); (4) the bursa angularis oris is found only in firmisternal genera; (5) dermal scutes (which he claimed to be "glandulo-muscular organs") on the digits occur in petropedetid ranids (as well as *Crossodactylus*); and (6) the breeding habits of dendrobatids "are found in no other Salientia except in the arthroleptid ranids" (p. 483), proposed "that the Dendrobatinae be redefined as a Neotropical subfamily of the Ranidae" (p. 483). Subsequent reviews either explicitly endorsed (e.g., Hecht, 1963: 31) or did not address (e.g., Tihen, 1965; Inger, 1967; Kluge and Farris, 1969) Griffiths's hypothesis of the relationships of dendrobatids.

However, Lynch (1971: 164; see also Lynch, 1973) supported Noble's hypothesis, arguing that elosiines (including *Crossodactylus*) and dendrobatids "agree in cranial morphology, vertebral columns, the T-shaped terminal phalanges, the dermal glandular pads on top of the digital pads, and in the presence, in at least some species of each group, of toxic skin secretions" (see fig. 14).

Lynch (1971: 164) also asserted that *Crossodactylus* and dendrobatids exhibit the ranoid pattern of thigh musculature, which "mitigates the importance of one of the criteria used by Griffiths (1963) to associate

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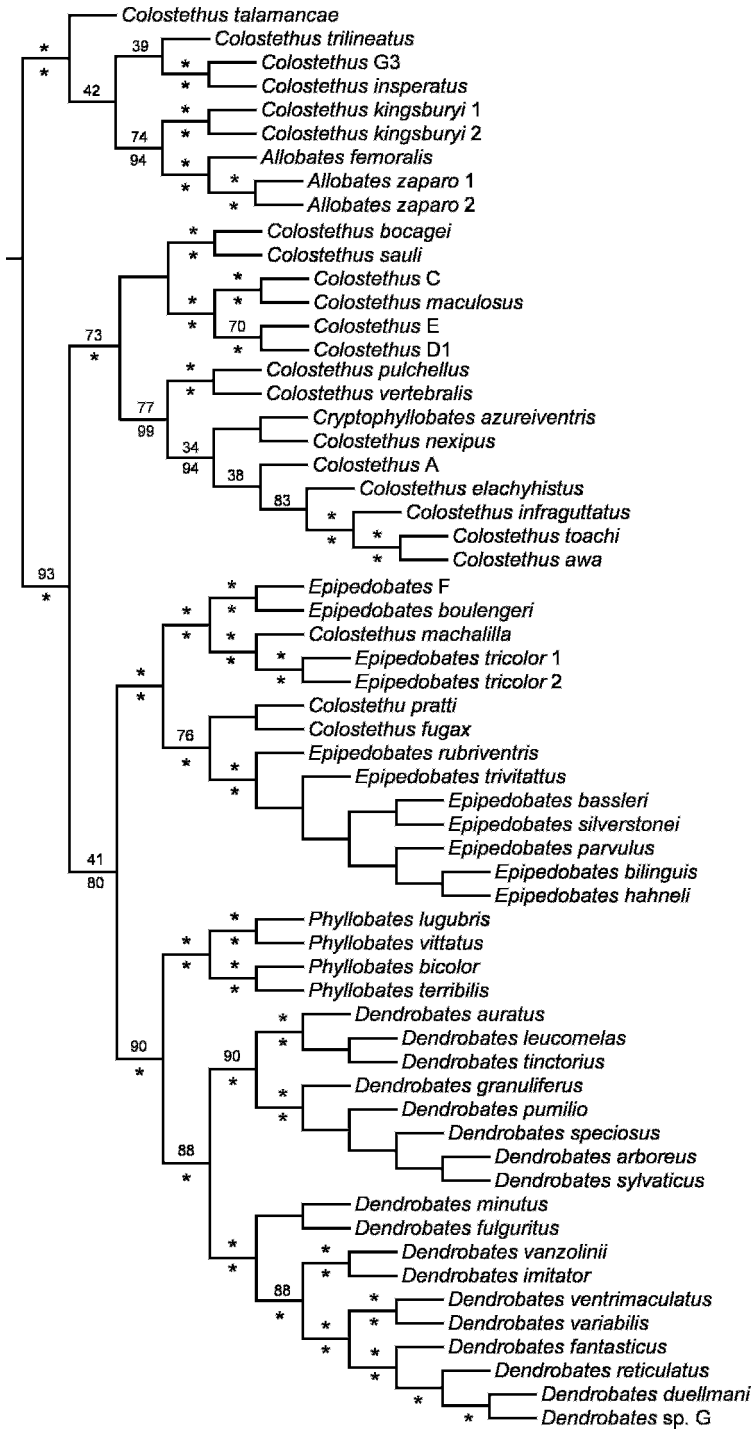

Fig. 11. Hypothesized phylogeny of dendrobatids, redrawn from Santos et al. (2003: 12794, fig. 1), based on unweighted parsimony analysis of the mitochondrial transcription unit H1 (ca. 2,400 bp), aligned with ClustalX (Thompson et al., 1997) ''under various parameters … and finally adjusted by eye to produce a parsimonious alignment'' whereby ''informative sites were minimized'' (Santos et al., 2003:

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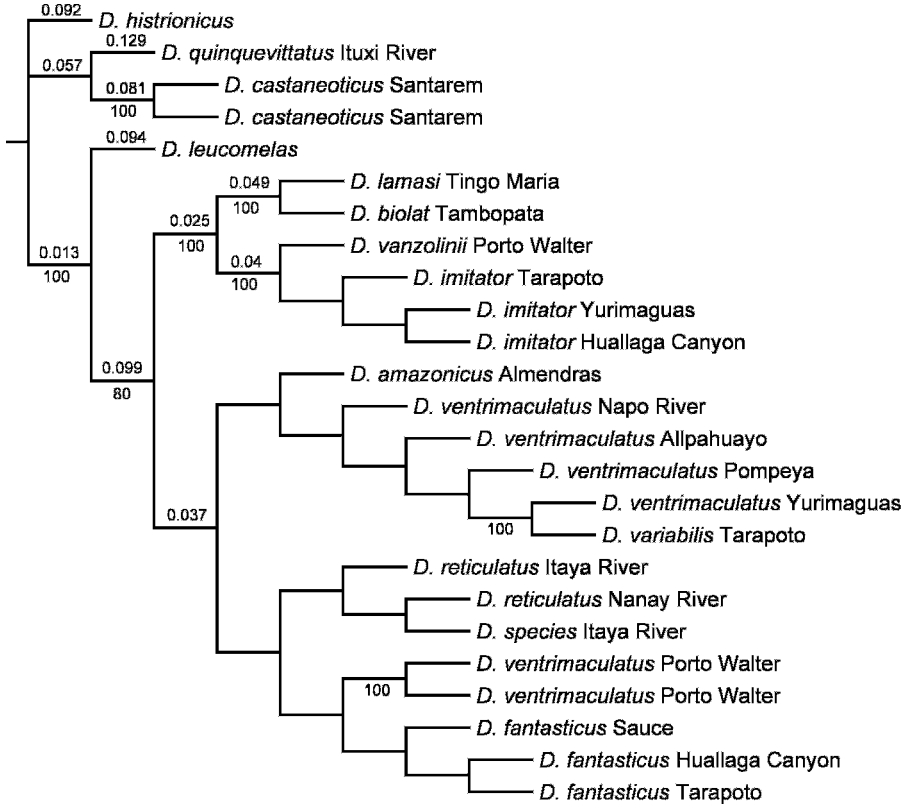

Fig. 12. Hypothesized phylogeny of *Dendrobates*, redrawn from Symula et al. (2003: 459, fig. 3), based on maximum likelihood (under the GTR + Γ model) analysis of cytochrome *b* and cytochrome oxidase I DNA sequences aligned with ClustalX (Thompson et al., 1997) (parameters not specified). Maximum likelihood branch lengths shown above branches, parsimony bootstrap frequencies shown below branches (frequencies >75% shown).

the dendrobatids as a Neotropical subfamily the Ranidae.'' Interestingly, Lynch (1971: 210–211) also indicated that there was ''considerable similarity in myology and osteology'' between the Neotropical leptodactyloid Elosiinae and Dendrobatidae and the African ranid subfamily Petropedetinae. Further, although he cautioned that his examination of the African taxa was not exhaustive, he stated that ''[t]he similarities are quite striking and probably reflect a community of ancestry rather than parallelism.''

Lynch's (1971, 1973) resurrected version of Noble's (1926) hypothesis stood for 15 years. For example, although Savage (1973) adopted Starrett's (1973) scheme of higher level relationships and did not discuss dendrobatid phylogeny per se, he followed Lynch (1971) in considering Dendrobatidae to be a South American, tropical, leptodactyloid derivative. Bogart (1973: 348) conjectured that ''Dendrobatidae may be derived chromosomally from a 26-chromosome ancestor, such as the leptodactylid *Elosia*'' (although he did not examine any African

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12793). Parsimony bootstrap frequencies shown above branches, frequency of clades among trees sampled in Bayesian analysis shown below branches. Stars indicate clades found in ≥95% of the replicates or sampled trees.

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Fig. 14. Hypothesized phylogeny of anurans, redrawn from Lynch (1973).

ranoid species for comparison). Duellman (1975) included Dendrobatidae in Bufonoidea (though not explicitly with *Crossodactylus*). Ardila-Robayo (1979) evaluated 68 characters and found two equally parsimonious topologies, both of which showed Dendrobatidae (''Phyllobatinae''; see Dubois, 1982, and Holthius and Dubois, 1983, for discussion of nomenclature) to be related to elosiines. Like Duellman (1975), Laurent (''1979'' 1980) and Dubois (1984) did not address dendrobatid relationships specifically, but they included Dendrobatidae in Bufonoidea (except that the latter replaced

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Fig. 13. Phylogeny of dendrobatids redrawn from Vences et al. (2003a: 219, fig. 3), based on maximum likelihood analysis (under the GTR + I + Γ model) of 368 bp of 16S rDNA aligned ''using the clustal option of Sequence Navigator (Applied Biosystems)'' (parameters not specified) and excluding ''all regions of the gene fragments that could not be clearly aligned among all taxa'' (p. 217). Numbers above branches are neighbor-joining bootstrap frequencies (frequencies >50% shown); numbers below branches are frequency of clades among trees sampled in Bayesian analysis (frequencies >70% shown).

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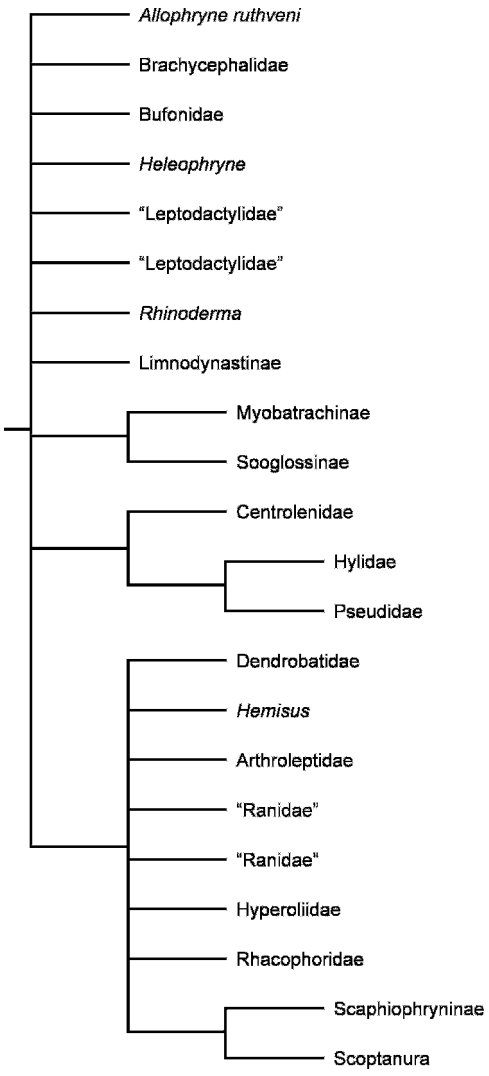

Fig. 15. Hypothesized phylogeny of neobatrachians, redrawn from Ford and Cannatella (1993).

Bufonoidea with the senior synonym Hyloidea).

Both the ranoid and hyloid hypotheses have suffered from mistaken observations. Against Griffiths (1959), Kaplan (1997) confirmed Noble's (1926) claim that the pectoral girdle of *Colostethus subpunctatus* overlaps in ontogeny (which had been denied by Griffiths), and Silverstone (1975a) and Grant et al. (1997) showed that Griffiths's claims regarding dendrobatid thigh musculature were also false. Against Lynch (1971), the thigh musculature in hylodines conforms with Noble's (1922) "bufonid" pattern, not the dendrobatid pattern (Grant et al., 1997: 31; see also Dunlap, 1960), and no species of hylodine tested by Myers and Daly was found to possess lipophilic alkaloids (Grant et al., 1997).

Fifteen years after Lynch (1971) resurrected the hyloid hypothesis, Duellman and Trueb (1986) resurrected the ranoid one. Based on a cladistic analysis of 16 characters, they placed Dendrobatidae in a ranoid polytomy, unrelated to South American leptodactylids. Myers and Ford (1986) did not address the phylogenetic position of dendrobatids, but they listed a number of diagnostic character-states for Dendrobatidae, including (1) the posterodorsal portion of the tympanum concealed beneath the massive superficial slip of the m. depresssor mandibulae, (2) the alary processs of the premaxilla tilted anterolaterally, (3) occurrence of a retroarticular process on the mandible, (4) absence of m. adductor mandibulae externus, (5) single anterior process on hyale, (6) the occurrence of digital scutes, and (7) the m. semitendinosus tendon of insertion piercing the tendon of the m. gracilis.

Shortly thereafter, Ford (1989) completed her doctoral dissertation on the phylogenetic position of Dendrobatidae, based on 124 osteological characters, and found that the most parsimonious solution placed Dendrobatidae as the sister taxon of the Old World ranoid family Arthroleptidae. That dissertation remains unpublished, but it was summarized by Ford and Cannatella (1993; see also Ford, 1993). They reiterated the dendrobatid synapomorphies given by Myers and Ford (1986) and cited Ford's dissertation as finding that "dendrobatids were nested within Ranoidea, close to arthroleptid and petropedetine ranoids" (p. 113; see fig. 15), but they did not list any synapomorphies in support of that hypothesis.

The phylogenetic position of Dendrobatidae alternated between the ranoid and hyloid hypotheses through the 1990s. Bogart (1991: 251–252) compared karyotypes, average measurements, and idiograms of several species of petropedetids and hylodines with dendrobatids and concluded that "*Hylodes* and other hylodine leptodactylids have the

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more similar karyotypes to the dendrobatid frogs.'' Blommers-Schlösser's (1993) redefined Ranoidea excluded Dendrobatidae, but she still considered Dendrobatidae to be part of the more inclusive ''firmisternal frogs'' group, which is equivalent to Ranoidea sensu lato. However, Blommers-Schlösser (1993) also proposed the novel hypothesis that Dendrobatidae is most closely related to microhylids, brevicipitids, and hemisotids in her Microhyloidea group. Hillis et al.'s (1993) combined analysis of the morphological data from Duellman and Trueb (1986) and their own 28S rDNA sequence data indicated that the hyloid hypothesis was more parsimonious than the ranoid hypothesis. Hedges and Maxson's (1993) neighbor-joining analysis of 12S mitchondrial DNA (mtDNA) sequences also placed dendrobatids among hyloids, as did Hay et al.'s (1995) and Ruvinsky and Maxson's (1996) neighbor-joining analyses 12S and 16S mtDNA data. Haas (1995) described an additional dendrobatid synapomorphy (viz., proximal ends of Certatobranchialia II and III free, lacking synchondritic attachment). He failed to find evidence of a ranoid relationship, but discovered a number of character-states shared with hyloid taxa; however, these characters are of uncertain polarity, and no hylodine was included to rigorously test Noble's hypothesis. Grant et al. (1997) discovered that a median lingual process occurs in many Old World ranoid genera (including those thought to be most closely related to dendrobatids) and several species of dendrobatids but failed to detect it in any nonranoid frog. Burton (1998a) reported a synapomorphy in the musculature of the hand (absence of caput profundum arising from carpals) in Dendrobatidae, *Hylodes*, and *Megaelosia*, but not the putative ranoid relatives (but note that this state also occurs in part or all of Ascaphidae, Bombinatoridae, Discoglossidae, Heleophrynidae, Hemisotidae, Pipidae, and Sooglosidae).

Additional support for the ranoid hypothesis has not been proposed, as most studies this decade have found dendrobatids to be nested among hyloids, if not directly related to hylodines. Vences et al.'s (2000) analysis of 12S and 16S mtDNA sequence data showed Dendrobatidae to group with hyloids, not ranoids, as did Emerson et al.'s (2000) analysis of 12S, $tRNA^{val}$, and 16S mtDNA data (although the latter authors also found Dendrobatidae to be polyphyletic, broken up by *Bufo valliceps* and *Atelopus chiriquiensis*). Haas's (2001) study of the mandibular arch musculature of larval and postmetamorphic amphibians included *Phyllobates bicolor*, which was found to possess the neobatrachian (plus pelobatid) synapomorphy (viz., presence of functionally differentiated m. levator mandibulae lateralis) and lack the three ranoid synapomorphies, hence leaving it in a ''hyloid'' polytomy. In an explicit cladistic analysis, Haas (2003) assembled a dataset composed of mostly larval characters (but including most traditionally important characters from adult morphology and behavior) and found Dendrobatidae to be sister to his two hylodine species (fig. 16). Vences et al. (2003a) also included two species of hylodines in their analysis of 12S and 16S mtDNA sequences, but they found dendrobatids to be sister to *Telmatobius simonsi*. Darst and Cannatella (2004) analyzed 12S, 16S, and $tRNA^{val}$ mtDNA sequences and found dendrobatids to be nested within Hylidae (parsimony result shown in fig. 17) or sister to a group consisting of ceratophryines, hemiphractines, and telmatobiines (maximum likelihood; topology not shown). Faivovich et al. (2005) were primarily interested in the relationships among hylids, but their outgroup sample was extensive; their analysis of nuclear and mitochondrial DNA placed dendrobatids as the sister group to the Hylodinae (topology not shown).

Summary of Historical Review

The picture that emerges from the review of the history of dendrobatid systematics is one of considerable conflict and confusion. There is near universal support for the monophyly of the family, which has not been seriously challenged since it was first proposed by Noble 90 years ago, but the phylogenetic position of Dendrobatidae has alternated between two predominant hypotheses: (1) deeply embedded among ranoids as the sister to petropedetids or arthroleptids or (2) deeply embedded among

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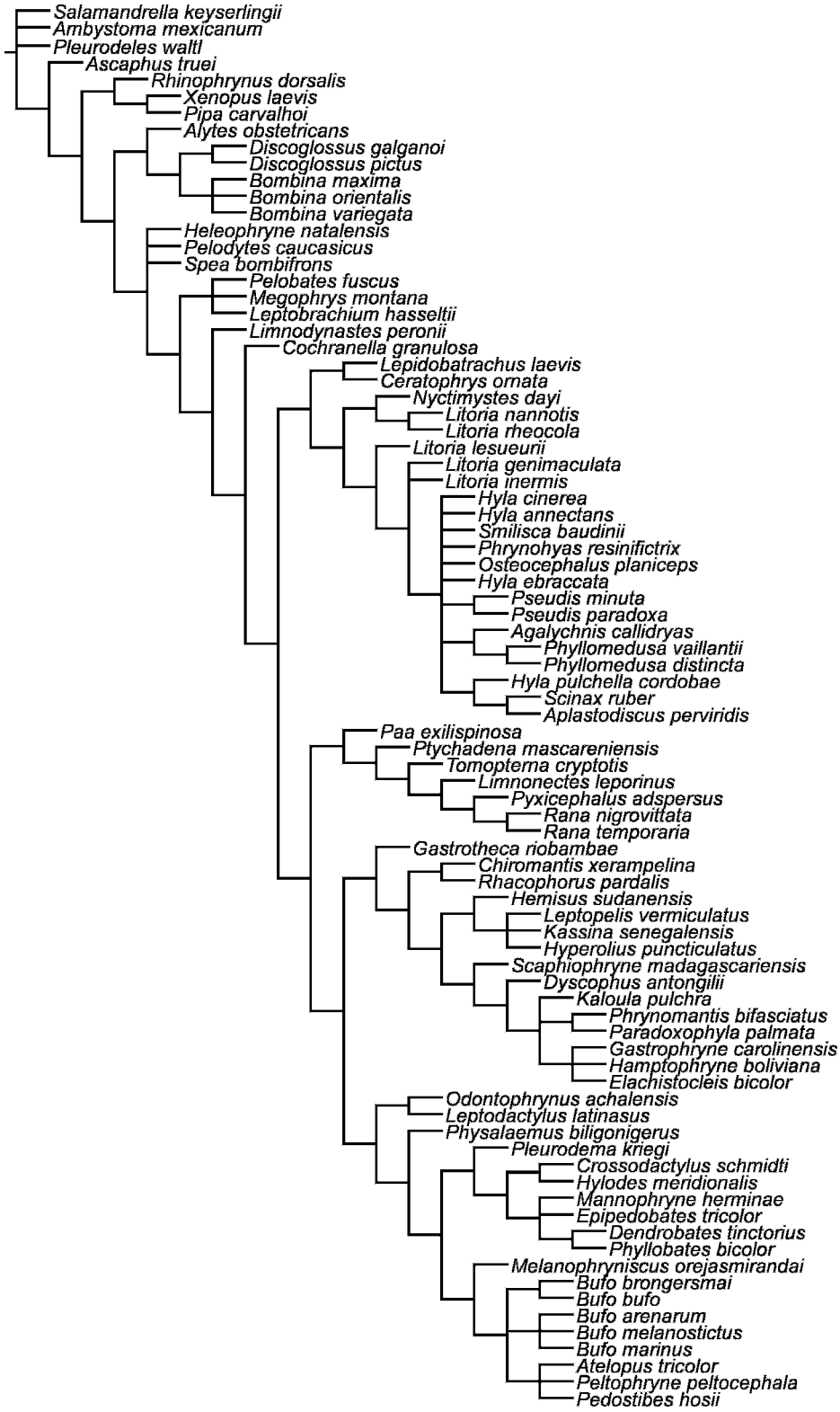

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hyloids as the sister to hylodines. Recent studies based on DNA sequences (mostly mtDNA) have favored the hyloid hypothesis, but there is extensive conflict in the details of both hypotheses. Within Dendrobatidae, the once uncontroversial monophyly of the aposematic taxa has been rejected by mtDNA studies, and there is little agreement on the monophyly and relationships among most genera. The monophyly of *Phyllobates* has been universally supported, although the relationships among its five species have not. To date, no study has combined DNA sequences with evidence from morphological, behavioral, and biochemical (alkaloid) sources, and all explicit phylogenetic analyses have included a limited sample of the diversity of dendrobatids.

PHYLOGENETIC PLACEMENT OF DENDROBATIDS AND OUTGROUP SAMPLING

Theoretical Background

Although the present study was not designed primarily to test the relationships between dendrobatids and other anurans, that question is key to selecting an adequate sample of outgroup taxa to rigorously test the relationships (including monophyly) and transformation series among dendrobatids. That is, the position taken in this study is that all nondendrobatids constitute "the outgroup," and outgroup taxa are sampled for the purpose of testing hypothesized patristic and cladistic relationships. Ideally, one would code all nondendrobatids for all included characters; however, given the practical impossibility of that ideal, prior knowledge of phylogeny and character variation must be used to inform sampling of those taxa most likely to falsify ingroup hypotheses (including ingroup monophyly), the scope and scale of outgroup sampling being limited primarily by practical limitations of time and resources (e.g., specimen and tissue availability, laboratory resources, computer power and time). The possibility always exists that expansion of the outgroup sample may lead to improved phylogenetic explanations—a consideration that points the way to increased testing in future research cycles.

Although this approach to outgroup sampling incorporates prior knowledge, it does so in an expressly non-Bayesian way. The effect of prior knowledge in Bayesian approaches is to constrain hypothesis preference toward prior beliefs about ingroup evolution. Here, prior knowledge is used heuristically to maximize the probability of falsifying prior beliefs about ingroup evolution (for discussion of heurism in phylogenetic inference see Grant and Kluge, 2003). That this "probability" is not frequentist, logical, or personal and is not formally quantifiable does not deny its relevance. The goal is to test phylogenetic hypotheses as severely as possible, and prior knowledge is key to that undertaking.

Empirical Background

As summarized above, the phylogenetic placement of Dendrobatidae is among the most controversial problems in anuran systematics. In part, this is because the two cladistic hypotheses that have emerged as the leading contenders are so radically contradictory, effectively placing dendrobatids at opposite extremes of the neobatrachian clade: dendrobatids are placed as sister to hylodine hyloids from South America or are allied to petropedetid or arthroleptid ranoids from Africa. Minimally, evaluation of these hypotheses would require a phylogenetic analysis of Neobatrachia, which was beyond the scope of the present study.

Nevertheless, in a recently completed study Frost et al. (2006) sampled 532 terminals for the mitochondrial H-strand transcription

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Fig. 16. Hypothesized phylogeny of anurans, redrawn from Haas (2003), based on parsimony analysis of larval and adult morphology.

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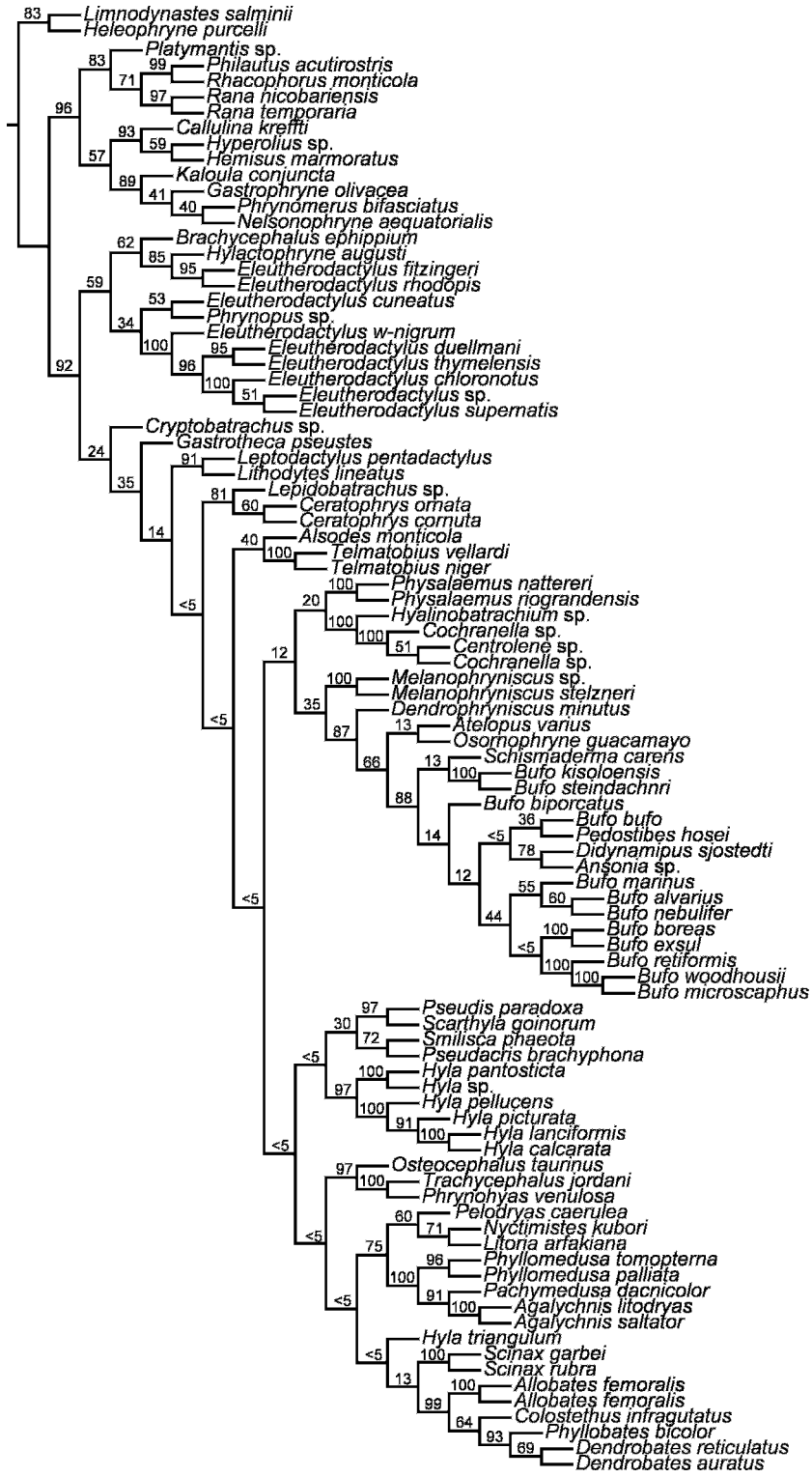

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unit 1 (H1; composed of 12S ribosomal, $tRNA^{val}$, and 16S ribosomal sequences), histone H3 (H3), tyrosinase, rhodopsin, seventh in absentia (SIA), 28S large ribosomal subunit, and Haas's (2003) morphological transformation series in a phylogenetic analysis of living amphibians. That study included approximately 9% of each of the ''major'' amphibian clades (caecilians, salamanders, and frogs), including eight species (and genera) of dendrobatids and all putative sister groups. Insofar as that study is the most extensive analysis of amphibian phylogeny undertaken to date, we used those results to inform outgroup sampling for the current study.

The Frost et al. (2006) study resulted in four trees of 126,929 steps, the relevant portion of which is shown in figure 18.

Relevant to the present study, Frost et al. (2006) corroborated the monophyly of Dendrobatidae. Furthermore, dendrobatids were not found to be closely related to petropedetids, arthroleptids, or any other ranoid and were instead nested deeply among hyloid taxa. Specifically, Dendrobatidae was found to be sister to *Thoropa*, those taxa were sister to Bufonidae, and that inclusive clade was sister to Cycloramphidae (including *Crossodactylus*, *Hylodes*, and *Megaelosia* as the sister clade of the remaining cycloramphids). Alternative hypotheses of the placement of Dendrobatidae (e.g., placed in a clade with *Crossodactylus*, *Hylodes*, and *Megaelosia*, as favored by Noble, 1926; Lynch, 1971; Haas, 2003; Faivovich, 2005) were tested explicitly by inputting constraint topologies for diagnosis and swapping, but they all required additional transformations (breaking up the *Thoropa* + Dendrobatidae clade required at least 39 extra steps).

Although detailed knowledge of the placement of *Thoropa* did not exist prior to that analysis, its placement as the sister of Dendrobatidae is unconventional, to say the least. No morphological synapomorphies have been proposed to unite these taxa, and it was expected that *Thoropa* would be nested among cycloramphids. Nevertheless, insofar as this is the most parsimonious solution found in the most complete study of amphibian relationships carried out to date, the Frost et al. (2006) hypothesis provides the starting point for further testing. Also, the immediately relevant nodes of the Frost et al. (2006) tree are all well supported (Bremer support for Dendrobatidae + *Thoropa* = 39, Dendrobatidae + *Thoropa* + Bufonidae = 30); considering that *Thoropa* was only scored for the mtDNA and H3 loci (i.e., over 1,500 bp of nuDNA were missing), the Bremer value for the *Thoropa* + Dendrobatidae clade is remarkably high. Furthermore, the general placement of Dendrobatidae is reminiscent of (but not identical to) Noble's (1922) Brachycephalidae, which included the dendrobatids, *Brachycephalus*, *Atelopus*, *Rhinoderma*, *Sminthillus* (now a synonym of *Eleutherodactylus*), *Geobatrachus*, and *Oreophrynella* (the latter two genera not sampled by Frost et al.). According to Frost et al. (2006), *Brachycephalus* and *Eleutherodactylus* are part of the distantly related Brachycephalidae (not shown in fig. 18), but *Atelopus* and *Rhinoderma* are placed in the same general neighborhood as Dendrobatidae. As such, the results of Frost et al. (2006) provide both an objectively defensible and subjectively ''reasonable'' basis for outgroup sampling, and we therefore sampled outgroup taxa from among these closely related groups.

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Fig. 17. Hypothesized phylogeny of anurans, redrawn from Darst and Cannatella (2004: 465, fig. 1), based on parsimony analysis of mitochondrial transcription unit H1 (ca. 2,400 bp), aligned with ClustalX (Thompson et al., 1997) ''under a variety of gap penalty weightings'', adjusted manually ''to minimize informative sites under the parsimony criterion'', using secondary structure models to help align ambiguous regions, and excluding regions ''for which homology of the sites could not be inferred'' (Darst and Cannatella, 2004: 463). Numbers are bootstrap frequencies.

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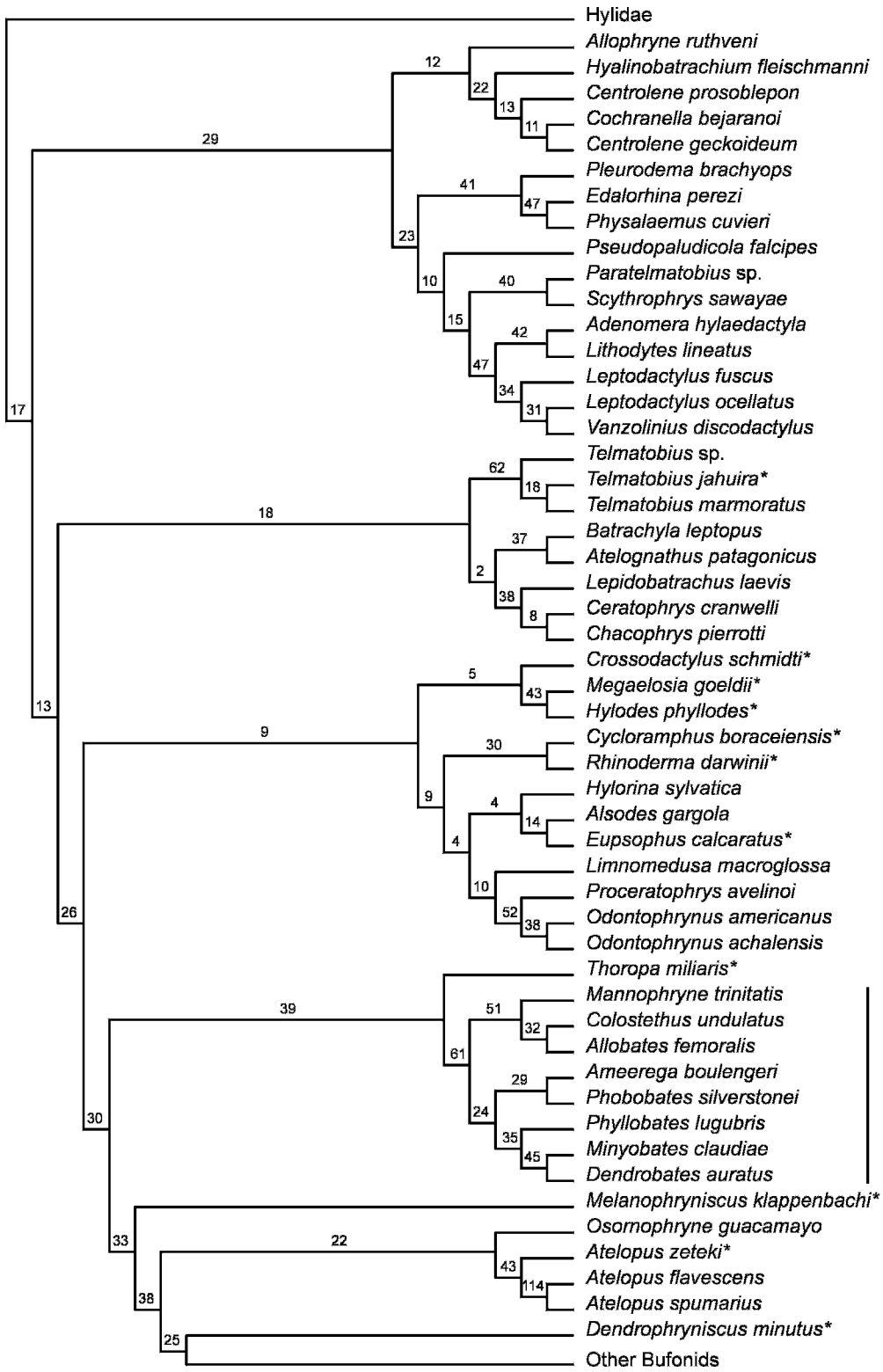

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Outgroup Sampling

In light of Frost et al.'s (2006) findings, it is clear that dendrobatids are not closely related to the Old World ranoids and are instead nested among New World hyloids. Despite the relatively high support for the relevant nodes, the actual sister-group relationship of Dendrobatidae remains controversial, and the present study aimed to further test this topology by including relevant morphological characters, additional molecular data, and additional taxa. Especially relevant is the large amount of missing data for *Thoropa* and the relatively low Bremer support (BS) for the monophyly of Cycloramphidae (BS = 9) and several of the cycloramphid nodes (BS as low as 4). With that in mind, we targeted the following 46 athesphatanuran outgroup taxa: *Allophryne ruthveni, Alsodes gargola, Atelognathus patagonicus, Atelopus spurrelli, Atelopus zeteki, Batrachyla leptopus, Centrolene geckoideum, Centrolene prosoblepon, Ceratophrys cranwelli, Chacophrys pierottii, Cochranella bejaranoi, Crossodactylus schmidti, Cycloramphus boraceiencis, Dendrophryniscus minutus, Edalorhina perezi, Eupsophus calcaratus, Hyalinobatrachium fleischmanni, Hypsiboas boans, Hyla cinerea, Osteocephalus taurinus, Hylodes phyllodes, Hylorina sylvatica, Lepidobatrachus laevis, Leptodactylus fuscus, Leptodactylus discodactylus, Leptodactylus hylaedactyla, Leptodactylus lineatus, Leptodactylus ocellatus, Limnomedusa macroglossa, Megaelosia goeldii, Melanophryniscus klappenbachi, Odontophrynus achalensis, Odontophrynus americanus, Paratelmatobius* sp., *Physalaemus gracilis, Pleurodema brachyops, Proceratophrys avelinoi, Pseudopaludicola falcipes, Rhaebo guttatus, Rhaebo haematiticus, Rhinoderma darwinii, Scythrophrys sawayae, Telmatobius jahuira, Telmatobius marmoratus, Telmatobius* sp., and *Thoropa miliaris*. *Hypsiboas boans* was designated as the root for analyses.

All but one of these species were the same ones used by Frost et al. (2006), the exception being *Atelopus spurrelli*, which we included because (1) sequences proved difficult to generate for the *Atelopus zeteki* tissue, so adding an additional species was necessary to ensure full coverage of molecular data, and (2) adequate whole specimens of this Chocoan endemic were available at AMNH to allow morphological study.

We included all molecular data from the Frost et al. (2006) analysis for these terminals. To these we added phenotyic characters and sequences for cytochrome oxidase *c* subunit I, cytochrome *b*, recombination activating gene 1, and several fragments that were missing from Frost et al. (2006) for 12 of those terminals (marked with an asterisk in fig. 18): *Atelopus spurrelli*, *Atelopus zeteki*, *Crossodactylus schmidti*, *Cycloramphus boraceiencis*, *Dendrophryniscus minutus*, *Eupsophus calcaratus*, *Hylodes phyllodes*, *Megaelosia goeldii*, *Melanophryniscus klappenbachi*, *Rhinoderma darwinii*, *Telmatobius jahuira*, *Thoropa miliaris*. These terminals were targeted for increased sampling because of their phylogenetic proximity to Dendrobatidae, phenotypic affinities, and the availability of whole specimens and other data (e.g., behavior, alkaloid profiles) to score phenotypic characters.

As discussed in greater detail below, with a single exception character-states were coded for each ingroup species and were not extrapolated from other species (e.g., we did not assume that all species of *Colostethus* lack lipophilic alkaloids and instead

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Fig. 18. Phylogenetic placement of Dendrobatidae according to Frost et al. (2006). The Frost et al. study sampled 532 terminals (direct optimization parsimony analysis under equal costs for all transformations; see text for details of dataset), 51 of which are included here to show the placement of Dendrobatidae with respect to its closest relatives. All of the terminals shown were included in the present study, including three representatives of Hylidae and two "other bufonids". Those targeted for additional genotypic and phenotypic evidence are marked in the figure with an asterisk (see text for details). Numbers are Bremer support values.

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only coded species that have been examined for alkaloids); however, we relaxed that requirement to incorporate additional information for outgroup taxa. Specifically, for *Crossodactylus* alkaloid data were derived from *Crossodactylus* sp. from Teresopolis, Río de Janeiro, Brazil (Flier et al., 1980; Grant et al., 1997; J. W. Daly, in litt. 09/15/00), chromosome number was assumed to be the same as in the other five species that have been karyotyped (Aguiar et al., 2004), and all other data were coded from *Crossodactylus schmidti*. For *Cycloramphus*, most data were taken from *Cycloramphus boraceiensis*, but osteological data were taken from *Cycloramphus fuliginosus*. For *Eupsophus*, DNA sequences and larval data were taken from *Eupsophus calcaratus*, whereas all other data were taken for *Eupsophus roseus* (for which material was available at AMNH); see Nuñez et al. (1999) for discussion of the identity of these two species. For *Hylodes*, most data were obtained from *Hylodes phyllodes*, but osteology was coded from *Hylodes nasus*. Finally, for *Melanophryniscus*, DNA sequences were taken from *Melanophryniscus klappenbachi*, whereas all other data were scored from *Melanophryniscus stelzneri* (which is better known and adequately represented at AMNH). Chromosome data were not available for *Megalosia goeldii*, and there is variation in chromosome number within the genus (Rosa et al., 2003). Insofar as there is no clear empirical evidence to ally *Megalosia goeldii* with any of the three species for which chromosome data have been reported, we coded *Megalosia goeldii* as polymorphic. The osteological data reported for *Thoropa miliaris* were taken from *Thoropa lutzi*. We assumed that *Telmatobius jahuira* has the same chromosome number as reported for all other species in the genus (Kuramoto, 1990). All other outgroup data were taken from single species.

MATERIALS AND METHODS

Conventions and Abbreviations

One of the goals of this study is to propose a monophyletic taxonomy that represents the phylogeny of dendrobatids. The inadequacy of the current taxonomy is widely recognized, and although the general scheme remains that of Myers (1987) and Myers et al. (1991), the recent application of Bauer's overlooked generic names (e.g., *Ameerega*), the recognition (as well as continued rejection) of Zimmermann and Zimmermann names (e.g., *Allobates*), the rejection (as well as continued recognition) of *Minyobates*, and the proposal of a new name (*Cryptophyllobates*) all indicate that dendrobatid taxonomy is currently in flux with no universally accepted standard around which to structure discussion of dendrobatid diversity. To avoid confusion due to disagreements between the current taxonomies and our proposal for a monophyletic taxonomy, we use binominals only in the introductory sections, above, and after proposing the new taxonomy. Elsewhere (e.g., in the character descriptions) we refer to species using only their trivial names (e.g., *fraterdanieli*). Currently, 247 nominal species of dendrobatids are recognized, very few of which have the same trivial names. Where giving only the trivial name would engender confusion, we include the author, e.g., *sylvaticus* Barbour and Noble versus *sylvaticus* Funkhouser. All species-group names and their original, approximate current, and proposed placements are listed in appendix 1. We also include several species that are undescribed or of unclear identity. For simplicity, we refer to these species by their localities as informal names within quotes (e.g., "Magdalena" in reference to an undescribed species from the Magdalena valley in Colombia, "Curuá-Una" for an undescribed species from the Rio Curuá-Una in Brazil) or as they have been reported in the literature (e.g., *Nephelobates* sp.). We also assigned unique sample identification numbers to all tissues used in this study, and these numbers are reported as unique terminal identifiers.

Commands used in computer programs are italicized. Sequences incorporated from GenBank are listed in appendix 4. Data for tissues (including GenBank numbers for DNA sequences) and specimens examined are listed in appendices 5 and 6, respectively, referenced with the permanent collection number for the voucher specimen or, if that is unavailable, the tissue collection number,

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as follows: **AMCC** (Ambrose Monell Cryo Collection, American Museum of Natural History, New York, USA), **AMNH** (American Museum of Natural History, New York, USA), **ARA** (Andrés Acosta field series; specimens at MUJ), **BB** (Boris Blotto field series), **BMNH** (The Natural History Museum, London, UK), **BPN** (Brice P. Noonan field series; specimens at UTA), **CFBH** (Célio F. B. Haddad specimen collection, Brazil), **CFBH-T** (Célio F. B. Haddad tissue collection, Brazil), **CH** (Colección Herpetológica, Panamá), **CPI** (D. Bruce Means field series, to be deposited at USNM), **CWM** (Charles W. Myers field series), **GB** (Godfrey Bourne field series), **IAvH** (Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Villa de Leyva, Colombia), **ICN** (Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá, Colombia), **IRSNB-KBIN** (Institut Royal des Sciences Naturelles de Belgique/Koninklijk Belgisch Instituut voor Natuurwetenschappen, Brussels, Belgium), **IZUA** (Instituto de Zoología, Universidad Austral de Chile, Valdivia, Chile), **JAC** (Jonathan A. Campbell field series), **JDL** (John D. Lynch field sereis), **JF** (Julián Faivovich field series), **KRL** (Karen R. Lips field series), **KU** (University of Kansas Natural History Museum, Lawrence, USA), **LACM** (Natural History Museum of Los Angeles County, Los Angeles, USA), **LR** (Lily Rodriguez field series), **LSUMZ** (Louisiana State University Museum of Natural Science, Baton Rouge, USA), **MACN** (Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Buenos Aires, Argentina), **MAD** (Maureen A. Donnelly field series), **MAR** (Marco Antonio Rada; specimens at MUJ), **MB** (Marcus Breece captive collection), **MJH** (Martin J. Henzl field series), **MLPA** (Museo de la Plata, Buenos Aires, Argentina), **MHNUC** (Museo de Historia Natural Universidad del Cauca, Popyán, Colombia), **MPEG** (Museu Paraense Emilio Goeldi, Belém, Brazil), **MRT** (Miguel Rodrigues tissue collection), **MUJ** (Museo de Historia Natural, Universidad Javeriana, Bogotá, Colombia), **MVZ** (Museum of Vertebrate Zoology, University of California at Berkeley, USA), **MZUSP** (Museu de Zoologia da Universidade de São Paulo, Brazil), **NK** (Museo de Historia Natural Noel Kempff Mercado, Santa Cruz, Bolivia), **OMNH** (Sam Noble Oklahoma Museum of Natural History, The University of Oklahoman, USA), **PK** (Philippe Kok field series; specimens at IRSNB-KBIN), **RDS** (Rafael de Sá tissue collection), **RG** (Ron Gagliardo, Atlanta Botanical Garden), **ROM** (Royal Ontario Museum, Toronto, Canada), **RWM** (Roy W. McDiarmid field series), **SIUC** (Southern Illinois University at Carbondale, USA), **UMFS** (University of Michigan Museum of Zoology, Ann Arbor, Michigan, USA, field series), **UMMZ** (University of Michigan Museum of Zoology, Ann Arbor, Michigan, USA), **USNM** (National Museum of Natural History, Smithsonian Institution, Washington DC, USA), **USNM-FS** (National Museum of Natural History, Smithsonian Institution, Washington DC, USA, field series), **UTA** (University of Texas at Arlington, USA), **UVC** (Universidad del Valle, Cali, Colombia), **WES** (Walter E. Schargel field series), **ZSM** (Zoologisches Museum, München, Germany). Phenotypic data are given in appendix 7; formatted files for all data may be downloaded from http://research.amnh.org/herpetology/downloads.htm.

General Analytical Approach: Theoretical Considerations

Choice of Phylogenetic Method

The general goal of phylogenetic systematics is to explain the diversity of life by discovering the evolutionary relationships among species, where inferred transformations from one character-state to another provide the means to choose among competing explanations. That is, phylogenetic hypotheses are composite explanations consisting of both hypotheses of homology (transformation series; Hennig, 1966; see Grant and Kluge, 2004) and hypotheses of monophyly (topology). Farris (1967) expressed this succinctly by analyzing the concept of evolutionary relationship into its component parts of patristic relationship and cladistic relationship.

Operationally, phylogenetic analysis begins by decomposing the observed diversity

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of living things into its minimal historical units: character-states (sensu Grant and Kluge, 2004) and species (sensu Kluge, 1990; see also Grant, 2002). Although character-states are the evidential basis that underlies phylogenetic inference, they are effectively "bundled" into individual organisms, populations, and species, which constrains the ways in which they evolve and how they may be explained (e.g., females and males evolve as parts of the same lineage; defensible phylogenetic explanations are therefore not permitted to place them in separate clades). Likewise, species, which are the historical entities related through phylogeny (Hennig, 1966), may be decomposed into independently heritable (and independently variable) parts, that is, character-states. This ontological transitivity of taxic and character evolution is the foundation of phylogenetic inference (cf. Farris, 1967).

Once these minimal units have been individuated, all possible historical relationships between character-states and species are defined by pure logic (Siddall and Kluge, 1997; Wheeler, 1998). Phylogenetic analysis proceeds by mapping hypothetical character-state relationships to hypothetical species relationships and evaluating the competing composite hypotheses in terms of the number of character-state transformations they entail.

All phylogenetic methods aim to minimize character transformations. Unweighted (equally weighted) parsimony analysis minimizes hypothesized transformations globally, whereas assumptions (expressed as differential probabilities or costs) about the evolution or importance (e.g., reliability) of different classes of transformations employed in maximum likelihood, Bayesian analysis, and weighted parsimony methods lead to the minimization of certain classes of transformations at the expense of others. Operational considerations aside (e.g., tree-space searching capabilities), disagreements between the results of unweighted parsimony analysis and the other methods are due to the increased patristic distance required to accommodate the additional assumptions.

Kluge and Grant (2006) reviewed the justifications for parsimonious phylogenetic inference previously considered sufficient, namely, conviction (Hennig, 1966), descriptive efficiency (Farris, 1979), minimization of ad hoc hypotheses of homoplasy (Farris, 1983), and statistical, model-based inference (maximum likelihood, Sober, 1988). Finding significant inconsistencies in all of those justifications, Kluge and Grant (2006) proposed a novel justification for parsimony. Drawing on recent advances in the understanding of phylogenetics as a strictly ideographic, historical science and parsimonious inference generally in the philosophy of science literature (e.g., Barnes 2000; Baker, 2003), they argued that by minimizing globally the transformation events postulated to explain the character-states of terminal taxa, equally weighted parsimony analysis maximizes explanatory power. As such, in the present study we analyzed the total, equally weighted evidence under the parsimony criterion (for additional discussion of character weighting and total evidence, see Grant and Kluge, 2003). Given the size and complexity of this dataset, a further advantage of parsimony algorithms (whether weighted or unweighted) is that thorough analysis could be achieved in reasonable times given available hard- and software.

Sources of Evidence

The empirical evidence of phylogenetic systematics consists of transformation series (i.e., the ideographic character concept of Grant and Kluge, 2004). Traditionally, transformation series were derived exclusively from such sources as comparative morphology, molecular biology, and behavior, but as technological advances have made DNA sequencing simpler and less costly, phylogenetic studies have come to rely increasingly on the genotypic evidence of DNA sequences to test phylogenetic hypotheses. The present study exemplifies this trend. Nevertheless, both kinds of data provide evidence of phylogeny, and each has its own suite of strengths and weaknesses.

An important strength of phenotypic data is that the complexity of observed variation allows the historical identity of each transformation series to be tested independently (Grant and Kluge, 2004). By carrying out progressively more detailed structural and developmental studies, researchers are able to

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refine their hypotheses about the homology of phenotypic variants. However, the phenotype is determined by both the directly heritable components of the genotype and the nonheritable effects of the environment. In contrast, an obvious strength of DNA sequence evidence is that, because DNA is the physical material of genetic inheritance, the potentially confounding effects of environmental factors are avoided altogether.

Nevertheless, DNA sequence character-states are maximally reduced to physico-chemically defined classes of nucleotides, of which there are only four (cytosine, guanine, adenine, and thymine). Whereas this simplicity is advantageous in many kinds of genetics studies, it poses a serious problem for phylogenetics, because no structural or developmental complexity to distinguishes nucleotides that share a common evolutionary history (i.e., those that are homologous, their physico-chemical identity owing to the same transformation event) from those that evolved independently (i.e., those that are homoplastic, their physico-chemical identity owing to independent transformation events). For example, in terms of object properties, all adenines are physico-chemically identical, regardless of whether or not they arose through the same or different transformation events. Moreover, DNA sequences evolve through complete substitutions of one nucleotide for another (meaning that there are no intermediate states from which to infer historical identity) or complete insertions and deletions (meaning that any given nucleotide could be homologous with any other nucleotide). Phylogenetic analysis of DNA sequences must therefore contend with the problem of discovering both transformations between nucleotides and the insertion and deletion of nucleotides. To visualize homologous nucleotides, multiple sequence alignments codify insertions and deletions (indels) as gaps, that is, placeholders that shift portions of the sequence to align homologous nucleotides into column vectors.

Nucleotide Homology and the Treatment of Indels

The method of inferring indels and nucleotide homology (i.e., alignment) and the subsequent treatment of indels in evaluating phylogenetic explanations are of critical importance in empirical studies because, as is now widely appreciated, a given dataset aligned according to different criteria or under different indel treatments may result in strong support for contradictory solutions (e.g., McClure et al., 1994; Wheeler, 1995). Many workers infer indels in order to align nucleotides but then either treat them as nucleotides of unknown identity by converting gaps to missing data, or they eliminate gap-containing column vectors altogether, either because they believe them to be unreliable or because the implementation of a method of phylogenetic analysis does not allow them (Swofford et al., 1996). Others argue that indels provide valid evidence of phylogeny but suggest that sequence alignment (homology assessment) and tree evaluation are logically independent and must be performed separately (e.g., Simmons and Ochoterena, 2000; Simmons, 2004).

The position we take here is that indels are evidentially equivalent to any other classes of transformation events and, as such, are an indispensable component of the explanation of the DNA sequence diversity. Furthermore, because nucleotides lack the structural and/or developmental complexity necessary to test their homology separately, hypotheses of nucleotide homology can only be evaluated in reference to a topology (Grant and Kluge, 2004; see also Wheeler, 1994; Phillips et al., 2000; Frost et al., 2001). In recognition of these considerations, we assessed nucleotide homology dynamically by optimizing observed sequences directly onto topologies (Sankoff, 1975; Sankoff et al., 1976) and heuristically evaluating competing hypotheses by searching tree space (Wheeler, 1996). This is achieved using Direct Optimization techniques (Wheeler, 1996, 2003a, 2003b, 2003c), as implemented in the computer program POY (Wheeler et al., 1996–2003).

In this approach, determination of nucleotide homology is treated as an optimization problem in which the preferred scheme of nucleotide homologies for a given topology is that which requires the fewest transformation events when optimized onto that topology, that is, that which minimizes patristic distance, thus providing the most parsimonious

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explanation of the observed diversity. Determining the optimal alignment for a given topology is NP-complete[2] (Wang and Jiang, 1994). For even a miniscule number of sequences, the number of possible alignments is staggering (Slowinski, 1998), making exact solutions impossible for any contemporary dataset, and heuristic algorithms are required to render this problem tractable. Likewise, finding the optimal topology for a given alignment is also an NP-complete problem (Garey and Johnson, 1977; Garey et al., 1977).

Phylogenetic analysis under Direct Optimization therefore consists of two nested NP-complete problems. POY searches simultaneously for the optimal homology/topology combination, and search strategies must take into consideration the severity and effectiveness of the heuristic shortcuts applied at both levels. In any heuristic analysis, a balance is sought whereby the heuristic shortcuts will speed up analysis enough to permit a sufficiently large and diverse sampling of topologies and homologies to discover the global optimum during final refinement, but not so severe that the sample is so sparse or misdirected that the global optimum is not within reach during final refinement. Ideally, indicators of search adequacy (e.g., multiple independent minimum-length hits, stable consensus; see Goloboff, 1999; Goloboff and Farris, 2001) should be employed to judge the adequacy of analysis, as is now reasonable in analysis of large datasets using prealigned data (e.g., in TNT; Goloboff et al., 2003). However, current hard- and software limitations make those indicators unreachable in reasonable amounts of time for the present dataset analyzed under Direct Optimization, and the adequacy of our analysis may only be judged intuitively in light of the computational effort and strategic use of multiple algorithms designed for large datasets (see below for details).

[2]This is a technical term referring to the computational complexity of problems (Cormen et al., 2001). Computational problems are classified according to the time complexity of their algorithmic solutions. Computationally easy problems can be solved in polynomial time (P) relative to the size of the problem. Nondeterministic polynomial (NP) problems cannot be solved in polynomial time, but a solution can be verified in polynomial time. No polynomial-time algorithm is known for NP-complete (NPC) problems, but it has not been proved that such an algorithm is impossible; if a polynomial-time algorithm is discovered for any NPC problem, it would apply to the entire class of problems.

Total Evidence

The majority of phylogenetic studies, even those legitimately considered "total evidence" (Kluge, 1989), examine either higher level or lower level problems. The former are designed to address relationships between putative clades of multiple species (usually discussed as species groups, genera, families, etc.) by targeting exemplars from each of those units and sampling relatively invariable character systems. The latter are designed to address species limits and relationships among closely related species (and often phylogeographic questions also), and character sampling focuses on more variable systems.

The nestedness of phylogenetic problems both enables and weakens this divide-and-conquer approach. Assuming the monophyly of a group, the relationships within that clade have no bearing on the relationships of that clade to other clades. And assuming the sister-group relationships between the ingroup and outgroup taxa, the relationships within the ingroup clade are independent of the relationships between that clade and more distant relatives. Nevertheless, although this is a defensible (provided the assumed monophyly and placement of the ingroup are supported by evidence) and presently necessary strategy, these assumptions may ultimately be found to be false, and their elimination allows hypotheses at both levels to be more severely tested and may lead to more globally parsimonious explanations. Furthermore, the ripple effects that cladistically distant optimizations may have throughout the topology are unpredictable, so that the inclusion of distant terminals that are not immediately relevant to a problem may affect local topology. The ultimate goal of total evidence is to analyze all evidence from all sources and all terminals at all levels simultaneously.

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There are many obstacles, computational and otherwise, that prevent this ideal from being achieved in the foreseeable future. A potential criticism of this study is that we did not include all of the data from Frost et al. (2006). We restricted the outgroup sample to Athesphatanura to prevent the already computationally challenging problem of analyzing 414 terminals from becoming even more intractable. However, once hard- and software improvements permit thorough analysis of larger datasets, studies that extend outgroup sampling beyond Athesphatanura will offer a test of our results. Insofar as this study was designed to test both the species limits of problematic taxa and the relationships among dendrobatid clades, and to further test the relationships between dendrobatids and other anurans by combining the data from Frost et al. (2006) with new data from key outgroup taxa, it is intended to be a step toward the total evidence ideal. That this study aimed to simultaneously address problems of such different hierarchic levels had important consequences in taxon sampling, character sampling, and the analytical strategy that was undertaken.

General Analytical Approach: Implementation

Taxon Sampling

Outgroup taxa and the rationale for their selection are discussed above (Phylogenetic Placement of Dendrobatids and Outgroup Sampling). Selection of ingroup terminals was governed by three considerations: (1) relevance to testing prior phylogenetic claims, (2) availability of tissues (or sequences on GenBank), and (3) availability of specimens for morphological study. In light of the many problems in species-level taxonomy, we also sought to sample as many localities as possible for problematic species.

To facilitate taxonomic changes, every effort was made to include type species of all dendrobatid genera. Both genotypic and phenotypic data were included for type species of as many genera as possible, including (genus name in parentheses): *azureiventris* (*Cryptophyllobates*), *bicolor* (*Phyllobates*), *femoralis* (*Allobates*), *inguinalis* (*Prostherapis*), *nocturnus* (*Aromobates*), *pulchellus* (*Phyllodromus*), *pumilio* (*Oophaga*), *reticulatus* (*Ranitomeya*), *silverstonei* (*Phobobates*), *steyermarki* (*Minyobates*), *tinctorius* (*Dendrobates*), *tricolor* (*Epipedobates*), and *trivittatus* (*Ameerega*). We did not include the type species *alboguttatus* (*Nephelobates*), *fuliginosus* (*Hyloxalus*), *latinasus* (*Colostethus*), or *yustizi* (*Mannophryne*), because adequate data were not available to allow their inclusion in the present study. Nevertheless, we included numerous, presumably closely related representatives of these genera and made taxonomic changes accordingly.

Phenotypic Character Sampling

We anticipate that a criticism of the present study will be that we were too catholic in the inclusion of phenotypic characters. It is common for morphological systematists to seek characters that are conservative at their level of interest, under the assumption that they are more informative or reliable indicators of relationship, either explicitly (e.g., Kluge, 1993) or, much more commonly, implicitly. As a result, much of the systematics literature—especially the precladistic literature—consists of special pleading for the validity (or not) of characters as ''higher-level'', ''family-level'', ''genus-level'', ''species-level'' or some other rank-specific indicator. Some characters (e.g., presence or absence of teeth, pectoral girdle architecture, skull morphology), it has been argued, are ''good'' genus- or family-level characters, others (e.g., external morphology, soft-anatomy) are ''good'' only at the level of species, and still others are unreliable and should be excluded in their entirety. We disagree.

For evolution to occur, all character transformation events must take place at (or below) the species level, and it is only subsequent cladogenetic events that effectively push character transformations back in history and bring them to delimit clades; there can be no natural law regulating variation of characters among clades. The historical debate over the phylogenetic relevance of anuran teeth illustrates the futility of that approach to systematics: maxillary teeth

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are absent in all species of Bufonidae—which would make this a conservative, phylogenetically informative character at the family level—but vary intraspecifically in some species of dendrobatids—making this a completely uninformative character according to that view. Given the conceptual definition of characters as transformation series (Grant and Kluge, 2004), all characters have the same evidential status in terms of their ability to test phylogenetic hypotheses. Arguments over the rank-specific relevance or reliability of characters depend on the reification of ranks and lead ultimately to the ad hoc dismissal or overlooking of evidence, and such procedures should be eliminated from systematics.

In addition to the novel characters and character-states discovered in the course of this study, our goal was to include all characters that have figured in debates on the monophyly, placement, and internal relationships of Dendrobatidae. However, because this study aims primarily to test relationships within Dendrobatidae and not the position of Dendrobatidae among other frogs, the sample of characters is strongly biased to reflect variation among dendrobatid terminals.

Numerous characters date to the 19th century (mainly Duméril and Bibron, Cope, Boulenger), and we do not always cite the original sources for these traditional characters. However, we do cite more recent papers that have addressed them in the context of dendrobatid systematics, and we cite original sources for all more recent characters. All phenotypic character-states for *caeruleodactylus*, *humilis*, and *nidicola* were coded from the literature (Lima and Caldwell, 2001; Caldwell et al., 2002a; La Marca et al., 2002; Caldwell and Lima, 2003). Other sources for phenotypic data are cited in the relevant sections below. For the purposes of discussion, phenotypic transformation series are classified broadly as morphological, larval, behavioral, and biochemical, the latter referring to alkaloid profiles. Specific problems or concerns regarding particular characters or character systems are discussed below independently. In anticipation of the expansion of the present dataset, we list states and show illustrations for taxa not included in the present analysis.

Comparative anatomical study aimed to delimit transformation series and not to describe dendrobatid (or outgroup) anatomy per se. We have illustrated either photographically or in line drawings those character-states we believe may cause confusion, and character names and descriptions were intended only to be sufficiently precise to allow hypotheses of homology to be tested. With the exception of characters related to the median lingual process, we coded anatomical characters only from gross dissection under a dissecting microscope. This is a limitation of the present study, as greater insight into character-state identity and homology would undoubtedly be gained from histology (e.g., consider the remarkable insights into pectoral girdle architecture attained by Kaplan, 2004). Osteological character-states were coded from dried or cleared and stained (alcian blue and alizarin red) skeletons. We considered tissue with alizarin red-positive crystals to be calcified and uniformly alizarin red-positive tissue to be ossified.

We applied either Lugol's solution or alcian blue to facilitate coding of muscle characters. All muscles are bound by fibrous connective tissue, so the distinction between tendinous and fleshy origins and insertions is one of degree: Tendinous insertions and origins have a confluence of muscle fibers on a distinct segment of fibrous connective tissue, whereas those that are fleshy appear to insert or originate directly on the adjacent structure. We consider a slip to be a distinct bundle of fasciculi isolated from adjacent fasciculi of the same muscle by epimysium.

We examined the histology of the tongues of several species to individuate characters of the median lingual process (Grant et al., 1997). Tissues were embedded in paraffin, sectioned at 6–10 μm, and stained using either hematoxylin and eosin (H&E) or a trichrome stain consisting of Alcian Blue, Periodic Acid and Schiff's reagent (PAS), and H&E. Specifically, we examined histological sections of *baeobatrachus*, *tepuyensis*, *panamensis*, and *auratus* (the latter two lacking the MLP). For comparison we examined the histology of *Arthroleptis variabilis*, *Mantidactylus femoralis*, *Phrynobatachus natalensis*, *P.*

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petropedetoides, *Platymantis dorsalis*, and *Staurois natator*, although none of these species were coded for the present study. We also performed detailed dissections of the tongues of *atopoglossus*, *Arthroleptis stenodactylus*, *Discodeles bufoniformis*, and *Discodeles opisthodon*.

In addition to the phenotypic characters individuated for this study, other sources of variation will undoubtedly yield novel characters. For example, spermatozoa ultrastructure is promising but has been examined in too few species to warrant inclusion in the present study. Garda et al. (2002) examined the spermatozoa of *flavopictus*, Aguiar et al. (2003) studied *femoralis* and an undescribed species referred by them to *Colostethus* (OMNH 37001–37002), and Aguiar et al. (2002) looked at the spermatozoa of *hahneli* and *trivittatus*. (For a recent review of spermatozoa in nondendrobatids, see Scheltinga and Jamieson, 2003).

Relevant to the placement of Dendrobatidae, Haas (2003) presented an impressive matrix of detailed morphological evidence scored across the diversity of anurans, much of which was derived from studies of larval anatomy. The evidential value of such data is manifest, but adequate samples were unavailable for most species included in this study. Haas found (see fig. 16, above) that the four included dendrobatids were monophyletic, and that their sister group was *Hylodes* + *Crossodactylus* (*Megaelosia* was not included in that study).

Bhaduri (1953) studied the urinogenital systems of diverse amphibians, including *auratus*, *tinctorius*, and *flotator* (as *Phyllobates nubicola flotator*). He noted several differences among these species, such as the greater posterior extension of the kidneys in *Dendrobates* than in *Phyllobates* (p. 56), but he nonetheless concluded that "[t]he structural similarities of the urinogenital organs which we have observed in these two genera lend further support to Noble's view [that *Dendrobates* and *Phyllobates* are closely related]" (p. 72). Although we scored some visceral characters (e.g., pigmentation of the testes, pigmentation of the large intestine), in light of time constraints and the fact that specific characters used by Bhaduri have not been used since and have therefore not played an important role in dendrobatid systematics, we did not study this system in detail.

Burton (1998a) argued that hand musculature supports a relationship between Dendrobatidae and Hylodinae, "as the unusual condition of lacking any fibrous connection to the *tendo superficialis* or the adjacent aponeurosis is almost restricted to the hylodine genera *Hylodes* and *Megaelosia*, and Dendrobatidae" (p. 8). However, the phylogenetic implications of this character are not clear-cut; assuming hylodine monophyly and a sister-taxon relationship with Dendrobatidae, as implied by Burton, the occurrence of this character-state would optimize as either independently evolved in Dendrobatidae and *Hylodes* + *Megaelosia* or as a synapomorphy of the inclusive clade with subsequent loss in *Crossodactylus*. We did not examine hand musculature in this study.

Trewavas (1933) included *tinctorius*[3] in her study of the anuran hyoid and larynx. We examined the osteology of this system but did not examine its musculature. Our experience with other groups suggests that hyoid musculature may be a rich source of characters, and these characters will be evaluated in the near future.

There are also several morphological variants that have been claimed as characters in the literature that we reject in the present study. First, La Marca (1994, 2004) claimed the occurrence of enlarged, fanglike maxillary teeth as a synapomorphy for *Nephelobates*, and they also have been reported for *Megaelosia* (e.g., Lynch, 1971) and *Aromobates* (Myers et al., 1991), among others. Although we agree with La Marca and Myers et al. that dendrobatid tooth morphology varies and that the teeth of *Aromobates* and *Nephelobates* seem strikingly elongate and recurved, we were unable to individuate transformations series for several reasons, as follows (see fig. 19).

[3]Given the taxonomic problems that plagued this species prior to Silverstone (1975a), and the given range as "South America", the identity of the "*Dendrobates tinctorius*" specimen(s) examined by Trewavas (1933) is unclear.

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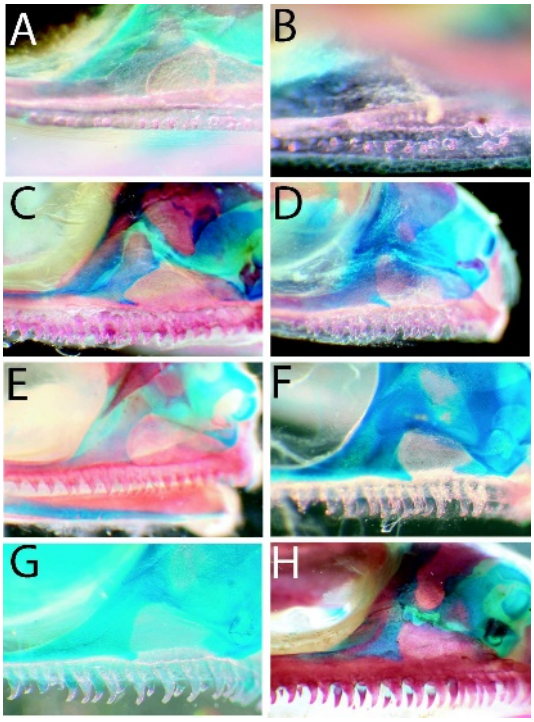

Fig. 19. Examples of variation in dendrobatid maxillary teeth. **A**, **B**: lateral (**A**) and lingual (**B**) views of *pictus* (UMMZ 184099). Note that the teeth do not protrude beyond the edge of the maxilla. **C**: lateral view of *riveroi* (AMNH 134144). **D**: lateral view of *subpunctatus* (UMMZ 221159). **E**: lateral view of *undulatus* (AMNH 159142). **F**: lateral view of *molinarii* (UMMZ 176207). **G**: lateral view of *dunni* (UMMZ 167131). **H**: lateral view of *nocturnus* (AMNH 129940).

(1) No appropriate reference point to assess relative tooth size has been proposed, and without this it is impossible to compare objectively the size of teeth in specimens of different species and varying body sizes and maxilla sizes and shapes (especially the shape and depth of the facial process). (2) Tooth size varies along the maxilla, and it is unclear which teeth should serve as the basis of comparison. (3) Superficial assessment of tooth size in cleared and stained specimens of a number of species suggested that variation is continuous, which must be accounted for when individuating transformations series. (4) All well-developed maxillary teeth (i.e., those that protrude beyond the edge of the maxilla) are recurved, at least in dendrobatids, and comparison of digital images (which eliminates the effect of relative size) shows the curvature of the so-called fanglike teeth of species referred to *Nephelobates* and *Aromobates* is no greater than those referred to *Colostethus*. In light of these considerations, we coded the presence and absence of maxillary teeth, as well as their structure, but not variation in size and shape.

Similarly, Lynch (1982) characterized *edwardsi* and *ruizi* as possessing a conspicuously large and elongate cloacal sheath (vent tube, anal sheath, embudo cloacal), and Rivero (1990 ''1988'') subsequently referred to these species as the *edwardsi* group of *Colostethus*. Later, La Marca (1994) also claimed the presence of a cloacal sheath as a synapomorphy for *Nephelobates*, although he made no reference to that structure in the *edwardsi* group. The cloacal sheath has now been included in numbered diagnoses in species descriptions (e.g., Lötters et al., 2003a), and Grant (1998) cited its synapomorphic occurrence as the basis for including *Colostethus lynchi* in the *edwardsi* group. More recently, Grant (2004) noted, without further comment, that ''examination of extensive material of most species of dendrobatids has caused me to doubt the validity of that character.''

The reason for that doubt is that, as shown in figure 20, only the two species originally placed in the *edwardsi* group (exemplified here by *edwardsi*) possess a conspicuously modified vent (cloacal sheath). Variations among other species of dendrobatids (including *lynchi*) are minor and cannot be distinguished from artifacts of preservation. Specimens that are positioned differently for fixation (whether floated in formalin or laid out in a fixing tray) vary in apparent vent morphology. For example, when a frog specimen is positioned in a fixing tray, the flaccid thigh muscles and loose skin may be pushed posterodorsally, causing the vent and adjacent tissue to ''bunch up'', or anteroventrally, causing the vent and adjacent tissue to be drawn downward, both of which alter the apparent prominence, length, and shape of the vent. Desiccation also affects vent prominence. In light of these observations, the cloacal sheath is restricted to the two known species of the *edwardsi* group. We did not include the cloacal sheath, thus delimited, in

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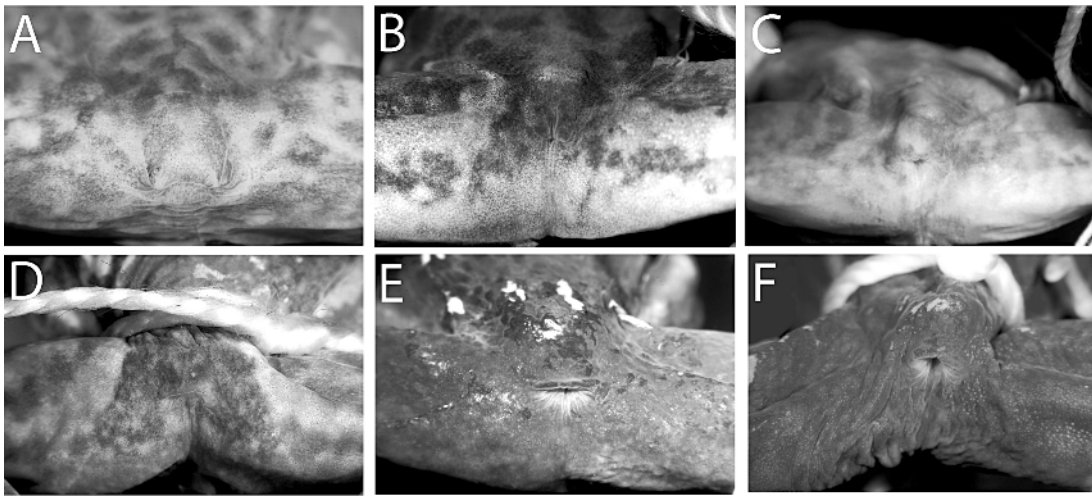

Fig. 20. Posterior view of several species of dendrobatids, showing variation in morphology of the vent. **A**: *edwardsi* (ICN 21936). Contrary to the other species depicted, the vent of *edwardsi* is conspicuously enlarged and elongated relative to that of other anurans. **B**: *molinarii* (UMMZ 176222, paratype), a species referred to *Nephelobates* by La Marca (1994). The vertical folds vary as an artifact of preservation. **C**: *alboguttatus* (AMNH 10503), the type species of *Nephelobates*. **D**: *trinitatis* (AMNH 125796), a species referred to *Mannophryne* by La Marca (1992). **E**: *petersi* (AMNH 42546). **F**: *petersi* (AMNH 42506). This species has never been claimed to be part of or closely related to *Nephelobates*. Note the differing prominence and apparent shape and size of the vent as an artifact of preservation.

the character matrix because we did not include *edwardsi* or *ruizi* due to inadequate material.

Finally, Savage (1968) was followed by Silverstone (1975a) in identifying dark pigmentation of the flesh as a synapomorphy of *Dendrobates* and *Phyllobates*. We paid considerable attention to this character, thanks largely to the numerous large series of skinned specimens collected by C. W. Myers and colleagues and deposited (cataloged and uncataloged) at AMNH. The variation we observed is much more complicated than the simple pigmented/unpigmented of Savage and Silverstone. Pigmentation occurs in diffuse, irregular patches and varies continuously in intensity from being entirely lacking to a few black specks or intense dark gray or black. We were unable to delimit transformation series objectively, and therefore excluded pigmentation of the flesh from this study.

Genotypic Character Sampling

In light of the vastly different levels of diversity included in this study (from within localities to among families), we sought to sample genes of differing degrees of variability. We targeted the mitochondrial H-strand transcription unit 1 (H1), which includes 12S ribosomal, $tRNA^{val}$, and 16S ribosomal sequence, yielding approximately 2,400 bp generated in 5–7 overlapping fragments. We also targeted a 385-bp fragment of cytochrome *b* and a 658-bp fragment of cytochrome oxidase *c* subunit I (COI). In addition to those five mitochondrial genes, we targeted the nuclear protein coding genes histone H3 (328 bp), rhodopsin (316 bp), tyrosinase (532 bp), recombination activating gene 1 (RAG1, 435 bp), and seventh in absentia (SIA, 397 bp), and the nuclear 28S ribosomal gene (ca. 700 bp), giving a total of approximately 6,100 bp of nuclear and mitochondrial DNA. Primers used in PCR amplification and cycle sequencing reactions (and their citations) are given in table 1. Included in this study is a novel primer pair (RAG1 TG1F and TG1R) designed to amplify the RAG1 product using the web-based program Primer3 (Rozen and Ska-

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TABLE 1
PCR Primers Used in This Study[a]

Gene region	Primer name	Direction	Primer sequence (5′ to 3′)	Source
16S rDNA	AR	Forward	CGCCTGTTTATCAAAAACAT	Palumbi et al., 1991
	BR	Reverse	CCGGTCTGAACTCAGATCACGT	Palumbi et al., 1991
	Wilkinson2	Reverse	GACCTGGATTACTCCGGTCTGA	Wilkinson et al., 1996
	L2A	Forward	CCAAACGAGCCTAGTGATAGCTGGTT	Hedges, 1994
	H10	Reverse	TGATTACGCTACCTTTGCACGGT	Hedges, 1994
	MVZ59	Forward	ATAGCACTGAAAAYGCTDAGATG	Graybeal, 1997
	MVZ50	Reverse	TYTCGGTGTAAGYGARAKGCTT	Graybeal, 1997
	12s A-L	Forward	AAACTGGGATTAGATACCCCACTAT	Goebel et al., 1999
	12s F-H	Reverse	CTTGGCTCGTAGTTCCCTGGCG	Goebel et al., 1999
	12s L1	Forward	AAAAGCTTCAAACTGGGATTAGATACCCCACTAT	Feller and Hedges, 1998
12S rDNA	L13	Forward	TTAGAAGAGGCAAGTCGTAACATGGTA	Feller and Hedges, 1998
	Titus I	Reverse	GGTGGCTGCTTTTAGGCC	Titus and Larson, 1996
$tRNA^{val}$	tRNAval-H	Reverse	GGTGTAAGCGARAGGCTTTKGTTAAG	Goebel et al., 1999
cytochrome	LCO1490	Forward	GGTCAACAAATCATAAAGATATTGG	Folmer et al., 1994
oxidase *c* subunit I	HCO2198	Reverse	TAAACTTCAGGGACCAAAAAATCA	Folmer et al., 1994
cytochrome *b*	MVZ 15-L	Forward	GAACTAATGGCCCACACWWTACGNAA	Moritz et al., 1992
	H15149	Reverse	AAACTGCAGCCCCTCAGAAATGATATTTGTCCTCA	Kocher et al., 1989
rhodopsin exon 1	Rhod1A	Forward	ACCATGAACGGAACAGAAGGYCC	Bossuyt and Milinkovitch, 2000
	Rhod1C	Reverse	CCAAGGGTAGCGAAGAARCCTTC	Bossuyt and Milinkovitch, 2000
	Rhod1D	Reverse	GTAGCGGAAGAARCCTTCAAMGTA	Bossuyt and Milinkovitch, 2000
tyrosinase exon 1	TyrC	Forward	GGCAGAGGAWCRTGCCAAGATGT	Bossuyt and Milinkovitch, 2000
	TyrG	Reverse	TGCTGGCRTCTCTCCARTCCCA	Bossuyt and Milinkovitch, 2000
histone H3	H3F	Forward	ATGGCTCGTACCAAGCAGACVGC	Colgan et al., 1999
	H3R	Reverse	ATATCCTTRGGCATRATRGTGAC	Colgan et al., 1999
28S rDNA	28sV	Forward	AAGGTAGCCAAATGCCTCATC	Hillis and Dixon, 1991
	28SJJ	Reverse	AGTAGGGTAAAACTAACCT	Hillis and Dixon, 1991
recombination activating gene 1	RAG1 TG1F	Forward	CCAGCTGGAAATAGGAGAAGTCTA	This study
	RAG1 TG1R	Reverse	CTGAACAGTTTATTACCGGACTCG	This study
	R1-GFF	Forward	GAGAAGTCTACAAAAAVGGCAAAG	Faivovich et al., 2005
	R1-GFR	Reverse	GAAGCGCCTGAACAGTTTATTAC	Faivovich et al., 2005
seventh in absentia[b]	SIA1 (T3)	Forward	TCGAGTGCCCCGTGTGYTTYGAYTA	Bonacum et al., 2001
	SIA2 (T7)	Reverse	GAAGTGGAAGCCGAAGCAGSWYTGCATCAT	Bonacum et al., 2001

[a] The gray line separates mitochondrial (above) and nuclear (below) loci. See text for PCR and cycle sequencing protocols.

[b] These primers were used with the universal T3 and T7 primers following Bonacum et al. (2001).

letsky, 2000), available at http://frodo.wi.mit.edu/cgi-bin/primer3/primer3_www.cgi. As discussed below, the amount of sequence data analyzed per terminal varied (fig. 21), ranging from 426 bp (*subpunctatus* obtained from GenBank) to 6,245 bp (*chlorocraspedus* 385), with a mean of 3,740 bp per terminal.

As noted above, we targeted loci that varied to differing degrees to test hypotheses of relationships at all levels, and we included multiple samples from the same and different localities of the same species in an effort to address problems in alpha taxonomy. We attempted to sequence all loci for at least one sample from every locality, but we did

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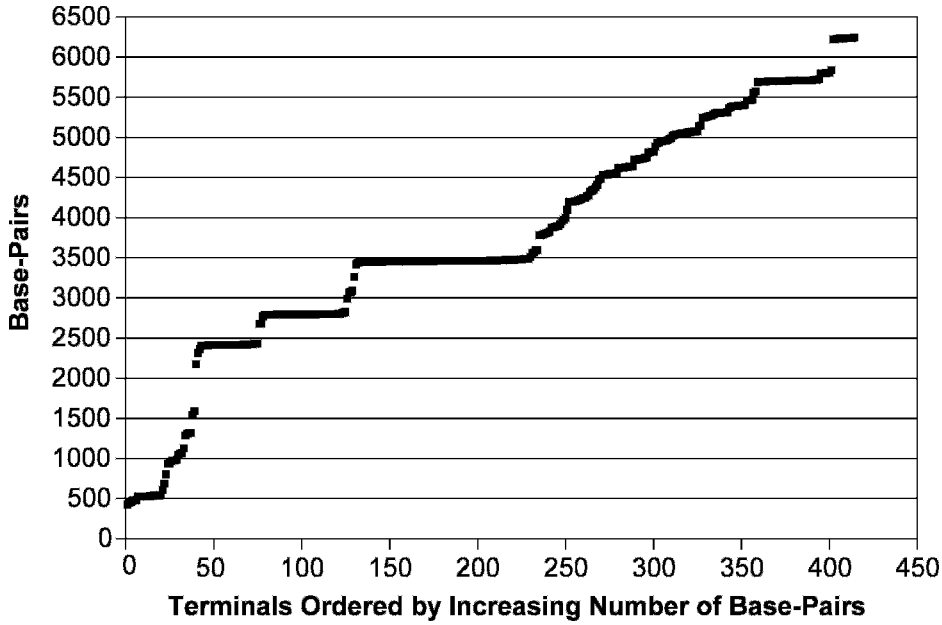

Fig. 21. Number of DNA base-pairs analyzed per terminal. For specific terminal data see appendices 4 and 5.

not sequence nuclear loci for all samples. We chose this strategy because early work on this project showed the nuclear loci to be generally less variable and usually identical in all samples from a given locality.

We augmented our own data with sequences from GenBank, listed in appendix 4, in order to include otherwise unsampled ingroup species and additional localities for taxonomically problematic species, that is, the dataset analyzed includes all species on GenBank as well as samples of some species from multiple localities. Nevertheless, we did not include all GenBank data. First, we only included loci for which we also generated data. For example, we did not include Widmer et al.'s (2000) cytochrome *b* data because their fragment did not overlap with ours. Second, although we included multiple samples to address taxonomic problems, we did not include all samples from population-level studies (e.g., Symula et al., 2003), as such dense intraspecific sampling was not required and would have impeded analysis by unnecessarily expanding the dataset.

Laboratory Protocols

Whole cellular DNA was extracted from frozen and ethanol-preserved tissues (liver or muscle) using the Qiagen DNeasy kit following the manufacturer's guidelines. PCR amplification was carried out in 25-µl reactions using puRe Taq Ready-To-Go Beads (Amersham Biosciences). The standard PCR program consisted of an initial denaturing step of 3 min at 94°C, 35–40 cycles of 1 min at 94°C, 1 min at 45–62°C, and 1–1.25 min at 72°C, followed by a final extension step of 6 min at 72°C. PCR-amplified products were cleaned and desalted using either the ARRAYIT kit (TeleChem International) on a Beckman Coulter Biomek 2000 robot or AMPure (Agencourt Biosciences Corporation). Cycle-sequencing using BigDye Terminators v. 3.0 (Applied Biosystems) was run in 8-µl reactions, and products were cleaned and desalted by standard isopropanol-ethanol precipitation or using cleanSEQ (Agencourt Biosciences Corporation). Sequencing was done on either an ABI 3700 or ABI 3730XL automated DNA sequencer. Contigs (sets of overlapping sequences) were assembled and edited using Sequencher (Gene Codes).

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Molecular Sequence Formatting

To enable integration of incomplete sequence fragments (particularly those from GenBank; see Taxon Sampling Strategy and Character Sampling Strategy, above), accelerate cladogram diagnosis, and reduce memory requirements under Iterative Pass Optimization, we broke complete sequences into contiguous fragments. (This also improves the performance of POY's implementation of the parsimony ratchet; see Heuristic Tree Searching, below.) We did so sparingly, however, as these breaks constrain homology assessment by prohibiting nucleotide comparisons across fragments, that is, it is assumed that no nucleotides from fragment X are homologous with any nucleotides from fragment Y. As the number of breaks increases, so too does the risk of overly constraining the analysis and failing to discover the globally optimal solution.

We therefore inserted as few breaks as were necessary to maximize the amount of sequence data included, minimize the introduction of nucleotides of unknown identity into the sequences (see Character Sampling Strategy, above), and attain maximum length fragments of around 500 bases (see table 2). Breaks were placed exclusively in highly conserved regions (many of which correspond to commonly used PCR primers), as recovery of such highly invariable regions is generally alignment-method independent (unpublished data) and therefore does not prevent discovery of global optima. These highly conserved regions were identified via preliminary ClustalX (Thompson et al., 1997) alignments under default parameters and examination using BioEdit (Hall, 1999). Except for their usefulness in placing fragments derived from different PCR primers and detecting errors, these preliminary alignments were used solely for the purpose of identifying conserved regions; they did not otherwise inform or constrain our phylogenetic analysis. Once appropriate conserved regions were identified, fragments were separated by inserting pound signs (#) at break points. Thus, the multiple fragments of the mitochondrial H1 unit remain in the same file and order, for example.

TABLE 2
Summary of DNA Sequence Data[a]

Sequence	Approx. no. basepairs	No. fragments	No. terminals
Mitochondrial H-strand transcription unit 1	2400	16	414
Cytochrome *b*	385	3	318
Cytochrome *c* oxidase I	658	2	234
Recombination activating gene 1	435	2	128
28S	700	2	136
Histone H3	328	1	169
Rhodopsin	316	1	154
Seventh in absentia	397	2	135
Tyrosinase	532	2	54

[a] Approximate number of base pairs refers to complete sequences.

Total Evidence Analysis

We did not discriminate between classes of evidence in the phylogenetic analyses. To allow the molecular data to have bearing on problems of species taxonomy, we treated every specimen sequenced as a separate terminal, that is, we did not fuse putatively conspecific specimens into a single polymorphic terminal, which would prevent the molecular data from addressing alpha taxonomic problems and require that all decisions on species identity be made prior to phylogenetic analysis. Loci not sequenced for particular terminals—either because the primers failed or because other syntopic conspecifics were sequenced instead—were treated as missing for those terminals.

There are three possible methods of incorporating phenotypic evidence for specimens judged to be conspecific but coded separately for genotypic data.

1. Phenotypic characters may be coded for each specimen separately. The shortcomings of this method are numerous: (a) This approach excludes background knowledge that informs but is not explicitly encoded in the character matrix, such as mating behavior and ontogeny. This could result in males, females, and juveniles being grouped in separate clades. (b) Similarly, tissue samples usually are not available for specimens representing all relevant

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semaphoronts. As such, many semaphoront-specific characters would be excluded from analysis or have to be coded without being matched with the molecular evidence. (c) For this approach to be applied consistently, evidence obtained from specimens in other studies would also have to be rejected, such as alkaloid profiles and vocalizations and other behaviors, or also scored separately for each individual. Strict application of this approach is clearly infeasible and would result in the exclusion of extensive evidence.

2. The phenotypic data for the species as a whole can be duplicated for each molecular terminal.
3. The phenotypic data for the species as a whole can be entered for a single molecular terminal, with those characters treated as missing for other (putatively) conspecific terminals.

The latter two options offer more defensible approaches. The second method has the advantage of minimizing ambiguous optimizations due to missing entries, which may be crucial in examining the evolution of some of the most interesting phenotypic characters (e.g., behaviors). The third approach appears to have the advantage of maximizing the severity of the molecular test of species identity, that is, terminals judged conspecific on phenotypic grounds could not be held together on those grounds alone in phylogenetic analysis. Although we see some validity to this argument, given the relative sizes of the phenotypic and genotypic partitions (ca. 170 characters vs. ca. 6,100 unaligned base pairs), we see no a priori reason to expect morphology to overwhelm the DNA sequence data. Moreover, the identical entries that would potentially hold those specimens together in the face of molecular evidence are, in fact, apomorphies for the species, and total evidence analysis demands that they be considered as such. That is, the goal in total evidence analysis is not to test the results of one data partition against another, but to allow all evidence to interact simultaneously to identify the hypothesis that best explains all the evidence.

As such, we opted to duplicate the morphological entries coded for the species, that is, each conspecific terminal was given identical entries in the phenotypic matrix. Phenotypic characters not expressed in the sequenced semaphoront (e.g., testis color in female specimens) were scored and species-level phenotypic polymorphisms were coded as ambiguities. A caveat is that we did not associate GenBank sequences with phenotypic data unless we lacked our own genotypic data for the taxon (e.g., *sauli*), and then only for one sample if more than one was on GenBank (e.g., we associated the phenotypic entries for *kingsburyi* with AY364549 only).

With a single exception, the reported ingroup characters were scored for single species (see Outgroup Sampling, above, for coding of outgroup species). The exception was *alagoanus*, for which the morphological characters were scored from specimens of *olfersioides*. The two species were named on the basis of few differences between small samples, and study of external morphology of larger samples from a greater number of localities suggests they may be conspecific (V.K. Verdade, personal commun.), although additional data from color in life, vocalizations, and DNA sequences have yet to be examined. DNA sequences were generated for *alagoanus*, but whole specimens were not available for examination. Tissue samples were unavailable for *olfersioides* (which has not been observed in Rio de Janeiro since approximately 1980 and may be extinct; C.F.B. Haddad, personal obs.), but numerous museum specimens were available for morphological study. As such, we combined the data from these two species under the asumption that they represent a unique clade; we refer to the resulting terminal as *alagoanus* because most of the evidence was scored from that species.

Simultaneous phylogenetic analysis was performed using the program POY (Wheeler et al., 1996–2003) version 3.0.11a and the MPI version 3.0.12a-1109195780.71. All POY runs were parallelized across 95 processors of the AMNH 256-processor Pentium 4 Xeon 2.8 GHz cluster or 16–32 processors of the 560-processor mixed 512 mHz and 1 GHz cluster. Results were visualized using Winclada (Nixon, 1999–2002), and we verified POY results and analyzed implied alignments using NONA (Goloboff, 1999) spawned from Winclada. Although character weighting was used heuristically in tree searching (see below), evidence was weighted equally to assess tree optimality.

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Heuristic Character Optimization

Numerous algorithms of varying exhaustiveness have been proposed to optimize unaligned DNA sequences on a given topology. Our search strategy employed three Direct Optimization algorithms; in order of increasing exhaustiveness and execution time, these were Fixed-States Optimization (Wheeler, 1999), Optimization Alignment (Wheeler, 1996), and Iterative Pass Optimization (Wheeler, 2003b).

Although Fixed-States Optimization was proposed as a novel means of conceptualizing DNA sequence homology (Wheeler, 1999), we employed it here simply as a heuristic shortcut. Because Fixed-States is so much faster than the Optimization Alignment algorithm, it allowed more thorough sampling of the universe of trees for subsequent refinement under more exhaustive optimization algorithms. Our general strategy was therefore to examine a large pool of initial candidate trees quickly under Fixed-States and submit those trees as starting points for further analysis under Optimization Alignment. Because the potential exists for the globally optimal tree (or trees that would lead to the global optimum when swapped under a more exhaustive optimization algorithm) to be rejected from the pool of candidates under the heuristic algorithm, we also generated a smaller pool of candidate trees under Optimization Alignment. The resulting optimal and near-optimal candidate trees were then submitted to final evaluation and refinement under Iterative Pass optimization using *iterativelowmem* to reduce memory requirements. (For details on tree-searching algorithms, see Heuristic Tree Searching, below.)

We did not employ the *exact* command during most searches, although we did use it in the final stages of analysis to allow accurate matrix-based length verification (Frost et al., 2001). To verify lengths reported in POY, we output the implied alignment (Wheeler, 2003a) and binary version of the optimal topology in Hennig86 format with *phastwincladfile* and opened the resulting file in Winclada (Nixon, 1999–2002). Because each topology may imply a different optimal alignment, when multiple optimal topologies were obtained we examined them separately by inputting each as a separate file using *topofile*. Examination of the implied alignments, whether formatted as Hennig files or as standard alignments (*impliedalignment*), grants another opportunity to detect errors in formatting or sequencing.

Heuristic Tree Searching

Efficient search strategies for large datasets are, to a certain degree, dataset dependent (Goloboff, 1999), and, as discussed above, common indicators of sufficiency are impractical given current technological limitations. Therefore, rather than apply a simple, predefined search strategy (e.g., 100 random addition Wagner builds + TBR branch swapping), we employed a variety of tree searching algorithms, spending more time on those that proved most efficient. Optimal trees from different searches were pooled for tree-fusing and TBR swapping, all of which was followed by refinement under Iterative Pass Optimization (Wheeler, 2003b). The search strategy is summarized in table 3.

Random addition sequence Wagner builds (RAS) were performed holding one or three trees. We conducted searches without *slop* or *checkslop*, both of which increase the pool of trees examined by swapping suboptimal trees found during the search; although these steps can be highly effective, initial trials showed they were too time consumptive for the present dataset.

The parsimony ratchet (Nixon, 1999) was proposed for analysis of fixed matrices. Given that under dynamic homology there are no prespecified column vectors to be reweighted, the original approach had to be modified. In the current version of POY, the ratchet is programmed to reweight randomly selected DNA fragments. The present dataset was broken into 31 fragments (see table 2), so *ratchetpercent 15* randomly reweighted five fragments, regardless of their length or relative position. We reweighted 15–35% of the fragments and applied weights of 2–35 times.

As a complementary approach, we also performed quick searches (few random addition sequence Wagner builds + SPR) under indel-transversion-transition costs of 3-1-1, 1-

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TABLE 3
Summary of Tree Searching Methods Combined in Overall Search Strategy[a]

Abbreviated name	Description
RAS	Random addition sequence Wagner builds.
Constrained RAS	As above, but constrained to agree with an input group inclusion matrix derived from the consensus of topologies within 100–150 steps of present optimum.
Subset RAS	Separate analysis of subsets of 10–20 taxa. Resulting topologies used to define starting trees for further analysis of complete dataset.
Ratcheting (fragment reweighting)	Ratcheting as programmed in POY, with 15–35% of DNA fragments selected randomly and weighted 2–8×, saving 1 minimum length tree per replicate.
Ratcheting (transformation reweighting)	Ratcheting approximated by applying relative indel–transversion–transition weights of 3–1–1, 1–3–1, and 1–1–3, saving all minimum length trees for analysis under equal weights.
Constrained tree fusing and/or ratcheting (fragment)	As above, but with current optimum input as a starting tree, and constrained to agree with an input group inclusion matrix derived from the consensus of topologies within 100–150 steps of present optimum.
Tree fusing	Standard tree fusing followed by TBR branch swapping.
Manual rearrangement	Manual movement of branches of current optimum.

[a] Different runs combined multiple procedures, and all runs included SPR and/or TBR refinement. See text for details and references.

3-1, and 1-1-3 and included the resulting topologies in the pool of trees submitted to fusing and refinement under equal weights, following the general procedure of d'Haese (2003). Reweighting in this method is not done stochastically and therefore differs from both Nixon's (1999) original version and POY's implementation of the ratchet and technically is not a simulated annealing or Metropolis-Hastings-type strategy like the others; however, because it weights sets of transformations drawn from throughout the entire dataset, it is likely to capture different patterns in the data and may actually be a closer approximation to the original ratchet than POY's implementation. Both approaches are effective methods to escape local optima.

We also performed constrained searches by calculating the strict consensus of trees within an arbitrary number of steps of the present optimum, saving the topology as a treefile, constructing the group inclusion matrix (Farris, 1973) in the program Jack2Hen, and then employing *constraint* in the subsequent searches. To calculate the consensus we included trees within 100–150 steps of the current optimum, the goal being to collapse enough nodes for swapping to be effective, but few enough nodes for significant speedups in RAS + swapping to find optimal arrangements within the polytomous groups (see Goloboff, 1999: 420). This is effectively a manual approximation of Goloboff's (1999) consensus-based sectorial search procedure, the main difference being that we collapsed nodes based only on tree length and not relative fit difference (Goloboff, 1999; Goloboff and Farris, 2001).

Using constraint files generated in the same way, we also input the current optimum as a starting point for fusing and/or ratcheting. This strategy avoids spending time on RAS builds of the unconstrained parts of the tree (which tend to be highly suboptimal) and seeks to escape local optima in the same way as unconstrained ratcheting, discussed above; however, there is a trade-off in that the arrangements may be less diverse but are likely to be, on average, closer to optimum, than those examined through RAS.

As a further manual approximation of sectorial searches, we analyzed subsets of taxa separately by defining reduced datasets with *terminals* files that listed only the targeted terminals. Rigorous searches (at least 100 RAS + TBR for each of the reduced datasets) of these reduced datasets were then performed, and the results were then used to specify starting topologies for additional searching of the complete dataset.

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Static matrices may be thoroughly analyzed in a fraction of the time required to perform an equivalent analysis under dynamic homology. We therefore output implied alignments of current optima from POY and ran multiple replicates of RAS + 50 rounds of the parsimony ratchet using Winclada and NONA. Improvements were not always attained through this procedure, but when they were, we then input the optimal cladogram(s) from the static search as a starting point for further analysis in POY.

As a final attempt to discover more parsimonious solutions, we also rearranged branches of current optima manually. As a general search strategy this would obviously be highly problematic, if for no other reason than that it would bias analyses. However, we performed this step primarily to ensure that the "received wisdom" and other arrangements were evaluated explicitly in the analysis. The procedure was to open the current optimum in Winclada, target taxa whose placement was strongly incongruent with current taxonomy, and move them to their expected positions (or in polytomies, depending on the precision of the expectations). The resulting topologies were saved as treefiles that were read into POY as starting topologies for diagnosis and refinement (e.g., tree fusing). In this way we ensured that the more heterodox aspects of our results were not due to simply failing to evaluate the more orthodox alternatives during the automated searches.

Heuristic Data Exploration

To estimate support (sensu Grant and Kluge, 2003), we calculated Bremer (decay) values for all nodes present in the strict consensus of equally parsimonious solutions (Bremer, 1994). To accomplish this we output the implied alignment and optimal trees in Hennig86 format using *phastwincladfile*, converted it to NEXUS format in Winclada, and then generated a NEXUS inverse-constraints batch file in PRAP (Müller, 2004), which was analyzed in PAUP* 4.0b10 (Swofford, 1998–2002). Bremer analysis consisted of 1 RAS + 5 iterations of the parsimony ratchet (reweighting 25% of characters by 2) for each clade. More thorough analysis involving more rigorous tree searches of the unaligned data would undoubtedly lower the estimates; as is always the case with heuristic analysis, the Bremer values reported are an upper bound.

Species Identification

One of the goals of this study was to address problems in determining species identity. Through the course of the study species were identified on phenotypic grounds. Here we examine the bearing of evidence from DNA sequences and phylogenetic analysis on alpha taxonomic problems (see also Total Evidence Analysis, above).

As a means of identifying species limits, the results of phylogenetic analysis should be interpreted in light of several caveats: (1) Phylogenetic analysis presupposes that the genealogical relationships among the entities analyzed are phylogenetic (Davis and Nixon, 1992); as such, it will impose a hierarchy even on entities that are related tokogenetically, for example. In such cases, the branching structure would be an analytical artifact and finding that a species is or is not monophyletic would be irrelevant. (2) Species are historical individuals, and, as such, all parts of a given species need not form a clade (Skinner, 2004; see also Frost and Kluge, 1994). Incongruence between the history of different parts and the whole may be due to any number of natural phenomena, such as lineage sorting and partial/temporary introgression, none of which denies the historical individuality of the species. (3) Given a cladogram alone, there is no objective basis for identifying species limits, that is, there is no way to discriminate intra- from interspecific hierarchic structure without additional information. For example, dividing a pectinate cladogram of N terminals into 1 species, $N - 1$ species, and N species are all cladistically valid delimitations. As such, phylogenetic structure can only disconfirm hypotheses of species identity (but consider points 1 and 2); finding that the parts of a putative species form a clade does not deny that the clade may be composed of multiple species.

In spite of the above caveats, phylogenetic analysis is a valid (if fallible) species discovery operation (Frost et al., 1998). Conceptually, species are minimal historical individu-

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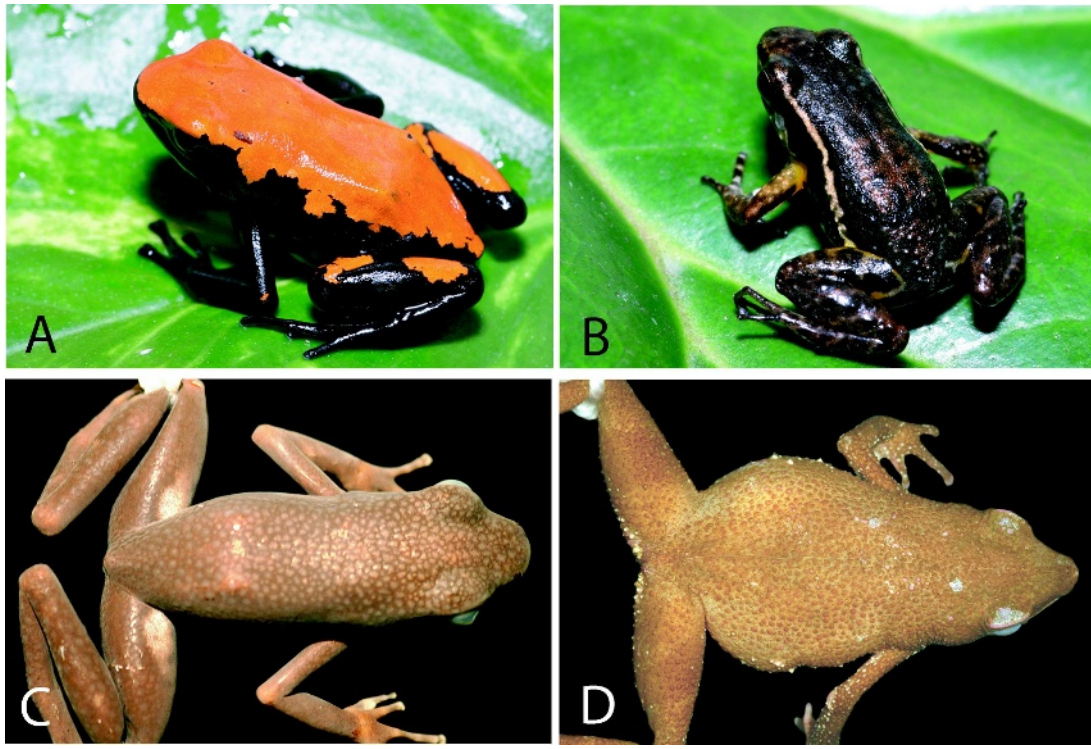

Fig. 22. Character 0, dorsal skin texture. **A**: State 0, smooth (*galactonotus*, AMNH live exhibit). **B**: State 1, posteriorly tubercular (*fraterdanieli*, MHNUC 364). **C**: State 2, granular (*macero*, AMNH 129473). **D**: State 3, spiculate (*Dendrophryniscus minutus*, AMNH 93856).

als, meaning that species boundaries occur at the point where the properties of contemporary individuals dissolve (Kluge, 1990; Grant, 2002). Historical individuality may therefore be apprehended both from ''below'' by discovering the constituent parts that interact and ''above'' by individuating entities that are historically distinct. Incongruence between the results of complementary discovery operations (those directed from above and below, in this case) indicates heuristically that further study is warranted (Grant, 2002). Ultimately, species individuation requires diagnostic characters, and phylogenetic analysis facilitates their discovery.

To address the limits of problematic species, we considered (1) cladogram topology (cladistic distance), (2) branch lengths (patristic distance), and (3) uncorrected pairwise distance[4] (uncorrected *p*, or number of base mismatches divided by total sequence length; no length variation was observed for this locus) of cytochrome *b* sequences within and between localities and/or closely related species. We focused on that sequence because (1) it is sufficiently variable and (2) it is almost completely represented in our dataset.

Our primary reason for including pairwise distances in this analysis is that they provide a rapid heuristic for species identification without conducting a complete phylogenetic analysis, in the same way that artificial dichotomous keys are efficient identification tools (Grant, 2002). We do not advocate using pairwise distances to delimit species. First, there is no justification for setting some arbitrary distance (e.g., 5%)—phenetic or otherwise—as ''sufficient'' for granting spe-

[4]This is usually referred to as sequence divergence. However, divergence is a phylogenetic concept synonymous with patristic distance (Farris, 1967). These pairwise comparisons are phenetic and are better characterized as dissimilarities or phenetic distances.

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cies status. Given variation in evolutionary rates and sampling density, it is expected that intraspecific variation may be greater in some species than interspecific variation among others. Indeed, the inability to distinguish between rate variation and artifacts due to taxon sampling (including extinction) casts doubt on all studies that base conclusions on degree of divergence or distance. What matters is the total evidence (including other loci, morphology, behavior, etc.) for the historical reality of the putative species and clades, for which character-state transformations must be identified to diagnose minimal historical individuals, not degree of similarity (pair- or otherwise). Second, as two-taxon statements, pairwise distances do not distinguish between symplesiomorphy and synapomorphy and therefore fail to explain the observed variation. Third, pairwise distance only discriminates among samples, that is, it is a relational concept and therefore cannot diagnose any particular entity (see Frost, 2000). Nevertheless, because they do not require extensive sampling or detailed analysis (phylogenetic or otherwise), pairwise comparisons are extremely fast and simple and therefore highly heuristic, and as such they are a useful starting point in examining species identity.

PHENOTYPIC CHARACTERS

0. Dorsal Skin Texture (fig. 22): smooth = 0; posteriorly granular = 1; strongly granular = 2; spiculate =3. Nonadditive.

Living and well-preserved anuran skin always has some texture, so even ''smooth'' skin may appear shagreen or faintly granular under high magnification. In state 0 all dorsal surfaces lack distinct tubercles or granules (e.g., *histrionicus*, *abditaurantius*). In state 1, granules or tubercles are scattered irregularly over the dorsal surfaces, being more distinct and prominent posteriorly, especially in the sacral region and on the thigh and/or shank, and absent or weaker and sparser anteriorly (e.g., *boulengeri*, *fraterdanieli*). These granules or tubercles are often distinctly elevated and conical. State 2 consists of rounded or flattened granules distributed densely and evenly (e.g., *granuliferus*, *parvulus*). Spiculate skin (state 3) is restricted to outgroup species; the skin of *Dendropryniscus minutus* is conspicuously spiculate, but in others (e.g., *Atelopus spurrelli*) the distinctly spiculate skin is only evident under magnification. Although state 1 is intermediate in the *amount* of granulation, the individual granules or tubercles of states 1 and 2 are qualitatively different, and there is no developmental evidence to suggest that transformations between states 0 and 2 pass through state 1.

Dorsal skin texture has generally been used descriptively in species-level taxonomic studies (e.g., Myers et al., 1995, in distinguishing between *pumilio* and *granuliferus*; Silverstone, 1976, in distinguishing between *femoralis* and *boulengeri*). Jungfer (1989) reviewed the ''red-backed granulated'' Amazonian dendrobatids but did not explicitly delimit them as a group.

Unlike some other anurans (e.g., centrolenids), skin texture of dendrobatids varies only minimally (or not at all) in relation to season and/or reproductive activity, with variation involving only the protuberance of granules or tubercles and not the occurrence of different states. Nevertheless, care must be exercised in coding this character (and others involving dermal structures) because it is prone to alteration due to preservation. Inadequately fixed or preserved specimens tend to lose granularity or even slough the epidermis. Even well-preserved specimens fixed according to the standard procedure of laying the specimen in a fixing tray prior to immersion in formalin are often less granular than they were in life. Conversely, granularity may be exaggerated in desiccated specimens. As noted by Myers and Daly (1979: 5, footnote 1), the best means of preserving skin texture (as well as other dermal characters such as hand and foot tubercles) is to float them completely in formalin immediately. (However, we do not mean to endorse this method generally, as it complicates examination of the vast majority of morphological characters.)

Heyer (1983: 322) provides electronmicrographs showing the skin texture for *Cycloramphus boraceiensis*. We coded *pulcherrimus* according to Duellman's (2004) description.

1. Paired Dorsal Digital Scutes: absent = 0; present = 1.

All species of dendrobatids have distinctive paired dermal scutes atop digital discs,

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although they may be inconspicuous on first and last digits and are generally most strongly expressed on the third finger and fourth toe (i.e., on discs that are most expanded). Noble (1926: 7) cited this character as evidence uniting dendrobatids in a single, exclusive group, and since then it has been used consistently to diagnose dendrobatids. Noble and Jaeckle (1928) examined the histology of the digital discs and illustrated (but did not discuss) the digital scutes of a specimen they identified as *Phyllobates latinasus* (actual species unknown but probably not *latinasus*; see Grant, 2004, for discussion of *latinasus* taxonomy) and *Hylodes nasus* (as *Elosia bufonia*). Noble (1931) noted the occurrence of the digital scutes in his Elosiinae (p. 504) and dendrobatids (p. 507). Although he did not explicitly state that it was homologous in the two groups, that was implied by his hypothesis that dendrobatids arose from "*Crossodactylus* or a form closely allied to it". He further observed (p. 520) that both dendrobatids and the African ranid Petropedetinae had "apparently identical" dermal scutes on the upper surface of each digit (he did not comment on the shared occurrence of this state in his Elosiinae), but he explained away this similarity as adding "one more to the many cases of parallel evolution in the Salientia". Liem and Hosmer (1973: 473) also noted that the myobatrachid genus *Taudactylus* has "expanded digital discs with a median longitudinal groove dorsally". Lynch (1979) illustrated the discs of groups known to possess digital scutes or scutelike structures. Lynch (1979: 7) clarified that the scutes are "flaplike structures", which distinguishes them from superficially similar digits of some *Eleutherodactylus* that exhibit only a median groove. La Marca (1995: fig. 9) provided scanning electron micrographs of the digital scutes of *collaris*, *herminae*, *oblitterata*, *neblina*, *olmonae*, *riveroi*, *trinitatis*, *yustizi*, and an undescribed species. Griffiths (1959: 482) claimed that the scutes are "really glandulo-muscular organs and probably function to facilitate adhesion to foliage etc.", but no evidence has been presented in support of his thesis and their functional significance remains unknown.

2. SUPERNUMERARY TUBERCLES ON HAND: absent = 0; present = 1.

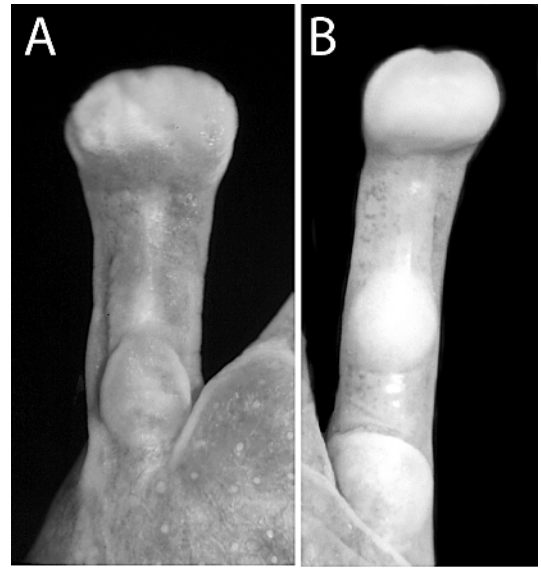

Fig. 23. Character 3, distal subarticular tubercle of finger IV. **A**: State 0, absent (*degranvillei*, AMNH 90876). **B**: State 1, present (*pictus*, AMNH 79209).

Most dendrobatids possess a large, subcircular palmar tubercle and an elliptical thenar tubercle. Many nondendrobatids also possess distinct supernumerary tubercles scattered over the fleshy part of the palm (e.g., Lynch and Duellman, 1997). As part of their polymorphism, some dendrobatids exhibit a tiny tubercle-like thickening on the outer edge (not the fleshy part) of the palm, but we do not consider this to be homologous with the supernumerary tubercles of other taxa.

3. DISTAL TUBERCLE ON FINGER 4 (fig. 23): absent = 0; present = 1.

Most dendrobatids possess both proximal and distal subarticular tubercles on finger IV (state 1). Grant and Rodríguez (2001) noted that in some species the distal tubercle on finger IV is absent (state 0) and that, although this is often associated with reduction in the length of finger IV (Character 4), some species that lack this tubercle show no reduction in finger length (e.g., *melanolaemus*, *pumilio*), which demonstrates the transformational independence of the two characters. This independence is further reinforced by examination of outgroup taxa, as *Thoropa miliaris* possesses a long finger IV and lacks the distal subarticular tubercle.

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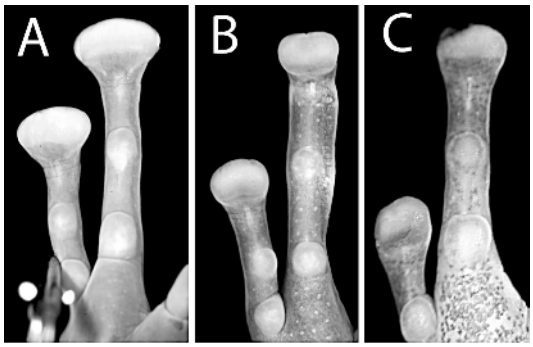

Fig. 24. Character 4, length of finger IV. **A**: State 0, surpassing distal subarticular tubrcle of finger III (*histrionicus*, AMNH 88259). **B**: State 1, reaching distal half of distal subarticular tubercle of finger III (*tricolor*, USNM 286082). Note also the strong preaxial swelling of finger III. **C**: State 2, not reaching distal subarticular tubercle of finger III (*insperatus*, KU 149684). Note also the absence of the distal subarticular tubercle of finger IV.

4. Finger IV Length (fig. 24): surpassing distal subarticular tubercle of finger III = 0; reaching distal half of distal subarticular tubercle of finger III = 1; not reaching distal subarticular tubercle of finger III = 2. Additive.

The length of finger IV is assessed by pressing it against finger III to determine if it extends well beyond the distal subarticular tubercle (state 0), reaches the distal half of, but does not surpass, the distal subarticular tubercle (state 1), or does not reach the distal subarticular tubercle (state 2). In the latter state, finger IV extends to a point approximately midway between the proximal and distal subarticular tubercles Although it is possible that we have conflated transformations involving the length of finger III, the fact that finger II reaches the distal half of the distal subarticular tubercle in all species supports indirectly the hypothesis that variation is due exclusively to transformations of finger IV, that is, if the observed variation is due to changes in the length of finger III, then the same change would also have had to affect the relative length of finger II. And it is further supported by the loss of the distal subarticular tubercle in species with a relatively short finger IV (see Character 3, above). Given the constancy of the length of finger II, this character is equivalent to the traditional taxonomic coding of finger IV versus finger II (i.e., when both are pressed against finger III, in state 0 IV is longer than II, in state 1 fingers IV and II are equal, and in state 2 IV is shorter than II).

5. Relative Lengths of Fingers I and II: I << II (II 1.2 or more times longer than I) = 0; I < II = 1; I = II = 2; I > II = 3. Additive.

Traditionally, the relative lengths of fingers I and II have been assessed by pressing these two fingers together at the point midway between the two digits. However, this is highly dependent on the investigator's judgment of the midway point between the two digits, that is, bringing finger I further toward finger II (or vice versa) can affect coding of this character. Kaplan (1997) measured the length of each finger from the same point at the base of the palmar tubercle to the tip of each finger, which is more precise and less prone to error, and we employed his method here. Kaplan's method also assumes that there are no carpal changes that affect the distance from the palm to finger tips differentially (no such variation was detected). Any method of measuring finger length requires that the fingers be straight; when well-preserved hands were unavailable, digits were straightened for measurement. In state 0 finger II is at least 20% longer than finger I; in state 1 finger II is less than 15% longer than finger I; in state 2 the fingers are subequal in length; in state 3 finger I is unambiguously longer than finger II.

Although developmental data are unavailable, gross morphology suggests that state transformations are due to variation in the length of finger I and not the length of finger II, that is, the length of finger II relative to finger III was not observed to vary, as it reaches the midlevel of the distal subarticular tubercle in all taxa. However, it is possible that two characters have been conflated, that is, one involving variation in the length of finger I, the other variation in the length of finger II. We did not attempt to relate the differences in relative lengths with the underlying osteology, which could also reveal that multiple characters have been conflated.

6. Digital Discs: absent = 0; present = 1.

The differentiation of the digital terminations into expanded discs with adhesive pads

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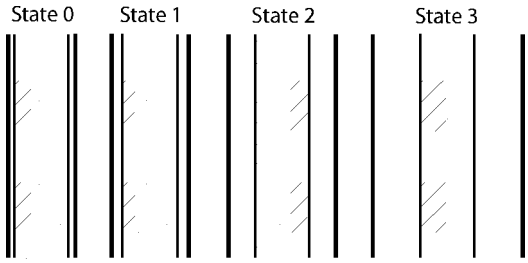

Fig. 25. Characters 7–10 and 31–35, schematic illustration of the four states observed in the expansion of digital discs. The digital shaft is indicated by the inner crosshatched area and the outer edges of the disc are indicated by the heavier outer line.

has long been used to infer anuran relationships (e.g., Cope, 1867). Numerous authors (e.g., Noble and Jaeckle, 1928; Green, 1979; Emerson and Diehl, 1980; Rivero et al., "1987" 1989; Ba-Omar et al., 2000) have examined the structure (and function) of the disc apparatus in a diversity of frogs and have found them to differ in only minor structural details (e.g., number of epidermal cell layers). We are unaware of any anuran that possesses finger discs but lacks toe discs (or vice versa), or that possesses discs on some but not all digits (although degree of expansion certainly varies among digits; see below). We have therefore treated the origin (and loss) of digital discs as a single transformation series. All dendrobatids possess digital discs, but they are absent in several of the sampled outgroup taxa.

7–10. Expansion of Finger Discs (fig. 25)

In the dendrobatid literature, expansion of finger discs is generally treated as one or at most two characters. Duellman and Simmons's (1988) standard diagnosis coded only the disc of finger III, and *Dendrobates* species descriptions often report the expansion of discs I and II–IV separately. However, there is no logical dependency between the discs of different digits, and the distribution of states in the matrix shows that the expansion of each digital disc is transformationally independent, and, as such, they are defensibly coded separately for analysis. A trend is that the disc of finger I is often (but not always) less expanded than those of the other fingers, but this does not violate the transformational independence of these characters.

We detected four discrete states in finger (and three in toe) disc expansion, shown schematically in figure 25. All dendrobatids have digital discs, so some degree of expansion is always detectable, although it may be extremely slight. This is exemplified by *elachyhistus* and *pumilio*, in which the disc of finger I appears unexpanded or at most weakly expanded (state 0). States 1 and 2 are found in most dendrobatids; state 3 is found in those species with greatly expanded discs (e.g., *tinctorius*). State 3 was only observed among fingers II–IV.

Polder (1973: 17) and Silverstone (1975a) claimed that some species of dendrobatids are sexually dimorphic in the expansion of the digital discs, with males possessing larger discs than females. Neither author provided quantitative data, however, and when Myers and Daly (1976b: 203) tested the claim quantitatively in *histrionicus* they found it to be unsupported. Although we detected (and coded) polymorphism in disc expansion in some species (including *histrionicus*), we concur with Myers and Daly (1976b) that it does not reflect differences between sexes. For example, in *leucomelas* the finger discs of male AMNH 137309 are larger than those of female AMNH 137310, but no more expanded than those of female AMNH 46051. We did not test the hypothesis that discs of males are *statistically* (i.e., on average) larger than those of females (Silverstone, 1975a: 8) because that question is unrelated to the problem of homologizing character-states and inferring transformation events (Grant and Kluge, 2003, 2004).

7. Finger Disc I: unexpanded = 0; weakly expanded = 1; moderately expanded = 2. Additive.

8. Finger Disc II: unexpanded = 0; weakly expanded = 1; moderately expanded = 2; greatly expanded = 3. Additive.

9. Finger Disc III: unexpanded = 0; weakly expanded = 1; moderately expanded = 2; greatly expanded = 3. Additive.

10. Finger Disc IV: unexpanded = 0; weakly expanded = 1; moderately expanded = 2; greatly expanded = 3. Additive.

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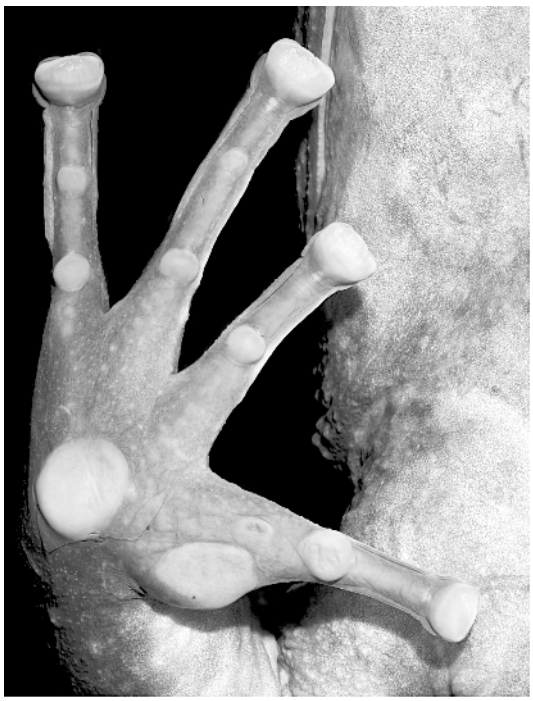

Fig. 26. Characters 11–18, finger fringes. In *Megaelosia goeldii* (AMNH 103949) fringes are present on pre- and postaxial edges of all fingers.

11–18. Finger Fringes (fig. 26)

The occurrence and extent of lateral keels and/or fringes on fingers and toes has been cited in most alpha taxonomic studies of dendrobatids for the past several decades at least (e.g., Edwards, 1971). Duellman and Simmons (1988: 116) noted that "the development of fringes on the fingers is variable, so standard comparison is made with the second finger." Nevertheless, as discussed above in reference to expansion of digital discs, because the fringes on each edge of each finger vary independently we coded them as separate characters.

Although lateral dermal expansions of the digits are commonly described in the dendrobatid literature, explicit delimitations of character-states are generally lacking, which has led to considerable confusion. They are generally referred to as either keels or fringes. As noted by Lynch and Duellman (1997: 33) for species of *Eleutherodactylus*, "there is a continuum from keels to fringes, and in some cases the distinction is arbitrary." Although such arbitrariness is relatively harmless in descriptive taxonomic studies, the cumulative effect of arbitrary delimitations can be disastrous in phylogenetic analyses. Coloma (1995: 6–7) noted that fringes may be absent, poorly developed, or well developed. He further clarified that "[w]hen it was difficult to distinguish between a real fringe and a preservation artifact, I describe the dermal modification as a 'keel' ", which, although explicit, actually engenders greater confusion because keels are generally considered to be real dermal modifications (e.g., Lynch and Duellman, 1997).

The strength of keeling (extent of dermal thickening) varies extensively, leading La Marca (1996 "1994": 6) to differentiate between keels and fringes as "very low" and "conspicuous but not folding around the toes", respectively. However, although we agree that these descriptors encompass the observed variation, and despite numerous dissections, we were unable to individuate character-states objectively. Any attempt to subdivide state 0 into multiple character-states must overcome two difficulties: (1) apparently continuous variation (as suggested by external examination and gross dissections) and (2) the fact that these dermal expansions are highly prone to postmortem modification, either due to desiccation (as indicated by Coloma, 1995) or simply as an artifact of preservation (and variation in preservation techniques). It is likely that the greater precision attained through histological study could overcome both of these problems, but that was beyond the scope of the present study. For the purpose of phylogenetic analysis, we individuated only two character-states: fringes absent (state 0) and fringes present (state 1).

In state 0, the extent of lateral dermal expansion varies from absent (i.e., the side of the digit is smoothly rounded and there is no detectable dermal thickening along the lateral margin) to conspicuously keeled. In state 1, the skin that extends from the dorsal surface extends ventrad and appears to fold over the side of the digit, which we refer to as a fringe (see fig. 26). In ventral (palmar) view the folding over can be seen to create a deep longitudinal crease or groove. We have not

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detected evidence that the folding over varies as an artifact of preservation, providing a basis to distinguish this state objectively. This state is approximately equivalent to La Marca's (1996 ''1994'': 6) ''flaps'', which he diagnosed as ''folding around the toes''. The strength of fringes varies from a weak flap (e.g., toes of *degranvillei*) to a strong flap that wraps around much of the ventral surface of the digit (the latter condition found only on toes; see below), but we were unable to delimit distinct states.

Webbing between the fingers does not occur in any dendrobatid we examined. Donoso-Barros (1965 ''1964'': 486) described ''rudimentary web between 2nd and 3rd fingers'' in *riveroi*, but finger webbing was not reported by La Marca (1996 ''1994'') and is absent in the specimens we examined. Similarly, Coloma (1995) described and illustrated webbing between the fingers in an undescribed species (as *Colostethus chocoensis*; see Grant et al., 1997: 24, footnote 13), and Grant et al. (1997: 25) mentioned the possible occurrence of webbing on the hands of *atopoglossus*. However, closer examination of the same specimens of ''*Colostethus chocoensis*'' and *atopoglossus* revealed that the apparent webbing is due to flattening of the loose skin of the hand, as considered by Grant et al. (1997). Lynch (1971: 30) reported similar mistaken reports among ''leptodactyloids''.

11. FINGER FRINGE: I preaxial: absent = 0; present = 1.

12. FINGER FRINGE: I postaxial: absent = 0; present = 1.

13. FINGER FRINGE: II preaxial: absent = 0; present = 1.

14. FINGER FRINGE: II postaxial: absent = 0; present = 1.

15. FINGER FRINGE: III preaxial: absent = 0; present = 1.

16. FINGER FRINGE: III postaxial: absent = 0; present = 1.

17. FINGER FRINGE: IV preaxial: absent = 0; present = 1.

18. FINGER FRINGE: IV postaxial: absent = 0; present = 1.

19. METACARPAL RIDGE (fig. 27): absent = 0; weak = 1.

The metacarpal ridge or fold is a dermal thickening running from the postaxial edge of the base of finger IV along the outer edge of the palm toward the palmar tubercle. In most species an edge is formed where the relatively flattened palm meets the rounded side of the hand, but we did not consider this to be a metacarpal ridge unless dermal thickening could be detected, either by gross inspection or by making a transverse incision. Although there is some variation among species in the degree of expression of the metacarpal ridge, it was minor and we were unable to delimit discrete states. As with other dermal characters, the metacarpal ridge may be exaggerated or lost as an artifact of preservation.

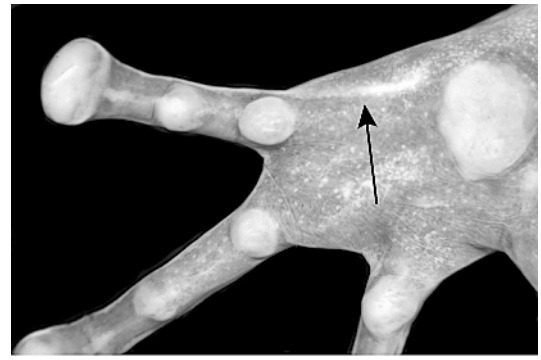

Fig. 27. Character 19, metacarpal ridge. State 1, present (*abditaurantius*, ICN 9853).

20–21. FINGER III SWELLING

Reproductively active males of numerous dendrobatids present swollen third fingers, a condition that is unknown in nondendrobatids. The ''swelling'' is due to the occurrence of extensive glandular tissue, the large granules often being evident in gross dissection or even through the skin. In light of the important role this character has played in recent discussions of dendrobatid systematics (e.g., Myers et al., 1991; but see Myers, 1991), we review its usage here.

Although a number of species possessing a distinctly enlarged third finger in males had been described previously (e.g., *trilineatus*, the holotype of which is a male), the first worker to describe and illustrate the swollen third finger was Dunn (1924: 7–8) for *nubicola*. Descriptions of ''digital dilatations'' or ''enlargements'' in the earlier literature referred to the expanded digital disc appara-

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tus (e.g., Cope, 1867: 130, 1887: 55). When Dunn (1931) named *flotator*, he grouped it with *nubicola* based in part on the shared occurrence of the swollen third finger in males. Dunn (1933) noted that males of *panamensis* possess a swollen third finger, but he did not attribute any phylogenetic significance to the observation.

Over the 50 years following Dunn's first report of the swollen third finger in males, the state of the third finger was mentioned sporadically in diagnoses and descriptions (e.g., among papers that deal with species with swollen third fingers in males, it was mentioned by Dunn, 1931, 1957; Funkhouser, 1956; Savage, 1968; Cochran and Goin, 1970: 60 [only for their *Phyllobates inguinalis*, as "flanges" on the third finger of males]; Edwards, 1971; and Silverstone, 1971, 1976; but not by Cochran and Goin, 1964; Cochran, 1966; or Silverstone, 1975b), but was not illustrated again until 1974, when Edwards provided a schematic representation in his unpublished (but widely distributed; see Myers et al., 1991: 30, footnote 14) dissertation (Edwards, 1974a).

The character has been mentioned fairly consistently since 1974, but miscoding is common, probably due in part at least to the inadequacy of Dunn's (1924) and Edwards's (1974a) illustrations, both of which depicted (1) roughly equal expansion on both sides (preaxial and postaxial) of the digit and (2) distally exaggerated swelling, neither of which is found in all (or even most) of the species with swollen third fingers. Similarly, although accurate for a few species, Duellman and Simmons's (1988: 117) description that "the basal segment of the third finger is distinctly swollen in males" does not apply to most of the species with clearly swollen third fingers in males (and none of the species they addressed in their paper). The expansion of the third finger can be much more subtle than Dunn's (1924) and Edwards's (1974a) illustrations suggest, and significant variation occurs in the extent and location of the swelling.

Silverstone (1976: 33) noted in his account of *tricolor* that not all adult males of a given sample may express the swollen third finger, a finding that was corroborated more generally by Myers et al. (1991), who speculated that expression is likely under hormonal control. This and additional difficulties related to the coding of this character were discussed by Myers et al. (1991, 1998, see especially fig. 4), Myers (1991), Myers and Donnelly (1997), and Grant and Rodríguez (2001).

20. Finger III Swelling in Adult Males: absent = 0; present = 1.

This character was scored for *awa* from Coloma (1995) because no adult males were included in the series we examined.

21. Morphology of Swollen Third Finger in Males (fig. 28): pre- and postaxial swelling = 0; weak preaxial swelling = 1; strong preaxial swelling = 2; swelling extending from wrist, mainly preaxial on digit = 3. Nonadditive.

22. Carpal Pad (fig. 29): absent = 0; present = 1.

Myers and Donnelly (2001) discovered the carpal pad in *undulatus*. It consists of a conspicuous nonglandular thickening and heavy melanosis of the skin above the wrist of males. We did not find this character to be present in any other species, but we include it here in anticipation of future discoveries.

23. Male Excrescences on Thumb: absent = 0; present = 1.

Although nuptial excrescences are common among outgroup taxa, most dendrobatids lack nuptial excrescences (state 0), the sole exception being *oblitterata*, which was reported as possessing nuptial excrescences (state 1) by La Marca (1995: 66).

We coded *Telmatobius jahuira* for this character following Lavilla and Ergueta (1995).

24. Morphology of Male Excrescences on Thumb: large, cornified spines = 0; small, uncornified spines = 1; nonspinous asperities = 2. Additive.

Lavilla and Ergueta (1995: 49, translated freely from the Spanish) described the nuptial excrescences of *Telmatobius jahuira* as "few cornified spines separated by large, unkeratinized spaces".

25. Female Excrescences on Thumb: absent = 0; present (large, cornified spines) = 1.

See Noble (1931: 122, 126) for illustrations and comments on the large, cornified spines

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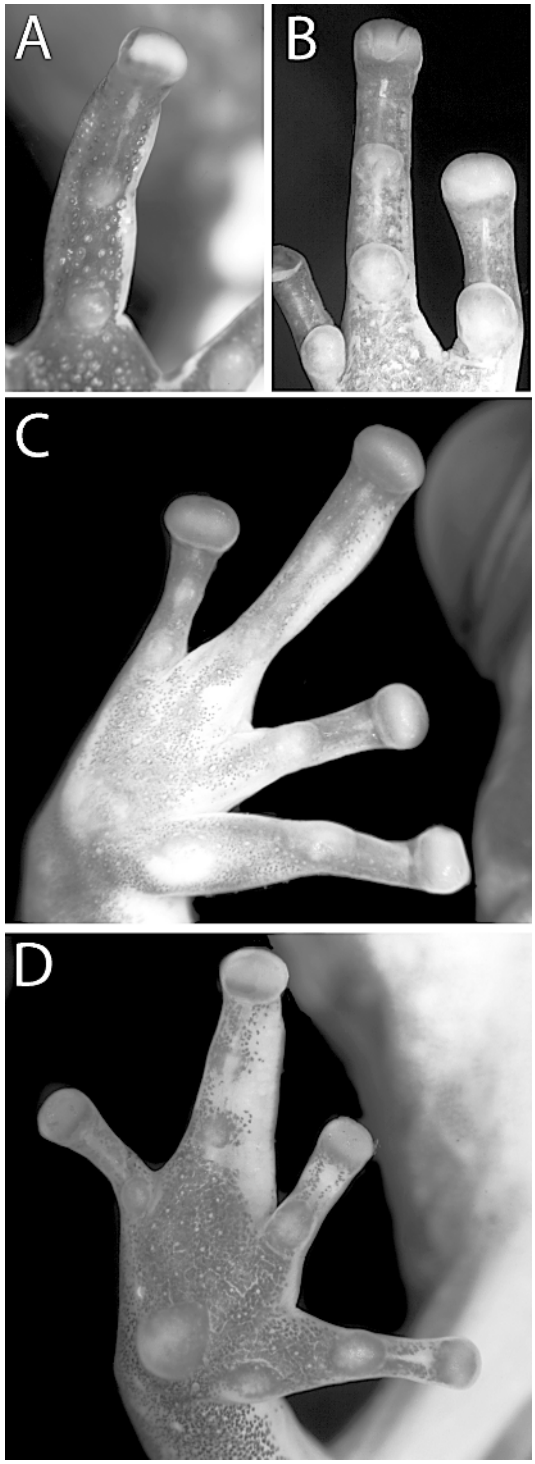

Fig. 28. Character 21, morphology of swollen third finger in males. **A**: State 0, pre- and postaxial swelling (*mertensi*, ICN 43698). **B**: State 1, weak preaxial swelling (*insperatus*, KU 149676). **C**: State 2, strong preaxial swelling (*nubicola*, AMNH 114574). **D**: State 3, swelling extending from wrist, mainly preaxial on digit (*baeobatrachus*, AMNH 140650).

on the thumb of females of species of *Crossodactylus*.

26. THENAR TUBERCLE (fig. 30): absent or small, inconspicuous swelling = 0; large, conspicuous, well-defined tubercle = 1.

Most dendrobatids have a conspicuous, protuberant, elliptical thenar (inner metacarpal) tubercle (state 1). Silverstone (1975a) noted that the thenar tubercle is inconspicuous or absent in *leucomelas* (state 0). Likewise, Caldwell and Myers (1990) illustrated and discussed the absence of the thenar tubercle in *castaneoticus* and *quinquevittatus*, which they interpreted as a synapomorphy uniting these two species in an exclusive clade (they did not make comparisons with *leucomelas*). Other species also exhibit the same morphology (e.g., *pumilio*).

Caldwell and Myers (1990: 16) noted some variation in the expression of the thenar tubercle in *quinquevittatus*; in some specimens it is altogether undetectable, whereas in others "possible vestiges of it" were detected as "possibly represented by slight epidermal thickening". Our observations concur with theirs. Given the propensity for such subtle dermal features to be lost as an artifact of preservation (due to skin sloughing, desiccation, or inadequate fixation, among other causes), we combined the apparent complete absence and inconspicuous epidermal thickening as state 0. Expression of the thenar tubercle is not dependent on overall body size; *leucomelas* is quite large, and the thenar tubercles of the small species *nubicola* and *stepheni* (roughly the same snout-vent length as *pumilio*) are large and well defined.

27. BLACK ARM GLAND IN ADULT MALES: absent = 0; present = 1.

This character was identified, discussed, and illustrated photographically by Grant and Castro-Herrera (1998; see also Grant and Ardila-Robayo, 2002) and used to delimit the *ramosi* group. It remains unclear if this patch of black, thickened tissue on the

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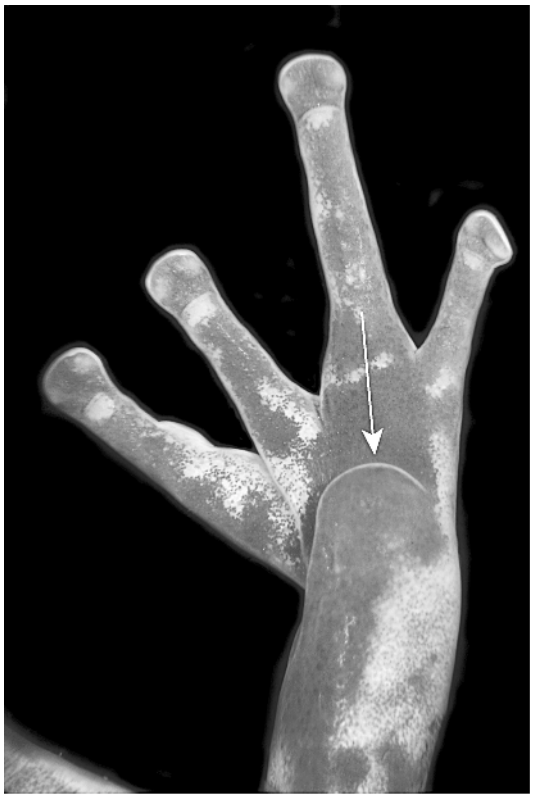

Fig. 29. Character 22, male supracarpal pad (*undulatus*, AMNH 159134).

ventral and medial surfaces of the distal extreme of the upper arm and often extending onto the inner surface of the lower arm is glandular, but its absence in females and juveniles and exaggeration in sexually active males suggests it is involved in amplexus and probably under hormonal control. In addition to the species listed by Grant and Ardila-Robayo (2002), this character is also present in *anthracinus* and the undescribed species referred to herein as ''Ibagué''.

28. TARSAL KEEL: absent = 0; present = 1.

The tarsal keel is a dermal structure that extends obliquely along the plantar surface of the tarsus. Regardless of its point of origin (see Character 29), it always terminates medially, not on the margin of the tarsus (see Character 30). Silverstone (1975a, 1976) used variation in this structure to diagnose species groups in *Dendrobates* and *Phyllobates*, and Lynch (1982) cited the loss of the tarsal keel in *edwardsi* and *ruizi* to delimit the *edwardsi* group of *Colostethus*.

Silverstone (1975a: 8) treated the ''tarsal fold'' and ''tarsal tubercle (at the proximal end of the tarsal fold)'' as separate characters. He considered the tarsal fold to be present in all *Dendrobates* and the tarsal tubercle to be both present and absent in

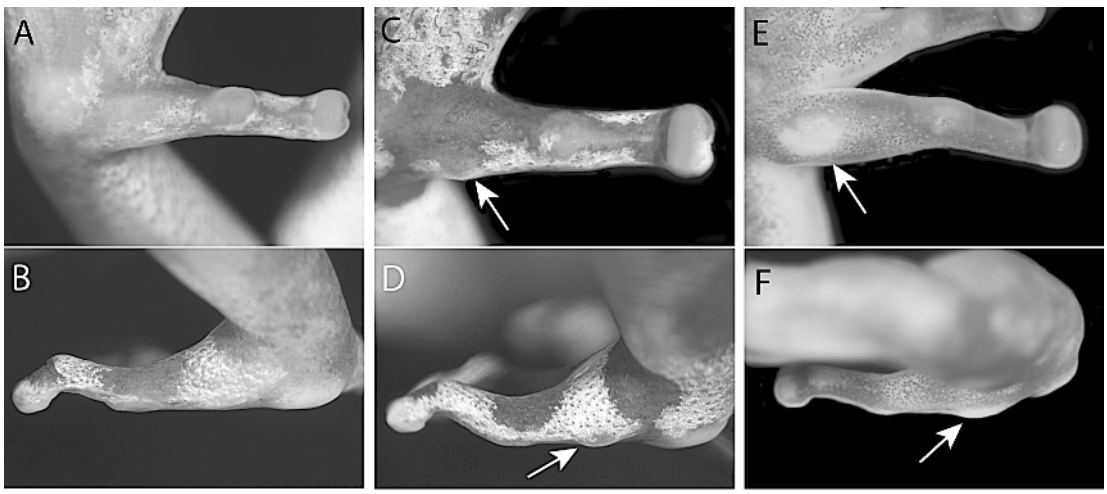

Fig. 30. Character 26, thenar tubercle. **A**, **B**: State 0, absent or small, inconspicuous swelling (*pumilio*, AMNH 102262). In this specimen, the thenar tubercle appears absent in both palmar aspect and profile. **C**, **D**: Another specimen of the same species (*pumilio*, AMNH 102263). In this specimen, the thenar tubercle is inconspicuous but clearly seen in profile (also scored as state 0). **E**, **F**: State 1, large, conspicuous, protuberant tubercle (*nubicola*, AMNH 114574).

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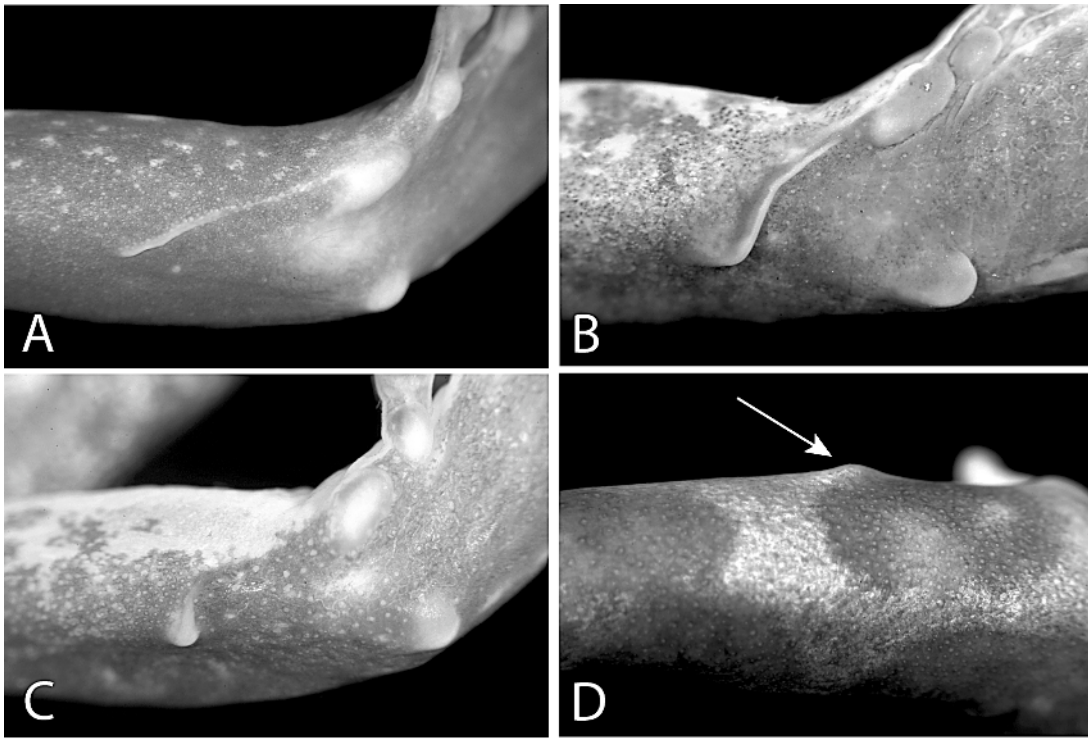

Fig. 31. Character 29, morphology of tarsal keel. **A**: State 0, straight or very weakly curved, extending proximolaterad from preaxial edge of inner metatarsal tubercle (*imbricolus*, AMNH 102082). **B**: State 1, tuberclelike and strongly curved at proximal end, extending from metatarsal tubercle (*degranvillei*, AMNH 90876). **C**: State 2, short, tuberclelike, curved or directed transversely across tarsus, not extending from metatarsal tubercle (''Neblina species'', AMNH 118657). **D**: State 3, weak, short dermal thickening, not extending from metatarsal tubercle (*pumilio*, AMNH 102261). The hind limb is rotated to view the inconspicuous tarsal keel in profile.

Dendrobates. However, the tarsal fold and tarsal tubercle form a single structure, the tubercle simply being an increased thickening of the proximal portion of the keel. This is especially clear in many nonaposematic dendrobatids (which were not the focus of Silverstone's work) in which the proximal end of the keel is conspicuously enlarged and may be described as tubercle-like, but is sharply curved to run across the tarsus and does not conform to the rounded structures usually referred to as tubercles.

29. MORPHOLOGY OF TARSAL KEEL (fig. 31): straight or very weakly curved, extending proximolaterad from preaxial edge of inner metatarsal tubercle = 0; tubercle-like (i.e., enlarged) and strongly curved at proximal end, extending from metatarsal tubercle = 1; short, tubercle-like, curved or directed transversely across tarsus, not extending from metatarsal tubercle = 2; weak, short dermal thickening, not extending from metatarsal tubercle = 3. Additive.

30. TARSAL FRINGE (fig. 32): absent = 0; present = 1.

The tarsal fringe consists of a conspicuous dermal flap that runs along the entire length of the preaxial edge of the tarsus; it is continuous with the fringe on toe I. The tarsal fringe differs from the tarsal keel (characters 28, 29) in that the latter extends proximolaterad across the tarsus to terminate at roughly the middle of the tarsus on the plantar surface, whereas the former never crosses the tarsus and extends along its entire length.

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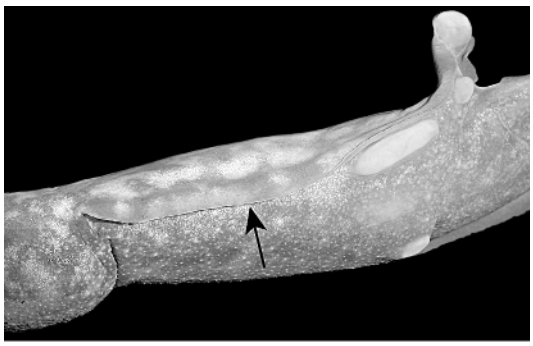

Fig. 32. Character 30, tarsal fringe. State 1, present (*Megaelosia goeldii*, AMNH 103950).

31–35. Expansion of Toe Discs

Like finger discs, dendrobatid literature generally treats the degree of expansion of toe discs as a single character. However, as discussed above under finger discs, toe discs vary independently of one another and are defensibly treated as separate characters. Toe discs exhibit three of the four character-states found in fingers; the greatest expansion found in finger discs (finger disc state 3) does not occur in toe discs. (Character-states are figured schematically in fig. 25, above.)

31. Toe Disc I: unexpanded = 0; weakly expanded = 1; moderately expanded = 2. Additive.

32. Toe Disc II: unexpanded = 0; weakly expanded = 1; moderately expanded = 2. Additive.

33. Toe Disc III: unexpanded = 0; weakly expanded = 1; moderately expanded = 2. Additive.

34. Toe Disc IV: unexpanded = 0; weakly expanded = 1; moderately expanded = 2. Additive.

35. Toe Disc V: unexpanded = 0; weakly expanded = 1; moderately expanded = 2. Additive.

36–45. Toe Webbing

Webbing has been used consistently in dendrobatid systematics since Noble (1923, 1926) diagnosed *Phyllobates* from *Hyloxalus* on the basis of reduced webbing. Although webbing can be argued to form a single, integrated functional unit (as can the entire organism), functional independence is at most secondary to historical independence in phylogenetic inference (Grant and Kluge, 2004), and there is ample evidence that the extent of webbing along each edge of each digit varies independently. Coding follows the nomenclature proposed by Savage and Heyer (1967) and subsequently modified by Myers and Duellman (1982), which quantifies webbing in terms of the number of free phalanges, assessed in relation to subarticular tubercles (e.g., in Character 40, state 6, the two distal phalanges are free of webbing). We consider toe fringes (defined as for fingers, above) to be homologous with webs. We do not consider lateral fringes that meet between the toes to constitute a web unless it is expanded relative to lateral fringes, that is, if the continuous lateral fringes are broader at the base than along the sides of the digits, we construe this as being a web.

Among the sampled outgroup taxa, McDiarmid (1971: 33) noted that the interdigital webbing of *Atelopus* and *Dendrophryniscus* "is not a membrane, as defined by Peters (1964) but rather a thickened integumentary connection between digits, similar to the webbing encountered in many of the more terrestrial anurans, such as toads of the genus *Bufo*." This suggests that the interdigital webbing of these species may not be homologous with that of other anurans. Nevertheless, although the distinction is clear in *Dendrophryniscus minutus*, it is less so in the sampled species of *Atelopus*, and we have therefore treated webbing as a single transformation series and allowed character congruence to be the ultimate arbiter (although much more extensive sampling of relevant taxa will be required to fully resolve the question).

36. Webbing: Toe I Preaxial: absent = 0; fringe = 1.

37. Webbing: Toe I Postaxial: absent = 0; fringe = 1; 2 = 2; 1.5 = 3; 1 = 4; 0 = 5. Additive.

Coloma (1995: 51) reported basal webbing (**I**2–3.5**II**) for *talamancae* and *toachi*, but there is no trace of webbing in the specimens we examined in this study.

38. Webbing: Toe II Preaxial: absent = 0; 2.5 = 1; 2 = 2; 1 = 3; 0 = 4. Additive.

Coloma (1995: 51) reported basal webbing (**I**2–3.5**II**) for *talamancae* and *toachi*, but

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there is no trace of webbing in the specimens we examined.

39. WEBBING: TOE II POSTAXIAL: absent = 0; 2 (without fringe) = 1; 2 (with fringe) = 2; 1.5 = 3; 1 = 4; 0 = 5. Additive.

40. WEBBING: TOE III PREAXIAL: absent = 0; fringe = 1; 3.5 (without fringe) = 2; 3.5 (with fringe) = 3; 3 = 4; 2.5 = 5; 2 = 6; 1.5 = 7; 1 = 8. Additive.

Coloma (1995: 51) reported more extensive webbing (equivalent to state 4) for *talamancae* than we observed (state 2).

41. WEBBING: TOE III POSTAXIAL: absent = 0; 3 without fringe = 1; 3 with fringe = 2; 2.5 = 3; 2 = 4; 1.5 = 5; 1 = 6. Additive.

42. WEBBING: TOE IV PREAXIAL: absent = 0; 4 without fringe = 1; 4 with fringe = 2; 3.5 = 3; 3 = 4; 2.5 = 5; 2 = 6; 1 = 7. Additive.

43. WEBBING: TOE IV POSTAXIAL: absent = 0; fringe = 1; 4 = 2; 3.5 = 3; 3 = 4; 2.5 = 5; 2 = 6; 1 = 7. Additive.

Coloma (1995: 51) reported basal webbing (**IV**4.5–3**V**) in *talamancae*, but there is no trace of webbing in the specimens we examined.

44. WEBBING: TOE V PREAXIAL: absent = 0; fringe = 1; 2.5 (with fringe) = 2; 2 = 3; 1.5 = 4; 1 = 5. Additive.

45. WEBBING: TOE V POSTAXIAL: absent = 0; fringe = 1.

This character was coded for *insulatus*, *pulcherrimus*, and *sylvaticus* Barbour and Noble from Duellman (2004), who reported it as absent in them all.

46. METATARSAL FOLD (fig. 33): absent = 0; weak = 1; strong = 2. Additive.

The metatarsal fold is a dermal thickening running from the postaxial edge of the base of toe V (often coextensive with the fringe, if present) along the outer edge of the sole toward the outer metatarsal tubercle. In most species an edge is formed where the relatively flattened sole meets the rounded side of the foot, but we did not consider this to be a metatarsal ridge or fold unless actual dermal thickening could be detected, either by gross inspection or by dissection. A weak metatarsal fold (state 1) is a ridge; strong dermal folds (state 2) are often folded over or angled relative to the surface of the sole.

47. CLOACAL TUBERCLES: absent = 0; present = 1.

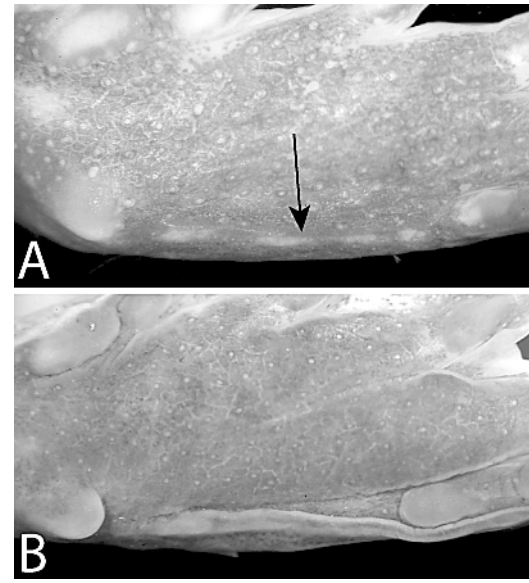

Fig. 33. Character 46, metatarsal fold. **A**: State 1, weak (''Neblina species'', AMNH 118657). **B**: State 2, strong (*degranvillei*, AMNH 90876).

Grant et al. (1997) identified and figured this pair of tubercles adjacent to the cloaca near the base of the thighs. They also discussed difficulties in scoring this character due to postmortem artifacts.

48–66. EXTERNAL COLORATION

Much of the diversity of dendrobatids involves variation in external color and color pattern. Among species referred to *Colostethus*, for example, variation in the pattern of lateral stripes and ventral color serves as one of the main tools for diagnosis. However, color and color pattern are perhaps the most confounding–and therefore undersampled in this study–sources of variation. Several aposematic dendrobatids (e.g., *pumilio*, *histrionicus*, and *tinctorius*) are renowned for their astonishing intra- and interpopulational variation in color and color pattern, and the difficulties posed by this immense and often continuous and overlapping variation can be immediately appreciated by glancing at a few pages of Myers et al.'s (1976b) account of *histrionicus*. Practically speaking, the three main difficulties are (1) detection of objective boundaries between different characters and character-

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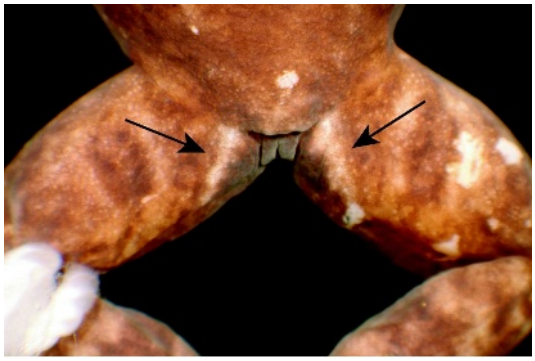

Fig. 34. Character 49, pale paracloacal mark. State 1, present (*degranvillei*, AMNH 90880).

states, (2) requirement of many states per character, and (3) distinguishing between color and color pattern. We made every effort to incorporate as much of the variation as possible, but much of it was overwhelming. Also, for ease of coding (especially preserved specimens) we focused more on color pattern than color, but by doing so we undoubtedly conflated characters and character-states. For example, we scored both *auratus* and *reticulatus* as having the thighs pale with dark spots, even though the thighs are different colors. Future studies will undoubtedly advance considerably beyond the current project by scoring more of this diversity of color and color pattern.

48. Iridescent Orange or Golden Spot at Dorsal Limb Insertions: absent = 0; present = 1.

Note that the photo of *quinquevittatus* in Caldwell and Myers (1990: 11) shows that this character is not redundant with or nonindependent of the thigh coloration characters.

49. Pale Paracloacal Mark (fig. 34): absent = 0; present = 1.

This is a pale, elongate mark at the base of the thigh. The shape of the spot varies from a straight vertical line to a sickle extending as a pale longitudinal stripe along the *posterior* surface of the thigh. The paracloacal mark originates adjacent to the vent at the base of the thigh, not in the groin or on the top the thigh (as does the pale mark in *femoralis*, for example; see character 50).

50. Thigh Dorsal Color Pattern (fig. 35): pale with dark spots (forming reticulum when spots are close together) = 0; solid dark = 1; dark with pale spots/bands = 2; solid pale = 3; brown with dark brown

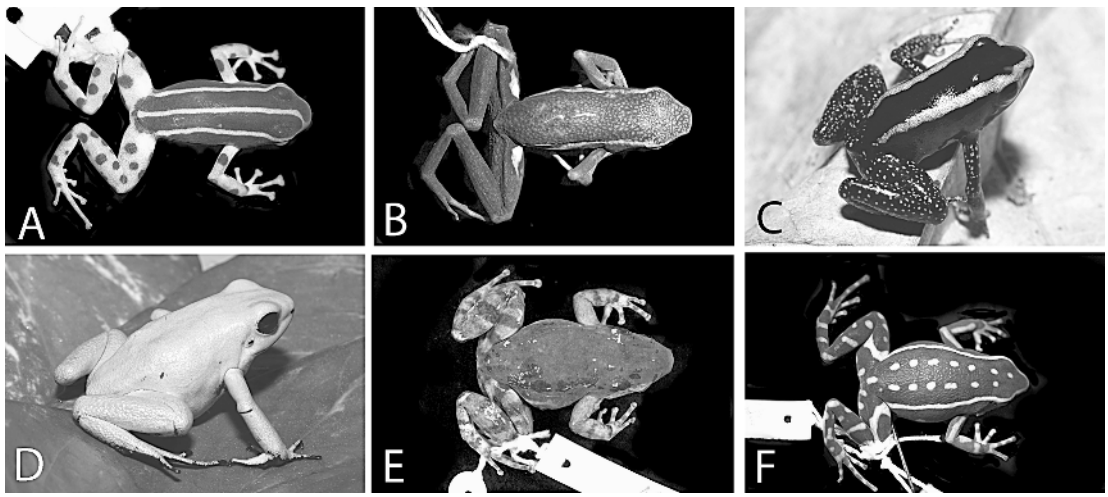

Fig. 35. Character 50, dorsal thigh color pattern. **A**: State 0, pale with dark spots (*quinquivittatus*, AMNH 124069). **B**: State 1, solid dark (*petersi*, AMNH 111000). Note that the pale spot is confined to the inguinal regions and does not extend onto the dorsal surface of the thigh. **C**: State 2, dark with pale spots/bands (*aurotaenia*, AMNH live exhibit). **D**: State 3, solid pale (*terribilis*, AMNH live exhibit). **E**: State 4, brown with dark brown bands/blotches (*inguinalis*, LACM 42409). **F**: State 5, dark with pale longitudinal stripe (*flavopictus*, AMNH 88642).

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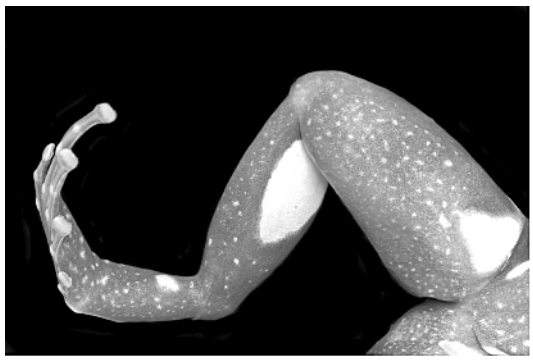

Fig. 36. Character 51, discrete pale proximoventral calf spot. State 1, present (*imbricolus*, AMNH 102082).

bands/blotches = 4; dark with pale longitudinal stripe = 5. Nonadditive.

51. Discrete Pale Proximoventral Calf Spot (fig. 36): absent = 0; present = 1.

Silverstone (1975a, 1975b) used the absence (state 0) and presence (state 1) of a discrete, pale spot on the proximal portion of the concealed surface of the shank to diagnose species and species groups. In life it is a bright flash mark. A number of species (e.g., *fraterdanieli*) have bright flash coloration on the concealed surface of the shank, but it does not form a discrete spot and we therefore follow Silverstone in scoring this character as absent for those species.

52–57. Pale Lateral Stripes

Edwards (1974a) used the combinations of pale lateral stripes (or lines) to diagnose species of *Colostethus*, identifying dorsolateral, oblique lateral, and ventrolateral stripes. Previous workers (e.g., Savage, 1968) had drawn attention to these characteristics as well, but Edwards standardized the distinction between the three stripes and has been followed by most authors. Nevertheless, caution must be employed when consulting the literature, as terminology varies. For example, what is referred to here as the oblique lateral stripe was referred to as a dorsolateral stripe by Edwards (1971) and Haddad and Martins (1994), and consistently as the inguinal stripe by La Marca (e.g., 1985, 1996 ''1994'', 1998 ''1996''; see also Myers and Donnelly, 2001). Duellman and Simmons (1988) discussed these characters as ''pale longitudinal stripes'', and Coloma (1995) followed their usage. Duellman (2004) distinguished between the oblique lateral and dorsolateral stripes in his Summary of Taxonomic Characters but used them interchangeably in the text (e.g., *idiomelus* and *sylvaticus* are diagnosed as lacking oblique lateral stripes and possessing dorsolateral stripes, but the converse is true for both species; e.g., see Duellman's figs. 5F and 6F).

Edwards (1974a) was concerned only with the mostly cryptically colored dendrobatids then referred to *Colostethus* and not the more conspicuously colored species referred to *Dendrobates* and *Phyllobates*. The broader sample of the present study showed that there are (at least) two distinct ''dorsolateral'' stripes, which we have designated A (Character 52) and B (Character 53), the latter also having been confused previously with the oblique lateral stripe.

52. Dorsolateral Stripe A (Does Not Drop to Thigh; fig. 37): absent = 0; present in juveniles only (i.e., lost ontogenetically) = 1; anterior, narrow, faint = 2; complete = 3. Nonadditive.

This dorsolateral stripe runs posteriad from the eyelid toward the tip of the urostyle. It does not cross the flank toward the groin (oblique lateral stripe), nor does it drop to the top of the thigh (dorsolateral stripe B). Myers et al. (1978) reported that in *bicolor* and *terribilis* the dorsolateral stripe is present in juveniles and lost ontogenetically (state 1). This ''loss'' is peculiar, however, as it is due to the hypertrophy of the bright dorsolateral stripes that expand ontogenetically to cover the entire dorsum, thus creating a uniformly colored, stripeless color pattern.[5] In state 2, the dorsolateral stripe is short, narrow, and inconspicuous (often more conspicuous in juveniles than adults), running from the

[5]In a captive breeding colony, A. Haas (in litt., 08/08/05) observed that ''yellow coloration appeared between the stripes (i.e., not a hypertrophy of the stripes); thus the process was more like filling in the gap between the stripes'', suggesting that the dorsolateral stripes are retained but concealed by the surrounding coloration. Further investigation into this character-state is warranted.

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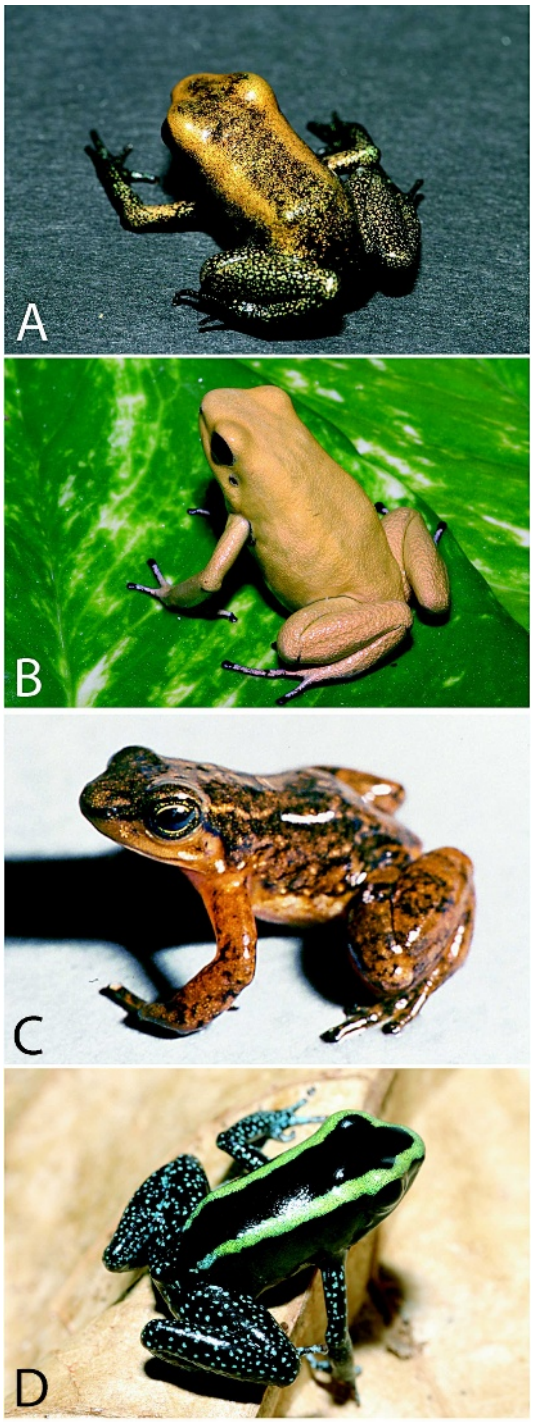

Fig. 37. Character 52, dorsolateral stripe A. **A**, **B**: State 1, present in juveniles (**A**), absent in adults (**B**) (*terribilis*, **A**: captive-raised specimen; **B**: AMNH live exhibit). **C**: State 2, anterior, narrow, faint (*atopoglossus*, holotype UVC 12068). **D**: State 3, complete (*aurotaenia*, AMNH live exhibit).

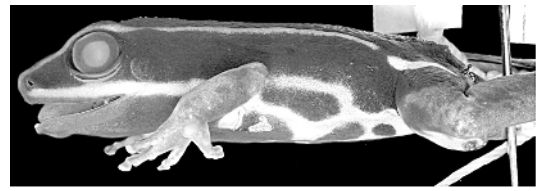

Fig. 38. Character 53, dorsolateral stripe B. State 1, present (*femoralis*, AMNH 140646).

posterior edge of the eye to a point just past the insertion of the arm. When present, the dorsolateral stripe of most species is complete, reaching or surpassing the level of the sacrum, and persists in adults (state 3).

The ontogenetic loss of the dorsolateral stripe is suggestive of additivity (i.e., absent ↔ present in juveniles only ↔ present throughout ontogeny); however, given the peculiarity of this particular "loss" through expansion, the additivity absent ↔ present throughout ontogeny ↔ present in juveniles only may be more appropriate. Regardless, it is unclear where state 2 would fit into this series, as there is no evidence that the dorsolateral stripe extends posteriorly through development, nor that state 2 is the result of reduction from a complete dorsolateral stripe. We therefore did not specify the additivity of this transformation series.

53. Dorsolateral Stripe B (Drops to Top of Thigh, Not Groin; fig. 38): absent = 0; present = 1.

This dorsolateral stripe extends posteriad from the eyelid along the dorsolateral edge of the body and turns abruptly ventrad at a position immediately anterior to the thigh. This stripe was considered to be dorsolateral by Silverstone (1975a) and Caldwell and Myers (1990) for *quinquevittatus*, but oblique lateral ("lateral") by Silverstone (1976) for *femoralis*. The confusion is understandable, as its path is intermediate between these two characters. Unlike the oblique lateral stripe, it does not run diagonally along the flanks but remains dorsal until almost the level of the thigh, but unlike dorsolateral stripe A, it drops toward the thigh posteriorly.

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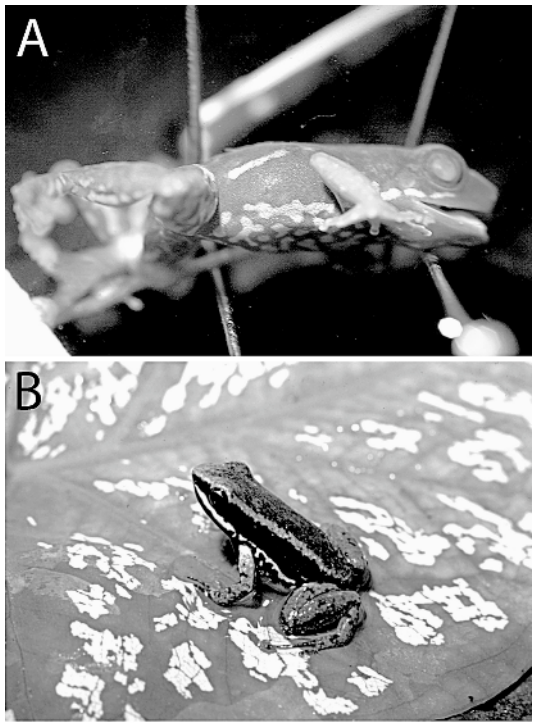

Fig. 39. Character 54, ventrolateral stripe. **A**: State 1, wavy series of elongate, interconnected spots (*espinosai*, AMNH 104875). In this specimen the spotting forms a fairly contiguous wavy stripe, but it is common for the elongate spots to be separated, forming a broken stripe. **B**: State 2, straight (*talamancae*, AMNH 69829, photo by R. Zweifel). Note also that the pale dorsolateral stripe does not drop toward the thigh posteriorly (Character 52, state 3).

54. VENTROLATERAL STRIPE (fig. 39): absent = 0; wavy series of elongate spots = 1; straight = 2. Nonadditive.

The ventrolateral stripe (VLS) runs along the ventral edge of the flank between the belly and the usually dark coloration of the flank. It may be present as a wavy series of elongate, often interconnected spots (state 1) or as a straight line (state 2). The ventrolateral stripe can be difficult to detect in preserved specimens, even those in which the ventrolateral stripe was prominent in life, because of the degradation of iridophores, especially in taxa with fairly pale ventral surfaces. In some of these cases the ventrolateral stripe can be detected as a lack of melanophores. However, the iridophores break down fairly quickly in preservative, often revealing a deeper layer of underlying melanophores invisible in living or freshly preserved specimens.

Coloma (1995: 47–48) reported that some specimens of *pulchellus* have "an interrupted white ventrolateral line", but we did not observe this in the specimens examined. Caldwell and Lima (2003) reported the ventrolateral stripe as absent and described the holotype of *nidicola* as having "irregular white blotches, not forming a stripe". However, a wavy VLS is evident in the photograph shown in their figure 3B (gravid female). Among the *trivittatus* specimens examined, the ventrolateral stripe is present in all specimens from Suriname but absent in all but one of the specimens from Peru (AMNH 43204, in which it is a series of small elongate spots on the left and a single, large elongate spot on the right).

55. OBLIQUE LATERAL STRIPE: absent = 0; present = 1.

The pale oblique lateral stripe extends from the groin diagonally across the flanks toward the eye.

56. OBLIQUE LATERAL STRIPE LENGTH (fig. 40): partial = 0; complete = 1.

Edwards (1974b) distinguished oblique lateral stripes (OLS) that extend from the groin part-way to the eye (partial, state 0) or all the way to the eye (complete, state 1). There is some individual variation in the anterior extension of the partial OLS, but it usually terminates prior to and does not extend past the level of the insertion of the arm. There is no evidence that the stripe develops from one end to the other, which is why we did not combine length with presence/absence as an additive multistate character (i.e., absent ↔ partial ↔ complete).

Edwards (1974b: 10) described the OLS of *sauli* as incomplete, which is supported by both his painting (p. 6) and the color plate of the same specimen in Coloma (1995: plate 1A). However, Coloma (1995) explicitly compared *sauli* only to those species having a complete oblique lateral stripe, and we have also observed it to be complete. We therefore scored this character as polymorphic.

57. OBLIQUE LATERAL STRIPE STRUCTURE (fig. 41): solid = 0; series of spots = 1; diffuse = 2. Nonadditive.

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Fig. 40. Character 56, oblique lateral stripe length. **A**: State 0, partial (*panamensis*, AMNH 69836, photo by R. Zweifel). **B**: State 1, complete (*fraterdanieli*, MHNUC 364).

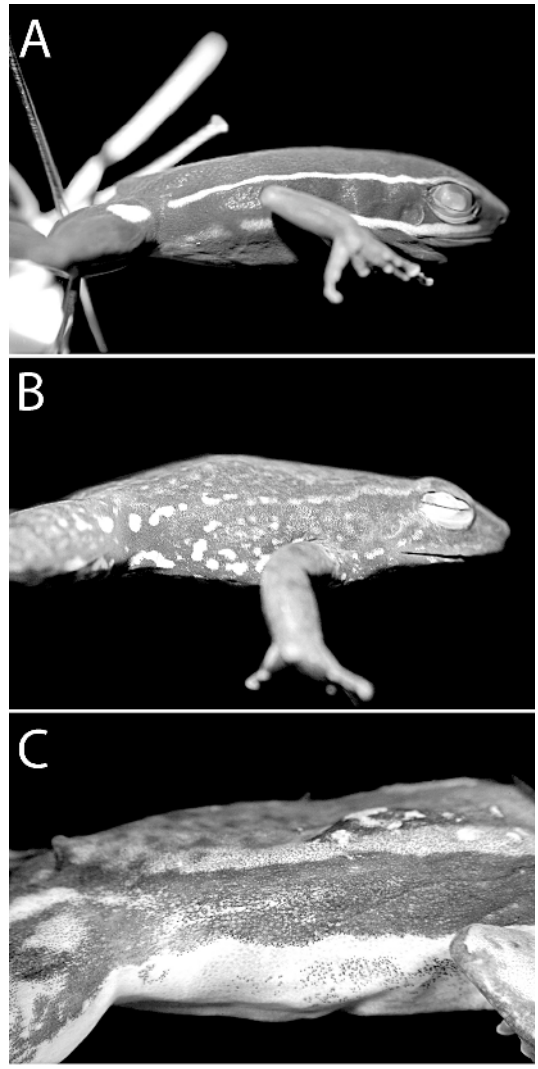

Fig. 41. Character 57, oblique lateral stripe structure. **A**: State 0, solid (*pulchripectus*, AMNH 137290). **B**: State 1, series of spots (*mertensi*, ICN 43698). **C**: State 2, diffuse (*trilineatus*, AMNH 171974).

The oblique lateral stripe (OLS) of most species consists of a solid line of pale pigmentation (e.g., *nubicola*; state 0). Lynch and Ruiz-Carranza (1985) identified state 1 (series of well-defined spots) in *agilis*, and Myers et al. (1991: 2, 3, figs. 1, 3) illustrated it photographically for *nocturnus*. Grant and Rodríguez (2001) discussed variation in this character and described and illustrated photographically state 2. As shown in Grant and Rodríguez (2001: 9, fig. 6), state 2 may also include spots, but they are smaller, less distinct, and arranged irregularly (not in a line).

58. GULAR–CHEST MARKINGS (fig. 42): absent = 0; present = 1.

A number of species from the Andes of southern Colombia, Ecuador, and Peru possess highly variable dark spots or blotches on the posterolateral portion of the gular–chest region. Myers et al. (1991) compared these markings with the collars of several Venezuelan species and considered the possibility that they may be homologous. We code them as different transformations series here, the difference being that the gular–chest markings are always separated medially and do not form a continuous transverse band.

Coloma (1995: 10) reported several variants in the shape and pattern of the gular–

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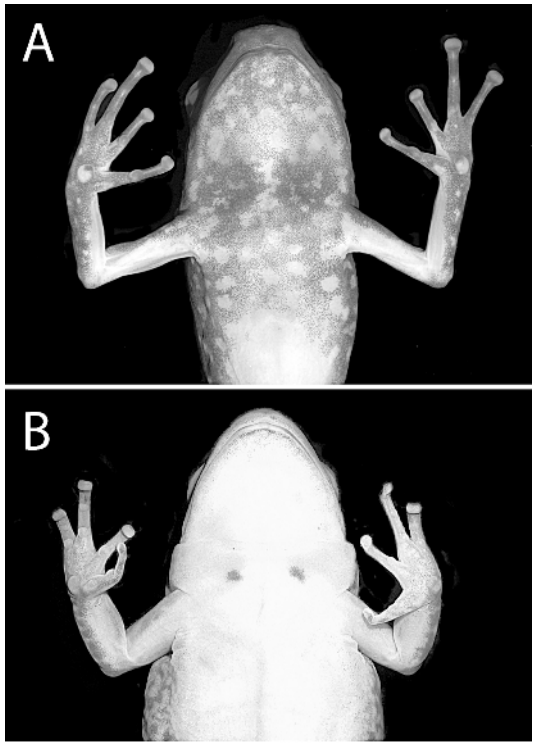

Fig. 42. Character 58, markings on gular–chest region, state 1 (present). **A**: Diffuse, white-spotted blotches (*awa*, AMNH 111542). **B**: Discrete, small dark spots (*vertebralis*, USNM 28232). Despite their differing shapes and patterns, we treated the occurrence of these markings as a single character-state.

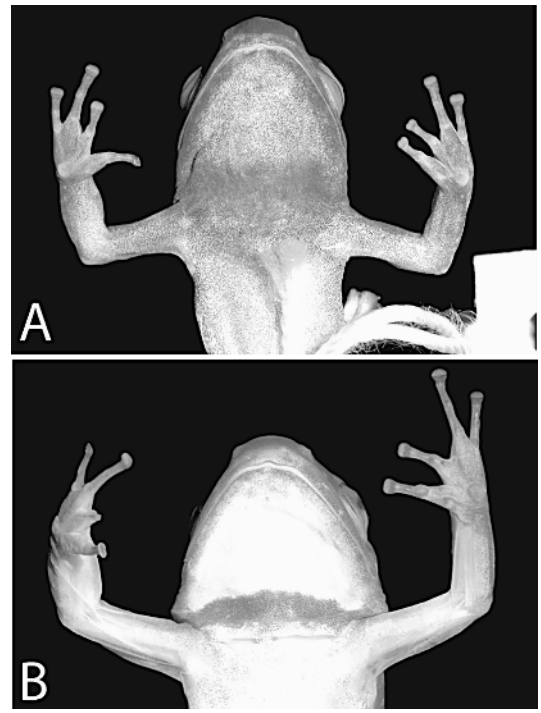

Fig. 43. Character 59, dermal collar, state 1 (present) in *trinitatis*. **A**: Male (UMMZ 167474). **B**: Female (UMMZ 167471). In this species, the dermal collar of males is diffuse and broad, but is clearly distinguished from the fainter gray stippling of the adjacent surfaces.

chest markings. Much of this variation is intraspecific, and Coloma reported ontogenetic changes. Consequently, until this variation is better understood, we treated all of these variants as homologous and subsumed their occurrence within a single character-state. Although Coloma (1995: 10) discussed them in the same context, the markings on the mental region and the pair of spots on the posterior chest do not occur in the same region, and we did not treat them as part of this transformation series.

Coloma (1995) reported the presence of diffuse bandlike markings in *bocagei*, but it was absent from all the specimens we examined.

59. Dark Dermal Collar (fig. 43): absent = 0; present = 1.

The dermal collar (''chest markings'' of La Marca, 1995) is a continuous transverse band of dark pigmentation that extends across the posterior throat, anterior to the arms. Although La Marca (1996 ''1994'') reported sexual variation in its occurrence, we observed it to be present in adults of both sexes of all species that possess the dermal collar (although we did observe polymorphism in males of *neblina*), so we did not code males and females as separate semaphoronts.

Rivero (1978 ''1976'': 330; translated from the Spanish) noted that ''[i]n almost all specimens [of *leopardalis*] a faint dark collar may be detected, never as clear and well defined as in *C. collaris*, and generally confined to the sides of the throat.'' Similarly, Myers et al. (1991) noted the occurrence of faint collarlike pigmentation on the throat of many specimens of *nocturnus*. Closer examination and dissection revealed that

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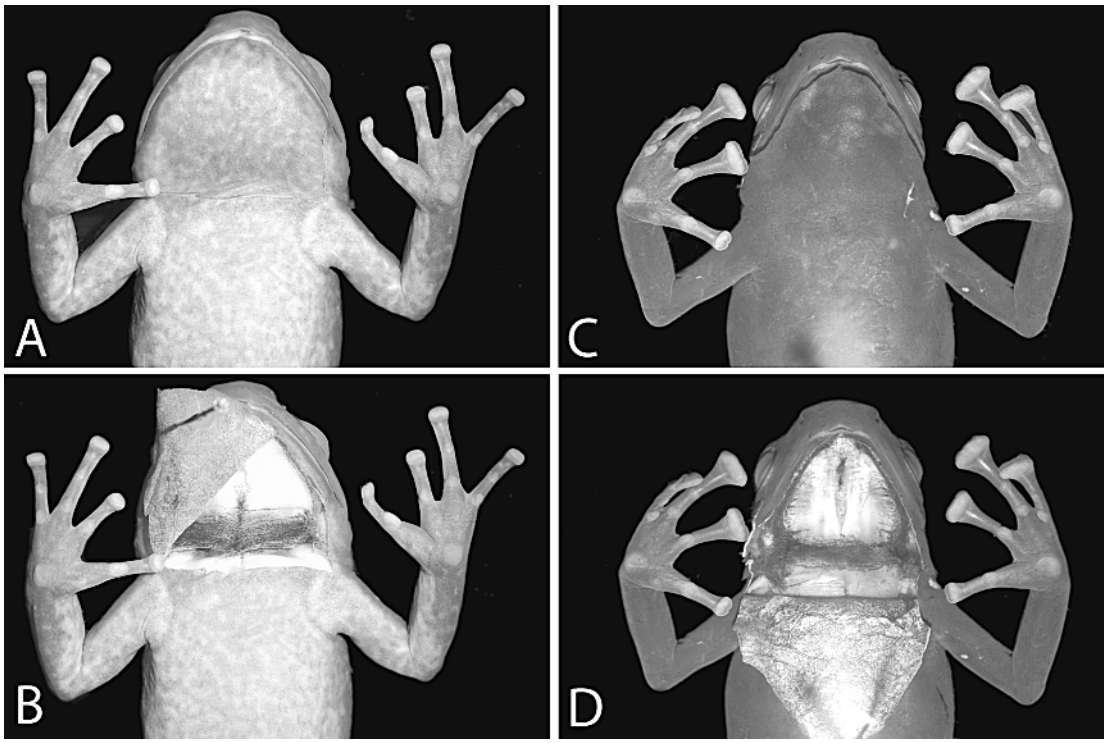

Fig. 44. Extensive subdermal melanosis of the collar region. **A**, **B**: *nocturnus* (AMNH 130008). **C**, **D**: *galactonotus* (AMNH 128233). Note also the irregular (clumped) stippling or faint, diffuse spotting in **A** (character 61, state 6; see below).

these dark collars are not caused by melanophores in the skin, as they are in other collared species (e.g., *collaris*), but instead by melanophores in the epimysium of the m. interhyoideus and connective tissue in the hyomandibular sinus (i.e., anterior to the pectoral apparatus) that are visible through the semitranslucent skin (fig. 44). The density of melanophores varies among individuals, with males having greater density (and therefore a more prominent collar) than females. Dense subdermal pigmentation may also occur in species with dark dermal pigmentation (e.g., *galactonotus*; see fig. 44), and individuals with dermal collars may (or may not) also present extensive subdermal pigmentation. In *leopardalis* (e.g., UMMZ 17170) the subdermal pigmentation is not as concentrated but still accounts for the faint collar reported by Rivero. Some degree of melanosis of the collar region is widespread among dendrobatids. However, as observed in pigmentation of the flesh generally, variation is continuous from a few melanophores scattered across the throat to a solid subdermal collar. As discussed above, we suspect there are valid transformation series here, but we were unable to delimit them objectively for the present study.

60. Dark Lower Labial Stripe (fig. 45): absent = 0; present = 1.

In *fraterdanieli* Grant and Castro-Herrera (1998) indicated the occurrence of a distinctive dark (black or brown) line along the lower lip and contrasting with the pale adjacent coloration.

61–64. Male and Female Throat and Abdominal Coloration

The color and color pattern of the throat and abdominal regions of adult males and females provide some of the most useful characters for discriminating among species of dendrobatids. Sexual dimorphism is com-

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Fig. 45. Character 60, dark lower lip line. State 1, present (*fraterdanieli*, MHNUC 364).

mon, especially in throat color and color pattern, but most states occur in both sexes.

In a series of field experiments, Narins et al. (2003) showed that both vocalization and pulsation of the dark vocal sac of *femoralis* are necessary to elicit aggressive responses, and they have experimented with this system to reveal the extent of temporal and spatial integration of these stimuli required for an aggressive response (Narins et al., 2005). Given the extent of species- and sex-specific variation in throat coloration in many dendrobatids, it is likely that integration of visual and vocal cues will be found to be widespread. To date Narins et al.'s investigations have only examined aggressive male–male interactions in this single species, but application of their procedures more generally promises to reveal fascinating insights into the role of throat coloration in aggresive and other interactions between males, females, and juveniles across multiple species.

A few points apply to the coding of all the following characters. First, as discussed above, we emphasized color pattern over color. Second, spotting, marbling, and reticulation form a continuous gradient that, though unambiguous in the extremes, we were unable to delimit objectively. We therefore treated these as a single character-state, although we undoubtedly overlooked additional transformations by doing so. Third, it may be difficult to discriminate between pale spotting/reticulation/marbling on a dark background versus dark spotting/reticulation/marbling on a pale background, as the distinction has to do with adjacent coloration and the relative concentration of pale and dark pigmentation. Many species are unambiguously one or the other, but others were either ambiguous or exhibited both states and were therefore coded as polymorphic. Fourth, we also treated irregular stippling (i.e., clumped stippling) and the occurrence of diffuse dark spotting as a single state because we were unable to discriminate two states objectively. Finally, the collar and gular–chest markings (characters 58, 59) are independent of the region referred to as the throat. For our purposes, throat refers to the region of the central gular region, that is, the area of the vocal sac in males.

61. MALE THROAT COLOR (figs. 44A, 46): pale, free or almost free of melanophores = 0; dark due to absence of iridophores = 1; evenly stippled = 2; pale with discrete dark spotting/reticulation/marbling = 3; solid dark = 4; dark with discrete pale spotting/reticulation/marbling = 5; irregular (clumped) stippling or faint, diffuse spotting = 6. Nonadditive.

In state 0 (pale, free or almost free of melanophores) the throat appears immaculate, but closer inspection may reveal sparse, inconspicuous melanophores. State 1 (dark due to absence of iridophores) is conspicuous in life but may easily be overlooked in preserved specimens. See Grant and Castro-Herrera (1998) for this character-state in life. The spotting/reticulation/marbling of the vocal sac is often irregular. State 6 (dark with pale medial stripe) is restricted to only *boulengeri* and *espinosai*. In both species the medial "stripe" varies from one or more elongate spots to a solid stripe. Also, the adjacent dark surfaces sometimes include scattered pale spots. States 0–5 are shown in figure 46; state 6 is shown in figure 44A.

62. FEMALE THROAT COLOR (fig. 47): pale, free or almost free of melanophores = 0; irregular (clumped) stippling or faint, diffuse spotting = 1; solid dark = 2; dark with discrete pale spotting/reticulation/marbling = 3; pale with discrete dark spotting/reticulation/marbling = 4; dark with pale medial longitudinal stripe = 5. Nonadditive.

63. MALE ABDOMEN COLOR (fig. 48): pale, free or almost free of melanophores = 0; pale with discrete dark spotting/reticulation/mar-

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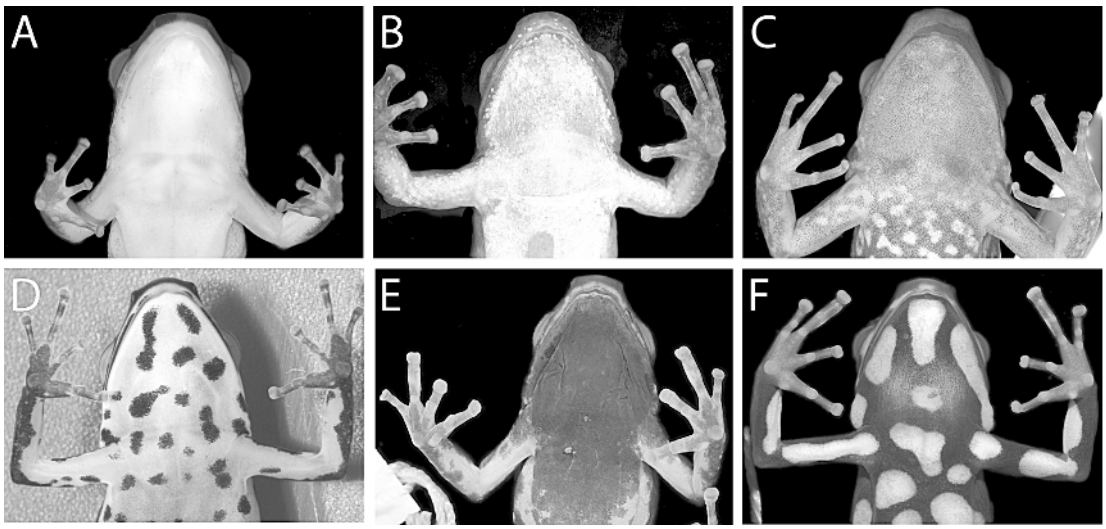

Fig. 46. Character 61, male throat color. **A**: State 0, pale, free or almost free of melanophores (''Neblina species'', AMNH 118689). **B**: State 1, dark due to absence of iridophores (*abditaurantius*, ICN 9853). This character-state is inconspicuous in preserved specimens but obvious in living or recently prepared specimens. **C**: State 2, evenly stippled gray (*infraguttatus*, AMNH 104846). Note that the gular–chest markings (character 58) of *infraguttatus* do not interfere with the even stippling of the throat. **D**: State 3, pale with dark spots (''*nubicola*-spC'', MHNUC 321). **E**: State 4, solid dark (*inguinalis*, LACM 42329). **F**: State 5, dark with discrete pale spotting/reticulation/marbling (*tricolor*, USNM 286082).

bling = 1; evenly stippled = 2; dark with discrete pale spotting/reticulation/marbling = 3; irregular (clumped) stippling or faint, diffuse spotting = 4; solid dark = 5. Non-additive.

64. Female Abdomen Color (fig. 49): pale, free or almost free of melanophores = 0; pale with discrete dark spotting/reticulation/marbling = 1; solid dark = 2; dark with discrete pale spotting/reticulation/marbling = 3; irregular (clumped) stippling or faint, diffuse spotting = 4; evenly stippled = 5. Nonadditive.

Coloma (1995: 54) described *vertebralis* as having ''dark stippling on abdomen in females, darker in males''; however, none of the females in the series AMNH 17458, 17604–08, 140977–141011 possesses any stippling on the abdomen (but all males do). Although we coded *riveroi* as having the abdominal region evenly stippled, in life it is posteriorly orange (Donoso-Barros, 1965 ''1964'').

65. Iris Coloration (fig. 50): lacking metallic pigmentation and pupil ring = 0; possessing metallic pigmentation and pupil ring = 1.

Silverstone (1975a: 8) noted that in life the iris of the species he included in *Dendrobates* is ''black (or rarely dark brown) and is never reticulated''. Similarly Silverstone (1976: 3) stated that in the species he included in *Phyllobates* ''the iris is black or brown (rarely bronze) and never reticulated''. We diagnose this character somewhat more precisely, but we believe our intentions are the same.

The iris coloration of most dendrobatids includes metallic pigmentation (bronze, copper, gold, silver) producing a metallic iris with a black reticulated pattern or a black iris with metallic flecks. Additionally, a distinct metallic ring around the pupil invariably occurs in irises with metallic pigmentation. A number of the aposematic dendrobatids lack all metallic pigmentation in the iris, giving rise to the solid black or brown iris mentioned by Silverstone.

This character can only be coded from living specimens. We dissected the eyes of preserved specimens of several species but

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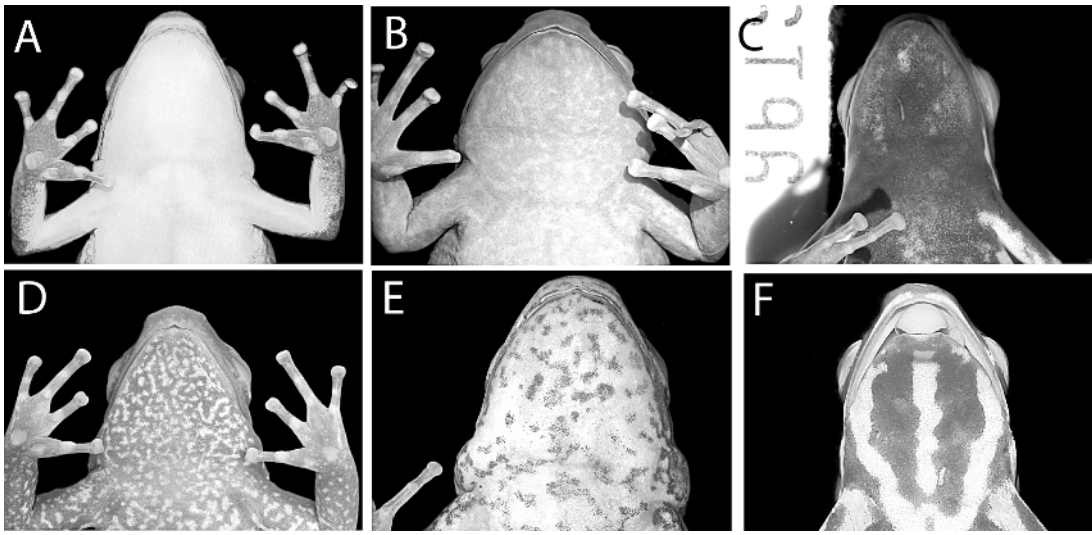

Fig. 47. Character 62, female throat color. **A**: State 0, pale, free or almost free of melanophores (*undulatus*, AMNH 159128). **B**: State 1, irregular (clumped) stippling or faint, diffuse spotting (*nocturnus*, AMNH 130018). **C**: State 2, solid dark (*hahneli*, AMNH 96190). **D**: State 3, dark with discrete pale spotting/reticulation/marbling (*imbricolus*, AMNH 102083). **E**: State 4, pale with discrete dark spotting/reticulation/marbling (*fraterdanieli*, AMNH 148021). **F**: State 5, dark with pale medial longitudinal stripe (*boulengeri*, USNM 145281).

failed to detect differences between pigmented and unpigmented irises. We therefore relied on explicit field notes, personal observations, and high-quality photographs. In addition to personal observations and unpublished field notes and photographs, this character was scored from the following published accounts: *arboreus* (Myers et al., 1984); *aurotaenia* (Silverstone, 1976; Lötters et al., 1997a); *azureiventris* (Kneller and Henle, 1985; Lötters et al., 2000); *awa* (Coloma, 1995); *baeobatrachus* (Lescure and Marty, 2000); *bicolor* (Myers et al., 1978; Lötters et al., 1997a); *bocagei* (Coloma, 1995); *boulengeri* (Silverstone, 1976); *caeruleodactylus* (Lima and Caldwell, 2001); *claudiae* (Jungfer et al., 2000); *delatorreae* (Coloma, 1995); *degranvillei* (Boistel and de Massary, 1999; Lescure and Marty, 2000); *elachyhistus* (Coloma, 1995; Duellman, 2004); *flotator* (Savage, 2002), *Eupsophus roseus* ([for *E. calcaratus*] Nuñez et al., 1999); *granuliferus* (Myers et al., 1995; Savage, 2002); *herminae* (La Marca, 1996 ''1994''); *Hylodes phyllodes* (Heyer et al., 1990); *ideomelus* (Duellman, 2004); *imitator* (Symula et al., 2001); *infraguttatus* (Coloma, 1995); *insperatus* (Coloma, 1995); *insulatus* (Duellman, 2004); *kingsburyi* (Coloma, 1995); *lehmanni* Myers and Daly (Myers and Daly, 1976b); *lugubris* (Silverstone, 1976; Savage, 2002); *macero* (Rodríguez and Myers, 1993; Myers et al., 1998); *machalilla* (Coloma, 1995); *molinarii* (La Marca, 1985); *nexipus* (Frost, 1986; Hoff et al., 1999); *nidicola* (Caldwell and Lima, 2003); *nocturnus* (Myers et al., 1991); *nubicola* (Savage, 2002), *parvulus* (Silverstone, 1976); *pictus* (Köhler, 2000); *petersi* (Rodríguez and Myers, 1993; Myers et al., 1998); *pulchellus* (Coloma, 1995); *pulchripectus* (Silverstone, 1975a); *pulcherrimus* (Duellman, 2004); *pumilio* (Myers et al., 1995; Savage, 2002); *quinquevittatus* (Caldwell and Myers, 1990); *reticulatus* (Myers and Daly, 1983); *rubriventris* (cover of Herpetofauna 19(110); see also Lötters et al., 1997b); *sauli* (Coloma, 1995); *silverstonei* (Myers and Daly, 1979); *speciosus* (Jungfer, 1985); *sylvaticus* Barbour and Noble (Duellman, 2004); *sylvaticus* Funkhouser (Myers and Daly, 1976b [as *histrionicus*]; Lötters et al., 1999); *talamancae* (Coloma, 1995); *terribilis* (Myers et al., 1978); *toachi* (Coloma, 1995); *trinitatis* (Wells, 1980c; La Marca,

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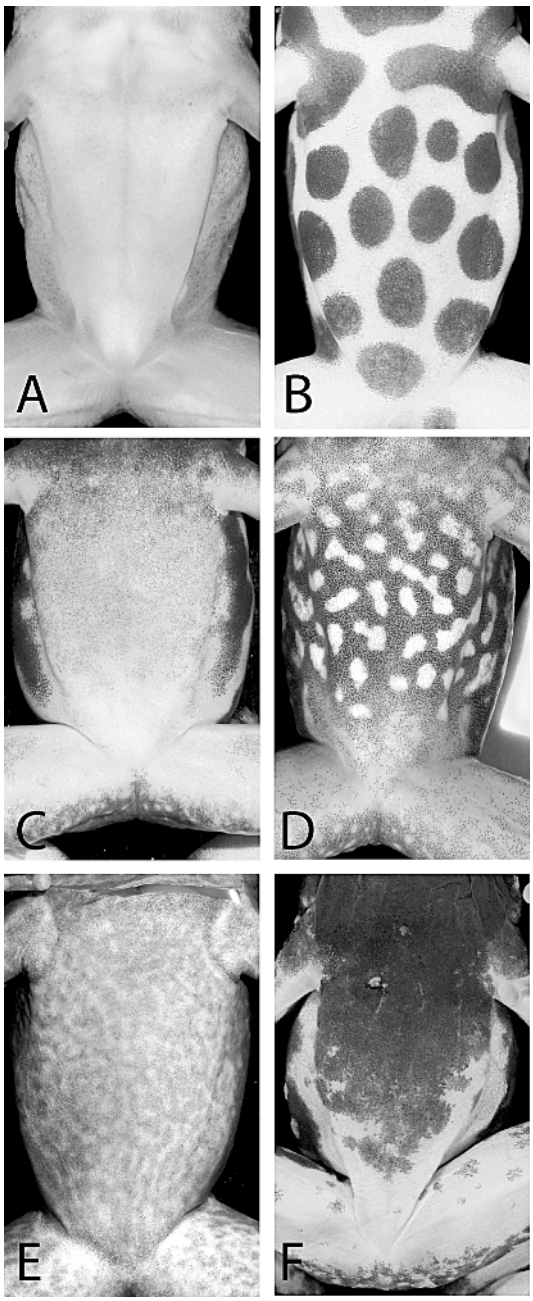

Fig. 48. Character 63, male abdomen color. **A**: State 0, pale, free or almost free of melanophores (''Neblina species'', AMNH 118689). **B**: State 1, pale with discrete dark spotting/reticulation/marbling (*quinquevittatus*, AMNH 124069). **C**: State 2, evenly stippled (*talamancae*, AMNH 113893). **D**: State 3, dark with discrete pale spotting/reticulation/marbling (*infraguttatus*, AMNH 104846). **E**: State 4, irregular (clumped) stippling or faint, diffuse spotting (*nocturnus*, AMNH 130012). **F**: State 5, solid dark (*inguinalis*, LACM 42329).

1996 ''1994''); *trivittatus* (Myers and Daly, 1979); *undulatus* (Myers and Donnelly, 2001); *vanzolinii* (Myers, 1982); *ventrimaculatus* (Lötters, 1988 [as *quinquevittatus*]; Lescure and Bechter, 1982 [as *quinquevittatus*]); *vertebralis* (Coloma, 1995); *vicentei* (Jungfer et al., 1996b); *vittatus* (Silverstone, 1976; Savage, 2002); *zaparo* (Silverstone, 1976).

66. Large Intestine Color (fig. 51): unpigmented = 0; pigmented anteriorly = 1; pigmented extensively = 2. Additive.

The large intestine of most species is unpigmented (state 0), being either white or (when distended) translucent. In some species, heavy melanosis forms a solid black coloration extending posteriad from the front of the large intestine. In state 1 the melanosis is confined to the anterior quarter of the large intestine; in state 2 it extends beyond the midlevel of the large intestine. The ontogeny of this character invariably progresses from state 0 through state 1 to state 2, which we interpret as evidence for the additivity of this transformation series.

67. Adult Testis (Mesorchium) Color (fig. 52): unpigmented = 0; pigmented medially only = 1; entirely pigmented = 2. Additive.

Testis color is scored from adults only. In all dendrobatids we have examined, testis pigmentation increases ontogenetically, with the mesorchia of juveniles being invariably entirely unpigmented white (state 0) and melanosis beginning medially (state 1) and eventually covering the testis entirely (state 2), forming either a dark reticulum or a solid dark color. Ontogenetic series show this character to develop from state 0 to state 1 to state 2, which we interpret as evidence of additivity.

Polymorphism among adults is rare. Grant (2004) found that of 40 specimens of *panamensis* scored, the left testes of two were unpigmented whereas the right testes were pigmented brown. Grant (2004) also documented unusual variation in the testis pigmentation of *inguinalis*. Testes of all adults

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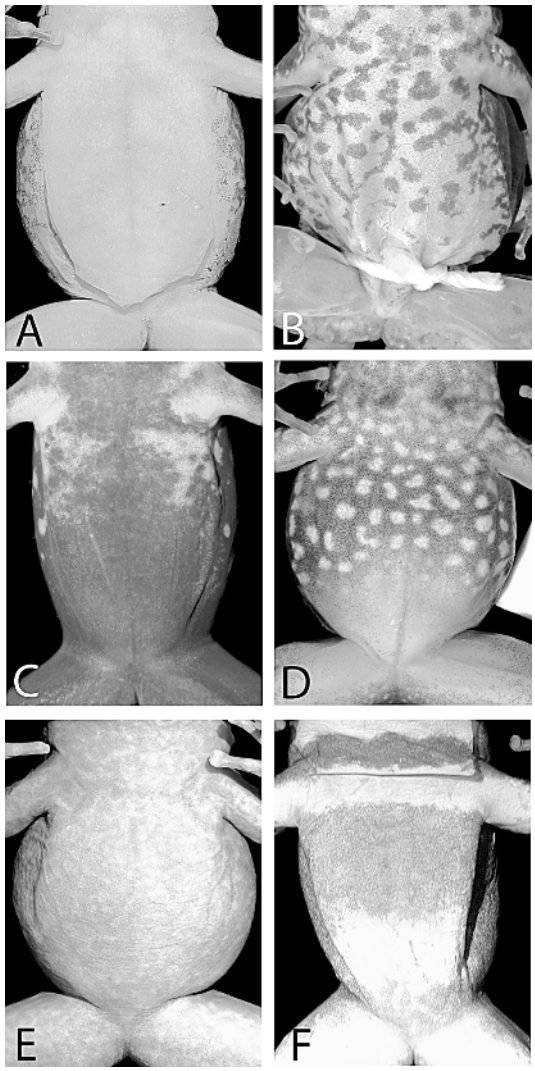

Fig. 49. Character 64, female abdomen color. **A**: State 0, pale, free or almost free of melanophores (*undulatus*, AMNH 159128). **B**: State 1, pale with dark spotting/reticulation/marbling (*fraterdanieli*, AMNH 39360). **C**: State 2, solid dark (*silverstonei*, AMNH 91845). **D**: State 3, dark with discrete pale spotting/reticulation/marbling (*infraguttatus*, AMNH 104849). **E**: State 4, irregular (clumped) stippling or faint, diffuse spotting (*nocturnus*, AMNH 130018). **F**: State 5, evenly stippled (*riveroi*, AMNH 134141).

had some degree of dark pigmentation, but it varied from being confined to medial and anterior surfaces to engulfing the entire testis; this variation was not correlated with adult

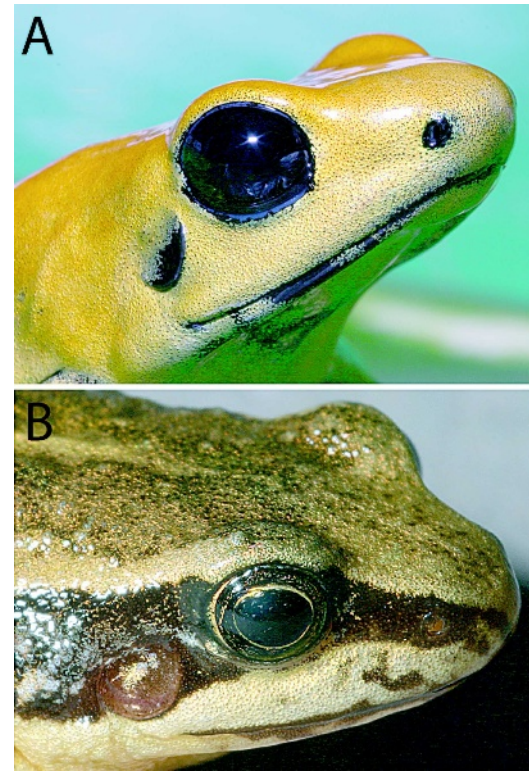

Fig. 50. Character 65, iris coloration. **A**: State 0, lacking metallic pigmentation and pupil ring (*bicolor*, AMNH live exhibit). **B**: State 1, with metallic pigmentation and pupil ring (*subpunctatus*, uncataloged MUJ specimen from Colombia: Bogotá, D.C., campus of Universidad Nacional de Colombia).

size, extent of dark ventral pigmentation, or maturity. It is likely that such variation is hormonally controlled and related to sexual activity, but no evidence exists to support this conjecture. Among the included outgroup taxa, Lötters (1996) reported that, although most species of *Atelopus* possess permanently unpigmented testes, in some species the testes become pigmented with the onset of the breeding season.

68. Color of Mature Oocytes (fig. 53): unpigmented (uniformly white or creamy yellow) = 0; pigmented (animal pole brown or black) = 1.

The entire oocyte may be white or creamy yellow (state 0) or differential localization of pigment granules in the animal cortex may give rise to a dark (brown or black) animal

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hemisphere and white or creamy yellow vegetal hemisphere (state 1).

Duellman and Trueb (1986) explained egg pigmentation as an adaptation to exposure to sunlight, and they listed a number of anuran groups in support of that hypothesis. However, it is unclear if that adaptive explanation holds among dendrobatids, given that many species with pigmented eggs lay clutches that are not exposed to sunlight. For example, Myers and Daly (1979) found "a clutch of 30 eggs … on a curled dry leaf that was completely concealed by another leaf of the cut-over forest floor", yet that species has pigmented eggs. It has also been conjectured (e.g., Duellman and Trueb, 1986) that this melanosis either raises egg temperature by better absorbing ambient heat or provides protection from exposure to ultraviolet radiation. Missing from previous discussions is an evaluation of the polarity of the transformations. Until this is evaluated through phylogenetic analysis, it is impossible to know if a particular instance of pigmentation (or lack of pigmentation) is apomorphic (and therefore a candidate for an explanation of adaptation) or symplesiomorphic.

Duellman and Trueb (1986: 535) reported that *Rhinoderma darwinii* possesses unpigmented ova, but specimens examined had pigmented ova.

69. M. SEMITENDINOSUS INSERTION (figs. 54, 55): "bufonid type" (ventrad) = 0; "ranid type" (dorsad) = 1.

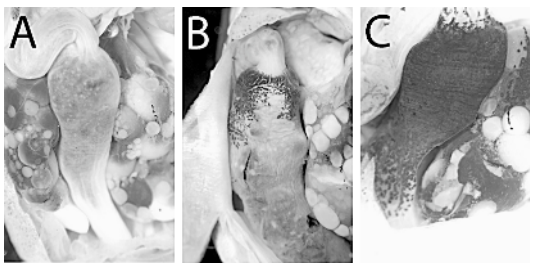

Fig. 51. Character 66, large intestine color. **A**: State 0, unpigmented ("Neblina species", AMNH 118679). Note that the distended tissue is translucent. **B**: State 1, anteriorly pigmented (*pratti*, SIUC 07654). **C**: State 2, extensively pigmented (*beebei*, ROM 39631).

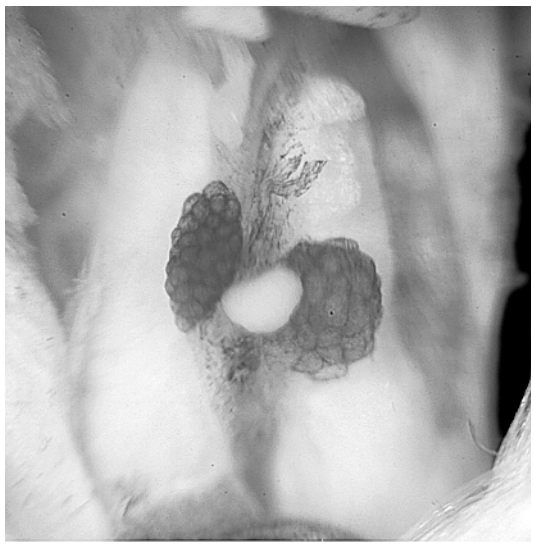

Fig. 52. Character 67, adult testis (mesorchium) color. State 2, entirely pigmented testes (*claudiae*, AMNH 124257) in ventral view.

Noble's (1922) seminal work brought thigh musculature to the forefront of studies of anuran relationships, and since then the path of insertion of the distal tendon of the m. semitendinosus has played an important role in discussions of dendrobatid relationships (reviewed by Grant et al., 1997). Noble identified two predominant morphologies: (1) the putatively primitive "bufonid type" in which the tendon of the m. semitendinosus inserts ventrad to the tendon of insertion of the mm. gracilis complex, and (2) the putatively derived "ranid type" in which it inserts dorsad to the mm. gracilis.

Noble also reported a number of "intermediate" morphologies, including that of dendrobatids. However, the m. semitendinosus of dendrobatids clearly inserts dorsal to

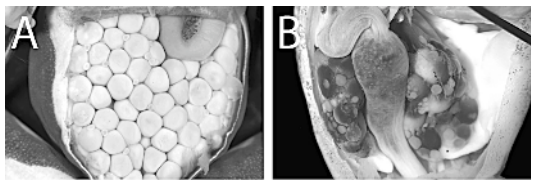

Fig. 53. Character 68, mature ova color. **A**: State 0, white or yellowish (*Atelopus spurrelli*, AMNH 50983). **B**: State 1, pigmented (brown) ("Neblina species", AMNH 118679).

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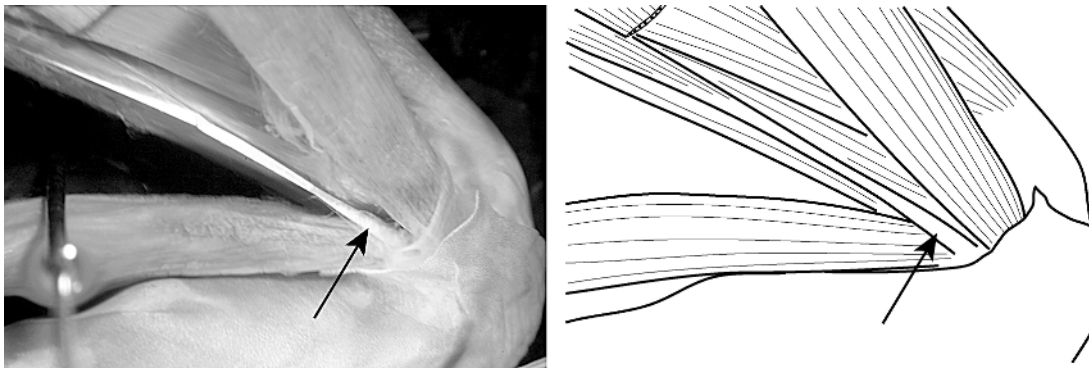

Fig. 54. Character 69, m. semitendinosus insertion. Photograph (left) and outline drawing (right) of ventral view of distal thigh of *Thoropa miliaris* (AMNH 17044), showing state 0, ventrad ''bufonid'' path of insertion. Arrow indicates the m. semitendinosus tendon of insertion.

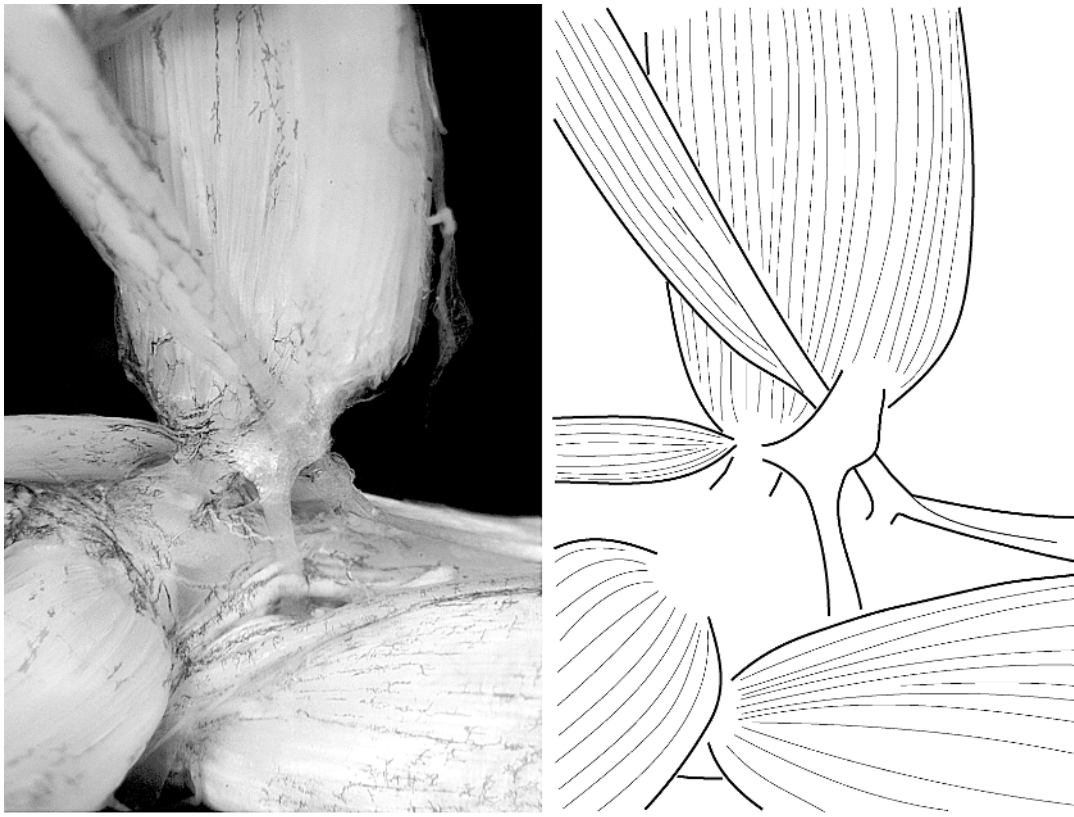

Fig. 55. Character 70, m. semitendinosus binding tendon. State 1, present (*aurotaenia*, AMNH 161109), photograph (left) and outline drawing (right) showing view of the concealed surface of the knee. The mm. gracilis complex is deflected ventrally to reveal the dorsad ''ranid'' path of the m. semitendinosus and the secondary binding tendon that straps it to the outer edge of the mm. gracilis complex.

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the mm. gracilis, the apparent intermediacy owing to a secondary binding tendon (see Character 70, below). Similarly, Noble interpreted intermediate morphologies as providing evidence for the "inward migration" of the tendon of insertion of the m. semitendinosus from the presumptively primitive "bufonid" position to the derived "ranid" position. However, he relied on *phylogenetic* evidence to establish character additivity, not ontogenetic (or other) evidence. The groups Noble considered most primitive had "bufonid type" insertion, those he thought were most derived had "ranid type", and variants were treated as intermediate between the two. Such reasoning is obviously fallacious, as it conflates the premises of analysis with the conclusions. We are unaware of developmental evidence of inward migration of the m. semitendinosus tendon of insertion from the "bufonid" to the "ranid" position.

70. M. Semitendinosus Binding Tendon (fig. 55): absent = 0; present = 1.

As first described and illustrated by Noble (1922: 41 and plate XV, fig. 6)[6], the dendrobatid thigh has a well-defined binding tendon[7] that straps the m. semitendinosus distal tendon to the dorsal edge of the inner surface of the mm. gracilis complex (state 1; fig. 55). In some large species, such as *palmatus* and *nocturnus*, this binding tendon is robust and conspicuous, giving the impression that the distal tendon of the m. semitendinosus actually pierces or penetrates the distal mm. gracilis tendon (e.g., Dunlap, 1960: 66). However, even in these species the m. semitendinosus tendon does not pass *through* the tendinous tissue, but rather *between* the binding tendon and the gracilis muscle (therefore differing from myobatrachids; Noble, 1922; Parker, 1940). This tendinous tissue also forms a secondary tendon that inserts on the inner (posterior) surface of the proximal head of the tibiofibula. Another secondary tendon is often present, arising near the ventral edge of the inner surface of the m. gracilis and leading to the thick sheet of connective tissue that wraps around the knee. Distal to the binding tendon, the m. semitendinosus tendon expands to insert along the long axis of the ventral surface of the tibiofibula.

71. M. Levator Mandibulae Externus Division: undivided ("s") = 0; divided ("s + e") = 1.

In her dissertation, Starrett (1968[8]) found that the jaw adduction musculature of dendrobatids includes a single muscle originating from the zygomatic ramus of the squamosal that lies deep (internal, medial) to the mandibular ramus of the trigeminal nerve (V_3), which she interpreted as the presence of the m. adductor posterior mandibulae subexternus and absence of the m. adductor mandibulae externus superficialis, or condition "s" in her system (state 0). Silverstone (1975a) found this in all 41 species he examined, and other workers (Myers et al., 1978, 1991; Myers and Daly, 1979; Myers and Ford, 1986; Grant et al., 1997; Grant, 1998) have found this in almost all dendro-

[6]We examined the thigh musculature of AMNH 13472, the *palmatus* specimen drawn by Noble, and confirmed that his illustration is accurate in its depiction of the path of the m. semitendinosus tendon of insertion. However, his illustration is erroneous with regard to the m. gracilis minor and the insertion of the mm. adductor longus and adductor magnus. The m. gracilis minor is no longer present on the left thigh of AMNH 13472, but on the right it is an inconspicuous, narrow, thin muscle that merges distally with the m. gracilis major to share a common tendon of insertion, a morphology that conforms with all of our previous observations of dendrobatid thighs; we have never observed the m. gracilis minor to be as thick and broad as indicated by Noble's illustration. In fact, in many species the m. gracilis minor is completely undetectable distal to midlength of the thigh. Similarly, although the mm. adductor longus and adductor magnus remain independent along most of the length of the femur, they fuse distally to share a common insertion in the dendrobatids we have examined, including AMNH 13472.

[7]We follow Noble's (1922: 41) terminology, except that the appropriate term for connective tissue that extends from muscle to periosteum (of the tibiofibula or femur, in this case) is *tendon*, not *ligament*.

[8]Although generally we did not take characters from unpublished sources, the influence of this dissertation in anuran systematics has been so great that it would be inappropriate to ignore this work.

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batids (see below). Our observations conform with the accounts of previous workers, with the exception that fibers generally originate on the anterior edge of the annulus tympanicus as well. In addition to the "s" morphology, among other frogs Starrett (1968) reported the presence of both muscles, or "s + e" in her system (state 1), as well as the absence of the m. adductor posterior mandibulae subexternus and presence of the m. adductor mandibulae externus superficialis, "e" (not observed in the present study).

Haas (2001) reevaluated the homology of these muscles based on detailed developmental studies across the diversity of amphibians. He concluded that the "subexternus" and "externus" muscles are actually different portions of the same muscle (slips, in our terminology; see Materials and Methods, above)—the m. levator mandibulae externus profundus and m. levator mandibulae externus superficialis, respectively. As such, Starrett's (1968) three conditions ("s", "e", and "s + e") involve two distinct transformation series: (1) the m. levator externus is constant in both "s" and "e" and the transformation series is formed by changes in the position of V_3, deep (internal, medial) in the "s" and superficial (external, lateral) in the "e"; (2) "s + e" is formed by the division of the m. levator mandibulae externus into profundus and superficialis slips, with V_3 lying between them. Because we did not observe the "e" condition in any of the species coded for morphology in the present study, we scored only the latter transformation series.

The sole published exception to the undivided m. levator mandibulae externus ("s"; state 0) morphology in dendrobatids is *nocturnus*, in which Myers et al. (1991) found the m. levator externus of some specimens (or one side) to form two distinct slips ("s + e"; state 1). Myers et al. (1991) interpreted this observation as possibly indicative of both the ranoid origin of dendrobatids and the primitiveness of *nocturnus* within the dendrobatid clade. The only other exception we observed was a specimen of *vanzolinii* (AMNH 108332) in which V_3 pierces the m. levator mandibulae externus. However, we did not code the superficial and medial fibers as different slips (i.e., "s + e") because the fibers are tightly bound both dorsal and ventral to the nerve and are not segregated by connective tissue septa (as they are in *nocturnus*, for example) and therefore do not form distinct slips (for similar individual variation, see Lynch, 1986). That said, only a single specimen was available for dissection, and the symmetry of this morphology suggests that further study may reveal a phylogenetically relevant change in the path of V_3.

Additional intraspecific variation was observed in *Hylodes phyllodes*. Of the 11 frogs in the series AMNH 103885–95, in 2 (AMNH 103888, 103890) V_3 runs medial to a distinct m. levator mandibulae externus superficialis ("s + e"; state 1) on both sides of the head, whereas the remaining 9 specimens all lack that slip ("s"; state 0). As in *nocturnus*, and in contrast to *vanzolinii*, the lateral fibers form a distinct slip. Indeed, in *H. phyllodes* all of the lateral fibers appear to originate on the rim of the annulus tympanicus, whereas the medial slip originates from the squamosal. Although this latter consideration is suggestive of nonhomology of the m. levator mandibulae externus superficialis in these taxa, we coded them as the same state and subjected that hypothesis to the test of character congruence.

72–75. M. Depressor Mandibulae

Starrett (1968) identified three distinct slips of the m. depressor mandibulae of dendrobatids: a massive, superficial slip originating from the dorsal fascia overlying the scapula and m. levator posterior longus, a deeper slip originating from the otic ramus of the squamosal, and an additional slip of fibers originating on the tympanic annulus. The combined morphology was codified as $DFSQ_dAT$. Lynch (1993: 37) refined the delimitation of this condition as "one in which some number of superficial fibers of the squamosal portion of the *m. depressor mandibulae* extend medial to the crest of the otic ramus of the squamosal and overlie the fibers of the *m. levator posterior longus*." Silverstone (1975a) confirmed that all 41 species of dendrobatids he examined have this morphology, and this was further confirmed in additional species by Myers and coworkers (e.g., Myers et al., 1978, 1991; Myers and Daly, 1979; Myers and Ford, 1986).

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Lynch (1993) rejected the anatomical findings of Starrett (1968), at least as they applied to *Eleutherodactylus*. Of greatest relevance to dendrobatids is his finding (pp. 37–38) that the superficial "DF" fibers actually are "bound tightly to deeper fibers … that originate on the lateral face of the otic ramus of the squamosal". That is, the fibers from the two origins are not segregated by connective tissue septa and therefore do not constitute distinct slips. Our dissections confirm Lynch's observations in dendrobatids and the sampled outgroup taxa as well, leading us to follow him in discarding Starrett's terminology.

Nevertheless, regardless of whether the depressor muscle is divided into distinct slips or not, the variation in fiber origins constitutes a valid transformation series. In all specimens examined, some fibers originate from the otic ramus of the squamosal. In all dendrobatids examined, the vast majority of fibers originates form the dorsal fasciae. Lynch (1993) referred to the portion of the m. depressor mandibulae that originates medial to the crest of the squamosal on the m. temporalis as a "dorsal flap", and we follow his terminology here (Character 73). We scored as Character 74 the origin of fibers posterior to the crest of the squamosal. The occurrence of fibers originating on the posterior edge of the annulus tympanicus is coded in Character 75.

Manzano et al. (2003) presented an extensive survey of the m. depressor mandibulae in anurans. Among dendrobatids, they examined *auratus*, *pictus*, and *subpunctatus*. Our observations and coding conform generally with theirs, with the following exceptions: (1) Manzano et al. did not recognize the dorsal flap as a separate character. (2) Manzano et al. reported that the superficial "slip" of *auratus* is divided into anterior and posterior "slips", whereas that of *pictus* and *subpunctatus* consists of a single, wide, fan-shaped muscle. We examined 20 uncataloged AMNH skinned carcasses of *auratus* from Isla Tobago, Panama, constituting 40 depressor muscles. In that series, variation is continuous between an uninterrupted fan-shaped muscle, the occurrence of a slight division across the thoracic sinus, and well-defined separate branches, with conspicuous bilateral asymmetry in some specimens. Given the continuous variation, we were unable to delimit states objectively. Moreover, the degree of individual variation suggests that the differences are likely nongenetic, although we cannot offer any direct evidence to that effect. (3) Manzano et al. reported fibers originating from the annulus tympanicus in *Rhinoderma darwinii*. However, although we observed fibers to extend toward the annulus, in the specimens we examined (AMNH 37849, 58082), the fibers invariably run along the cartilage and ultimately attach to the squamosal.

72. M. Depressor Mandibulae Dorsal Flap: absent = 0; present = 1.

73. M. Depressor Mandibulae Origin Posterior to Squamosal: absent = 0; present = 1.

74. M. Depressor Mandibulae Origin on Annulus Tympanicus: no fibers originating from annulus tympanicus = 0; some fibers originating from annulus tympanicus = 1.

Among dendrobatids, the fibers that attach to the annulus tympanicus are generally deep and easily overlooked, but careful dissection showed them to be present in all dendrobatids examined.

75. Tympanum and m. Depressor mandibulae relation: tympanum superficial to m. depressor mandibulae = 0; tympanum concealed superficially by m. depressor mandibulae = 1.

Myers and Daly (1979: 8) pointed out that in dendrobatids "the large superficial slip of the *depressor mandibulae* muscle tends to slightly overlap the tympanic ring and, in any case, holds the skin away from the rear part of the tympanum, thus accounting for the fact that the tympanum is only partially indicated externally" (see also Myers and Ford, 1986; Myers et al., 1991). Daly et al. (1996) further discussed this character and compared conditions found in *Mantella*.

76. Vocal Sac Structure: absent = 0; median, subgular = 1; paired lateral = 2. Nonadditive.

This character was coded following Liu (1935). Although we coded the vocal sac for the sampled species *Megaelosia goeldii*, in which males lack vocal sacs and slits and presumably do not call (Giaretta et al., 1993),

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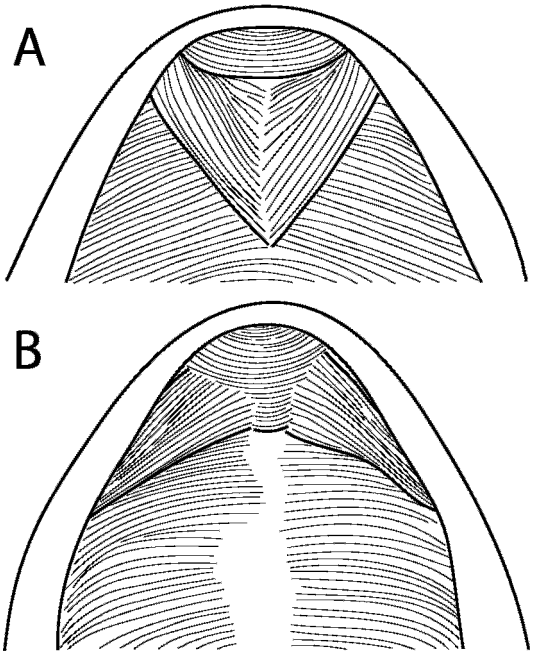

Fig. 56. Character 79, M. intermandibularis supplementary element morphology. **A**: State 0, anterolateral (*Rhinoderma darwinii*, AMNH 37849). **B**: State 1, anteromedial (*trinitatis*, uncataloged AMNH specimen, part of series collected with AMNH 87392–93).

other species of *Megaelosia* possess paired lateral vocal sacs (e.g., *M. lutzae*; Izecksohn and Gouvêa, 1987 "1985"). Lynch (1971) reported the state for *Eupsophus roseus* (coded for *E. calcaratus*).

77–78. M. INTERMANDIBULARIS SUPPLEMENTARY ELEMENT (fig. 56)

Tyler (1971) described variation in superficial throat musculature of hylids and other anurans, reporting the differentiation of the m. intermandibularis to form a supplementary element in two species of *Colostethus* [as *Calostethus*], two species of *Dendrobates*, and two species of *Phyllobates*. He did not list the species of dendrobatids he examined or describe the dendrobatid condition in any detail. La Marca (1995: 45) noted the occurrence of "supplementary elements of the anterolateral type attached to the ventral surface of the *m. submentalis*". Of relevance to the current study, Burton (1998b) also reviewed the occurrence and variation in supplementary elements of numerous Neotropical hyloid groups.

The treatment of the supplementary element in phylogenetic analysis is somewhat problematic, as the homology of the elements in different taxa is debatable. Following Tyler's (1971) terminology, dendrobatids possess an anterolateral element: Fibers originate on the lingual surface of the anterior portion of the mandible and run anteriomediad to insert on the ventral surface of the m. submentalis, with the more posterior fibers underlying (superficial to) the deeper fibers of the m. intermandibularis. Tyler also identified apical and posterolateral elements in other groups of anurans, and these conditions have been largely supported by subsequent workers. Tyler (1971) effectively treated each of the morphologies as nonhomologous (i.e., the differences in morphologies was treated as evidence that each of the supplementary elements was independently derived), but other workers have treated them as a homologous entity with subsequent variation (e.g., Burton, 1998b; Mendelson et al., 2000).

The shared origin of the supplementary element on the lingual surface of the mandible superficial to the deeper primary sheet of the m. intermandibularis and the fact that the different morphologies never co-occur are sufficient evidence to treat the supplementary elements of different anurans as a homologous structure. We therefore submitted the hypothesis of supplementary slip homology to the simultaneous test of character congruence by coding its occurrence as one character and the variation in the element as a second character.

77. M. INTERMANDIBULARIS SUPPLEMENTARY ELEMENT OCCURRENCE: absent = 0; present = 1.

78. M. INTERMANDIBULARIS SUPPLEMENTARY ELEMENT ORIENTATION: 0 = anterolateral; 1 = anteromedial.

Among the sampled species that possess the supplementary element, we observed two patterns. In the first (state 0), the fibers radiate anterolaterally from a sagittal raphe. In the second, the fibers extend anteromedially from the mandible. Burton (1998b) reported both of these morphologies for a variety of Neotropical "leptodac-

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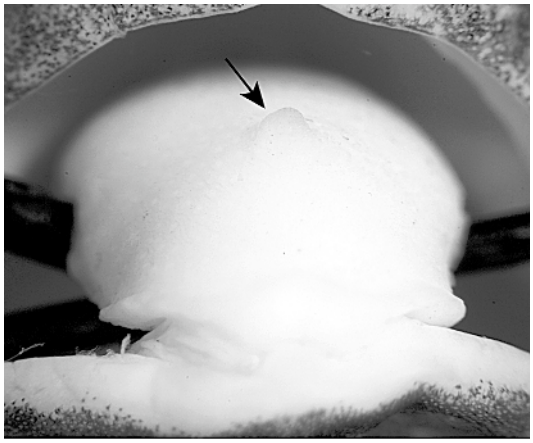

Fig. 57. Anterior view of the open mouth of the dendrobatid *praderioi* (CPI 10203) showing the short, tapered median lingual process (MLP).

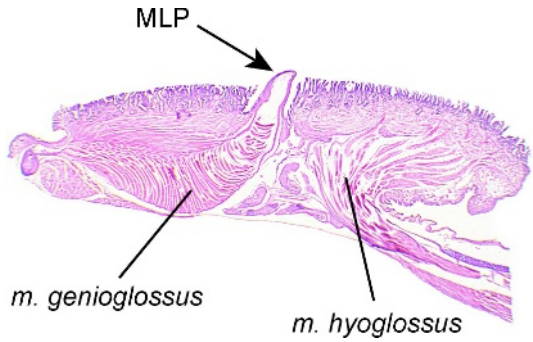

Fig. 58. Longitudinal histological section of the tongue of *baeobatrachus* (AMNH 140672) showing that the median lingual process (MLP) is an extension of the m. genioglossus. Note lack of muscle fibers toward the tip of the MLP.

tylids''. However, our coding deviates from Burton's (1998b) in that he treated species with anterolateral supplementary slips (e.g., *Hylodes* spp.) and without supplementary slips but having all fibers directed mediad or anterolaterad (e.g., *Thoropa miliaris*) as ''variants of the same general pattern'' (pp. 67–68). Burton based this decision on ''the fact that two of these variants may occur within the same genus (e.g., *Cycloramphus*), or within the same species (*C[audiverbera]. caudiverbera*)'' (p. 67). Co-occurrence of this nature does not constitute evidence of character-state identity (if it did, polymorphism would be conceptually impossible), and we scored *Hylodes phyllodes* and *Thoropa miliaris* differently.

Manzano and Lavilla (1995) reported an apical supplementary element in *Rhinoderma darwinii*; according to the terminology employed herein, it is anterolateral (state 0).

79–86. Median Lingual Process (figs. 57, 58)

Grant et al. (1997) discovered the median lingual process (MLP; fig. 57) in dendrobatids and documented its occurrence and variation throughout Anura (for additional dendrobatid records, see Myers and Donnelly, 1997; Grant and Rodríguez, 2001). Of greatest interest was the finding that an apparently homologous modification of the tongue occurs in dendrobatids and several Old World ranoids (including the putative sister group postulated by Griffiths, 1959) but is entirely lacking among all hyloid taxa. The functional significance of the MLP remains unknown. Variation in the MLP has been illustrated extensively by Grant et al. (1997) and Myers and Donnelly (1997); here we provide illustrations for novel characters.

As a first effort to understand the distribution and diversity of the MLP, Grant et al. (1997) allocated the observed variation to four ''types''. For phylogenetic analysis it was necessary to decompose those types into their component transformation series. Given the relevance of this anatomical structure to the placement of Dendrobatidae, we examined the histology of the tongues of eight species to gain a better understanding of its structure. Additional data were gathered through gross dissection. Although several of the characters we observed do not vary among the MLP-possessing taxa sampled in the present study, they vary independently in the broader context of the evolution of the MLP in anurans, and we therefore score all of these characters here.

To discover differences between the type C processes of Old World and New World taxa, we examined the histology of two species of the dendrobatids *tepuyensis* and *baeobatrachus*, and we compared them to *Phrynobatrachus natalensis* and *Phrynobatrachus petropedetoides*. These two species of

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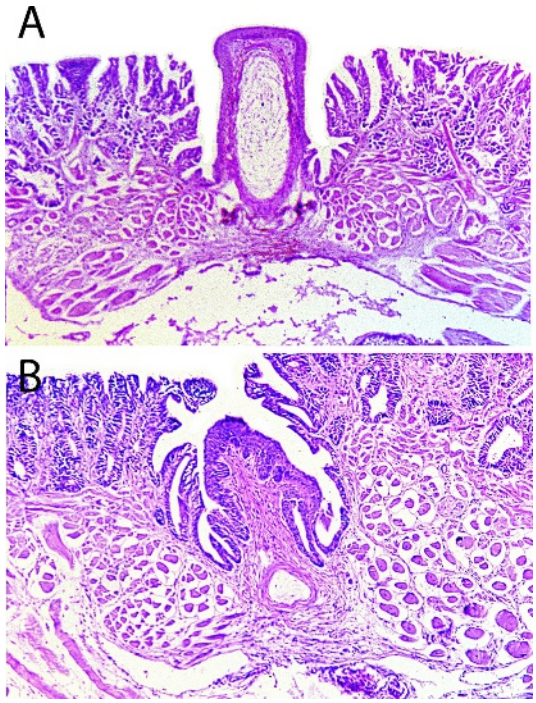

Fig. 59. Character 84, median lingual process (MLP) retractility, state 1 (retractile). **A**: Transverse section of a protruded MLP in *Phrynobatrachus natalensis* (AMNH 129714). **B**: Transverse section of a retracted MLP in *Phrynobatrachus petropedetoides* (AMNH 129626).

Phrynobatrachus have retractile type C processes, which we hoped would maximize the morphological differences between them and the nonretractile type C processes of the dendrobatids. To gain insight into the mechanism of retraction and protrusion, one of the specimens of *Phrynobatrachus petropedetoides* had the MLP fully protruded, whereas the other one had it retracted below the surface of the tongue. We also examined the type A processes of *Arthroleptis variabilis*, *Mantidactylus femoralis*, *Platymantis dorsalis*, and *Staurois natator* (the latter two species were included only for comparative purposes to delimit transformation series more rigorously and were not coded for phylogenetic analysis). Due to lack of specimens, we did not examine any type B or D processes.

The MLP of all examined taxa (i.e., types A and C, retractile and nonretractile) is formed through the same modification of

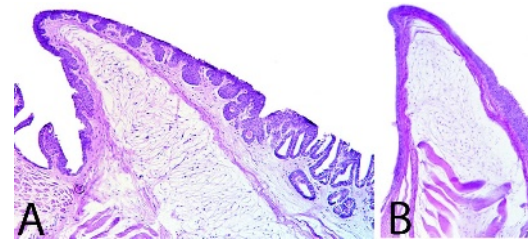

Fig. 60. Character 86, median lingual process (MLP) epithelium. **A**: State 0, glandular (*Phrynobatrachus petropedetoides*, AMNH 129593). The surface of the MLP is pitted with invaginations of the epithelium that form alveolar glands. **B**: State 1, nonglandular (*Phrynobatrachus natalensis*, AMNH 129732). The alveolar glands are absent, and the surface of the MLP consists of unmodified stratified epithelium.

the basal portion of the m. genioglossus, supporting the hypothesis that they are homologous structures. As seen in sagittal and transverse section of *baeobatrachus* (fig. 58) the m. genioglossus basalis is extended dorsally to protrude above the lingual surface as the median lingual process. In all taxa, muscle fibers are replaced distally by loose, presumably collagenous connective tissue, with elastic fibers forming the walls of the process. Although we did not stain specifically for nervous tissue, no major nerves were detected within the MLP. Additional histological findings are discussed below under the relevant characters.

79. MLP OCCURRENCE: absent = 0; present = 1.

To count the origin of the MLP as a single event (and not as multiple origins of each of the nested characters), we scored the occurrence of the MLP as a separate character. That is, species that lack the MLP were scored as state 0 for this character and missing ("–") for the remaining MLP characters.

80. MLP SHAPE: short, bumplike = 0; elongate = 1.

We considered the MLP to be short and bumplike if it its length (height) was no greater than its width at the base and elongate if its length was greater than its width at the base.

81. MLP TIP: blunt = 0; tapering to point = 1.

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82. MLP TEXTURE: smooth = 0; rugose = 1.

Grant et al. (1997) found most MLPs to be smooth relative to the lingual surface (state 0) but that in some species the MLP is rugose, textured like the adjacent surfaces of the tongue.

83. MLP ORIENTATION WHEN PROTRUDED: upright = 0; posteriorly reclined = 1.

When protruded, Grant et al. (1997) reported upright MLPs pointing straight dorsad (state 0) and posteriorly reclined MLPs (state 1).

84. MLP RETRACTILITY (fig. 59): nonretractile = 0; retractile = 1.

Following the reasoning of Grant et al. (1997), retractility was inferred from the position of the MLP in preserved specimens. We were unable to detect any histological differences between retractile and nonretractile processes. However, the fact that even very small series of some species show the MLP in various stages of retraction whereas very large samples of others do not include a single retracted lingual process suggests that this is not merely an artifact of preservation.

Comparison of retracted and protruded processes provides some clues as to the mechanism involved in retractility. As seen in figure 59A of the protruded process of *Phrynobatrachus natalensis* in transverse view, the connective tissue that extends to the tip of the MLP is very loose, with large spaces between the fibers and fibroblasts. In contrast, in a specimen of *Phrynobatrachus petropedetoides* with the MLP completely retracted below the surface of the tongue (fig. 59B), the loose connective tissue is much denser with no spaces between the fibers and fibroblasts, reminiscent of a squeezed sponge. This is characteristic of hydrostatic organs such as the feet of mollusks and suggests that protrusion and retraction of the MLP is achieved by the displacement of some sort of fluid.

85. MLP-ASSOCIATED PIT: absent = 0; present = 1.

Grant et al. (1997) noted the absence (state 0) and presence (state 1) of a pit immediately posterior to the MLP into which fits the posteriorly reclined MLP of some species. Although all of the species with posteriorly reclined MLPs sampled in the present study also have an associated pit, the observations of Grant et al. (1997) establish the transformational independence of the two characters.

86. MLP EPITHELIUM (fig. 60): glandular = 0; nonglandular = 1.

In state 0 the surface of the MLP is pitted with invaginations of the epithelium that form alveolar glands, as occur over the rest of the surface of the tongue. In state 1, these glandular invaginations do not occur, and the MLP is covered in unmodified, stratified epithelium.

87–98. LARVAE

In addition to specimens examined, larval data were taken from Ruthven and Gaige (1915), Fernández (1926), Funkhouser (1956), Donoso-Barros (1965 "1964"), Savage (1968), Duellman and Lynch (1969), Hoogmoed (1969), Edwards (1971, 1974b), Lynch (1971), McDiarmid (1971), Silverstone (1975a; 1976), Lescure (1976), Duellman (1978, 2004), Myers and Daly (1979), Cei (1980), Lescure and Bechter (1982), Heyer (1983), La Marca (1985), Lavilla (1987), Formas (1989), Caldwell and Myers (1990), Donnelly et al. (1990), Heyer et al. (1990), Mijares-Urrutia (1991), Myers et al. (1991), van Wijngaarden and Bolaños (1992), Rodríguez and Myers (1993), Haddad and Martins (1994), Juncá et al. (1994), Coloma (1995), Ibáñez and Smith (1995), La Marca (1996 "1994"), Mijares-Urrutia and La Marca (1997), Kaplan (1997), Lötters et al. (1997b), Grant and Castro-Herrera (1998), Faivovich (1998), Lindquist and Hetherington (1998), Lötters et al. (2000), Caldwell et al. (2002a), Caldwell and Lima (2003), Nuin (2003), and Castillo-Trenn (2004).

87. LARVAL CAUDAL COLORATION: vertically striped = 0; scattered melanophores clumped to form irregular blotches = 1; evenly pigmented = 2. Additive.

Caldwell et al. (2002a) figured the larvae of *caeruleodactylus* and *marchesianus*, the tails of which possess conspicuous, dark, broad, vertical stripes (state 0). The larval tails of the majority of species possess variable amounts of irregular, scattered melanophores clumped to form diffuse blotches, ranging from in-

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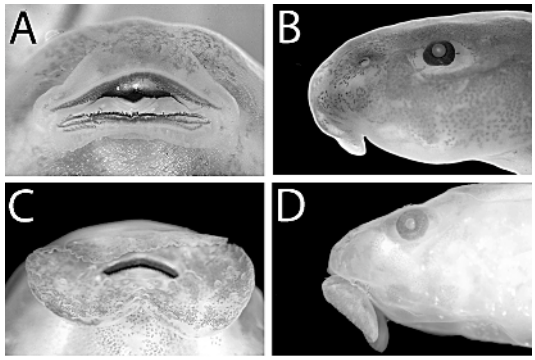

Fig. 61. Character 88, larval oral disc. **A**, **B**: Ventral (**A**) and lateral (**B**) views of State 0, ''normal'' (''Neblina species'', AMNH 118673). **C**, **D**: Ventral (**C**) and lateral (**D**) views of State 1, umbelliform disc (*nubicola*, AMNH 94849). Note also the submarginal papillae scattered over the surface of the oral disc (character 91).

conspicuous reticulation to large blotches (state 1). There is extensive ontogenetic and individual variation in the amount and intensity of this diffuse spotting, as documented for *kingsburyi* by Castillo-Trenn (2004), which prevented dividing the variation observed within this character-state into additional states. In some species, the larval tails are evenly pigmented brown, gray, or black (state 2).

88. LARVAL ORAL DISC (fig. 61): ''normal'' = 0; umbelliform = 1; absent = 2; suctorial = 3. Nonadditive.

As described by Haas (2003: 54), ''[t]he oral disk is formed by the upper and lower lips, i.e., flat, more or less expansive flaps of skin set off from the mouth and jaws and commonly bearing labial ridges with keratodonts.'' What is here referred to as the ''normal'' larval oral disc (state 0) consists of a thick, fleshy upper lip that is fully attached medially and lacks marginal papillae and a lower lip that is entirely free but relatively narrow and bears marginal papillae. The umbelliform (funnel-shaped) oral disc (state 1; fig. 61) is greatly enlarged relative to state 0. The upper lip is free and the marginal papillae extend around the entire circumference of the disc. Among dendrobatids, state 1 is known only in *flotator*, *nubicola*, and two unnamed species not included in this study. Dendrobatids that lack the oral disc (state 2) are endotrophic. The suctorial oral disc (state 3) is confined to the outgroup.

89. LATERAL INDENTATION OF LARVAL ORAL DISC: absent (not emarginate) = 0; present (emarginate) = 1.

90. MARGINAL PAPILLAE OF LARVAL ORAL DISC: short = 0; enlarged = 1; greatly enlarged = 2. Additive.

The marginal papillae of most dendrobatids (e.g., *boulengeri*) are numerous (>50 in late stages) and relatively small (state 0).[9] The marginal papillae of some species (e.g., *pumilio*) are fewer (<30 in late stages) and uniformly larger (state 1). For illustrations exemplifying this state, see Silverstone (1975a) and Haddad and Martins (1994). The remarkable larvae of *caeruleodactylus* and *marchesianus* possess only 12–18 (in late stages) greatly and irregularly enlarged marginal papillae (state 2). For illustrations of this state, see Caldwell et al. (2002a).

91. SUBMARGINAL PAPILLAE OF LARVAL ORAL DISC (fig. 61): absent = 0; present = 1.

Among dendrobatids, submarginal papillae (see Altig and McDiarmid, 1999a) are known to occur only in larvae with umbelliform oral discs (e.g., *nubicola*). However, nondendrobatids that lack umbelliform discs also possess submarginal papillae (e.g., *Duellmanohyla uranochroa*; see Altig and McDiarmid, 1999b), demonstrating the transformational independence of these two characters.

92. MEDIAN GAP IN MARGINAL PAPILLAE OF LOWER LABIUM: absent = 0; present = 1.

Among dendrobatids, the median gap in the marginal papillae of the lower labium was illustrated and discussed by Myers and Daly (1980; see also 1987) and was claimed by them to be a synapomorphy for *abditus*, *bombetes*, and *opisthomelas*; Ruiz-Carranza and Ramírez-Pinilla (1992) added *virolinensis* to the group.

[9]Castillo-Trenn (2004) documented ontogenetic variation in the number of marginal papillae in *kingsburyi*, ranging from 18 in stage 25 to 62 in stage 34. However, the relative size and density of papillae remains constant, that is, as the tadpole grows the number of marginal papillae increases while the size of each papilla remains approximately the same.

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93. Anterior Larval keratodont Rows: 0 = 0; 1 = 1; 2 = 2. Additive.

Haddad and Martins (1994) reported the absence of anterior keratodont rows in *hahneli*, and we confirmed their observations in tadpoles of early stages. However, tadpoles of later stages possess a single anterior keratodont row, and we therefore coded this species as state 1. The unusual shape of the mouth, illustrated by Haddad and Martins, is retained until metamorphosis.

94. Posterior Larval keratodont Rows: 0 = 0; 1 = 1; 2 = 2; 3 = 3. Additive.

Haddad and Martins (1994) reported the absence of posterior keratodont rows in *hahneli*, and we confirmed their observations in small (e.g., stages 25 or 26) tadpoles. However, tadpoles of later stages possess two posterior keratodont rows, and we therefore coded this species as state 2.

95. Larval Jaw Sheath: absent = 0; lower jaw only, not keratinized = 1; entire, keratinized = 2. Additive.

96. Larval Vent Tube Position: dextral = 0; median = 1.

Myers (1987) claimed the position of the larval vent tube among the differences between *Minyobates* and *Dendrobates*, with the former possessing the putatively primitive dextral position (state 0) and the latter being medial (state 1). Myers and Daly (1979) reported ontogenetic variation from dextral to median in *silverstonei*, and Donnelly et al. (1990) later reported that the vent tube of *aurotaenia*, *lugubris*, *terribilis*, and *vittatus* migrates from medial at Gosner (1960) stages 24 and 25 to dextral by stage 37 (or earlier). Caldwell and Myers (1990: 8) reported the frequency of dextral, sinistral, and median vent tubes in *castaneoticus* and summarized variation in this character and noted that "the rare sinistral condition [is] so far known only in the variation of the *Dendrobates quinquevittatus* complex." Similar intraspecific variation has been reported in other anurans as well (e.g., Altig and McDiarmid, 1999a). Because ontogenetic series were unavailable for most dendrobatids, we coded the position of the larval vent tube as observed in the most developed larvae examined. As such, for example, we coded the vent tube of *aurotaenia*, *lugubris*, *terribilis*, and *vittatus* as dextral.

97. Spiracle: absent = 0; present = 1.

Among the coded dendrobatids, the unusual condition of the absence of the spiracle has been reported for only *degranvillei* (Lescure, 1984) and *nidicola* (Caldwell and Lima, 2003), both of which possess endotrophic larvae.

98. Lateral Line Stitches: absent = 0; present = 1.

The lateral line system is composed of receptor organs (mechanoreceptive neuromasts and electroreceptive ampullary organs) and the nerves that innervate them, both of which develop from the lateral line placodes (Schlosser, 2002a). Insofar as is known, the lateral line system is entirely lacking only in direct developing anurans, but the accessory organs (stitches) derived from the primary neuromasts fail to develop in some species of multiple families of anurans (Schlosser, 2002b). That is, the apparent absence of the lateral line system in these taxa is due to the absence of the stitches. The occurrence of stitches varies among dendrobatids, and we coded their absence (state 0) and presence (state 1). Only transverse stitches have been reported for anurans (Schlosser, 2002b), and dendrobatids are no exception.

Stitches have been reported (as the lateral line system), described, and/or illustrated by several authors (e.g., Mijares-Urrutia, 1991; La Marca, 1996 "1994"; Myers and Donnelly, 1997, 2001; Castillo-Trenn, 2004), but they are frequently overlooked, and their absence is usually not reported (e.g., Duellman, 2004). Although stitches are large and conspicuous in some species, they are barely detectable in others, owing to their small size and the pigmentation of the surrounding areas, so it is not safe to assume that failure to mention the lateral line stitches signifies their absence. As such, when coding character-states from the literature, we scored the lateral line stitches as absent when the authors were explicit or provided adequate illustrations or unusually thorough descriptions that (we assume) would have noted stitches had they been visible.

In addition to the presence and absence of stitches, we observed variation in the system of rami they form. However, as also observed by Castillo-Trenn (2004) in *kingsburyi* and R. W. McDiarmid (personal commun.) in other

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anurans, we found that the pattern of rami varies extensively within species, and too little is known about ramus ontogeny and other variation to allow transformation series to be delimited at present.

99–116. BEHAVIOR

The behavior of a number of dendrobatids has been documented and, beginning with Noble (1927), interpreted phylogenetically by several authors (e.g., Myers and Daly, 1976b; Weygoldt, 1987; Zimmermann and Zimmermann, 1988; Summers et al., 1999b). However, although behavior is unquestionably a valid source of evidence of phylogenetic relationships, its interpretation as phylogenetic characters requires special attention because particular behaviors are context dependent. Certain aspects of the behavioral repertory of a given species may be stereotyped and consistent across populations, but behavioral differences among populations have been documented (e.g., Myers and Daly, 1976b), and variation among individuals and over time (especially under different conditions) in the same individual are well known (especially in vocalizations; e.g., Juncá, 1998; Grant and Rodríguez, 2001), and the (external and/or internal) causes of this variation are, for the most part, a complete mystery. Even highly stereotyped responses may be context dependent, which casts some degree of doubt on the significance of observations made on captive specimens and the validity of comparisons to wild individuals. In light of these potential problems, we proposed hypotheses of homology of behaviors judiciously.

An example of overinterpretation of behavioral observations is Zimmermann and Zimmermann (1988), who performed a phenetic analysis of 62 variables (including vocalizations and larval morphology) for 32 species. We disregarded some of their "characters" because they are invariable in the ingroup and most of the outgroup (e.g., pulsation of flanks and/or throat; upright posture; female follows male; inflate body), defined too subjectively or arbitrarily to allow comparison (e.g., oviposition near a stream; male defends large territory, male defends small territory), demonstrably nonindependent (e.g., larvae carnivorous and/or herbivorous and larvae mostly herbivorous, microphagous), or are otherwise problematic. For example, their character "larvae carried singularly or in group" is problematic because, although differences almost certainly exist among species (*bombetes* has only been observed to carry up to three tadpoles [T. Grant, personal obs.; A. Suárez-Mayorga, personal commun.], whereas *fraterdanieli* carries up to at least 12 [T. Grant, personal obs.], and *palmatus* nurse frogs transport up to 31 tadpoles [Lüddecke, 2000 "1999"]), the number of dorsal tadpoles observed is highly variable (e.g., Myers and Daly, 1979: 326, reported a male *silverstonei* found carrying a single larva and two others carrying nine larvae; see also Lüddecke, 2000 "1999": 315, table 3) due, potentially at least, to differences in clutch size, egg survivorship, rate of development, and the fact that a single load of tadpoles may be deposited all at once or one or a few at a time (Ruthven and Gaige, 1915). Clearly there are legitimate transformation series hidden in these observations, but more information is needed before characters can be delimited.

There is extensive missing data for behavioral characters, which necessarily limits the impact of these characters on the present analysis. However, one of our motivations for coding it nonetheless is that standardized codification facilitates future work. One of the most difficult aspects of individuating and scoring transformation series for phylogenetic analysis is that the behaviors are often complex and the ways they may be described by different observers may vary greatly. By delimiting and scoring these characters, we hope to draw attention to them for use in future comparative behavioral studies. Especially problematic are absences; for the present purposes, we coded conspicuous behaviors not reported in detailed studies as absent, but it is possible that they were simply not noticed. A similar problem is that even detailed notes may fail to mention expected observations, such as diurnal activity in dendrobatids. We did not make assumptions regarding the latter characters and only scored them from personal observation or explicit statements.

In addition to personal observations and unpublished field notes, behavioral data (not

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including vocalizations) were taken from the following published sources: Dunn (1933, 1941, 1944), Eaton (1941), Trapido (1953), Test (1954, 1956), Funkhouser (1956), Stebbins and Hendrickson (1959), Sexton (1960), Savage (1968, 2002), Duellman and Lynch (1969, 1988), Hoogmoed (1969), Mudrack (1969), Myers (1969, 1982, 1987), Edwards (1971), Lynch (1971), Crump (1972), Silverstone (1973, 1975a, 1975b,1976), Polder (1974), Durant and Dole (1975), Lescure (1975, 1976, 1991), Lüddecke (1976, 2000 ''1999''), Wells (1978, 1980a, 1980b, 1980c), Myers et al. (1978, 1984), Myers and Daly (1976a, 1979, 1980, 1983), Cei (1980), Limerick (1980), Weygoldt (1980, 1987), Vigle and Miyata (1980), Zimmermann and Zimmermann (1981, 1984, 1985, 1988), Kneller (1982), Hardy (1983), Heyer (1983), Dixon and Rivero-Blanco (1985), Jungfer (1985, 1989), Frost (1986), Formas (1989), Summers (1989, 1990, 1992, 1999, 2000), Caldwell and Myers (1990), Praderio and Robinson (1990); Aichinger (1991), Morales (1992), van Wijngaarden and Bolaños (1992), Brust (1993), Duellman and Wild (1993), Giaretta et al. (1993), Rodríguez and Myers (1993), Juncá et al. (1994), Kaiser and Altig (1994), Coloma (1995), Cummins and Swan (1995), Jungfer et al. (1996a), La Marca (1996 ''1994'', 1998 ''1996''), Caldwell (1997), Fandiño et al. (1997), Grant et al. (1997), Caldwell and de Araújo (1998, 2004, 2005), Juncá (1998), Grant and Castro-Herrera (1998), Morales and Velazco (1998), Boistel and de Massary (1999), Caldwell and de Oliveira (1999), Haddad and Giaretta (1999), Hoff et al. (1999), Summers et al. (1999b), Köhler (2000), Kok (2000), Lescure and Marty (2000), Lötters et al. (2000), Bourne et al. (2001), Downie et al. (2001), Hödl and Amézquita (2001), Lima et al. (2001, 2002), Myers and Donnelly (2001), Summers and Symula, (2001), Caldwell and Lima (2003), Giaretta and Facure (2003, 2004), Lima and Keller (2003), Grant (2004), Lehtinen et al. (2004), Toledo et al. (2004), and Summers and McKeon (2004).

99. ADVERTISEMENT CALLS: buzz = 0; chirp = 1; trill = 2; retarded trill = 3. Nonadditive.

Male advertisement calls played an important role in the systematics studies of Myers and Daly (e.g., 1976b). For example, the *histrionicus* group of Myers et al. (1984) is delimited, in part, by a synapomorphic ''chirp'' call. Data are available for numerous species (for partial review, see Lötters et al., 2003b), but their use in systematics has been predicated on their identification as a buzz (Myers and Daly, 1976b: 225), chirp (Myers and Daly, 1976b: 226), trill (Myers et al., 1978: 325), retarded trill (Myers and Daly, 1979: 18), or retarded chirp (Myers and Burrowes, 1987: 16), and the diversity of dendrobatid calls extends far beyond these few types. Although Lötters et al. (2003b) aimed to expand and standardize the definitions of these calls, they were aware that known calls of most species of dendrobatids do not correspond to any of these types, and additional characterizations such as peeps, cricketlike chirps, croaks, whistled trills, or harsh peep train (e.g., Rodríguez and Myers, 1993; Grant and Castro-Herrera, 1998; Bourne et al., 2001) have been employed, although none of these is defined precisely.

It is clear that these call types are composites of temporal and spectral transformation series that should be decomposed into independent characters for phylogenetic analysis. Unfortunately, the necessary analysis of advertisement call variation was outside the scope of the present study, and we scored advertisement calls according to the published scheme in order to test prior hypotheses (e.g., the buzz call as a synapomorphy of the *histrionicus* group). This is highly suboptimal, mainly because (1) many species were scored as unknown simply because their calls did not fit within the current classification and not because data were unavailable, and (2) extensive information on spectral and temporal modulation could not be incorporated. We hope this may be rectified in future studies. Species were coded according to Lötters et al. (2003b).

100. MALE COURTSHIP: STEREOTYPED STRUT: absent = 0; present = 1.

Dole and Durant (1974), Wells (1980a), and Lüddecke (2000 ''1999'') reported the occurrence of this behavior (state 1) in *collaris*, *panamensis* (as *inguinalis*; see Grant, 2004), and *palmatus*, respectively. Lüddecke (2000 ''1999'': 309, see also p. 210 for illustration) described it as ''a stereotyped

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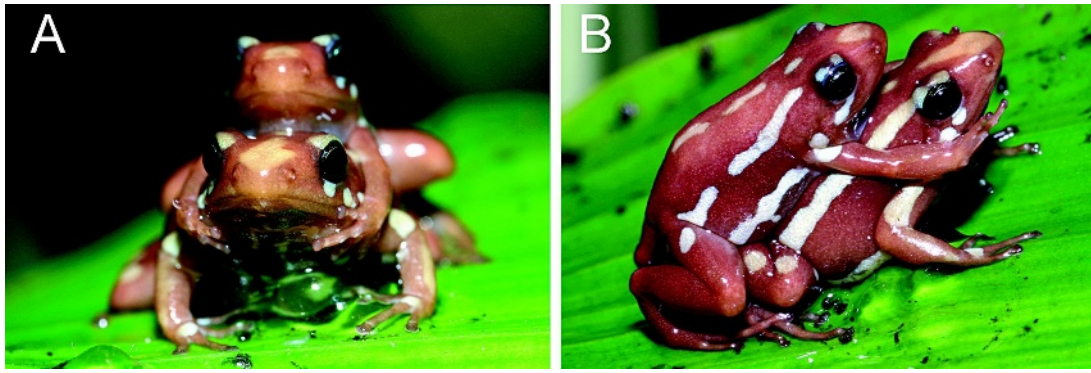

Fig. 62. Character 105, reproductive amplexus. State 2, cephalic amplexus (*anthonyi*, AMNH live exhibit) shown in anterior (**A**) and lateral (**B**) aspects.

rigid-looking strut [the male] performs in the silent intervals between advertisement calls''.

101. MALE COURTSHIP: JUMPING UP AND DOWN: Absent = 0; present = 1.

Wells (1980c: 195) described this character as follows:

> When a female or brown male moved near a calling black male, the usual response of the black male was to jump up and down on his calling perch. … Often the male would run for a few centimeters and jump so that his front feet rose 1–2 mm off the ground. Similar behavior has been reported in a closely related species (*C. collaris*), although males of that species apparently leap higher off the substrate than do male *C. trinitatis*.

102. FEMALE COURTSHIP: CROUCHING: absent = 0; present = 1.

According to Lüddecke (2000 ''1999'': 309), in this behavior the female crouches in front of, but does not slide underneath, the male.

103. FEMALE COURTSHIP: SLIDING UNDER MALE: absent = 0; present = 1.

Lüddecke (2000 ''1999'': 309) reported for *palmatus* that the female crouches and then ''slides completely under the male'' as one of the final stages of courtship.

104. TIMING OF SPERM DEPOSITION: after oviposition = 0; prior to oviposition = 1.

In 1980 both Limerick (1980) and Weygoldt (1980) reported that sperm deposition in *pumilio* appears to occur prior to oviposition (state 1). This unusual occurrence has since been reported for additional species by several authors (Jungfer, 1985; Weygoldt, 1987; Jungfer et al., 1996a, 2000; Lötters et al., 2000). Jungfer et al. (1996a) claimed this as a synapomorphy of *Dendrobates* and rationale for placing *Minyobates* in its synonymy, as done subsequently by Jungfer et al. (2000). Nevertheless, several species of *Dendrobates* sensu Jungfer et al. have been explicitly reported to have post-oviposition fertilization (e.g., *histrionicus* fide Zimmermann, 1990: 69; *arboreus* fide Myers et al., 1984: 15), which suggests that the phylogenetic interpretation of this character is not as straightforward as Jungfer et al. implied.

Fig. 63. Character 109, dorsal larval transport. State 1, present (*fraterdanieli*, specimens at UVC). This male nurse frog was transporting 12 tadpoles.

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105. Reproductive Amplexus (fig. 62): absent = 0; axillary = 1; cephalic = 2. Nonadditive.

Myers et al. (1978: 324–325) first described and illustrated cephalic amplexus in *tricolor*. Although reproductive amplexus is absent in numerous dendrobatids (a variety of pseudoamplectant positions–including cephalic grasping–may be employed in aggressive and/or courtship behavior), cephalic amplexus was cited by numerous authors (e.g., Duellman and Trueb, 1986; Myers and Ford, 1986; Myers et al., 1991) as a dendrobatid synapomorphy, with the absence in numerous dendrobatids explained as a derived loss. A similar amplectant position was reported for *Hypsiboas faber* by Martins and Haddad (1988), but the sampled outgroup species exhibit axillary amplexus.

106. Cloacal Apposition: absent = 0; present = 1.

Crump (1972: 197) first reported the occurrence of this character-state in *granuliferus*, in which the male and female face opposite directions and bring their cloacae into contact.

107. Egg Deposition Site: aquatic = 0; terrestrial: leaf litter, soil, under stones = 1; terrestrial: phytotelmata = 2. Additive.

This character is coded additively to reflect the increasing or decreasing degree of association with ground-level standing or flowing water.

108. Egg Clutch Attendance: none = 0; male = 1; female = 2; both = 3. Nonadditive.

See discussion of sex of nurse frog (Character 110, below) for the rationale behind treating biparental care as a separate state instead of polymorphism.

109. Dorsal Tadpole Transport (fig. 63): absent = 0; present = 1.

Noble (1927: 103) noted that his grouping of dendrobatids on morphological grounds "receives an eloquent support from life history data" as well, pointing out that males of species of *Dendrobates* and *Phyllobates* transport tadpoles on their back to pools (state 1), and, further, that "[n]o other Salientia have breeding habits exactly like *Dendrobates* and *Phyllobates*" (p. 104). For the present purposes, we refer only to dorsal transport by genetic parents (see below), and we follow Ruthven and Gaige (1915: 3) in referring to the parent that performs larval transport as the *nurse frog*.

Among outgroup taxa, males of *Rhinoderma darwinii* transport larvae, which Laurent (1942: 18) claimed as evidence of close relationship to dendrobatids. However, male *Rhinoderma* transport young in their hypertrophied vocal sacs (see Noble, 1931: 71 for illustration), whereas dendrobatids transport tadpoles on their backs. Several other anurans transport their young on their backs (e.g., *Hemiphractus*, *Stefania*, *Gastrotheca*), but they do so beginning with the egg clutch, whereas in dendrobatids transport is exclusively post-hatching. Among Neotropical anurans, the only species reported to have terrestrial (nontransported) eggs and dorsally transported tadpoles is *Cycloramphus stejnegeri* (Heyer and Crombie, 1979). Tadpole transport is not known for the sampled species of *Cycloramphus* (*C. boraceiensis*), but Giaretta and Facure (2003) reported male egg attendance (also present in *C. dubius* and *C. juimiria*; C.F.B. Haddad, personal obs.), which leaves open the possibility of tadpole transport. Outside of the Neotropics, apparently identical parental care occurs in the dicroglossids *Limnonectes finchi* and *L. palavanensis* (Inger and Voris, 1988) and the sooglossid *Sooglossus sechellensis* (Lehtinen and Nussbaum, 2003). In the hemisotid *Hemisus marmoratus*, maternal tadpole transport may occur as the female digs a subterranean tunnel to a water body (Lehtinen and Nussbaum, 2003).

Dorsal tadpole transport by parents is here coded as a single transformation series, but even the extremely limited evidence available suggests this is much more complex and probably involves multiple characters. Stebbins and Hendrickson (1959: 509) reported in *subpunctatus* that "[t]he tadpoles are anchored to the back of the frog by a sticky mucus." Myers and Daly (1980: 19) further noted that

> [i]n some dendrobatids, this attachment is accomplished solely by mere surface adhesion between the mucus and the tadpoles' flattened or slightly concave bellies, and the larvae are easily moved about and dislodged. … In other dendrobatids … the mucus attachment seems

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almost gluelike and the tadpoles are very resistant to being dislodged.

To this we add only that it is common for tadpoles to wriggle around freely on the nurse frog's back without being prodded (especially if few tadpoles are being transported by a large frog, such as *bicolor*), giving the impression that they adjust themselves to the nurse frog's movements.

Ruiz-Carranza and Ramírez-Pinilla (1992) studied the histology of the contact surfaces of nurse frogs and transported tadpoles in *virolinensis* and found numerous modifications in both the dorsal integument of the nurse frog and the ventral integument of the larvae. Lüddecke (2000 ''1999'') found experimentally that recently hatched larvae of *palmatus* did not mount a rubber model moistened with water, mounted but immediately abandoned a rubber model treated with either male or female skin secretions, and would only mount and settle on a live frog, with no sexual discrimination. In a less controlled experiment with hatching *anthonyi* T. Grant found that gently touching the jelly capsule with a finger was sufficient to stimulate hatching, immediate mounting, settling, and attachment (i.e., the tadpoles remained attached to the finger submerged in water for >1 min until they were forcibly dislodged); however, the male nurse frog had already removed most of the tadpoles from the clutch, which may have ''primed'' the remaining embryos for hatching and transport. As coded in Character 110, the sex of the nurse frog varies among species, and little is known about the biology of this kind of sex role reversal. Much more research is required to understand the evolution of dorsal tadpole transport in dendrobatids.

110. Sex of Nurse Frog: male = 0; female = 1; both = 2. Nonadditive.

Among species that transport larvae, the role of the nurse frog is typically assumed by one sex (Wells, 1978, 1980a, 1980b, 1980c). However, in some species, both sexes have been observed carrying tadpoles. Myers and Daly (1983) found experimentally that in *anthonyi* (as *tricolor*) the father was normally responsible for tadpole transport and would actively prevent the mother from approaching the developing clutch, but that removal of the male shortly after breeding led to female brood care and larval transport. They suggested that parental care is competitive, that is, the sexes compete to care for the offspring. This is at least consistent with Aichinger's (1991) observation of 38 male nurse frogs and only a single female nurse frog. Caldwell and de Araújo (2005) reported that in *brunneus* and *femoralis* males usually transport larvae but females will occasionally perform this role, and Silverstone (1976: 38) reported nurse frogs of both sexes for *petersi*. It is unknown how widespread this behavior is (i.e., if both sexes are usually potential carriers, even though one sex predominantly assumes this role, as in *tricolor*), but it is not universal. It is unknown how widespread this behavior is (i.e., if both sexes are usually potential carriers, even though one sex predominantly assumes this role, as in *tricolor*), but it is not universal. Host Lüddecke (in litt., 08/31/00) found experimentally that *palmatus* does *not* exhibit this behavior; in his experiments, Lüddecke found that mothers ate their eggs when the fathers were removed. As noted for Character 108, Lüddecke (2000 ''1999'') also found that tadpoles mounted males or females indiscriminately, which suggests that a potential for female transport may be primitive.

Given the paucity of experimental data, it is unclear if all cases of both sexes transporting tadpoles are the result of the same mechanism and/or a transformation event. For the time being, we coded each species based on available information. We have therefore scored species as having males (state 0), females (state 1), or both sexes (state 2) assume the role of nurse frog. This character individuation will undoubtedly require modification as more data are obtained on this behavior.

We coded biparental transport as a separate state rather than an ambiguous polymorphism because the behavioral modifications required to achieve biparental care do not apply to male or female care alone, that is, it involves more than just the co-occurrence of states 1 and 2. Also, we did not specify any particular additivity for this transformation series, as there is no evidence that the shift between sexes requires a cooperative (or competitive) intermediate bi-

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parental stage (although this could be indicated by phylogenetic analysis).

Savage (2002) reported male nurse frogs in *talamancae*, and Summers and McKeon (2004: 62, fig. 3) scored *femoralis*, *hahneli* (as "*hahnei*"), *talamancae*, and *trilineatus* (as "*trilieatus*") as having exclusively male parental care. However, nurse frogs of both sexes have been reported for *femoralis* (Silverstone, 1976; Lescure, 1976; for a recent report see Caldwell and de Araújo, 2005), *hahneli* (as *pictus*; Aichinger, 1991) and *trilineatus* (Aichinger, 1991), and exclusively female nurse frogs have been reported for *talamancae* (Grant, 2004 and references therein). Insofar as Savage and Summers and McKeon did not dispute those reports or provide specimen documentation for confirmation, we dismiss their reports as erroneous.

Adding to the behavioral complexity and the difficulty in coding this character, Weygoldt (1980) found in *pumilio* that mothers transport their larvae to water, whereas males may perform nonparental infanticide by transporting unelated tadpoles and not depositing them in water, thus achieving sexual interference. As noted above, we did not score nonparental transport as part of this transformation series.

111. Larval Habitat: ground level pool or slow-flowing stream or other body of water = 0; phytotelmata = 1; nidicolous = 2. Nonadditive.

Note that there is a logical dependency between larval habitat and dorsal tadpole transport (Character 108) in that nidicolous larvae are, by definition (Altig and Johnston, 1989; McDiarmid and Altig, 1999), not transported. Nevertheless, the two characters are not coextensive and are clearly independent: Lack of transport may also be associated with either state, and nurse frogs may transport larvae to either a ground level body of water or phytotelm.

Although "phytotelm" often refers to chambers above ground (e.g., bromeliads), technically the term applies to any chambers in a plant. Moreover, whether on or above the ground, these phytotelmata are expected to be biologically equivalent (e.g., both microhabitats offer limited space, nutrients, and other resources, and have a potentially high risk of predation), and we therefore did not discriminate between ground-level and higher phytotelmata. For example, we followed Caldwell and de Araújo (1998; 2004) in scoring *castaneoticus* as a phytotelm breeder because it uses Brazil nut husks.

112. Larval Diet: detritivorous = 0; predaceous = 1; oophagous = 2; endotrophic = 3. Nonadditive.

The vast majority of anurans have detritivorous tadpoles (state 0). We assumed that larvae found in ground level pools or streams or other large bodies of water (i.e., state 0 of Character 111) are detritivorous; unless diet is actually known, larvae of other habitats were coded as unknown ("?") for this character. Numerous species of dendrobatids are aggressive predators that consume con- and heterospecific tadpoles and arthropod larvae as an important component of their diet (Caldwell and de Araújo, 1998; state 1). Several species consume sibling oocytes (oophagous, state 2), either exclusively (*histrionicus* group; Limerick, 1980) or as part of a predaceous diet (state 1; e.g., *vanzolinii*; Caldwell and de Oliveira, 1999). We coded the latter taxa as polymorphic (see also Character 113, provisioning of oocytes for larval oophagy).

Four species with endotrophic larvae (state 3) have been described: *chalcopis* (not included in this study), *degranvillei*, *nidicola*, and *stepheni* (for review and description of *nidicola* see Caldwell and Lima, 2003). Some amount of larval growth prior to deposition (e.g., during transport; Wells, 1980b) is probably widespread, but complete endotrophy is much more limited and tends to be correlated with a variably reduced morphology. Nevertheless, the unmodified larva of *chalcopis* (Kaiser and Altig, 1994) demonstrates the transformational independence of endotrophy and the various morphological reductions (see also Altig and Johnston, 1989). Likewise, the occurrence of endotrophy is independent of tadpole habitat: *degranvillei* is transported (Lescure and Marty, 2000; tadpole transport was also predicted for *chalcopis* by Juncá et al., 1994), whereas the remaining endotrophic tadpoles are nidicolous.

113. Provisioning of Oocytes for Larval Oophagy: biparental = 0; female only = 1.

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Caldwell and de Oliveira (1999) reported provisioning of eggs for consumption by sibling tadpoles in *vanzolinii*, as did Bourne et al. (2001) in *beebei*. In these species, egg provisioning is stimulated by male courtship behavior and is therefore biparental (state 0), and larval diets include a variety of foods (for additional records, see Lehtinen et al., 2004). In other oophagous species (e.g., *histrionicus*) tadpole care is undertaken exclusively by the female. An alternative way to delimit state 1 is as obligate oophagy, as it appears that tadpoles of these species feed only on eggs (obligate oophagy demonstrated experimentally for *pumilio* by Brust, 1993; Pramuk and Hiler, 1999), whereas the others are predaceous (Caldwell and de Araújo, 1998).

Zimmermann and Zimmermann (1988) reported biparental provision of oocytes in *ventrimaculatus* (as *quinquevittatus*) in captivity, but Summers et al. (1999b) reported exclusively male care in Peruvian *ventrimaculatus*. Caldwell and Myers (1990) hypothesized that *ventrimaculatus* is a complex of cryptic species, which is supported by this behavioral variation.

114. ADULT ASSOCIATION WITH WATER: aquatic = 0; riparian (<3 m from water) = 1; independent of water (up to ca. 30 m from water) = 2. Additive.

Myers et al. (1991) characterized *nocturnus* as aquatic, which they contrasted with species such as *panamensis* (as *inguinalis*; see Grant, 2004) and *latinasus*, which are riparian and independent of streams, respectively. Postmetamorphic frogs of any species may be found in or near water, and environmental variation must be taken into account (i.e., during dry seasons or at drier localities frogs that are otherwise found well into the forest will congregate near sources of water), but the degree of commitment to or dependency on an aquatic environment segregates dendrobatids into at least three groups. Among dendrobatids, *nocturnus* appears to be the only aquatic species, that is, individuals are generally found immersed in water (state 0). A much greater number of dendrobatids are riparian (state 1). These species are almost entirely confined to the areas immediately adjacent to streams, where they establish and defend streamside territories (e.g., Wells, 1980a, 1980c). When disturbed these species seek refuge in water and *not* in leaf litter or debris beside the stream. The third group of species is effectively independent of water (state 3). As noted by Funkhouser (1956: 78) for *espinosai*, these species "scurry under debris for safety; they do not take to water even when it is close by", and territorial and courtship behaviors occur well away from ground water. Despite their relative independence from water, the density of these frogs may be greater nearer to streams, even in extremely wet environments such as the Colombian Chocó (T. Grant, personal obs.) where general moisture requirements are unlikely to be a limiting factor. This is probably due to reproductive factors: Many of these species are known to transport larvae from terrestrial nests to streams or ground-level pools, and it is predictable that selection would favor preference for sites closer to more permanent, larger bodies of water.

A potential fourth character-state is arboreality. For example, Myers et al. (1984) named *arboreus* in recognition of that species' arboreal habitat preference, whereas other species (e.g., *fraterdanieli*) are active exclusively on the ground and only climb into vegetation (never more than 1 m) to sleep. However, between these two extremes lie variations that defy simple codification. For example, *bombetes* is a leaf-litter frog that climbs up to 30 m above ground to deposit larvae in bromeliads (T. Grant, personal obs.; A. Suárez-Mayorga, personal commun.). Similarly, *histrionicus* forages in leaf litter on the ground but calls from perches in vegetation above ground (Silverstone, 1973; Myers and Daly, 1976b). Clearly there are evolutionary transformation events embedded in these behavioral variations, but the extent to which variation is obligate or facultative is unclear, and we have chosen to group putatively arboreal and terrestrial species as state 2. Assuming the additivity of this transformation series, the transformation from state 1 to state 2 applies to all of these species (as coded), and we have failed to recognize the additional transformation(s) from state 2a (terrestrial) to state 2b (arboreal).

115. DIEL ACTIVITY: nocturnal = 0; diurnal = 1.

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Myers et al. (1991) cited the transformation from nocturnal to diurnal activity as evidence for the monophyly of all dendrobatids minus *nocturnus*. As has been noted by several authors (e.g., Myers et al., 1991; Coloma, 1995; Duellman, 2004), some other species (e.g., *riveroi*, *bocagei*, *nexipus*) exhibit crepuscular or limited nocturnal activity, at least facultatively (e.g., on brightly moonlit nights). Although the conditions that surround this behavior are unclear, we coded these species as polymorphic.

116. Toe Trembling: absent = 0; present = 1.

We have observed several species to exhibit toe trembling or toe tapping, whereby usually the fourth toe (sometimes also the third) trembles or twitches rapidly up and down. Little is known about this behavior. Most observations derive from captive individuals, and there is no known function. It does not appear to be involved in intraspecific visual communication, as individuals do not alter their behavior notably when an individual begins toe trembling, and toe trembling may be observed in individuals that are isolated or in groups. Toe trembling is not continuous and only occurs in active frogs. However, although quantitative data are lacking, onset and/or vigor of toe trembling in dendrobatids does not seem to correlate with any particular stimulus and does not obviously originate as an epiphenomenon (Hödl and Amézquita, 2001). Toe trembling may (or may not) occur while foraging and during inter- and intraspecific interactions with individuals of the same or opposite sex. Hartmann et al. (2005) reported toe (and finger) trembling for the hylid *Hyspiboas albomarginatus*, which they interpreted to be visual signaling.

117. Hyale Anterior Process: absent = 0; present = 1.

All dendrobatids examined possess a single anterior process on each hyale (state 1), and it is both present and absent (state 0) in the sampled outgroup species. Myers and Ford (1986) cited the occurrence of a second anterior process on the hyalia of *Atopophrynus syntomopus* as evidence that it is not a dendrobatid; we did not sample this taxon in the present study and therefore did not test their hypothesis.

118. Shape of Terminal Phalanges: T-shaped = 0; knobbed = 1.

Following Lynch's (1971) terminology, the species sampled in this study possess T-shaped and knobbed phalanges.

119–128. Epicoracoids

Pectoral girdle architecture has been key in all discussions of dendrobatid relationships since Boulenger (1882). Character-states have generally been delimited in terms of the overlap or fusion of the epicoracoids and/or the presence or absence of epicoracoid horns (for historical usages, see Kaplan, 2004), with the epicoracoids of dendrobatids characterized as entirely fused and nonoverlapping and lacking epicoracoid horns, as in "firmisternal" taxa.[10] However, this is clearly an oversimplification (e.g., Noble, 1926; Kaplan, 1994, 1995, 2000, 2001, 2004). Recently, Kaplan (2004) divided girdle architecture variants into separate transformation series relating to degree of fusion (freedom) and overlap (nonoverlap), and he proposed explicit character-states, which we employ here.

Of most relevance to the problem of dendrobatid phylogeny, Noble (1926) claimed that the entirely fused epicoracoids of *subpunctatus* overlap during ontogeny, a finding that was challenged by Griffiths (1959), Lynch (1971a), and Ford (1989), but ultimately vindicated by Kaplan (1995). However, Kaplan (1995) interpreted differences between the overlap in *subpunctatus* and "arciferal" taxa (e.g., *Bufo*) as evidence that the overlap is nonhomologous and therefore not evidence of common ancestry (contra Noble, 1926).

[10]We place "firmisternal" and "arciferal" in quotes and use the terms to denote the taxa they have been associated with rather than the pectoral girdle morphology they purport to designate. Both firmisterny and arcifery are clearly complexes of characters (Kaplan, 2004), the conflation of which has led to much unnecessary confusion in anuran systematics. Although it may be appropriate to treat them as single units in functional studies, the only defensible approach in phylogenetics is to treat each transformationally independent character independently, and we concur with Kaplan that the terms should be abandoned.

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To date, the only dendrobatid in which overlap has been detected is *subpunctatus*. Kaplan (1995: 302) also examined *abditaurantius* (adult), *palmatus* (adult), and *virolinensis* (Gosner, 1960, stages 42–43) and "did not find any evidence of overlap", and Griffiths (1959) reported that overlap is absent in *trinitatis* (not *trivittatus*, as reported by Kaplan, 1995).

Although we did not perform the detailed histology necesary to score these characters precisely, epicoracoid morphology has played an important role in all previous discussions of dendrobatid phylogeny and we believe it would be inappropriate to exclude it altogether. Therefore, although we are cognizant of the potential errors that may be incorporated into the analysis, we coded degree of fusion and overlap in adults (or near adults) as precisely as possible through examination of cleared and stained whole specimens. Although Kaplan (1995: 301) stated that in *subpunctatus* "the girdle halves overlap in adults except for a small area of ventral fusion", this was not visible in cleared and stained specimens, and so for consistency we coded this species as lacking overlap. Insofar as we did not detect overlap in any other dendrobatid, and Kaplan (1995) argued that overlap in *subpunctatus* is nonhomologous with the overlap of "arciferal" taxa, coding the occurrence of overlap in this taxon would result in an autapomorphy and therefore would not affect the results of the present analysis.

119. Epicoracoid Fusion: fused from anterior tips to posterior tips = 0; fused from anterior tips of epicoracoids to level midway between the posterior levels of the procoracoids and the anterior ends of the coracoids, free posteriorly = 1; fused from anterior tips to a level slightly posterior to medial ends of clavicles, free posteriorly = 2. Additive.

States 0, 1, and 2 correspond to states E, C, and A, respectively, of Kaplan (2004: 94). State 1 is intermediate in the degree of fusion, which we considered to be evidence for the hypothesis of $0 \leftrightarrow 1 \leftrightarrow 2$ additivity for this transformation series.

120. Epicoracoid Overlap: nonoverlapping = 0; overlapping from level slightly posterior to level of procoracoids to anterior level of sternum = 1; overlapping from level between posterior level of procoracoids and anterior ends of coracoids to posterior level of coracoids = 2; overlapping from level slightly posterior to medial ends of clavicle to level slightly posterior to anterior level of sternum = 3. Nonadditive.

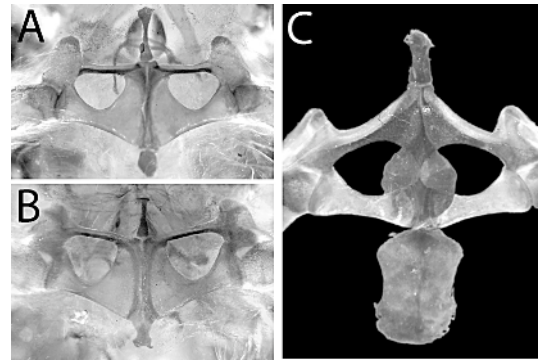

Fig. 64. Character 121, angle of clavicles. **A**: State 0, directed laterad (*steyermarki*, AMNH 118572). **B**: State 1, directed anteriad, approximately parallel to the posterior margin of the coracoid (*opisthomelas*, AMNH 102582). **C**: State 2, directed anteriad (*Eupsophus roseus*, KU 207501).

States 0, 1, 2, and 3 correspond to states B, E, C, and A, respectively, of Kaplan (2004: 94). Because variation in overlap involves complex changes in epicoracoid structure, we were unable to find evidence to select one hypothesis of additivity over another; we therefore treated this character nonadditively.

121. Angle of Clavicles (fig. 64): directed laterally = 0; directed posteriorly = 1; directed anteriorly = 2. Nonadditive.

In most dendrobatids each clavicle runs laterad, perpendicular to the sagittal plane (state 0). In some species, the clavicles are directed posteriad, running approximately parallel to the posterior margin of the coracoid (state 1). Clavicles directed anteriad (state 2) are confined to certain species in the outgroup. The intermediacy of the laterally directed clavicles is suggestive of additivity; however, pectoral girdle ontogeny does not proceed in this way, and we therefore scored this transformation series nonadditively.

122. Acromion Process: cartilaginous, distinct = 0; fully calcified (or ossified), continuous with clavicle and scapula = 1.

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The acromion processes of some taxa are cartilaginous (state 0) in mature specimens, whereas in others they are extensively calcified or ossified (state 1). We did not distinguish between extensive calcification and ossification. As with other osteological characters that vary ontogenetically (characters 127, 134–138), adult females are most extensively ossified.

123. PREZONAL ELEMENT (OMOSTERNUM): absent = 0; present = 1.

124. PREZONAL ELEMENT (OMOSTERNUM) ANTERIOR EXPANSION: not expanded distally, tapering to tip = 0; weakly expanded, to 2.5× style at base of cartilage or equivalent = 1; extensively expanded distally, 3.5× style or greater = 2. Additive.

125. PREZONAL ELEMENT (OMOSTERNUM) SHAPE OF ANTERIOR TERMINUS: rounded or irregularly shaped = 0; distinctly bifid = 1.

126. PREZONAL ELEMENT (OMOSTERNUM) SHAPE OF POSTERIOR TERMINUS: simple = 0; notched, forming two struts = 1; continuous with epicoracoid cartilage = 2. Nonadditive.

127. PREZONAL ELEMENT (OMOSTERNUN) OSSIFICATION: entirely cartilaginous = 0; medially ossified (cartilaginous base and tip) = 1; basally ossified (cartilaginous tip) = 2; entirely ossified = 3. Additive.

128. SUPRASCAPULA ANTERIOR PROJECTION: cartilaginous = 0; heavily calcified = 1.

129. STERNUM SHAPE: simple (rounded, irregular) = 0; medially divided = 1.

The posterior termination of the sternum is either simple (rounded or irregularly shaped; state 0) or distinctly divided medially, forming either two prongs or two broad, rounded lobes. We also observed independent variation in the lateral expansion of the sternum. For example, even though the sternum of both species is medially divided, in *panamensis* (UMMZ 167459) it is broadly expanded, whereas in *juanii* (ICN 5097) the sternum is tapered. However, we also observed confounding intermediate and other variation and were unable to individuate states objectively for the current study.

130. ZYGOMATIC RAMUS OF SQUAMOSAL (fig. 65): elongate, slender, pointed = 0; very long and slender = 1; robust, truncate, and elongate = 2; shorter and less robust but still well defined = 3; well defined, moderate length, abruptly directed ventrad = 4; inconspicuous, poorly differentiated = 5; very small, inconspicuous, hooklike = 6; miniscule bump = 7; robust, elongate, in broad contact with the maxilla = 8. Nonadditive.

The zygomatic ramus of the squamosal varies extensively and forms a series of complex morphological transformations. In state 0, the zygomatic ramus is elongate (approximately half the length of the ascending ramus and extending well anterior past the tympanic ring), slender, gently curved, and pointed. State 1 is a very long and slender process. State 2 is robust, truncate, and elongate (extending anterior to the tympanic ring, but not as long as state 2). State 3 is shorter and less robust than state 2 but is still a conspicuous shaft that usually extends anterior to the tympanic ring. Like the processes of states 0, 1, and 2, the axis of state 3 is at most only weakly inclined toward the maxilla. The zygomatic ramus of state 4 is also well defined, but it is distinctly and abruptly directed ventrad, its axis pointing almost straight down at the maxilla, that is, a line from the zygomatic ramus would intersect the posterior extreme of maxilla, and it does not extend anterior to the tympanic ring. State 5 is an inconspicuous, poorly differentiated process. The zygomatic ramus of most of the sampled species is a very small, inconspicuous, hooklike process (state 6). McDiarmid (1971) considered the zygomatic ramus to be absent in *Melanophrynis-*

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Fig. 65. Character 130, zygomatic ramus of squamosal. **A**: State 0 (*Eupsophus roseus*, KU 207501). **B**: State 1 (*Cycloramphus fuliginosus*, KU 92789). **C**: State 2 (*nocturnus*, AMNH 130041). **D**: State 2 shown in a dissected whole specimen (*palmatus*, AMNH 20436). **E**: State 3 (*trinitatis*, AMNH 118389). **F**: State 4 (*trivittatus*, AMNH 118428). **G**: State 5 (*espinosai*, AMNH 118417). **H**: State 6 (*bocagei*, UMMZ 182465). **I**: State 7 (*Melanophryniscus stelzneri*, AMNH 77710). **J**: State 8 (*Megaelosia goeldii*, AMNH 103952; squamosal colored red).

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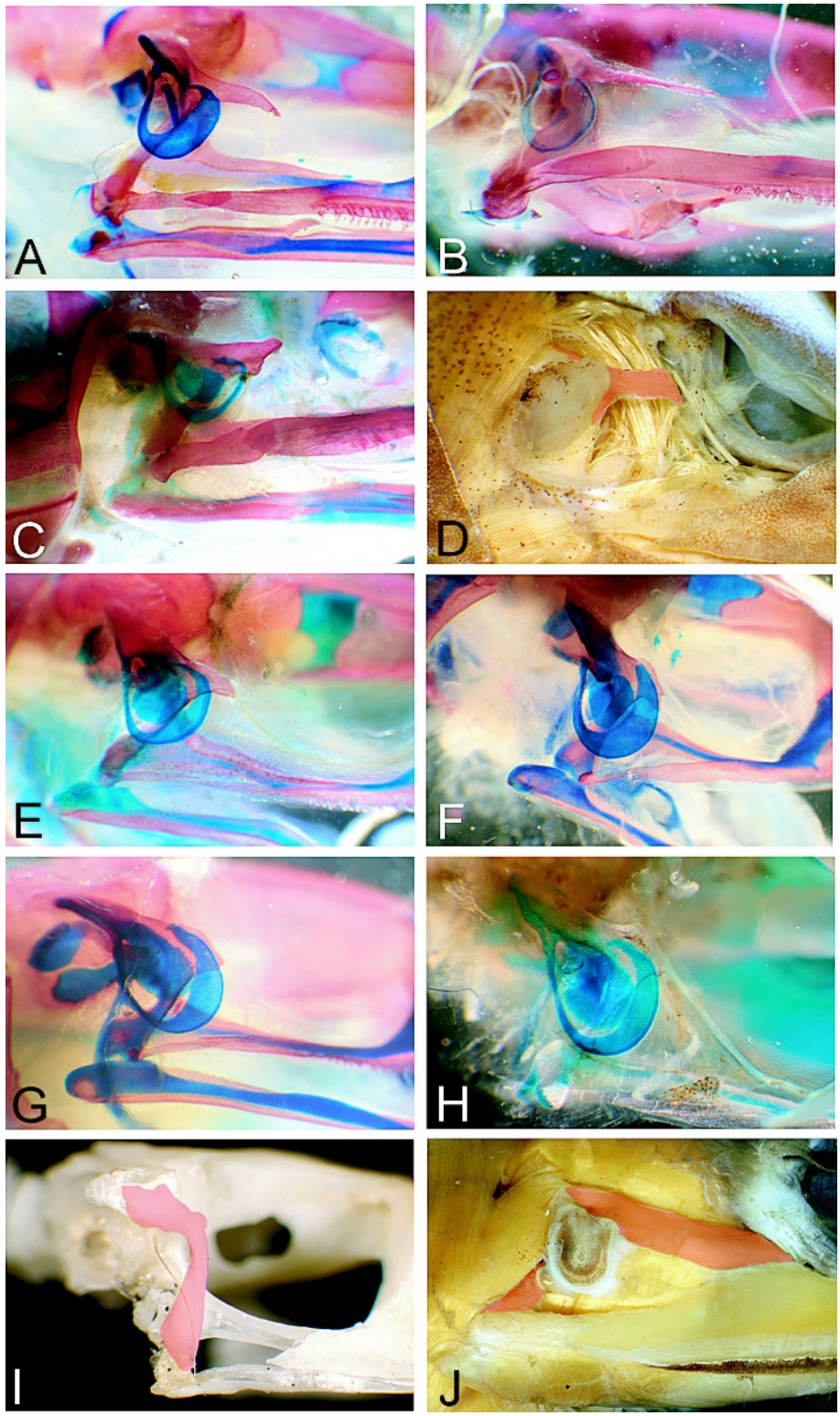

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cus; however, we detected a miniscule bump (state 7) in *Melanophryniscus stelzneri*, which we considered to be homologous with the zygomatic ramus. (Regardless, we did not observe this state in any other species included in the present analysis, so coding it as "absent" or "a miniscule bump" has no bearing on the outcome of analysis.) In *Megaelosia goeldii*, the robust zygomatic ramus extends anteroventrad to be in broad contact with the maxilla (state 8).

131. ORIENTATION OF ALARY PROCESS OF PREMAXILLA: directed anterolaterally = 0; directed dorsally = 1; directed posterodorsally = 2. Additive.

Myers and Ford (1986) claimed the anterolaterally tilted alary process as a synapomorphy of dendrobatids, although several other taxa also share this state (e.g., Lynch, 1971). We treated this transformation series additively ($0 \leftrightarrow 1 \leftrightarrow 2$) based on the argument that the rearrangement in skull architecture required to alter the orientation of the alary process would necessitate passing through the intermediate stage.

132. PALATINES: absent = 0; present = 1.

Variation in the occurrence of the palatine bones among dendrobatids has been documented by numerous authors (e.g., Silverstone, 1975a; Myers and Ford, 1986), and Kaplan (1997) interpreted the character phylogenetically. Trueb (1993) considered the neobatrachian palatine to be nonhomologous with the palatine of other vertebrates, and she is almost certainly correct. Nevertheless, this bone would unquestionably be identified as a palatine if anurans were found to be rooted on a neobatrachian. As such, the validity of Trueb's distinction rests on the phylogenetic position of neobatrachians, that is, it is a conclusion of phylogenetic analysis, not a premise. We therefore follow Haas (2003) in referring to this bone as the palatine.

133. QUADRATOJUGAL–MAXILLA RELATION: overlapping = 0; separated = 1.

In dendrobatids, the quadratojugal and maxilla are never in contact or tightly bound but are instead loosely bound by ligamentous tissue. In some species, the two bones overlap (state 0), whereas in others the anterior tip of the quadratojugal does not reach the level of the posterior tip of the maxilla.

134. NASAL–MAXILLA RELATION (fig. 66): separated = 0; in contact = 1.

The nasal and maxilla may be separate (state 0) or contact each other. We did not distinguish between overlap and fusion because gross examination under a dissecting microscope proved inadequate to determine the status of many specimens and the necessary histological study was infeasible for the present study.

135. NASAL–SPHENETHMOID RELATION (fig. 67): free, separate = 0; overlapping or fused = 1.

In state 0, the nasal and sphenethmoid do not overlap, whereas in state 1 those bones are either overlapping or fused. We did not distinguish between overlapping and fusion as the necessary histological analysis was infeasible for the present study.

136. FRONTOPARIETAL FUSION: entirely free = 0; fused posteriorly = 1; fused along entire length = 2. Additive.

Ontogenetic variation in frontoparietal fusion suggests that it proceeds anteriorly. We therefore treated this character additively.

137. FRONTOPARIETAL–OTOCCIPITAL RELATION: free = 0; fused = 1.

Among dendrobatids, there is variation in the relation of the frontoparietal and otoccipital (i.e., the fused prootic and exoccipital; Lynch, 1971: 52), being free (state 0) in some taxa and fused (state 1) in others. Lynch (1971) documented variation in this character in numerous outgroup taxa.

138. EXOCCIPITALS: free, separate = 0; fused sagittally = 1.

The exoccipital portions of the fused otoccipital bones (see Lynch, 1971: 52) may be separated by cartilage (i.e., chondrocranial ossification may be incomplete; state 0) or may be fused sagittally (state 1). A further potential state is for them to abut but not fuse, but we did not observe this among the specimens examined.

139. MAXILLARY TEETH: absent = 0; present = 1.

Variation in the occurrence of teeth has been used consistently in dendrobatid systematics (see Grant et al., 1997 for discussion). In the more recent literature, Edwards (1971: 147) stated that dendrobatids "can be divided into two groups—those species lack-

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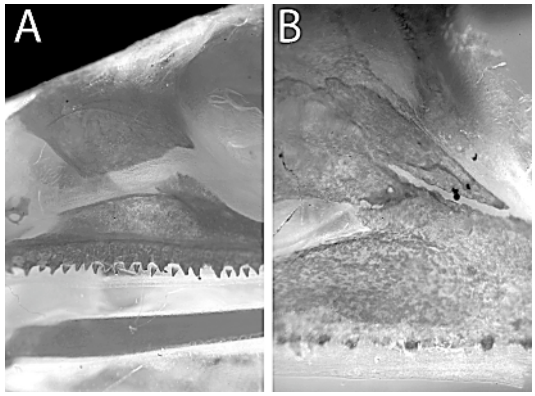

Fig. 66. Character 134, nasal–maxilla relation. **A**: State 0, nasal and maxilla broadly separated (*silverstonei*, AMNH 91847). **B**: State 1, greater magnification showing nasal and maxilla overlapping or fused (*bassleri*, AMNH 43402).

ing maxillary teeth (*Dendrobates*) and those having maxillary teeth (*Phyllobates* and *Colostethus*).'' Silverstone (1975a) showed that the situation is more complicated due to character conflict and polymorphism. (See also Materials and Methods for uncoded variation in maxillary tooth size and shape.)

140. MAXILLARY TOOTH STRUCTURE: pedicellate = 0; nonpedicellate = 1.

Most anurans have pedicellate teeth, whereby the tooth is divided into a pedicel and crown (Parsons and Williams, 1962). Parsons and Williams (1962: 377) examined the teeth of *bocagei* (as *Phyllobates bocagii*) and *palmatus* (as *Phyllobates granuliventris*) and found that ''the division is certainly not marked in gross structure and is quite probably lacking.'' Myers et al. (1991: 11) further pointed out that there is no ''pattern of physical separation of crowns from pedicels (breakage is irregular)'', and that ''the loss or significant obfuscation of the usual amphibian pedicellate condition warrants attention as a possible synapomorphy for the Dendrobatidae.'' We coded tooth structure from gross examination of cleared and stained specimens only, although histological study is required to address this problem decisively.

141. VOMERINE TEETH: absent = 0; present = 1.

142. RETROARTICULAR PROCESS OF MANDIBLE (fig. 68): absent = 0; present = 1.

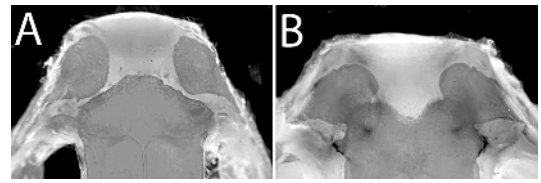

Fig. 67. Character 135, nasal–sphenethmoid relation. **A**: State 0, separate (*bassleri*, AMNH 43402). **B**: State 1, overlapping or fused (*nocturnus*, AMNH 130014). In this case the nasals clearly overlap but are not fused with the sphenethmoid, but in other species the distinction between the bones is not as clear.

Myers and Ford (1986) noted the occurrence of a retroarticular process on the mandible as a distinguishing characteristic of dendrobatids, and Ford and Cannatella (1993) listed it as one of two unique synapomorphies. Although many dendrobatids are characterized by conspicuously elongate retroarticular processes, Myers et al. (1991: 11) noted that in *nocturnus* the process is ''present, but always short (compared with other dendrobatids) although somewhat variable in length.'' As shown in figure 68, there is considerable interspecific variation in the length of the retroarticular process. However, we were unable to delimit states, in part because no clear choice for a standard reference point has been identified.

143. EXPANSION OF SACRAL DIAPOPHYSES (fig. 69): unexpanded = 0; moderately expanded = 1; strongly expanded = 2. Additive.

The shape of the sacral diapophyses has been used since Boulenger (1882). Ford (1989) mistakenly cited Duellman and Trueb (1986) as having placed Dendrobatidae among ranoids based in part on their sharing round-shaped sacral diapophyses (Duellman and Trueb did not include that character in their matrix), but it has, nonetheless, played an important role in anuran systematics.

The state found in dendrobatids has usually been referred to as round or cylindrical (e.g., Duellman and Trueb, 1986), but the sacral diapophyses are invariably elliptical in cross section. For this reason we refer instead to the degree of expansion of the sacral diapophyses. Emerson (1982) quantified expansion by measuring the angle formed by

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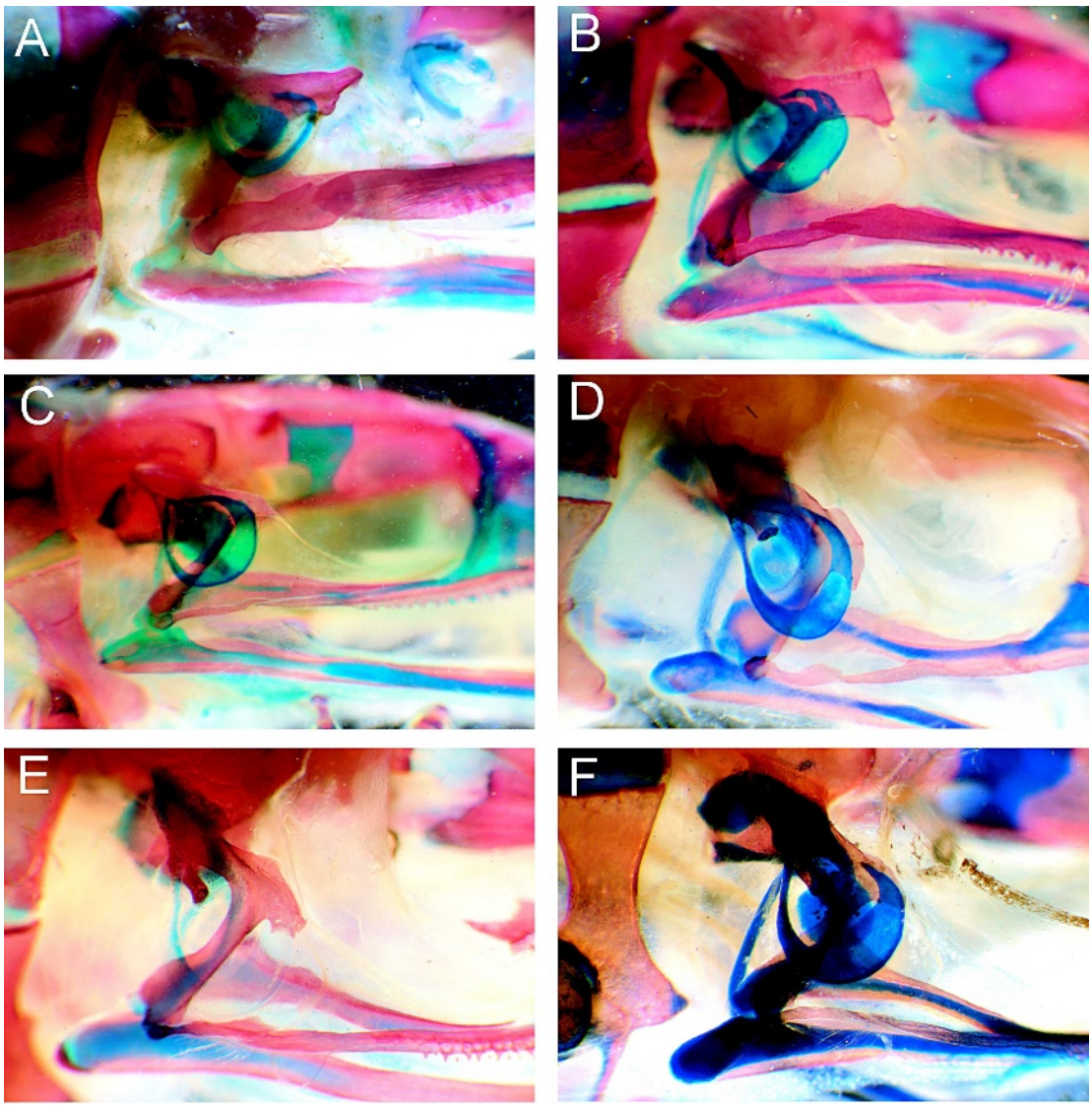

Fig. 68. Length variation in character 142, retroarticular process of the mandible. **A**: *nocturnus*, AMNH 130041. **B**: *riveroi*, AMNH 134142. **C**: *vittatus*, AMNH 118386. **D**: *lehmanni* Myers and Daly, AMNH118442. **E**: *pratti*, AMNH118364. **F**: "Neblina species", AMNH 118667.

the expansion. Here we code this character as the ratio of the width of the tip of the diapophysis to the width of the base of the diapophysis. Variation is not continuous; all states are separated by gaps. Unexpanded diapophyses are subequal at the base and tip. Moderately expanded diapophyses are 1.5–2.5 times wider at the tip than at the base; greatly expanded diapophyses are at least 2.7 times greater at the tip. Sacral diapophyses often bear irregular flanges that we did not include in the measurement of width.

144–146. VERTEBRAL FUSION

Noble (1922: 15) reported fusion of vertebrae 2 + 3 and 8 + 9 (i.e., 8 + sacrum) in two species of dendrobatids (*pumilio* [as *Dendrobates typographicus*] and probably *histrionicus* or *sylvaticus* Funkhouser [dis-

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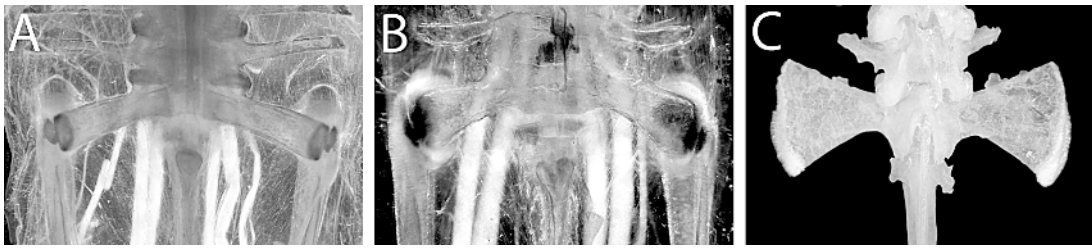

Fig. 69. Character 143, expansion of sacral diapophyses. **A**: State 0, unexpanded (*riveroi*, AMNH 134143l). **B**: State 1, moderately expanded (*pumilio*, AMNH 118514). **C**: State 2, greatly expanded (*Melanophryniscus stelzneri*, AMNH 77710).

cussed under the tentative name *Dendrobates tinctorius*]). Silverstone (1975a: 5) summarized his observations of vertebral fusion in dendrobatids as "absent in the 17 specimens of *Colostethus* examined, present in only two of the 29 specimens of *Phyllobates* examined, and present in 28 of the 46 specimens of *Dendrobates* examined." He also noted that vertebral fusion varies intraspecifically, and we also found intraspecific variation among equivalent semaphoronts.

144. VERTEBRA 8 AND SACRUM: free = 0; fused = 1.

145. VERTEBRAE 1 AND 2: free = 0; fused = 1.

Myers et al (1991:11) reported ventral fusion of vertebrae 1 and 2 in *nocturnus* (AMNH 130047); however, close examination showed that the vertebrae are tighly bound by ligamentous tissue but are not fused.

146. VERTEBRAE 2 AND 3: free = 0; fused = 1.

147–172. ALKALOID PROFILES

Dendrobatid frogs are known to possess a diverse array of over 450 alkaloids (Daly et al., 1999; J. W. Daly, in litt., 01/25/05). Use of alkaloid profiles as transformation series is complicated, in part, because it appears that "some, if not all … 'dendrobatid alkaloids' may have a dietary origin" (Daly et al., 1994a; see also Myers and Daly, 1976b: 194–197; Myers et al., 1995), which means that the occurrence of a given alkaloid may be determined not by the genotype but by availability of the dietary source in the environment (making this a nonheritable characteristic, i.e., not a character). Saporito et al. (2003) identified a species of siphonotid millipede as the likely dietary source of spiropyrrolizidine and Saporito et al. (2004) identified certain species of formicine ants as the natural dietary source of two pumiliotoxins found in *pumilio*. Dumbacher et al. (2004) identified melyrid beetles as the probable dietary source of batrachotoxins for the New Guinean passerine birds *Pitohui* and *Ifrita* and further conjectured that this is the likely source of the alkaloids in *Phyllobates* as well. There is often considerable variation in the alkaloid profiles of conspecifics from both the same and disjunct populations (e.g., Myers et al., 1995). Captive reared offspring of wild-caught, toxic frogs are nontoxic if fed crickets and fruit flies, but readily accumulate alkaloids if present in the diet (either as a pure supplement to a fruit fly diet or in leaf-litter arthropods; Daly et al., 1992, 1994a, 1994c).

Nevertheless, despite the environmental dependency, there is also clearly a heritable aspect to the alkaloid uptake system. It has been found experimentally that *azureiventris*, *panamensis*, and *talamancae* do not accumulate detectable amounts of alkaloids when ingested from the diet (Daly et al., 1994c; Daly, 1998). Furthermore, among sequestering species there is differential accumulation, as suggested indirectly by the occurrence of different alkaloid profiles among microsympatric species (Daly et al., 1987; Myers et al., 1995) and demonstrated directly by feeding experiments (Daly et al., 1994c, 2003; Garraffo et al., 2001), that is, the uptake systems of different species either (1) are capable of sequestering only a subset of the alkaloids ingested in the diet or (2) vary drastically in the efficacy of accumulation of different classes of alkaloids. Either way, this variation is heritable. Furthermore, Daly et al. (2003) demonstrated selective alkaloid modification

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by certain dendrobatid species and not others (see Character 171). As with all phenotypic characters, the expression of alkaloid characters is due to the combination of genotype plus environment (for a detailed discussion of the meaning of "genetic" see Sarkar, 1998). Hypotheses of homology can therefore be proposed defensibly, albeit cautiously, for alkaloid profiles.

Given that it is the *capability* to accumulate a class of toxin that is treated as the character, we coded alkaloid profiles as "any instance" (Campbell and Frost, 1993). That is, we treated the demonstrated occurrence of a given class of alkaloid in one or more populations of a species as evidence that the entire species is capable of accumulating that class of alkaloid (i.e., it is coded as present), even if that class of alkaloid was not detected in all samples. This is not intended as a general endorsement of that method of codifying polymorphism (for theoretical arguments, see Grant and Kluge, 2003, 2004), but rather as a consequence of this *particular* biological problem. Given current understanding of the alkaloid uptake system of these frogs, it is most likely that the absence of a class of alkaloid in some but not all individuals is due to dietary deficiency and not a character-state transformation. This assumption is testable, and it may be found that (1) this assumption is borne out (i.e., the alkaloid is sequestered when present in the diet), (2) such species are truly polymorphic (i.e., character history and species history do not track each other perfectly, either due to ancestral polymorphism, a character-state transformation event subsequent to the most recent cladogenetic event, or some other phenomenon), or (3) multiple species have been conflated. This is exemplified by *lugubris*:

> Only one of several populations of *P*[*hyllobates*] *lugubris* had barely detectable amounts of batrachotoxins. Some but not all populations had trace levels of other alkaloids. … Alkaloids including a batrachotoxin, were fed to captive-raised *P. lugubris* and found to be readily accumulated into skin (J. W. Daly, unpublished results). Thus, the frog has a functional accumulating "system" and the lack or near lack of alkaloids in wild-caught frogs must reflect low availability or non-targeting of alkaloid- or batrachotoxin-containing arthropods. (J. W. Daly, in litt. 02/02/00).

It is also possible that a species is capable of accumulating an alkaloid not detected in *any* population because the dietary source of the precursor is absent at all sampled localities (i.e., failure to detect accumulation in wild-caught specimens does not decisively demonstrate that the species is incapable of sequestration). However, by coding these taxa as lacking the ability to accumulate the toxin we incorporated all available evidence. The hypothesis that a taxon is incapable of accumulating a class of toxin is falsifiable and can be tested both by examining more specimens and populations and through feeding experiments. For example, although no histrionicotoxin could be detected in wild *lehmanni* Myers and Daly (Myers and Daly, 1976b), Garraffo et al. (2001: 421) report that "[f]eeding experiments indicated that *D. lehmanni* readily accumulated histrionicotoxin into skin when fed alkaloid-dusted fruit flies."

Although a dietary source is either known or assumed for dendrobatid alkaloids, the actual arthropod(s) responsible have yet to be discovered for the vast majority of these, that is, most of the alkaloids are unknown elsewhere in nature. Potential sources were reviewed by Daly et al. (1993: 226, 2005). For example, pyrrolizidines are known to occur in the ants *Solenopsis xenovenenum*, *Monomorium* spp. from New Zealand, and *Megalomyrmex* from Venezuela. Pyrrolidines (including 2,5-pyrrolidines, known among amphibians only in dendrobatids) occur in *Solenopsis*, *Monomorium*, and *Megalomyrmex*. Decahydroquinolines were detected in extracts of virgin queens of the thief ant *Solenopsis* (*Diphorhoptrum*) *azteca* from Puerto Rico. 3,5-Disubstituted indolizidines occur in ants of the genera *Monomorium* and *Solenopsis*. Coccinellines were first discovered in the ladybug beetles Coccinellidae. Monocyclic piperidines occur in *Solenopsis*. Spiropyrrolizidine is likely sequestered from a millipede (Saporito et al., 2003), two pumiliotoxins found in *pumilio* are obtained from formicine ants (Saporito et al., 2004), and scheloribatid mites are the probable source of a third pumiliotoxin in *pumilio*

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(Takada et al., 2005). The source of batrachotoxins in dendrobatids remains unknown, although melyrid beetles are likely (Dumbacher et al., 2004).

That the actual dietary source is unknown is an important consideration, given the discovery by Daly et al. (2003) that some species convert dietary pumiliotoxin to allopumiliotoxin via a specific hydroxylation event (see Character 171, below). Whereas prior to this discovery it was assumed that all of the over 450 alkaloids known in these frogs were incorporated without modification into the skin, one must consider the possibility that some portion of this diversity of alkaloids may result from the modification of precursors. Nevertheless, it is unclear how widespread metabolic conversion may be, as the following 12 alkaloid classes have been administered in feeding experiments with no evidence for any metabolism (J. W. Daly, in litt., 01/25/05): batrachotoxin, histrionicotoxins, allopumiliotoxins, decahydroquinolines, 3,5-pyrrolizidines, 3,5-indolizidine, 5,8-indolizidine, 5,6,8-indolizidine, pyrrolidine, piperidine, spiropyrrolizidine, and coccinelline-like tricyclics.

Given the dietary origin of the alkaloids and how little is known about the alkaloid uptake system, we were conservative in delimiting alkaloid characters for phylogenetic analysis. Instead of coding the occurrence of each of the over 450 dendrobatid alkaloids as a separate character, we scored the occurrence of the major and minor classes of alkaloids, following Daly et al. (1987, 1993) and incorporating more recent developments (e.g., Daly et al., 1994c, 2003, 2005; Daly, 1998; Garraffo et al., 1993, 1997, 2001; Daly et al., 1999; Mortari et al., 2004; J. W. Daly, in litt., 01/25/05). We followed Myers (1987) and Myers et al. (1995) in coding 3,5-indolizidines and 5,8-methylindolizidines as distinct characters. In only coding the occurrence of general classes of alkaloids, we consciously overlooked more refined, potentially phylogenetically informative data in an attempt to avoid introducing error due to the nature of alkaloid accumulation in these frogs. Furthermore, in the majority of species, numerous alkaloids of the same class co-occur, which suggests that sequestration acts at the level of the class of alkaloid, not individual alkaloids; that is, it appears that it is the ability to sequester alkaloids with certain chemical properties that evolves, not the ability to sequester a *particular* alkaloid.

We did not distinguish between major, minor, and trace occurrences of alkaloids (i.e., we treated all as "present"), but, following Daly's recommendation (J. W. Daly, in litt., 02/02/00), we did not consider "trace, trace" occurrences as evidence of presence of an alkaloid, as merely having recently consumed an alkaloid-containing prey item could give this result.[11] We also did not discriminate based on uptake efficiency. For example, although uptake of piperidines is poor in most species (e.g., *auratus*, in which they are trace alkaloids), and uptake of piperidine **241D** appears highly efficient in *speciosus* (in which this is a major or minor alkaloid), we coded piperidines identically (i.e., present). It should be clarified that, despite the fact that the trivial names of the classes of alkaloids are often derived from species that possess it (e.g., pumiliotoxin from *pumilio*), compounds are assigned to a class based on molecular structure and chemical properties, not taxonomic distribution.

It has been speculated that certain alkaloids could share common precursors, specifically a 2,6-disubstituted(dehydro)piperidine as a precursor in the biosynthesis of histrionicotoxins, gephyrotoxins, indolizidines, and decahydroquinolines (Daly et al., 1987: 1065), and more generally that the monocyclic piperidines are possible precursors for the more complex, piperidine-ring-containing alkaloids and the monocyclic pyrrolidines for the more complex, pyrrolidine-ring-containing dendrobatid alkaloids (Daly et al., 1993: 251). Nevertheless, with the exception of allopumiliotoxin **267A** (see Character 171), there is no evidence that they

[11]Daly et al. (1987: 1078) reported a trace occurrence of alkaloid **181B**, a 5,8-methylindolizidine, from a single population of *femoralis* at Napo, Ecuador. However, J. W. Daly (in litt., 02/02/00) informed T. Grant that this was a trace, trace amount, and he recommended that this not be treated "as evidence for significant ability for accumulation of alkaloids in the species".

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share a common biosynthetic origin, and even if they do, this would pertain to the arthropods, not the frogs' uptake system. Historical independence is demonstrated by the fact that no classes of alkaloids share identical taxonomic distributions.

We coded unambiguously only those species whose alkaloid profiles have been examined; taxa whose profiles have not been examined were coded as unknown ("?"). The discovery that an untested species is embedded within a toxic clade would provide a strong prediction that the species may also sequester alkaloids and would therefore guide chemists in their search for novel, potentially useful toxins. Negative findings often are not explicitly reported in the literature; however, in cases where species have been examined using techniques that would detect a particular compound and the compound was not reported, we coded it as absent (e.g., epibatidine). If there was any doubt as to the tests samples were subjected to, we coded the character as unknown ("?").

Data were taken from reviews (Daly et al., 1987, 1993, 1999), the primary literature (Tokuyama et al., 1992; Garraffo et al., 1993, 2001; Badio and Daly, 1994; Myers et al., 1995; Daly et al., 1997., 2003; Fitch et al., 2003; Saporito et al., 2003; Mortari et al., 2004; Darst et al., 2005), and an exhaustive summary of published and unpublished alkaloid profiles and corrections to previous accounts provided by John W. Daly (in litt., 01/25/05). To facilitate coding from the literature we list the individual nonsteroidal alkaloids for each class, following the convention of Daly et al. (1987). We did not include unclassified alkaloids, although they may provide relevant information once their structures are elucidated. We did not list unpublished alkaloids in the character descriptions (although we did code their presence in the matrix), and we only listed alkaloids that occur in the species sampled in the present study.

147. Ability to Sequester Alkaloids: absent = 0; present = 1.

We coded the general ability to sequester alkaloids separately from the individual classes of alkaloids sequestered in order to count the gain and loss as a single transformation event. We scored species that are incapable of sequestering any alkaloid as state 0 for this character and missing ("–") for all other lipophilic alkaloid characters; we coded species that are able to sequester any alkaloid as state 1 for this character and present and absent for each of the particular alkaloid classes. That is, although the origin of the ability to sequester alkaloids necessarily entails the ability to sequester some particular class(es) of alkaloid(s) (i.e., there is a logical relation of nested dependency between these characters), the fact that no taxon possesses only a single class of alkaloid would mean that the alternative approach of treating each origin and loss as entirely unrelated events would count the origin of sequestration as multiple events. The biological assumption underlying this coding is that there exists a single genetic basis for the sequestration of all classes of lipophilic alkaloids and that modifications to it account for the differential ability to sequester distinct classes. This assumption is consistent with the limited understanding of the uptake mechanism but has not been subjected to critical test (i.e., no attempt has been made to isolate the genetic basis of sequestration).

Darst et al. (2005) reported the occurrence of alkaloids based on thin layer chromatography, which allowed us to score several additional species. Unfortunately, that method does not discriminate between or lead to the identification of different alkaloids, so this is the only character that can be coded from their results.

148. Batrachotoxins (BTX): absent = 0; present = 1.

The steroidal batrachotoxins are known to occur in only five species of frogs (*aurotaenia*, *bicolor*, *lugubris*, *terribilis*, and *vittatus*), and their shared occurrence was treated as evidence of the monophyly of those species in a restricted *Phyllobates* (Myers et al., 1978). Given the extreme toxicity of BTX relative to other dendrobatid alkaloids, the ability of these frogs (and the inability of other dendrobatids) to sequester BTX is likely related to their modified sodium channel that is insensitive to BTX (as demonstrated for *aurotaenia* and *terribilis*; Daly et al., 1980).

149. Histrionicotoxins (HTX): absent = 0; present = 1.

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235A, 237F, 239H, 259A, 261A, 263C, 265E, 283A, 285A, 285B, 285C, 285E, 287A, 287B, 287D, 291[a].

Alkaloid **283A′** (found in *sylvaticus* Funkhouser) is closely related to and was treated as an HTX by Daly et al. (1987), but it was not included by Daly et al. (1993) or Daly et al. (2005).

150. PUMILIOTOXIN (PTX): absent = 0; present = 1.

207B, 209F, 225F, 237A, 251D, 253F, 265D, 265G 267C, 267D, 277B, 281A, 293E, 297B, 305B, 307A, 307B, 307D, 307F 307G, 307H, 309A, 309C, 321A, 323A, 325B, 353A.

151. ALLOPUMILIOTOXINS (aPTX): absent = 0; present = 1.

225E, 237B, 241H, 251I, 253A, 267A, 297A, 305A, 307C, 309D, 321C, 323B, 325A, 339A, 339B, 341A, 341B, 357.

152. HOMOPUMILIOTOXINS (hPTX): absent = 0; present = 1.

223G, 249F, 251L, 256R, 265N, 317, 319A, 319B, 321B.

153. DECAHYDROQUINOLINE (DHQ): absent = 0; present = 1.

193D, 195A, 209A, 209J, 211A, 211K, 219A, 219C, 219D, 221C, 221D, 223F, 223Q, 223S, 231E, 243A, 245E, 249D, 249E, 251A, 253D, 267L, 269AB, 269A, 269B, 271D, 275B.

154. 3,5-DISUBSTITUTED PYRROLIZIDINES: absent = 0; present = 1.

167F, 195F, 209K, 223B, 223H, 237G, 251K, 253I, 265H, 265J, 267H.

167F and **209K** were formerly classified as the 3,5-disubstituted indolizidines **167B** and **209D**.

155. 3,5-DISUBSTITUTED INDOLIZIDINES: absent = 0; present = 1.

195B, 211E, 223AB, 223R, 237E, 239AB, 239CD, 239E, 249A, 271F, 275C, 275F.

156. 5,8-DISUBSTITUTED INDOLIZIDINES: absent = 0; present = 1.

181B, 193E, 197C, 203A, 205A, 207A, 209B, 209I, 217B, 219F, 221A, 221K, 223D, 223J, 225D, 231C, 233D, 235B, 237D, 237H, 239A, 239B, 239C, 239D, 239F, 239G, 241C, 241F, 243B, 243C, 243D, 245B, 245C, 245D, 251B, 251U, 253B, 263F, 257C, 259B, 261D, 271A, 273B, 279D, 295A, 295B.

157. DEHYDRO-5,8-INDOLIZIDINES: absent = 0; present = 1.

245F, 245H.

158. 5,6,8-INDOLIZIDINES: absent = 0; present = 1.

195G, 207Q, 223A, 231B, 233G, 237L, 249H, 251M, 253H, 259C, 263A, 263D, 265I, 265L, 267J, 273A, 275E, 277C, 277E, 279F, 293C.

159: 4,6-QUINOLIZIDINES: absent =0; present = 1.

195C, 237I.

160. 1,4-QUINOLIZIDINES: absent = 0; present = 1.

207I, 217A, 231A, 233A, 235E', 247D, 257D.

161. LEHMIZIDINES: absent = 0; present = 1.

275A.

162. EPIQUINAMIDE: absent = 0; present = 1.

196.

163. 2,5-PYRROLIDINE (PYR): present = 0; absent = 1.

183B, 197B, 223N, 225C, 225H, 277D, 279G.

164. 2,6-PIPERIDINES (PIP): absent = 0; present = 1.

197E, 211I, 211J, 213, 221L, 223K, 225B, 225I, 237J, 239I, 239L, 239O, 241D, 241G, 253J, 255A, 267K, 267C.

165. GEPHYROTOXIN (GTX): absent = 0; present = 1.

287C, 289B.

166. COCCINELLINE-LIKE TRICYCLICS: absent = 0; present = 1.

191B, 193A, 193C, 201B, 205B, 205E, 207J, 207P, 207R, 219I, 221G, 221M, 235M, 235P.

167. SPIROPYRROLIZIDINES: absent = 0; present = 1.

Referred to as pyrrolizidine oximes by Daly et al. (1993).

222, 236, 252A, 254.

168. INDOLIC ALKALOIDS (CHIMONANTHINE/CALYCANTHINE): absent = 0; present = 1.

346B, 346C.

169. EPIBATIDINES: absent = 0; present = 1.

208/210, 308/310.

170. NORANABASAMINE (=PYRIDYL-PIPERIDINES): absent = 0; present = 1.

This pyridine alkaloid is known in nature only from *aurotaenia*, *bicolor*, and *terribilis* (Daly et al., 1993, 1999).

239J.

171. PUMILIOTOXIN 7-HYDROXYLASE: absent = 0; present = 1.

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Feeding experiments by Daly et al. (2003) demonstrated the existence in several species of dendrobatids of an enantioselective mechanism that converts PTX (+)-**251D** to the more highly toxic allopumiliotoxin (aPTX) (+)-**267A**. That is, contrary to other alkaloid characters, which code the ability to sequester a class of alkaloid, this character applies to the occurrence of the 7-hydroxylase, as evidenced by the occurrence of the hydroxylated compound.

Coding this character is somewhat more complicated than coding the other alkaloid characters, because in this case occurrence of aPTX **267A** may be due to either (1) the hydroxylation of PTX **251D** or (2) the sequestration of aPTX **267A** from a dietary source (aPTX is known to occur in some arthropods). This creates the potential for both false negatives and false positives. Direct evidence for the occurrence of 7-hydroxylase may only be obtained through feeding experiments. Further evidence on the distribution of the pumiliotoxin 7-hydroxylase obtained indirectly from the alkaloid profiles of wild-caught specimens (see Daly et al., 2003: 11095, table 1) requires the assumption that all aPTX **267A** occurs through metabolism of ingested PTX **251D**, which, at least in the case of *anthonyi* (reported as *tricolor*; for taxonomy of these species, see Graham et al., 2004), is false (assuming multiple species have not been conflated). Daly et al. (2003) reported wild-caught specimens as possessing trace amounts of aPTX **267A**, but feeding experiments revealed that the species is incapable of hydroxylating PTX **251D** and the occurrence of aPTX **267A** represents a false positive for the presence of 7-hydroxylase. Nevertheless, in the absence of direct evidence from feeding experiments, such as is available for *anthonyi*, we coded all trace, minor, and major occurrences of aPTX **267A** as the presence of the 7-hydroxylase, which allows the results of phylogenetic analysis to serve as a tool for designing future feeding experiments to test hypothesized occurrence of 7-hydroxylase (e.g., finding that a species that possesses aPTX **267A** is embedded in a clade of species incapable of 7-hydroxylation would suggest the occurrence may be due to sequestration from a dietary source and not biosynthetic conversion).

Conversely, the absence of 7-hydroxylase can only be assured in the presence of PTX **251D**. We coded the failure to detect aPTX **267A** as "absent" (state 0) only when PTX **251D** was detected. If PTX **251D** was not detected (but other PTXs were), we coded this character as unknown ("?") (e.g., *truncatus*). If available evidence indicates that a species is incapable of sequestering pumiliotoxins, we coded this character as missing ("–") (e.g., *trivittatus*).

Direct evidence for the presence of the pumiliotoxin 7-hydroxylase through feeding experiments was found for *auratus*, *galactonotus*, and *castaneoticus*, and direct evidence for the absence of pumiliotoxin 7-hydroxylase through feeding experiments was found in *tricolor* and *bicolor* (Daly et al., 2003). Other species are coded on the basis of wild-caught specimens, with data derived from Daly et al. (1987, 1993, 2003).

172. TETRODOTOXIN (TTX): absent = 0; present = 1.

Daly et al. (1994b) reported the occurrence of TTX in *panamensis* (as *Colostethus inguinalis*; see Grant, 2004). They also examined aqueous extracts of eight additional species referred to *Colostethus* (the "*Colostethus* species" reported as being "common, nr Villa María, Caldas, Colombia" is *fraterdanieli*), and *nocturnus*, *pumilio*, and *bicolor*. Daly et al. (1994b: 283) cautioned that the negative results for *pumilio* and *bicolor* were based on methanol extracts,

> which would have extracted only minimal amounts of tetrodotoxin. … Thus, very low levels of tetrodotoxin-like compounds … might have escaped detection because of the low efficiency of methonol in extracting such compounds. But levels approaching those reported for *C. inguinalis* [= *panamensis*] … would have been detected even in methanol extracts.

173. CHROMOSOME NUMBER: 18 = 0; 20 = 1; 22 = 2; 24 = 3; 26 = 4; 28 = 5; 30 = 5. Additive.

Karyological data have been reported for 35 of the dendrobatids included in the present study: *panamensis* and *pumilio* (Duellman, 1967), *auratus* and *pumilio* (León, 1970), *trivittatus* (Bogart, 1970, 1973, 1991), *trinitatis* (Rada de Martínez, 1976), *auratus*, *gran-*

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uliferus, *histrionicus*, *lugubris*, *pumilio*, and *sylvaticus* Funkhouser (as *histrionicus* from NW Ecuador) (Rasotto et al., 1987), *conspicuus* [as *brunneus*], *femoralis*, *fraterdanieli*, *olfersioides*, *palmatus*, *pictus*, *subpunctatus*, *talamancae*, *trivittatus*, *truncatus*, *vanzolinii* [as *quinquevittatus*], *vertebralis*, and an undescribed species referred to *Colostethus* (Bogart, 1991), *caeruleodactylus*, *marchesianus* (sensu stricto; see Caldwell et al., 2002b) and two undescribed species referred to *Colostethus* (Veiga-Menoncello et al., 2003a), *nidicola* and *stepheni* (Veiga-Menoncello et al., 2003b), *chalcopis*, *leopardalis*, *herminae*, *neblina*, *olmonae*, and *trinitatis* (Kaiser et al., 2003), *flavopictus*, *femoralis*, *hahneli*, and *trivittatus* (Aguiar et al., 2002). Thirty of those species are included in the present study.

For outgroup taxa, data were taken from Kuramoto's (1990) review. Data published subsequently were taken from Silva et al. (2001) for *Cycloramphus boraceiensis*, Rosa et al. (2003) for *Megaelosia*, Ramos et al. (2002) for *Atelopus zeteki*, and Aguiar et al. (2004) for *Crossodactylus* and *Hylodes phyllodes*.

Coding chromosome variation as transformation series is complicated by imprecision in determining chromosome homology. For the most part, chromosomes are simply arranged according to size and named (numbered) consecutively. That all variation in chromosome morphology is reported in relation to chromosome identity (which is a function of relative chromosome size) is a serious problem. Rarely, more detailed considerations are brought to bear (e.g., see Bogart, 1991, regarding the homology of chromosome 4 in *pictus* and chromosome 5 in *trivittatus*), but this is done so infrequently as to be of little use in the present study. A further limitation of available karyological data relates to the variation in techniques and kinds of data reported. For example, nucleolar organizing regions (NORs) are reported for only 11 of the dendrobatids included in this study, and in just those few species at least six NOR states are apparent. Likewise, in light of the confounding variation he observed, Bogart (1991: 245) cautioned that "[i]t is evident that analysis of chromosome arms would be of little value for understanding karyotype evolution in the family Dendrobatidae. It is also evident that dendrobatid chromosomes have undergone extensive restructuring via translocations and inversions."

There are undoubtedly many additional transformation series in chromosome morphology, but we coded only chromosome number because (1) it is reported in all karyological studies, (2) it is less dependent on individual chromosome identity (see references above), and (3) it has been employed previously in studies of dendrobatid systematics. Nevertheless, inferring transformation series solely from chromosome number necessarily assumes that the same chromosome(s) are gained or lost in each change in total number of chromosomes, which future research will undoubtedly determine to have been an oversimplification.

RESULTS

General Results

Direct optimization parsimony analysis followed by the parsimony ratchet analysis of the implied alignment resulted in 37 equally parsimonious solutions of 46,520 steps. Forty nodes collapse in the strict consensus of these optimal topologies, all of which involve conspecific terminals only. Further swapping those 37 trees using the implied alignment recovered a total of 25,872 trees, with no additional nodes collapsed in the strict consensus. The CI (Kluge and Farris, 1969) and RI (Farris, 1989) for the phenotypic characters[12] on the total evidence solutions are 0.14 and 0.76, respectively. We begin by summarizing higher-level relationships, shown in figure 70, and proceed to the relationships among dendrobatids in figures 71–76. Rather than describe the cladogram and associated support values exhaus-

[12]Although one may calculate the CI and RI for DNA sequences based on the implied alignment, the significance of these homoplasy-based indices in the context of dynamic homology is questionable. Two equally parsimonious explanations may have different CIs and RIs, and explanations with the same CI and RI may have different costs. For details, see Kluge and Grant (2006).

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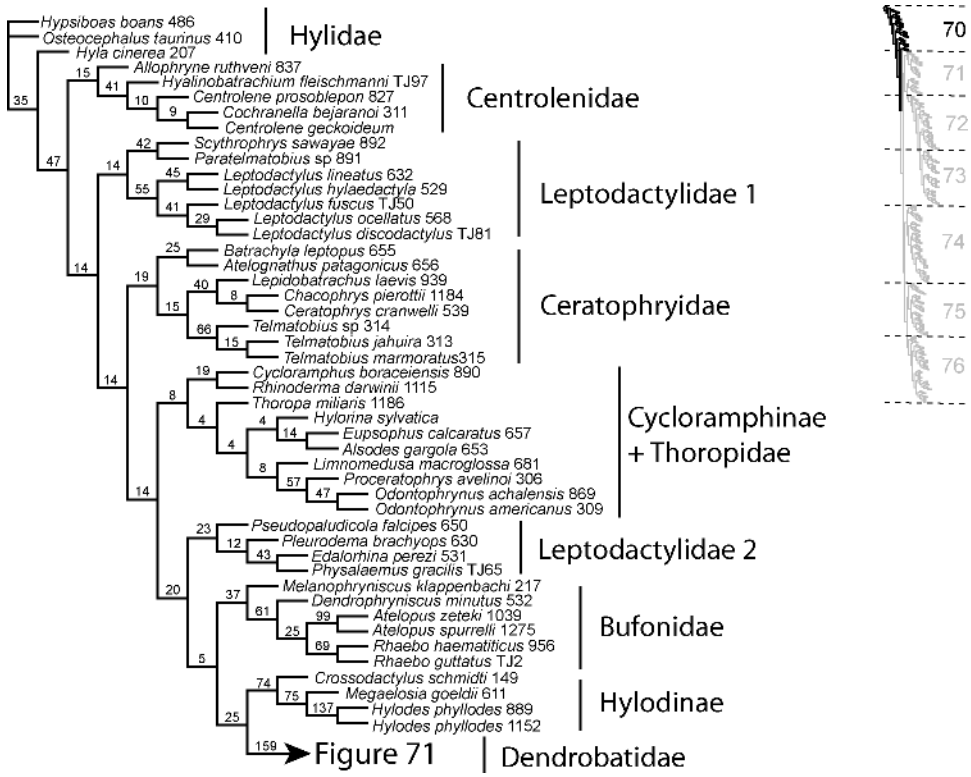

Fig. 70. Strict consensus of 25,872 most parsimonious trees of 46,520 steps: outgroup relationships and monophyly and placement of dendrobatids. Numbers above branches are Bremer support values. Family group names applied as in Frost et al. (2006). Cycloramphinae and Hylodinae were nested within Cycloramphidae in Frost et al.'s study. Numbers following terminal names are unique sample identifiers. Terminals without numbers or with alphanumeric identifiers (GenBank numbers) were not sequenced for the present study or Frost et al. (2006) and were taken from GenBank. Upper right inset shows entire cladogram and corresponding figure numbers, with present view in black.

tively, we emphasize information not depicted on the cladogram, especially the unambiguous transformations that delimit clades and the bearing of the current results on species-level problems. Only unambiguous synapomorphies shared by all most parsimonious trees are reported.

Dendrobatid Monophyly and Outgroup Relationships

Dendrobatid monophyly was supported strongly in the present analysis (fig. 70). Unambiguous phenotypic transformations include the loss of supernumerary tubercles on the hand (Character 2, 1 → 0), gain of the tarsal keel (Character 28, 0 → 1), the "ranid" type insertion of the distal tendon of the m. semitendinosus (Character 69, 0 → 1), gain of the m. semitendinosus binding tendon (Character 70, 0 → 1), occurrence of the dorsal flap of the m. depressor mandibulae (Character 72, 0 → 1), relation of the tympanum and m. depressor mandibulae (Character 75, 0 → 1), orientation of the m. intermandibularis supplementary element (Character 78, 0 → 1), maxillary tooth structure (Character 140, 0 → 1), the occurrence of the retroarticular process of the mandible (Character 142, 0 → 1), and the reduction in chromosome number from 26 to 24 (Character 175, 4 → 3). Behavioral synapomorphies include the loss of reproductive amplexus (Character 104, 1 → 0), the gain of dorsal tadpole transport

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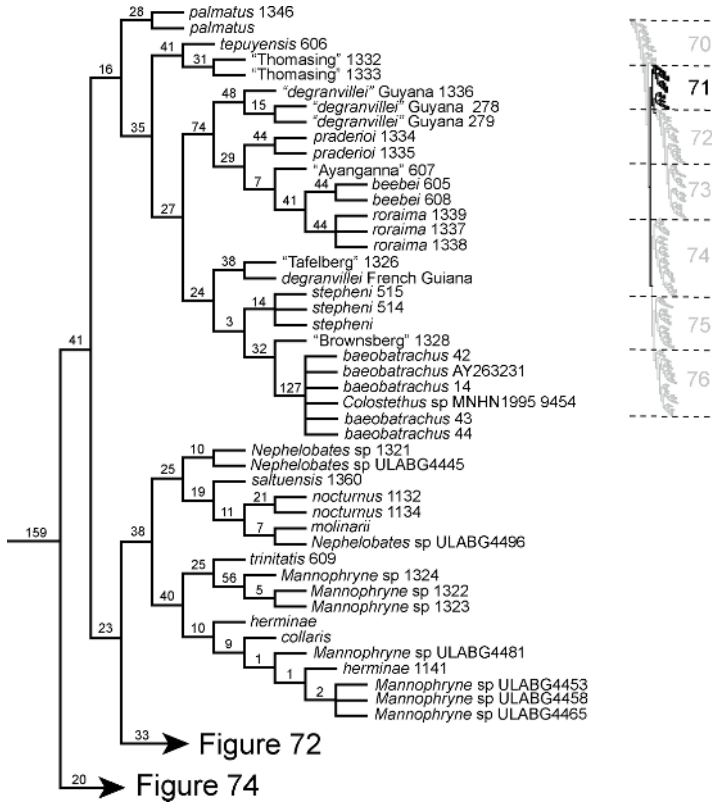

Fig. 71. Strict consensus of 25,872 most parsimonious trees of 46,520 steps: relationships among dendrobatids. Numbers above branches are Bremer support values. Numbers following terminal names are unique sample identifiers. Terminals without numbers or with alphanumeric identifiers (GenBank numbers) were not sequenced for the present study or Frost et al. (2006) and were taken from GenBank. Unidentified species taken from GenBank are labeled as originally published. Upper right inset shows entire cladogram and corresponding figure numbers, with present view in black.

(108, 0 → 1), and the origin of toe trembling (Character 115, 0 → 1).

Our results generally resemble those of Frost et al. (2006) regarding the phylogenetic position of dendrobatids and the relationships among outgroup taxa, but with a few significant exceptions. Of greatest relevance to the problem of dendrobatid relationships, the current study refuted Frost et al.'s (2006) placement of *Thoropa* and dendrobatids as sister groups and instead placed *Thoropa* inside Cycloramphidae, with Hylodinae recovered as the sister group of dendrobatids (as first suggested by Noble, 1926). In addition to the genotypic transformations that optimize unambiguously to this node, phenotypic transformations include the origin of digital scutes (Character 1, 0 → 1) and the formation of digital discs (Character 6, 0 → 1), the origin of T-shaped terminal phalanges (Character 118, 1 → 0), and the occurrence of an oblique lateral stripe (Character 55, 0 → 1). Except for the removal of hylodines and insertion of *Thoropa*, the relationships among cycloramphines are identical to those of Frost et al. (2006). As was found by Frost et al., the next more inclusive clade includes Bufonidae, and then Cycloramphinae.

The greatest difference between Frost et al.'s (2006) results and the present hypothesis involves the placement of leptodactylids. The clades here labeled Leptodactylidae 1 and Leptodactylidae 2 were a monophyletic

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TABLE 4
Percent Uncorrected Pairwise Distances Between Cytochrome *b* Sequences of *tepuyensis* and "Thomasing"[a]

	Sample ID	1	2	3
1	*tepuyensis* 606	—		
2	"Thomasing" 1332	4.4	—	
3	"Thomasing" 1333	4.4	0.0	—

[a] Gray lines separate species.

group in Frost et al.'s study, and that clade was sister to Centrolenidae, together forming the Amnibatrachia. Here, centrolenids are the sister of all included taxa except hylids, Leptodactylidae 1 is sister to all but the centrolenids and hylids, and Leptodactylidae 2 is sister to Bufonidae + Hylodinae + Dendrobatidae, that is, it is separated from Leptodactylidae 1 by ceratophryids and cycloramphines.

Relationships among Dendrobatids

The eastern Colombian species *palmatus* is sister to a clade that includes all species that possess the median lingual process (MLP) (fig. 71). Eight unambiguous phenotypic transformations unite *palmatus* with the MLP clade, including the origins of fringes on the preaxial edges of fingers II and III (Characters 13 and 15, $0 \rightarrow 1$).

Within the MLP clade, *tepuyensis* and the undescribed species "Thomasing" are relatively robust frogs with extensive webbing. Their monophyly is strongly supported (Bremer support = 41), although only a single phenotypic synapomorphy optimizes unambiguously to this node (expansion of toe disc I, Character 31, $1 \rightarrow 2$). Percent pairwise distances are shown in table 4.

The identification of sample 606 as *tepuyensis* will likely require revision. That species was described by La Marca (1998 "1996") from Auyántepui, whereas sample 606 was taken over 200 km away on Mt. Ayanganna (ca. 60 km WNW of Kaieteur, Guyana). Given the high degree of endemism of many tepui species, it is doubtful that these samples are conspecific. Nevertheless, we compared the voucher specimen of the tissue sample (ROM 39637, the only specimen of this species collected at this locality) to a series of 33 specimens of *tepuyensis* from the type locality and failed to detect diagnostic differences. Our prediction is that additional specimens and/or molecular data will reveal that these are different species, but for the present we apply the name *tepuyensis* to specimens from both localities. "Thomasing" is an undescribed species from Mt. Thomasing, Mazaruni-Potaro, Guyana.

The monophyly of the remaining species of the MLP clade is supported by three unambiguous phenotypic transformations: the gain of the pale paracloacal marks (Character 49, $0 \rightarrow 1$), completion of the oblique lateral stripe (Character 56, $0 \rightarrow 1$), and the origin of an endotrophic larval diet (Character 112, $0 \rightarrow 3$).

Among the species of this clade are several that resemble, superficially at least, *degranvillei*. Species delimitation is hindered by extensive morphological variation within syntopic series, making this a prime example of the relevance of DNA sequence data in discovering cryptic diversity. Samples 278, 279, and 1336 were all collected in Guyana (details below). Although we did not detect morphological differences, our results indicate that they are not conspecific with *degranvillei* sensu stricto. The *degranvillei* data obtained from GenBank were generated by Vences et al. (2003), who stated that their sample of *degranvillei* was from Saül, French Guiana, which is quite close to the type locality and, therefore, likely to represent *degranvillei* sensu stricto. We therefore refer to the Guyanan species as "*degranvillei.*" Cytochrome *b* sequences for the Vences et al. specimen were not available, but the pairwise distance between "Tafelberg" and the "*degranvillei*" is 17.5%.

The two samples of *praderioi* were collected at 1,310 m on Roraima, Guyana. Sample 1336 of the Guyanan "*degranvillei*" was also collected on Roraima but was taken at 1,075 m. The two remaining Guyanan "*degranvillei*"samples were taken in the Merume mountains, and "Ayanganna" was collected on Mt. Ayanganna, ca. 50 km WNW of Kaieteur, Guyana.

Despite the morphological similarity and geographic proximity of *praderioi* and "*degranvillei*" on Roraima, and only <300 m

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TABLE 5
Percent Uncorrected Pairwise Distances Between Cytochrome *b* Sequences of "*degranvillei*" from Guyana, *praderioi*, and the Undescribed Species "Ayanganna"[a]

	Sample ID	1	2	3	4	5	6
1	"*degranvillei*" 278 Mereme	—					
2	"*degranvillei*" 279 Mereme	0.3	—				
3	"*degranvillei*" 1336 Roraima	1.8	1.6	—			
4	"Ayanganna" 607	9.6	9.4	9.6	—		
5	*praderioi* 1334 Roraima	10.4	10.1	10.4	8.3	—	
6	*praderioi* 1335 Roraima	10.4	10.1	10.4	8.3	0.0	—

[a] Gray lines separate localities and species.

difference in elevation between the localities, the pairwise distance is 10.1–10.4% (see table 5). The pairwise distance between the three "*degranvillei*" samples is only 1.6–1.8%, despite the much greater geographic distance.

According to the topology alone, it is possible that "Ayanganna" and *praderioi* may be conspecific. Nevertheless, they differ morphologically (e.g., webbing) and at 8.3% of their cytochrome *b* sites, leaving little doubt that they are different species.

The sister species *beebei* and *roraima* are diminutive, geographically proximate species that both possess the median lingual process and breed in phytotelmata (for breeding behavior in *beebei*, see Bourne et al., 2001). Pairwise distances are shown for *beebei* and *roraima* in table 6. There is no confusion surrounding the identity of *beebei*, with the exception that the French Guianan species discussed under that name (e.g., Kok, 2000; Lescure and Marty, 2000) is not conspecific with *beebei* sensu stricto from Guyana (among other differences, the French Guianan species lacks the median lingual process).

La Marca (1998 "1996") described *roraima* based on a single immature specimen from 2,700 m near the peak of Mt. Roraima. Although there are several inconsistencies in La Marca's description and illustrations, and the immaturity of the holotype impedes identification, the material included in the present study was collected at the type locality and agrees with the description sufficiently to conclude that it is *roraima*. Samples 1337 and 1338 were taken from adults CPI 10216 and CPI 10217. Sample 1339 is from an untagged tadpole collected in a bromeliad, which establishes conclusively adult and larval conspecificity.

TABLE 6
Percent Uncorrected Pairwise Distances Between Cytochrome *b* Sequences of *beebei* and *roraima*[a]

	Sample ID	1	2	3	4	5
1	*beebei* 605	—				
2	*beebei* 608	0.3	—			
3	*roraima* 1337	5.7	5.5	—		
4	*roraima* 1338	5.5	5.2	0.3	—	
5	*roraima* 1339	5.7	5.5	0.5	0.3	—

[a] Gray lines separate species.

The clade composed of *baeobatrachus*, *degranvillei*, *stepheni*, "Tafelberg", and "Brownsberg" has a Bremer value of 24. Five unambiguous phenotypic changes occur at this node, including the loss of the distal subarticular tubercle on finger IV (Character 3, $1 \rightarrow 0$).

The nomenclatural history of *baeobatrachus* and *stepheni* is convoluted. The name "baeobatrachus" first appeared in Edwards's widely distributed but formally unpublished Ph.D. dissertation (Edwards, 1974a). The type locality Edwards intended to designate was Ducke Reserve in Amazonas State, just outside Manaus (Brazil). The two samples included here (514, 515) are from that locality. On the 15th anniversary of the completion of Edwards's dissertation, Martins (1989) described *stepheni* with the explicit intent of providing a name for Edwards's "baeobatrachus". The type locality of *stepheni* is Presidente Figueiredo, also in Amazonas State and approximately 100 km from Manaus. Apparently unaware of this development or the fact that Edwards's "baeobatrachus" was not an available name, and despite having cited a paper that deals with the reproductive biology of *stepheni* (viz.,

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TABLE 7
Percent Uncorrected Pairwise Distances Between Cytochrome *b* Sequences of *stepheni*, *baeobatrachus*, and the Undescribed Species "Tafelberg" and "Brownsberg"[a]

	Sample ID	1	2	3	4	5	6	7	8
1	*stepheni* 514	—							
2	*stepheni* 515	0.3	—						
3	*baeobatrachus* 14	17.4	17.1	—					
4	*baeobatrachus* 42	17.7	17.4	0.3	—				
5	*baeobatrachus* 43	17.4	17.1	0.0	0.3	—			
6	*baeobatrachus* 44	17.4	17.1	0.0	0.3	0.0	—		
7	"Tafelberg" 1326	19.0	19.2	16.9	17.1	16.9	16.9	—	
8	"Brownsberg" 1328	17.1	16.9	11.9	12.2	11.9	11.9	15.6	—

[a] Gray lines separate localities and species.

Juncá et al., 1994), in a popular article Boistel and Massary (1999) presented a color photograph and brief but validating diagnosis under the name *Colostethus baeobatrachus*. Boistel and Massary did not specify a type locality or voucher specimen, but Kok (2000) provided a complete redescription based on material from Montagne Belvédère in French Guiana and deposited at IRSNB. The four samples included here (14, 42, 43, 44) were taken from that series. Immediately thereafter, Kok (2001) determined that *baeobatrachus* and *stepheni* were indistinguishable and placed them in synonymy. Published sonograms of *stepheni* at Reserva Ducke (Juncá, 1998) and *baeobatrachus* in French Guiana (Lescure and Marty, 2000) are very similar, the sole potentially relevant difference occurring in the dominant frequencies: in *stepheni* it is given as 4.6–4.8 kHz and in *baeobatrachus* 5.12–5.83 kHz. Sample sizes are very small though, and such minor differences are commonly observed within species.

Nevertheless, the ca. 17% pairwise distance between the Reserva Ducke and Montagne Belvédère samples strongly suggests they are not conspecific (see table 7). Furthermore, tadpoles of *stepheni* are nidicolous with reduced mouth parts and a median vent tube (Juncá et al., 1994; Juncá, 1998), whereas a male nurse frog was collected at Serra do Navio, Amapá, Brazil transporting three tadpoles with fully developed mouth parts and dextral vent tube.[13] Assuming that the Montagne Belvédère and Serra do Navio samples are conspecific, there is strong evidence that these *baeobatrachus* and *stepheni* are not conspecific, despite the apparent lack of diagnostic characters in adult morphology. That *baeobatrachus* and *stepheni* are valid species is further supported by phylogenetic analysis, which places the undescribed species "Brownsberg" (1328), from Guyana, as sister to *baeobatrachus* to the exclusion of *stepheni*.

The remaining species, "Tafelberg" (sample 1326) is another undescribed species from Guyana that is closely related to (and potentially conspecific with) the GenBank *degranvillei* (see above for comments on the identity of this sample). Cytochrome *b* sequences were unavailable for the GenBank *degranvillei* sample and morphological comparisons were not made, but the number of unambiguous transformations in 12S and

[13] Lescure and Marty (2000: 320) also claimed differences in larval morphology between *stepheni* (described by Juncá et al., 1994) and *baeobatrachus* (described, according to Lescure and Marty, by Edwards, 1974a, in his dissertation). However, they failed to note that Edwards's description was based on free-swimming larvae from Reserva Ducke, and yet Juncá's nidicolous larvae were also from Reserva Ducke. This suggests that either (1) *stepheni* has both free-swimming, exotrophic and nidicolous, endotrophic larvae, (2) *stepheni* and *baeobatrachus* occur in sympatry at Reserva Ducke, or (3) Edwards's free-swimming tadpoles were not *stepheni*. Given that at least one additional dendrobatid (*Colostethus marchesianus* fide Juncá, 1998) occurs at Reserva Ducke and Edwards never explained his rationale for associating these tadpoles and adults, (3) is the most plausible explanation.

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Fig. 72. Strict consensus of 25,872 most parsimonious trees of 46,520 steps: relationships among dendrobatids. Numbers above branches are Bremer support values. Numbers following terminal names are unique sample identifiers. Terminals without numbers or with alphanumeric identifiers (GenBank numbers) were not sequenced for the present study or Frost et al. (2006) and were taken from GenBank. Unidentified species taken from GenBank are labeled as originally published. Upper right inset shows entire cladogram and corresponding figure numbers, with present view in black.

16S sequences that occur on the terminal branches (13 for ''Tafelberg,'' 14 for *degranvillei*) suggests they are not conspecific.

The other clade shown in figure 71 is composed mainly of species currently referred to *Aromobates*, *Mannophryne*, and *Nephelobates*. The monophyly of this clade is strongly supported (Bremer support = 38) and is delimited by 54 unambiguous genotypic changes, although there are no unambiguous phenotypic transformations at this node. Following the current taxonomy, *Aromobates nocturnus* and *Colostethus saltuensis* are nested within *Nephelobates*. The latter species was included in the *alboguttatus* group of Rivero (1990 ''1988''), but was excluded without comment when La Marca (1992) named his own version of the *alboguttatus* group formally as *Nephelobates*. Likewise, the affinities of *nocturnus* and the species of both *Nephelobates* and *Mannophryne* were noted when *Aromobates* was described (referring to those as yet unnamed genera as the *alboguttatus* and *collaris* groups, respectively; Myers et al., 1991), and Kaiser et al. (1994), Meinhardt and Parmelee (1996), and Grant et al. (1997) questioned the monophyly of those genera

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TABLE 8
Percent Uncorrected Pairwise Distances Between Cytochrome *b* Sequences of Syntopic Specimens of *undulatus*

	Sample ID	1	2	3
1	*undulatus* 331	—		
2	*undulatus* 332	0.8	—	
3	*undulatus* 333	0.3	1.0	—

relative to *Aromobates*. More specifically, prior to naming *Nephelobates*, La Marca (1993) considered *nocturnus* to be most closely related to his *alboguttatus* group, which is corroborated in this study.

Although *Nephelobates* is paraphyletic, the monophyly of the equally controversial *Mannophryne* is solidly corroborated in this analysis. This clade has a Bremer value of 40 and may be diagnosed morphologically by the synapomorphic dermal collar, which optimizes unambiguously to this node (Character 59, 0 → 1). The conclusions, based on morphological criteria, that the collarlike gular–chest markings of several Ecuadorian species (e.g., *elachyhistus*) are not homologous with the dermal collar of these Venezuelan species and that the diffuse collar of *nocturnus* is due to nonhomologous subdermal pigmentation (see Characters 58 and 59) are supported by the distant relationships of these taxa in the optimal cladograms.

Among the nominal species included in the cladogram, the *herminae* samples are not conspecific; at this time we are unable to speculate as to which of these (if either) corresponds to *herminae* sensu stricto. The cytochrome *b* sequences for the two samples of *nocturnus* are identical.

The clade shown in figure 72 is a large, primarily *cis*-Andean (east of the Andes) group. Ten unambiguous phenotypic transformations delmit this clade, including the origin of swelling of finger III in adult males (Character 20, 0 → 1) and the loss of palatines (Character 132, 1 → 0).

The sister of the remainder of this clade is *alagoanus*, from the Atlantic forest of Brazil, followed by the undescribed ''Neblina species'' and *undulatus*. ''Neblina species'' was collected at the base of the tepui Neblina, in Venezuela; the cytochrome *b* sequences of the two specimens are identical. Myers and Donnelly (2001) described *undulatus* from the Yutajé massif, also in Venezuela. The three samples were all collected in the same vicinity (see table 8 for pairwise distances).

Among the species included in the present analysis, the only *trans*-Andean (west of the Andes) species in this clade are the sister species *talamancae* and the undescribed ''Magdalena''. The affinities of *talamancae* have never been clear (e.g., Rivero, 1990 ''1988'' was unable to assign it to any of his groups), probably because it differs considerably from the *trans*-Andean species with which it was compared. However, the placement of these species among these *cis*-Andean species is strongly supported and highlights the overall resemblance of these species (e.g., for photographs of *talamancae* and *kingsburyi*, see Coloma, 1995). Moreover, the discovery of the undescribed ''Magdalena'' species fills in the gap in the distribution between *talamancae* and the remaining species.

''Magdalena'' and *talamancae* share the unambiguous transformation from an evenly stippled to solid dark throat in adult males (Character 61, 2 → 4). These two species are allopatric. ''Magdalena'' is known only from sites on the floor of the middle Magdalena river valley in Colombia, and *talamancae* is widespread from the Pacific lowlands of South America in Ecuador and Colombia north to Nicaragua. Pairwise distances for cytochrome *b* sequences of these species are shown in table 9. The *talamancae* samples are from two localities in Panama (Bocas del Toro: 325, 326; Coclé: 1147) and one in Nicaragua (361, 362, 408).

Although the most parsimonious cladogram recovers monophyletic Panamanian and Nicaraguan samples of *talamancae*, the genetic distances between the samples are consistent with the hypothesis of continuous gene flow. The greatest pairwise distance is between the samples from Nicaragua and Coclé, with the intermediate sample from Bocas del Toro also intermediate genetically.

Much of the diversity of small, brown, relatively nondescript *cis*-Andean dendrobatids has been associated with the old (see appendix 1) names *brunneus*, *marchesianus*, and *trilineatus*. Progress in documenting the

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TABLE 9
Percent Uncorrected Pairwise Distances Between Cytochrome *b* Sequences of *talamancae* and "Magdalena"[a]

Sample ID	1	2	3	4	5	6	7
1 *talamancae* 325 Bocas del Toro	—						
2 *talamancae* 326 Bocas del Toro	0.5	—					
3 *talamancae* 1147 Coclé	2.6	2.6	—				
4 *talamancae* 361 Nicaragua	5.2	5.2	5.7	—			
5 *talamancae* 362 Nicaragua	5.2	5.2	5.7	0.0	—		
6 *talamancae* 408 Nicaragua	5.2	5.2	5.7	0.0	0.0	—	
7 "Magdalena" 1358	16.1	16.6	16.1	15.6	15.6	15.6	—

[a] Gray lines separate localities and species.

diversity of Amazonian dendrobatids has been hindered by confusion surrounding these nominal species. Grant and Rodríguez (2001) clarified the identity of the western Amazonian *trilineatus*, and Caldwell et al. (2002b) redescribed *marchesianus* based on extensive new material and vocalizations from the type locality (in the vicinity of the Rio Uaupes in Amazonian Brazil) and clarified that all populations referred to that species from elsewhere (e.g., Santa Cecilia, Ecuador) were heterospecific (T. Grant has also examined material of this species from the adjacent region of Colombia). In the same year, Morales (2002 "2000") provided an account for *marchesianus* based on examination of a syntype and specimens from other localities, but his redescription is incomplete (e.g., it does not address intraspecific variation or make comparisons with other species) and disagrees in several key points with that of Caldwell et al. (2002b), as well as the Colombian material examined by T. Grant, and the account is therefore rejected. We included DNA sequences for numerous specimens referred to *trilineatus* by Grant and Rodríguez (2001), as well as material from the same or nearby localities, but we were unable to include sequences for *marchesianus* sensu stricto.

The remaining taxonomic problem involving an old name is *brunneus*. Grant and Rodríguez (2001) provided data for topotypic and other material, but they did not attempt to address decisively the problem of *brunneus* identity. La Marca et al. (2004) improved matters considerably by clarifying that the "*brunneus*" from northern Venezuela was in fact a new species (which they named *Colostethus pittieri*) most closely related to *humilis*. In what appears on the surface to be the most thorough study of the systematics of these frogs, Morales (2002 "2000") provided an account for *brunneus*. Like the remainder of the accounts in that paper—including those for the 11 new species named therein—the account of *brunneus* does not address variation within *brunneus* or compare that species to others and is therefore highly unsatisfactory. Nevertheless, Morales's account of *brunneus* is the most recent attempt to clarify its identity, and we therefore apply the name in his sense. We included DNA sequences from several of the specimens examined by Morales and referred by him to several species, including *brunneus* and his new species *conspicuus* and *gasconi*.

Although we apply the name *brunneus* in the sense of Morales (2002 "2000"), and samples 352 and 1278 were both referred to that species by him, Morales also referred sample 354 of a distantly related species from Curuá-Una (shown in fig. 73) to *brunneus*. The minimum pairwise distance between that sample and either of the others he referred to *brunneus* is 16.6%. We therefore exclude that sample from the pairwise comparisons in table 10 and instead include it with the other samples from Curuá-Una (see below). The pairwise cytochrome *b* distances between *brunneus* and its sister species from Parque Estadual Guajará-Mirim ("PEG-M2") are 14.3–15.3%.

Terminals identified as "PEG-M2" represent one of three undescribed species of dendrobatids collected at Parque Estadual

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TABLE 10
Percent Uncorrected Pairwise Distances Between Cytochrome *b* Sequences of *brunneus*

	Sample ID	1	2	3	4	5	6	7	8	9	10
1	*brunneus* 352	—									
2	*brunneus* 612	0.8	—								
3	*brunneus* 613	0.3	0.5	—							
4	*brunneus* 1264	0.0	0.8	0.3	—						
5	*brunneus* 1271	0.0	0.8	0.3	0.0	—					
6	*brunneus* 1278	1.0	0.3	0.8	1.0	1.0	—				
7	*brunneus* 1281	0.0	0.8	0.3	0.0	0.0	1.0	—			
8	*brunneus* 1286	1.3	0.5	1.0	1.3	1.3	0.3	1.3	—		
9	*brunneus* 1294	1.3	0.5	1.0	1.3	1.3	0.3	1.3	0.5	—	
10	*brunneus* 1316	0.8	0.0	0.5	0.8	0.8	0.3	0.8	0.5	0.5	—

Guajará-Mirim, Rondônia, Brazil (see table 11) The pairwise distances between the samples of this species and *brunneus* are 14.3–15.3%.

The next clade includes *juanii*, from Villavicencio, Colombia, *zaparo*, from eastern Ecuador, and the widespread *femoralis*. The monophyly of *zaparo* and *femoralis* is strongly supported (BS = 147), and they are united by 161 unambiguous transformations.

The occurrence of *zaparo* and *femoralis* in this clade of otherwise cryptically colored, nontoxic frogs conflicts strongly with the traditional placement of these species with bright, toxic species such as *petersi* and *pictus* (e.g., Silverstone, 1976). Nevertheless, the distant placement of these species found by previous studies (e.g, Santos et al., 2003; Vences et al., 2003a) could not be refuted by the inclusion of phenotypic and additional DNA evidence. Furthermore, both *femoralis* and *zaparo* appear to be incapable of accumulating alkaloids (Darst et al., 2005; J. W. Daly in litt., 02/02/00), which suggests that the remarkable resemblance of these nontoxic and toxic species may be due to Batesian mimicry.

The type locality of *femoralis* is Yurimaguas, Peru, but the taxon is distributed throughout much of the Amazon basin (Silverstone, 1976). Morphologically, specimens referred to *femoralis* exhibit minor variations in coloration (e.g., thickness of lateral stripes, size and extent of bright thigh flash marks; see Silverstone, 1976). We generated cytochrome *b* sequences for 17 samples of *femoralis* collected at the following eight localities, covering much of the nominal species' range (pairwise distances shown in table 12): Porto Walter, Acre, Brazil (397, 398, 1309); Cusco Amazónico, Madre de Dios, Peru (78, 128, 129); Cuyabeno, Sucumbíos, Ecuador (399, 400, 1306); Parque Estadual Guajará-Mirim, Rondônia, Brazil, (393, 394); Reserva Ducke, Amazonas, Brazil (520); Panguana, Huánuco, Peru (nearest to the type locality and therefore tentatively treated as *femoralis* sensu stricto) (526); Sipaliwini, Suriname (1325); Rio Curuá-Una, Pará, Brazil (395, 396, 1298).

The taxonomy of *zaparo* is less problematic, but we include it in table 12 as a point of reference for *femoralis*. Vences et al. (2003a)

TABLE 11
Uncorrected Pairwise Distances Between Cytochrome *b* Sequences of "PEG-M2"

	Sample ID	1	2	3	4	5	6
1	"PEG-M2" 617	—					
2	"PEG-M2" 618	1.3	—				
3	"PEG-M2" 1237	1.6	0.3	—			
4	"PEG-M2" 1276	1.3	0.5	0.8	—		
5	"PEG-M2" 1282	1.6	0.3	0.5	0.8	—	
6	"PEG-M2" 1289	1.6	0.3	0.0	0.8	0.5	—

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TABLE 12
Percent Uncorrected Pairwise Distances Between Cytochrome *b* Sequences of *femoralis* and *zaparo*[a]

	Sample ID	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
1	*femoralis* 397 PW	—																		
2	*femoralis* 398 PW	0.0	—																	
3	*femoralis* 1309 PW	0.0	0.0	—																
4	*femoralis* 78 CA	5.2	5.2	5.2	—															
5	*femoralis* 128 CA	5.2	5.2	5.2	0.0	—														
6	*femoralis* 129 CA	5.2	5.2	5.2	0.0	0.0	—													
7	*femoralis* 399 CU	11.7	11.7	11.7	14.3	14.3	14.3	—												
8	*femoralis* 400 CU	11.4	11.4	11.4	14.0	14.0	14.0	0.8	—											
9	*femoralis* 1306 CU	11.7	11.7	11.7	14.3	14.3	14.3	0.5	0.3	—										
10	*femoralis* 393 PEG-M	14.6	14.6	14.6	14.0	14.0	14.0	9.9	10.7	10.4	—									
11	*femoralis* 394 PEG-M	14.6	14.6	14.6	14.0	14.0	14.0	9.9	10.7	10.4	0.0	—								
12	*femoralis* 520 RD	13.8	13.8	13.8	14.0	14.0	14.0	10.4	10.7	10.4	7.3	7.3	—							
13	*femoralis* 526 PAN	12.7	12.7	12.7	13.3	13.3	13.3	9.9	10.7	10.4	7.3	7.3	3.9	—						
14	*femoralis* 1325 SIP	12.0	12.0	12.0	12.2	12.2	12.2	8.1	8.8	8.6	6.2	6.2	4.7	4.2	—					
15	*femoralis* 395 RCU	13.3	13.3	13.3	13.8	13.8	13.8	8.6	9.4	9.1	6.2	6.2	5.7	5.7	3.6	—				
16	*femoralis* 396 RCU	13.5	13.5	13.5	14.0	14.0	14.0	8.8	9.6	9.4	6.5	6.5	6.0	6.0	3.9	0.3	—			
17	*femoralis* 1298 RCU	13.3	13.3	13.3	13.8	13.8	13.8	8.6	9.4	9.1	6.2	6.2	5.8	5.7	3.6	0.0	0.3	—		
18	zaparo 321	13.3	13.3	13.3	13.0	13.0	13.0	12.2	12.0	12.2	14.3	14.3	14.6	15.6	13.3	14.3	14.6	14.3	—	
19	zaparo 328	13.0	13.0	13.0	12.7	12.7	12.7	12.5	12.2	12.5	14.6	14.6	14.8	15.3	13.5	14.6	14.8	14.5	0.3	—

[a] Gray lines separate localities and species. Abbreviations are: PW (Port Walter), CA (Cusco Amazónico), CU (Cuyabeno), PEG-M (Parque Estadual Guajará-Mirim), RD (Reserva Ducke), SIP (Sipaliwini), RCU (Rio Curuá-Una).

united these two species formally in *Allobates*. The species Duellman and Mendelson (1995) referred to as *zaparo* is a distantly related, probably toxic species (details discussed below).

As shown in table 12, the pairwise distances between *zaparo* and *femoralis* samples are 12.2–15.3%. Forty-three unambiguous transformations unite the *zaparo* samples, and 38 unite those of *femoralis*. Although the cladogram is consistent with the recognition of a single species for material currently referred to *femoralis* (i.e., the taxon is monophyletic), the extensive patristic and pairwise distances are suggestive of multiple species. Cytochrome *b* distance is low within localities (0.0–0.8%) and much higher between localities (3.9–14.6%). This is strongly suggestive that a different species occurs at each of these localities (i.e., eight species), which would

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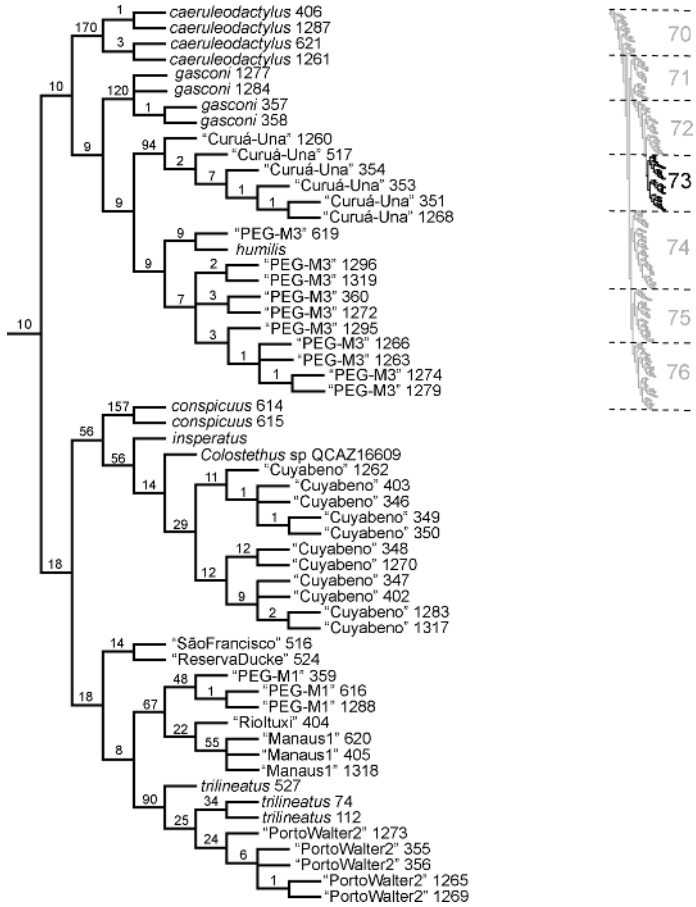

Fig. 73. Strict consensus of 25,872 most parsimonious trees of 46,520 steps: relationships among dendrobatids. Numbers above branches are Bremer support values. Numbers following terminal names are unique sample identifiers. Terminals without sample numbers were taken from GenBank. Note that Morales (Morales, 2002 ''2000'') identified ''PortoWalter2'' 356 as *gasconi*, and ''Curuá-Una'' 354 as *brunneus* (see fig. 72). Upper right inset shows entire cladogram and corresponding figure numbers, with present view in black.

greatly increase the known diversity of this clade.

Thirty-four unambiguous transformations establish the monophyly of the clade shown in figure 73, with a Bremer value of 10. The *caeruleodactylus*–''PEG-M3'' clade is united by 36 unambiguous transformations. Lima and Caldwell (2001) named *caeruleodactylus*, and Caldwell et al. (2002a) described its distinctive tadpole. Although we did not include *marchesianus* in the present analysis, the conspicuous dark vertical stripes on the tail and greatly enlarged marginal papillae provide evidence that it is the sister species of *caeruleodactylus* (see Caldwell et al., 2002a). Pairwise distances between specimens of *caeruleodactylus* are shown in table 13. The samples were collected at the type locality.

Sample 1277 from Rio Ituxi was referred to *gasconi* by Morales (2002 ''2000''), as was the distantly related sample 356 from Porto Walter (the pairwise distance between cytochrome *b* sequences of these two specimens is 15.6%). The type locality given for this species is ''Jainu on the left side of the Río Juruá, Amazonas, Brazil'' (Morales, 2002 ''2000'': 30, translated from the Spanish). Although Porto Walter is located on the Rio Juruá, Rio Ituxi is slightly closer, and on that basis we refer these terminals to *gasconi*.

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TABLE 13
Percent Uncorrected Pairwise Distances Between Cytochrome *b* Sequences of Syntopic Specimens of *caeruleoactylus*

Sample ID	1	2	3	4
1 *caeruleoactylus* 406	—			
2 *caeruleoactylus* 621	0.3	—		
3 *caeruleoactylus* 1261	0.0	0.3	—	
4 *caeruleoactylus* 1287	0.3	0.5	0.3	—

Comparison with topotypes will be required to confirm the identity of these samples. The pairwise cytochrome *b* distance between this species and *caeruleodactylus* is 14.0–14.5%, between this species and the undescribed ''Curuá-Una'' (see below) 13.5–14.2%, and between this species and ''PEG-M3'' 15.8–16.4%. Pairwise cytochrome *b* distances within *gasconi* are given in table 14.

Samples from near Rio Curuá-Una represent an undescribed species (''Curuá-Una''; see table 15). The pairwise distances between the samples of this species and those of ''PEG-M3'' (see below) are 9.9–10.9%. Morales (2002 ''2000'') referred sample 354 to the distantly related *brunneus*; as mentioned above, the minimum pairwise distance between this specimen and either of the others Morales referred to *brunneus* is 16.6%.

''PEG-M3'' is one of three undescribed species of dendrobatids collected at Parque Estadual Guajará-Mirim, Rondônia, Brazil. The pairwise distance between the samples of this species and ''Curuá-Una'' is 9.9–10.9% (for distances within ''PEG-M3'' see table 16). In the current analysis, *humilis* is nested within the samples of ''PEG-M3''. However, it is highly unlikely that the populations are conspecific: The sample of

TABLE 14
Percent Uncorrected Pairwise Distances Between Cytochrome *b* Sequences of *gasconi*[a]

Sample ID	1	2	3	4
1 *gasconi* 357	—			
2 *gasconi* 358	0.0	—		
3 *gasconi* 1277	0.3	0.3	—	
4 *gasconi* 1284	0.3	0.3	0.0	—

[a] Sample 1277 was referred to *gasconi* by Morales (2002 ''2000'').

humilis was collected at 2,100 m in the Venezuelan Andes (La Marca et al., 2002), whereas ''PEG-M3'' is from the Amazonian lowlands of western Brazil. Sequence data for *humilis* are limited to approximately 500 bp of 16S, so additional molecular data is likely to overturn this result. La Marca et al. (2004) considered *humilis* to be most closely related to their new species *pittieri*, which we did not test here.

The clade composed of *conspicuus*, *insperatus*, the unidentified Ecuadorian species reported by Santos et al. (2003; no locality given), and an undescribed species from Cuyabeno, Ecuador is well supported (Bremer support = 56) and united by 70 unambiguous transformations. The samples of the Brazilian species *conspicuus* were collected at Porto Walter and sample 614 was referred to *conspicuus* by Morales (2002 ''2000''). Bremer support for the monophyly of these specimens is 157, and 157 synapomorphies optimize to it unambiguously. The remaining three species in this clade (branch length = 62, Bremer support = 56) are all from Ecuador. Cytochrome *b* data are not available for *insperatus* and the unnamed ''*Colostethus* sp.'', but pairwise distances are

TABLE 15
Percent Uncorrected Pairwise Distances Between Cytochrome *b* Sequences of an Undescribed Species from Near the Rio Curuá-Una in Brazil[a]

Sample ID	1	2	3	4	5	6
1 ''Curuá-Una'' 351	—					
2 ''Curuá-Una'' 353	0.3	—				
3 ''Curuá-Una'' 354	0.3	0.0	—			
4 ''Curuá-Una'' 1260	0.8	0.5	0.5	—		
5 ''Curuá-Una'' 1268	0.0	0.3	0.3	0.8	—	
6 ''Curuá-Una'' 517	0.8	0.5	0.5	0.0	0.8	—

[a] Morales (2002 ''2000'') referred sample 354 to the distantly related *brunneus*.

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TABLE 16
Percent Uncorrected Pairwise Distances Between Cytochrome *b* Sequences of "PEG-M3"

	Sample ID	1	2	3	4	5	6	7	8	9
1	"PEG-M3" 360	—								
2	"PEG-M3" 619	0.0	—							
3	"PEG-M3" 1263	0.3	0.3	—						
4	"PEG-M3" 1272	0.0	0.0	0.3	—					
5	"PEG-M3" 1274	0.3	0.3	0.0	0.3	—				
6	"PEG-M3" 1279	0.3	0.3	0.0	0.3	0.0	—			
7	"PEG-M3" 1295	0.3	0.3	0.0	0.3	0.0	0.0	—		
8	"PEG-M3" 1296	0.0	0.0	0.3	0.0	0.3	0.3	0.3	—	
9	"PEG-M3" 1319	0.0	0.0	0.3	0.0	0.3	0.3	0.3	0.0	—

shown in table 17 for *conspicuus* and "Cuyabeno".

The remaining terminals in figure 73 are allied to *trilineatus*. In their redescription of *trilineatus* based on extensive material from Peru, Grant and Rodríguez (2001) noted variation within and between localities that could be representative of greater species diversity. The present study included DNA sequences of putative *trilineatus* samples from Cusco Amazónico, Madre de Dios, Peru (74 and 112; specimens not examined by Grant and Rodríguez, 2001, but referred explicitly to *trilineatus* by Morales, 2002 "2000") and Panguana, Huánuco, Peru (527; Grant and Rodríguez, 2001, referred material from this locality to *trilineatus*; Morales, 2002 "2000", referred specimens from this locality to *marchesianus*, but that species is endemic to the Rio Uaupes of Brazil and adjacent Rio Vaupés of Colombia; Caldwell et al., 2002a, 2002b; T. Grant, personal obs.). The type locality of Yurimaguas is closest to Panguana. Also included here are samples of one of two dendrobatid species collected at Porto Walter, referred to as "PortoWalter2". As mentioned above, one of these specimens (356) was referred to *gasconi* by Morales (2002 "2000"). A single sample each is available from São Francisco (516), Reserva Ducke (524), and Rio Ituxi (404), and several samples each from Parque Estadual Guajará-Mirim (359, 616, 1288), Manaus (620, 405, 1318), Cusco Amazónico (74, 112), and Porto Walter (355, 356, 1265, 1269, 1273).

The *trilineatus* clade has a Bremer support value of 18, with 25 unambiguous transformations at this node. As shown in figure 73 and table 18, the pattern of diversification is

TABLE 17
Percent Uncorrected Pairwise Distances Between Cytochrome *b* Sequences of *conspicuus* and an Undescribed Species from Cuyabeno, Ecuador[a]

	Sample ID	1	2	3	4	5	6	7	8	9	10	11	12
1	*conspicuus* 614	—											
2	*conspicuus* 615	0.0	—										
3	"Cuyabeno" 346	13.5	13.5	—									
4	"Cuyabeno" 347	12.5	12.5	1.6	—								
5	"Cuyabeno" 348	13.2	13.2	0.3	1.6	—							
6	"Cuyabeno" 349	14.0	14.0	0.5	1.8	2.3	—						
7	"Cuyabeno" 350	13.5	13.5	0.3	2.1	2.1	0.8	—					
8	"Cuyabeno" 402	12.5	12.5	1.6	0.0	1.8	2.1	1.8	—				
9	"Cuyabeno" 403	13.5	13.5	0.0	1.5	1.8	0.5	0.3	1.6	—			
10	"Cuyabeno" 1262	13.0	13.0	0.5	1.0	1.8	1.0	0.8	1.0	0.5	—		
11	"Cuyabeno" 1283	12.5	12.5	1.6	0.0	1.8	2.1	1.8	0.0	1.6	1.0	—	
12	"Cuyabeno" 1317	12.5	12.5	1.6	0.0	1.8	2.1	1.8	0.0	1.6	1.0	0.0	—

[a] Gray lines separate localities and species.

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TABLE 18
Percent Uncorrected Pairwise Distances Between Cytochrome *b* Sequences of *trilineatus* and Related Undescribed Species[a]

	Sample ID	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
1	SF 516	—																
2	RD 524	15.3	—															
3	PEG-M1 359	16.1	16.4	—														
4	PEG-M1 616	16.1	16.4	0.0	—													
5	PEG-M 1288	16.1	16.4	0.0	0.0	—												
6	RI 404	15.1	16.4	8.6	8.6	8.6	—											
7	MAN1 620	17.4	14.8	9.1	9.1	9.1	7.3	—										
8	MAN1 405	17.4	14.8	9.1	9.1	9.1	7.3	0.0	—									
9	MAN1 1318	17.7	15.1	9.4	9.4	9.4	7.3	0.3	0.3	—								
10	triPAN 517	14.3	16.9	15.6	15.6	15.6	16.4	16.1	16.1	16.4	—							
11	triCA 74	13.5	15.6	15.3	15.3	15.3	15.8	15.6	15.6	15.8	17.4	—						
12	triCA 112	13.8	15.3	15.6	15.6	15.6	16.1	15.3	15.3	15.6	17.7	0.3	—					
13	PW2 355	14.0	14.8	13.0	13.0	13.0	13.5	13.8	13.8	14.0	14.8	5.5	5.7	—				
14	PW2 356	13.5	14.3	13.0	13.0	13.0	13.5	13.8	13.8	14.0	14.3	6.0	6.2	0.5	—			
15	PW2 1265	13.8	14.6	12.7	12.7	12.7	13.2	13.5	13.5	13.8	14.5	5.7	6.0	0.3	0.3	—		
16	PW2 1269	14.0	14.8	13.0	13.0	13.0	13.5	13.8	13.8	14.0	14.8	6.0	6.2	0.5	0.5	0.3	—	
17	PW2 1273	14.0	14.8	12.7	12.7	12.7	13.2	13.5	13.5	13.8	14.5	6.0	6.2	0.5	0.5	0.3	0.5	—

[a] Abbreviations are as follows: MAN1 (''Manaus1''), PW2 (''PortoWalter2''), RD (''ReservaDucke''), RI (''RioItuxi''), ''PEG-M1'', SF (''SãoFrancisco''), triCA (*trilineatus* Cusco Amazónico), triPAN (*trilineatus*, Panguana). Gray lines separate localities.

suggestive of eight species—one at each locality. The minimum pairwise cytochrome *b* distances between localities is 5.7% between the *trilineatus* from Cusco Amazónico and the samples from Porto Walter. Despite the geographic and cladistic proximity of the Reserva Ducke and São Francisco samples, these samples (which are united by 25 unambiguous transformations) are separated by a patristic distance of 244 steps and their cytochrome *b* sequences are 15.3% different.

The clade shown in figure 74 is united by 89 unambiguous transformations, including reduction in the length of finger IV (Character 4, 0 → 1), lengthening of finger I (Character 5, 2 → 3), and swelling of finger III in adult males (Character 20, 0 → 1). The next clade, shown at the top of figure 74, includes the *nubicola* group and Silverstone's (1976) *tricolor* group + *machalilla*. This inclusive clade is delimited by 84 unambiguous transformations in DNA sequences.

The *nubicola* group, represented by *flotator*, *nubicola*, and the undescribed species ''*nubicola*-spC'' to be named by T. Grant and C. W. Myers (in preparation) is delimited by 46 unambiguous transformations, including the gain of a straight pale ventrolateral stripe (Character 54, 0 → 2), pale male abdomen color (Character 63, 3 → 0), anterior pigmentation of the large intestine (Character 66, 0 → 1), and several synapomorphies relating to the larval oral disc (Character 88, 0 → 1; Character 89, 1 → 0; Character 91, 0 → 1; and Character 94, 3 → 0). This clade includes data downloaded from GenBank that were attributed to *pratti* from western Colombia by Vences et al. (2003a). However, one of the authors of that study informed us that they did not examine a voucher specimen (S. Lötters, in litt. 2/23/2005), and *nubicola* and *pratti* occur in sympatry and are often confused by collectors. The three sampled species resemble each other greatly; the Central American species *flotator* was

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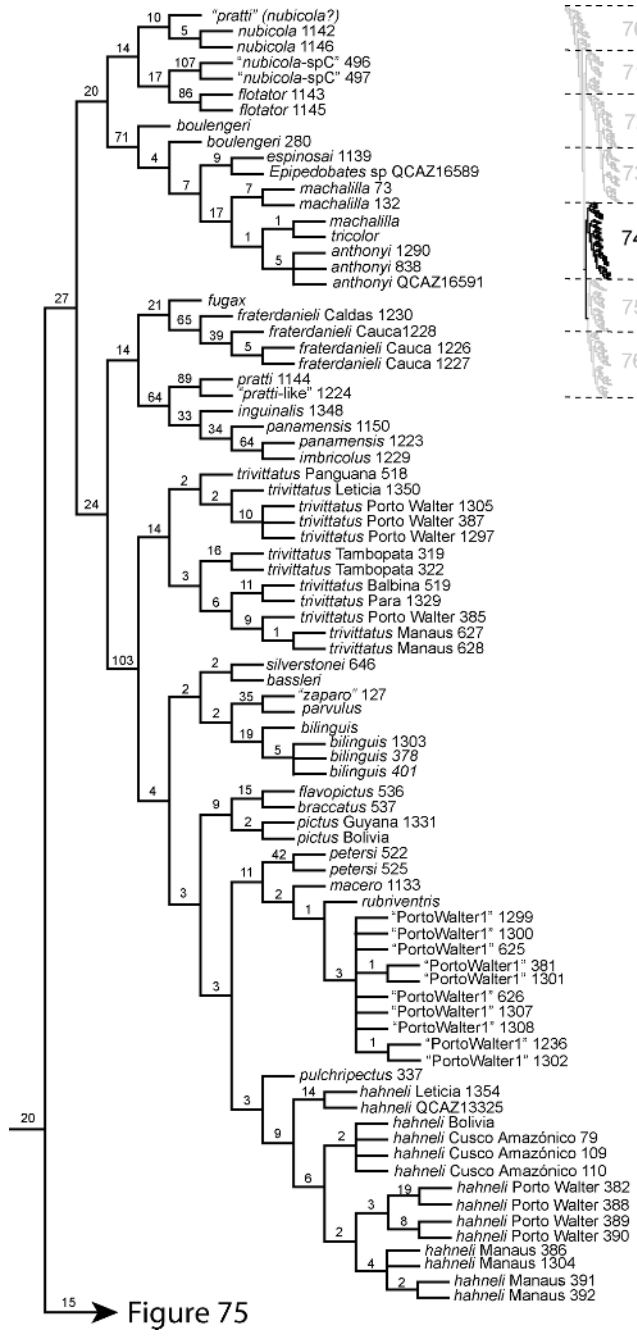

Fig. 74. Strict consensus of 25,872 most parsimonious trees of 46,520 steps: relationships among dendrobatids. Numbers above branches are Bremer support values. Numbers following terminal names are unique sample identifiers. Terminals without numbers or with alphanumeric identifiers (GenBank numbers) were not sequenced for the present study or Frost et al. (2006) and were taken from GenBank. Unidentified species taken from GenBank are labeled as originally published. Upper right inset shows entire cladogram and corresponding figure numbers, with present view in black.

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TABLE 19
Percent Uncorrected Pairwise Distances Between Cytochrome *b* Sequences of *flotator*, *nubicola*, and "*nubicola*-spC"[a]

Sample ID	1	2	3	4	5	6
1 *flotator* 1143	—					
2 *flotator* 1145	0.0	—				
3 *nubicola* 1142	18.4	18.4	—			
4 *nubicola* 1146	18.4	18.4	0.0	—		
5 "*nubicola*-spC" 496	15.3	15.3	22.1	22.1	—	
6 "*nubicola*-spC" 497	15.3	15.3	22.1	22.1	0.0	—

[a] Gray lines separate species.

considered a synonym of *nubicola* until 1995 (Ibáñez and Smith, 1995), but these two species are not sisters and differ in 18.4% of their cytochrome *b* sites (table 19).

The sister of the *nubicola* clade includes several taxonomically problematic taxa. Lötters et al. (2003b) noted differences in the vocalizations of *boulengeri* and concluded that more than one species was probably involved. Cytochrome *b* sequences are unavailable for the GenBank specimen for comparison, but only eight unambiguous transformations group *boulengeri* 280 with the other species of this clade. Cytochrome *b* sequences are also unavailable for GenBank specimen *Epipedobates* sp. QCAZ16589, but the occurrence of only four unambiguous transformations to distinguish it from *espinosai* 1139 suggests that it may be conspecific with *espinosai*. Like Santos et al. (2003), we found that *machalilla* is nested within this clade of otherwise toxic species. However, the specimens we sequenced fall together, whereas the Santos et al. sequence obtained from GenBank is sister to *tricolor*. Graham et al. (2004) reported this sample of *machalilla* to be most closely related to *anthonyi* instead of *tricolor*, although that conclusion was not supported in their analysis (the critical node had a Bremer value of 0). In our analysis, only a single unambiguous synapomorphy unites *tricolor* and *machalilla*, and the clade has a Bremer value of only 1. There is little unambiguous evidence to group these samples with *anthonyi* to the exclusion of *machalilla* samples 73 and 132 (only five transformations), but it is worth noting that samples 73 and 132 are united by 24 unambiguous transformations and differ in only 9.

Grant and Castro-Herrera (1998) noted the extensive within- and among-population variation in *fraterdanieli* and left open the possibility that this may be a complex of similar species. The samples of *fraterdanieli* were collected in Colombia near Popayán, Cauca, at approximately 1,800 m in the Cordillera Occidental (1226, 1227, 1228). An additional sample was collected at 2,800 m in the Departamento de Caldas in the Cordillera Central (1230). All localities face the Cauca valley. As seen in table 20, the three Cauca *fraterdanieli* cytochrome *b* sequences are identical. The pairwise distance between those samples and the Caldas specimen is 6.5%. Likewise, the three Cauca specimens are united by 42 unambiguous transformations, and the Caldas sample differs by an additional 63 unambiguous transformations. This pattern of diversity is strongly suggestive that these are two different species. The type locality of *frateranieli* is in the Cordillera Central in Antioquia, at approximately 1,900 m (Silverstone, 1971). Minimally, comparison with samples from lower elevations in the Cordillera Central is required to determine which of these populations (i.e., that from approximately the same elevation but much further south in the Cordillera Occidental or that from the Cordillera Central in roughly the same region but much higher elevation) is conspecific with *fraterdanieli* sensu stricto or if additional species have been conflated under this name.

The terminals labeled *pratti* 1144 and and "*pratti*-like" 1224 are morphologically indistinguishable but are almost certainly not conspecific. Sample 1144 was collected at El Copé, Coclé, central Panama, and 1224 is from Jungurudó, Darién, near the boarder

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TABLE 20
Percent Uncorrected Pairwise Distances Between Cytochrome *b* Sequences of *fraterdanieli*[a]

Sample ID	1	2	3	4
1 *fraterdanieli* Cauca 1226	—			
2 *fraterdanieli* Cauca 1227	0.0	—		
3 *fraterdanieli* Cauca 1228	0.0	0.0	—	
4 *fraterdanieli* Caldas 1230	6.5	6.5	6.5	—

[a] Gray lines separate localities.

TABLE 21
Percent Uncorrected Pairwise Distances Between Cytochrome *b* Sequences of *imbricolus*, *inguinalis*, and Two Distant Localities of *panamensis*[a]

Sample ID	1	2	3	4
1 *imbricolus* 1229	—			
2 *inguinalis* 1348	15.6	—		
3 *panamensis* 1150 El Copé	11.7	16.1	—	
4 *panamensis* 1223 Cana	3.9	14.8	11.4	—

[a] Gray lines separate species.

with Colombia. Roberto Ibáñez noted differences in their vocalizations (in litt., 12/20/2003). Further, only female nurse frogs are known to occur in *pratti* (Grant, 2004), whereas a male nurse frog was collected at Jungurudó. The behavioral sample size at the Darién locality is inadequate to eliminate the possibility that this is simply intraspecific variation, but these behavioral differences are further reinforced by the observation that, although these two samples are united by 104 unambiguous transformations, the patristic distance between them is 163. Finally, the pairwise distance between their cytochrome *b* sequences is 10.6%. As such, despite the lack of morphological differences between these frogs, there is considerable evidence that they represent different species. Resolution of this problem, though evidentially straightforward, is nomenclaturally complicated. The type locality of *pratti* is in western Colombia, and the relationship of topotypic *pratti* to either of these samples has not yet been assessed. The proximity of the Darién species to the type locality suggests it may be *pratti* sensu stricto, but direct evidence is required. As noted above, the specimen reported as *pratti* from western Colombia by Vences et al. (2003a) is probably a misidentified specimen of *nubicola*, but that too requires confirmation.

Grant (2004) removed *panamensis* from the synonymy of *inguinalis* on morphological grounds, and, although there are several points of resemblance, *imbricolus* differs extensively from both species (e.g., ventral coloration, color and definition of flash marks, degree of webbing, sexual dimorphism, and occurrence of tetrodotoxin). Although the identities of *inguinalis* and *imbricolus* are not problematic, *panamensis* is widespread and highly variable. Dunn (1933) and Savage (1968) drew attention to differences between western and eastern samples. Grant (2004) found that variation between localities was no greater than is observed in samples from each locality and therefore concluded that the samples of *panamensis* constituted a single species. The two *panamensis* samples included for DNA sequence data are from distant localities: 1150 is from El Copé in central Panama, whereas 1223 is from extreme eastern Panama at Caná, Darién at the eastern extreme of the distribution, near the Colombian border.

Both the cladistic results and the pairwise cytochrome *b* comparisons (table 21) support Grant's (2004) conclusion that *inguinalis* is not conspecific with the Panamanian species previously assigned to its synonymy. However, the present results suggest that the two samples of *panamensis* represent different species. The pairwise distance between the cytochrome *b* sequences for these two samples is 11.4%. Furthermore, the cladogram shows the western sample to be more closely related to *imbricolus*, from which its cytochrome *b* sequence differed by only 3.9%. Denser sampling at intervening localities, as well as additional data (e.g., vocalizations, behavior), are required to address this problem decisively.

The next large clade includes the majority of the species referred to *Phyllobates* by Silverstone (1976), *Ameerega* by Bauer (1986), and *Epipedobates* by Myers (1987). More specifically, it is equivalent to the combination of Silverstone's (1976) *pictus* and *trivittatus* groups, with the addition of species described subsequently. The clade is delimited by 131 unambiguous transformations, including the almost unique gain of

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TABLE 22
Percent Uncorrected Pairwise Distances Between Cytochrome *b* Sequences of *trivittatus*[a]

Sample ID	1	2	3	4	5	6	7	8	9	10	11	12	13
1 *trivittatus* 319 TAM	—												
2 *trivittatus* 320 TAM	0.0	—											
3 *trivittatus* 322 TAM	0.0	0.0	—										
4 *trivittatus* 385 PW	1.8	1.8	1.8	—									
5 *trivittatus* 387 PW	2.1	2.1	2.1	3.4	—								
6 *trivittatus* 1297 PW	2.1	2.1	2.1	3.4	0.52	—							
7 *trivittatus* 1305PW	2.1	2.1	2.1	3.4	0.52	0.52	—						
8 *trivittatus* 518 PAN	1.2	1.2	1.2	2.6	1.3	1.3	1.3	—					
9 *trivittatus* 1350 LET	2.1	2.1	2.1	3.4	1.6	1.6	1.6	1.3	—				
10 *trivittatus* 519 BAL	1.6	1.6	1.6	1.3	3.1	3.1	3.1	2.3	3.1	—			
11 *trivittatus* 627 MAN	1.3	1.3	1.3	0.5	2.9	2.9	2.9	2.1	2.9	0.8	—		
12 *trivittatus* 628 MAN	1.3	1.3	1.3	0.5	2.9	2.9	2.9	2.1	2.9	0.8	0.0	—	
13 *trivittatus* 1329 PAR	1.6	1.6	1.6	1.3	3.1	3.1	3.1	2.3	3.1	0.0	0.8	0.8	—

[a] Gray lines separate localities. Abbreviations are: TAM (Tambopata Reserve), PW (Porto Walter), PAN (Panguana), LET (Leticia), BAL (Balbina), MAN (Manaus), and PAR (Para).

conspicuously granular dorsal skin (Character 0, 1 → 2) and ability to sequester lipophilic alkaloids (Character 146, 0 → 1).

Unlike other widespread Amazonian species, such as *femoralis* (discussed above), and despite the known degree of external color and color pattern variation (Silverstone, 1976) of nominal *trivittatus*, the pattern and extent of diversity are not suggestive of more than a single species (see table 22). We included samples of *trivittatus* from seven localities covering (albeit sparsely) most of the known range of the species, as follows (listed approximately from southwest to northeast): Tambopata Reserve, Madre de Dios, Peru (319, 320, 322); Porto Walter, Acre, Brazil (385, 387, 1297, 1305); Panguana, Huánuco, Peru (518); Leticia, Amazonas, Colombia (1350); Balbina, north of Manaus, Amazonas, Brazil (519); south of Manaus, Amazonas, Brazil (627, 628); and Para, Suriname (1329).

The monophyly of *trivittatus* is established by 96 unambiguous transformations, and the pairwise cytochrome *b* distances between these samples and Guyanan *pictus* are 13.2–14.3% and southeastern Brazilian *flavopictus* are 10.9–12.5%. Conversely, the variation within *trivittatus* is low, despite the great distances between localities. Pairwise cytochrome *b* distances between localities are 0.5–3.4%. Although the higher values are as great as or greater than those between some closely related species (e.g., *auratus* and *truncatus*; see below), there are no major gaps (i.e., pairwise distances appear to vary continuously) or geographic trends, and cladistic relationships do not suggest historically isolated populations.

Duellman and Mendelson (1995) referred sample 127 from northern Peru to *zaparo*, but they also noted that theirs was the first record of that taxon outside the Río Pastaza drainage. The present results demonstrate conclusively that this species is not conspecific with *zaparo*, despite their morphological resemblance, and we therefore place the name in quotes. Sufficient data (e.g., locality) are unavailable to determine if "*zaparo*" and Santos et al.'s (2003) *parvulus* are conspecific.

One of the more unexpected species-level results is the grouping of the GenBank sample of *pictus* from Bolivia, near the type locality, with *pictus* 1331 from Guyana. Despite the great geographic distance between these localities, the samples appear to be conspecific.

"PortoWalter1" is another undescribed species from Porto Walter, Brazil. The sister of this species is *rubriventris*. Although only 12 unambiguous transformations diagnose "PortoWalter1" from *rubriventris* (three

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TABLE 23
Percent Uncorrected Pairwise Distances Between Cytochrome *b* Sequences of *hahneli*[a]

	Sample ID	1	2	3	4	5	6	7	8	9	10	11	12
1	*hahneli* 79 CA	—											
2	*hahneli* 109 CA	0.3	—										
3	*hahneli* 110 CA	0.3	0.0	—									
4	*hahneli* 382 PW	2.6	2.6	2.6	—								
5	*hahneli* 388 PW	2.9	2.9	2.9	0.3	—							
6	*hahneli* 389 PW	2.6	2.6	2.6	1.0	1.3	—						
7	*hahneli* 390 PW	3.1	3.1	3.1	1.6	1.8	1.0	—					
8	*hahneli* 1354 LET	7.5	7.3	7.3	6.8	7.0	6.0	6.5	—				
9	*hahneli* 386 MAN	2.1	2.1	2.1	2.1	2.3	2.1	2.6	7.3	—			
10	*hahneli* 391 MAN	2.1	2.1	2.1	2.1	2.3	2.1	2.6	7.3	0.0	—		
11	*hahneli* 392 MAN	2.1	2.1	2.1	2.1	2.3	2.1	2.6	7.3	0.0	0.0	—	
12	*hahneli* 1304 MAN	2.1	2.1	2.1	2.1	2.3	2.1	2.6	7.3	0.0	0.0	0.0	—

[a] Gray lines separate localities. Abbreviations are: CA (Cusco Amazónico), PW (Porto Walter), LET (Leticia), and MAN (Manaus).

"PortoWalter1" synapomorphies and nine *rubriventris* autapomorphies) only 566 bp of 16S data were available for *rubriventris*. Cytochrome *b* sequences are identical in samples of "PortoWalter1", except for sample 626, which differs from the others in a single nucleotide.

Like *trivittatus* and *femoralis*, *hahneli* is another widespread Amazonian species. The type locality for *hahneli* is Yurimaguas, Peru. We included 12 samples of *hahneli* from four localities, as follows: Cusco Amazónico, Peru (79, 109, 110), Leticia, Colombia (1354); south of Manaus, Brazil (386, 391, 392, 1304), and Porto Walter, Brazil (382, 388, 389, 390). Pairwise distances between the cytochrome *b* sequences of these samples are given in table 23, and these sequences differ from those of *pulchripectus* in 10.4–11.7% of their sites. The *hahneli* samples are united by 51 unambiguous transformations. The sample from Leticia differs from the others in 6.5–7.5% of its cytochrome *b* sequence—much more than occurs between other samples, despite the greater geographic distance between other samples (e.g., Cusco Amazónico and Manaus). Likewise, the clade containing the remaining *hahneli* samples is united by 31 unambiguous transformations. This suggests that samples from Leticia and other localities are not conspecific. It is unclear which of these species is conspecific with *hahneli* sensu stricto. The cytochrome *b* distances between the remaining *hahneli* localities are 2.1–3.1%. Although Santos et al. (2003) did not provide specimen data, the topology suggests their specimen (QCAZ-13325) is conspecific with the Leticia *hahneli*.

In figure 75, the Colombian species *subpunctatus* is sister to a clade diagnosed by 76 unambiguous transformations, including several changes in hand and foot morphology (Characters 13, 15, 36–44), the appearance of posteriorly angled clavicles (Character 121, $0 \rightarrow 1$), gain of palatine bones (Character 132, $0 \rightarrow 1$), and the shift to riparian habitat (Character 113, $2 \rightarrow 1$).

Santos et al. (2003) resurrected *maculosus* from synonymy with *bocagei*, where it had been placed by Coloma (1995). Key to that interpretation is the identity of the specimen they identified as *bocagei* sensu stricto, because that species falls out with *sauli* both here and in Santos et al.'s (2003) analysis. However, no locality or other data were provided for that specimen, and an alternative possibility is that the remaining samples (including those identified here as *bocagei* from Cuyabeno) are conspecific with topotypic *bocagei* and the sister of *sauli* is an undescribed species. Additional data are required to assess the alternative hypotheses.

Santos et al. (2003) also omitted locality data for the unidentified specimens *Colostethus* sp. QCAZ16511, *Colostethus* sp. QCAZ16504, and *Colostethus* sp. QCAZ-

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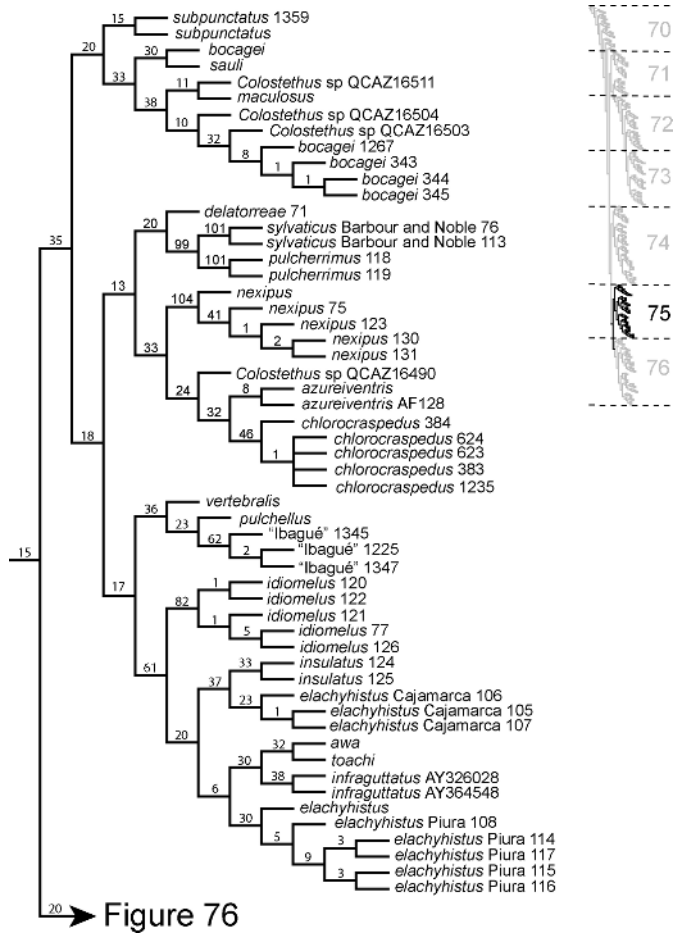

Fig. 75. Strict consensus of 25,872 most parsimonious trees of 46,520 steps: relationships among dendrobatids. Numbers above branches are Bremer support values. Numbers following terminal names are unique sample identifiers. Terminals without numbers or with alphanumeric identifiers (GenBank numbers) were not sequenced for the present study or Frost et al. (2006) and were taken from GenBank. Unidentified species taken from GenBank are labeled as originally published. Upper right inset shows entire cladogram and corresponding figure numbers, with present view in black.

16503, which complicates understanding the diversification of these dendrobatids. As noted above, one possibility is that these and related terminals are conspecific. Nevertheless, in light of the patristic distances between these terminals (128 steps between QCAZ16511 and QCAZ16504; 87 between QCAZ16504 and QCAZ16503), our provisional interpretation is that *Colostethus* sp. QCAZ16511 and *Colostethus* sp. QCAZ-16504 are different, possibly undescribed species, and that *Colostethus* sp. QCAZ16503 is conspecific with the terminals from Cuyabeno (e.g., patristic distance between QCAZ16503 *bocagei* 1267 = 8 steps). Although the topology is consistent with *Colostethus* sp. QCAZ16511 being conspecific with *maculosus* sensu Santos et al. (2003), 50 and 47 unambiguous transformations in mtDNA subunit H1 occur at these terminal nodes, respectively, suggesting they represent different species.

The clade composed of *delatorreae*, *pulcherrimus*, and *sylvaticus* Barbour and Noble is delimited by 38 unambiguous transformations. These species are all from mid- to high elevations in the Andes of northern Ecuador (*delatorreae*) and northern Peru (*pulcherrimus*

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TABLE 24
Percent Uncorrected Pairwise Distances Between Cytochrome *b* Sequences of *pulcherrimus* and *sylvaticus* Barbour and Noble[a]

	Sample ID	1	2	3	4
1	*pulcherrimus* 118	—			
2	*pulcherrimus* 119	0.3	—		
3	*sylvaticus* 76	13.0	13.3	—	
4	*sylvaticus* 113	13.0	13.3	0.0	—

[a] Gray lines separate species.

and *sylvaticus* Barbour and Noble). Duellman (2004) recently named *pulcherrimus* and compared it to the similar *sylvaticus* Barbour and Noble. The two samples of *pulcherrimus* (118 and 119) are topoparatypes (Cajamarca, Peru), and both samples of *sylvaticus* Barbour and Noble were collected at 2,820 m in Ayacaba, Peru. The species are closely related, but the pairwise distances between their cytochrome *b* sequences are 13.0–13.3% (see table 24) and each is diagnosed by approximately 100 unambiguous transformations.

The sister group to that clade includes *nexipus*, *azureiventris*, *chlorocraspedus*, and an unidentified species sequenced by Santos et al. (2003; no locality data given). The known species form a distinctive group of relatively brightly colored frogs with dorsolateral stripes, the latter being an unambiguous synapomorphy of the clade (Character 52, 0 → 3). In total, the clade is delimited by 51 unambiguous transformations. Lötters et al. (2000) proposed the genus *Cryptophyllobates* for the putatively aposematic *azureiventris*. However, Daly (1998:171) reported that in a feeding experiment this species did not accumulate dietary alkaloids. The recently described species *chlorocraspedus* is as brightly colored as *azureiventris*, and wild-caught samples lacked detectable levels of alkaloids also (J. W. Daly, in litt., 01/28/05). Although they were not included in the present study, the two recently named species *patitae* (Lötters et al., 2003a) and *eleutherodactylus* (Duellman, 2004) are also likely part of this clade. The samples of *chlorocraspedus* have identical cytochrome *b* sequences, with the exception of sample 385, which differs in two nucleotides (0.5%). Samples of *nexipus* were included from two localities at different elevations (Cataratas Ahuashiyacu, 14 km NE of Tarapoto, 730 m: 75, 130, 131; and San Martín, 6 km ESE of Shapaja, 300 m: 123). The specimen from the lower elevation is identical to two of the three specimens from the higher elevation; those specimens differ from one of the 730 m specimens in two nucleotides. Santos et al. (2003) omitted locality data for the sample they identified as *nexipus*, but 45 unambiguous transformations optimize to the terminal node (all from mtDNA subunit H1) and 42 unambiguous changes delimit the remaining specimens as a clade (all from Peru), suggesting that they may not be conspecific.

The terminals referred to as "Ibagué" are an undescribed species from the slopes of the Magdalena valley in Colombia (see table 25 for pairwise cytochrome *b* distances). The species possesses the black arm band in adult males and is thus the sole exemplar of the *ramosi* group included in present study (Grant and Castro, 1998; Grant and Ardila-Robayo, 2002). Other species that possess this structure (and are included in the *ramosi* group) are *anthracinus*, *cevallosi*, *fascianiger*, *exasperatus*, *lehmanni* Silverstone, *ramosi*, and *saltuarius*. "Ibagué" is nested in a clade with *vertebralis* and *pulchellus*, all of which are small, identically striped, and similarly colored Andean frogs. Forty-two changes optimize unambiguously to the node including *vertebralis* and 34 unambiguous transformations unite "Ibagué" with *pulchellus*.

Rivero (1991a) described *idiomelus* based on a single specimen (from Venceremos, Peru), but Duellman's (2004) account was based on extensive material, including adults and larvae from several localities; all of the samples sequenced in the present study were referred to *idiomelus* by Duellman (2004). Three specimens (120–122) are from 2,180 m at Abra Pardo de Miguel, San Martín, and the other two (77 and 126) are from 2,150 m at Pomachochas, Amazonas. The five specimens form a clade, but the Abra Pardo locality is paraphyletic with respect to Pomachochas. Pairwise cytochrome *b* distances are given in table 26.

Originally described from Loja, Ecuador, *elachyhistus* is a widespread, highly variable Andean species. Duellman (2004) recently redescribed *elachyhistus* from several locali-

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TABLE 25
Percent Uncorrected Pairwise Distances Between Cytochrome *b* Sequences of "Ibagué"[a]

	Sample ID	1	2	3
1	"Ibagué" 1225	—		
2	"Ibagué" 1347	0.3	—	
3	"Ibagué" 1345 La Mesa	0.5	0.3	—

[a] Gray lines separate localities.

ties in northern Peru, including those included in the present study. Based on the current results, it is clear two species have been conflated, a southern species from Cajamarca, Peru (105, 106, and 107), which is sister to *insulatus*, and a northern species from Piura, Peru (108, 114, 115, 116, 117); see table 27 for pairwise cytochrome *b* distances. Locality data were not given by Santos et al. (2003) for the GenBank *elachyhistus* included, but the data provided in GenBank report it as being from Ecuador, which suggests that the northern species is *elachyhistus* and the southern species is undescribed.

Although toxic species also occur elsewhere in the cladogram (e.g., *anthonyi*, *petersi*), the remaining clade, shown in figure 76, consists of exclusively brightly colored and (insofar as is known) toxic species. Evidence for the monophyly of this clade is given by 63 unambiguous changes, including origin of smooth dorsal skin (Character 0, $1 \rightarrow 0$), loss of the oblique lateral stripe (Character 55, $1 \rightarrow 0$), the loss of metallic pigmentation of the iris (Character 65, $1 \rightarrow 0$), use of phytotelmata as larval habitat (Character 110, $0 \rightarrow 1$), and origin of the ability to sequester lipophilic alkaloids (Character 147, $0 \rightarrow 1$).

The clade composed of *aurotaenia*, *bicolor*, *lugubris*, *terribilis*, and *vittatus* constitutes *Phyllobates* sensu Myers et al. (1978), and its monophyly is established by 146 unambiguous transformations, including the lengthening of finger I (Character 5, $2 \rightarrow 3$) and the ability to accumulate batrachotoxin (Character 148, $0 \rightarrow 1$). Species identities are uncontroversial, the sole potential exception being the possibility that *terribilis* represents the southern extreme of clinal variation of *bicolor* (Myers et al., 1978; Lötters et al., 1997a). That hypothesis is rejected in the current phylogenetic analysis, which places *aurotaenia* and *terribilis* as sister species to the exclusion of *bicolor*. This result is also consistent with cytochrome *b* pairwise distances (table 28). The pairwise distance between *terribilis* and *bicolor* is 7.0%, whereas the pairwise distance between *terribilis* and *aurotaenia* is only 5.7%. The two *lugubris* samples are from Panama (329) and Nicaragua (366), representing opposite extremes in the species' distribution. These specimens form a clade, and there is no indication in morphology or otherwise that *lugubris* may refer to more than a single species. Nevertheless, the distance between cytochrome *b* sequences of the two samples is 6.0%. The *terribilis* samples are from the type locality in western Colombia (1135) and bred in captivity (1232). The *aurotaenia*, *bicolor*, and one of the *vittatus* samples (839) were bred in captivity; the second *vittatus* sample is GenBank sequence AF128582.

Maxson and Myers (1985) proposed that the South American species *bicolor* and *terribilis* were sisters and were, in turn, sister to a clade composed of *lugubris*, *aurotaenia*, and *vittatus*, the latter two being sisters. In addition to a plausible biogeographic argument, *bicolor* and *terribilis* were grouped on the basis of the shared ontogenetic "loss"

TABLE 26
Percent Uncorrected Pairwise Distances Between Cytochrome *b* Sequences of *idiomelus*[a]

	Sample ID	1	2	3	4	5
1	*idiomelus* 120 Abra Pardo	—				
2	*idiomelus* 121 Abra Pardo	0.0	—			
3	*idiomelus* 122 Abra Pardo	0.0	0.0	—		
4	*idiomelus* 77 Pomachochas	0.5	0.5	0.5	—	
5	*idiomelus* 126 Pomachochas	0.5	0.5	0.5	0.0	—

[a] Gray lines separate localities.

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TABLE 27
Percent Uncorrected Pairwise Distances Between Cytochrome *b* Sequences of Two Species Currently Referred to *elachyhistus*[a]

	Sample ID	1	2	3	4	5	6	7	8
1	*elachyhistus* Cajamarca 105	—							
2	*elachyhistus* Cajamarca 106	0.3	—						
3	*elachyhistus* Cajamarca 107	0.0	0.3	—					
4	*elachyhistus* Piura 108	13.0	13.2	13.0	—				
5	*elachyhistus* Piura 114	11.4	11.7	11.4	2.1	—			
6	*elachyhistus* Piura 115	11.7	11.9	11.7	2.3	0.3	—		
7	*elachyhistus* Piura 116	11.7	11.9	11.7	2.3	0.3	0.0	—	
8	*elachyhistus* Piura 117	11.4	11.7	11.4	2.1	0.0	0.3	0.3	—

[a] Gray lines separate localities.

(through hypertrophy; see Character 52, above) of dorsolateral stripes (DLS). Widmer et al. (2000) tested that hypothesis with a 520-bp cytochrome *b* dataset and concurred that *bicolor* and *terribilis* were sister-species. However, they found that *aurotaenia* was placed in a clade with the other South American species, and that the two Central American species, *lugubris* and *vittatus*, were sisters. Our greatly enlarged dataset corroborates Widmer et al.'s (2000) hypothesis of Central and South American monophyly, but we found that *bicolor* is the sister of *aurotaenia* + *terribilis*. Maxson and Myers (1985; see also Myers et al., 1978) hypothesized that the persistent DLS was "a primitive pattern that is retained by the adults of *aurotaenia*, *lugubris*, and *vittatus*." According to our results, it is equally parsimonious for the persistent DLS to have evolved in the ancestor of *Phyllobates*, with either two "losses" of the DLS in adults in *bicolor* and *terribilis* or a single "loss" of the DLS in adults in the ancestor of the South American clade and reversion in *aurotaenia*, or for the DLS in juveniles only to be ancestral for *Phyllobates* and the persistent DLS to have evolved independently in *aurotaenia* and the ancestor of *lugubris* and *vittatus*.

Myers (1987) designated *steyermarki* as the type species of *Minyobates*, which he proposed for several species previously included in Silvestone's (1975a) *minutus* group of diminutive *Dendrobates*. Further, Myers hypothesized that *steyermarki* and its relatives were placed outside of a *Phyllobates* + *Dendrobates* clade that included the remainder of Silverstone's *minutus* group. In our results, *steyermarki* is placed as the sister species of all species traditionally associated with *Dendrobates*, including a clade that corresponds to the bulk of Silverstone's *minutus* group. The placement of these species in a clade exclusive of *Phyllobates* refutes Myers's hypothesis (but see discussion of *castaneoticus* and *quinquevittatus*, below), but is identical to the findings of Vences et al. (2003a). These clades are not strongly supported, owing to the lack of evidence for *steyermarki*, for which only phenotypic characters and 547 bp of 16S (the latter sequenced by Vences et al., 2003a) could be included.

Silverstone (1976) named the distinctive species *fulguritus* from the Chocó region of western Colombia, and the included sample is from near Bahía Solano. The sister-species *claudiae* and *minutus* strongly resemble each other morphologically. Nevertheless, their cytochrome *b* sequences are 8.1–8.3% dissimilar (see table 29). The monophyly of this group of three species is established by 69 unambiguous transformations, including the occurrence of dorsolateral and oblique lateral stripes (Characters 52 and 55) and the fusion of vertebrae 2 + 3 (Character 146, 0 → 1).

The sister group of the *fulguritus* clade contains most of the Amazonian species of Silverstone's *minutus* group. Evidence for the monophyly of this group is given by 67 unambiguous transformations, including the expansion of finger discs II–IV (Characters 8–10). Caldwell and Myers (1990) removed *ventrimaculatus* from the synonymy of *quinquevittatus* (see below), but they noted that the nominal taxon, which occurs throughout

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Fig. 76. Strict consensus of 25,872 most parsimonious trees of 46,520 steps: relationships among dendrobatids. Numbers above branches are Bremer support values. Numbers following terminal names are unique sample identifiers. Terminals without numbers or with alphanumeric identifiers (GenBank numbers) were not sequenced for the present study or Frost et al. (2006) and were taken from GenBank. Unidentified species taken from GenBank are labeled as originally published. Upper right inset shows entire cladogram and corresponding figure numbers, with present view in black.

the Amazon region from Peru to French Guiana, probably consists of a complex of similar species. Symula et al. (2003) presented molecular evidence that at least two distantly related species are included in Peruvian ''*ventrimaculatus*''. Assuming the validity of *amazonicus* and *variabilis* (but see Lötters and Vences, 2000, and Caldwell and Myers, 1990, respectively) the current results suggest five species of ''*ventrimaculatus*'', one at Rio Ituxi, Brazil (376, 377), a second at Manaus, Brazil (1310), a third at Leticia, Colombia

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TABLE 28
Percent Uncorrected Pairwise Distances Between Cytochrome *b* Sequences of *aurotaenia*, *bicolor*, *lugubris*, *terribilis*, and *vittatus*[a]

	Sample ID	1	2	3	4	5	6	7	8
1	*aurotaenia* 840 (CR)	—							
2	*bicolor* 1233 (CR)	6.0	—						
3	*lugubris* 329 Panama	16.6	17.9	—					
4	*lugubris* 366 Nicaragua	17.1	17.9	6.0	—				
5	*terribilis* 1135	5.7	7.0	17.7	18.7	—			
6	*terribilis* 1232 (CR)	5.7	7.0	17.7	18.7	0.0	—		
7	*vittatus* 839 (CR)	16.4	16.9	6.5	5.7	17.9	17.9	—	
8	*vittatus* (GB)	16.1	14.1	5.2	6.7	17.3	17.3	2.1	—

[a] CR = captive reared. GB = GenBank. Gray lines separate species.

(1349) and French Guiana (GenBank AY263248), a fourth at Pompeya, Ecuador (374), and a fifth at Porto Walter, Brazil (375, 1311). Although the cladogram does not falsify the hypothesis that the samples from Rio Ituxi and Manaus are a single species, 72 unambiguous synapomorphies unite the two Rio Ituxi specimens, 58 autapomorphies optimize unambiguously to the Manaus terminal node, and cytochrome *b* sequences differ in 8.1% of their sites (table 30). Despite the considerable geographic distance between the Leticia and French Guiana samples, they form a clade, and the patristic difference between them is minimal (14 steps; cytochrome *b* data are unavailable for the French Guiana sample); however, this is based on analysis of only 560 bp of 16S for the French Guiana specimen. The Leticia and Pompeya localities are closest to the type locality of Sarayacu, Ecuador, suggesting that one of them may be conspecific with *ventrimaculatus* sensu stricto.

TABLE 29
Percent Uncorrected Pairwise Distances Between Cytochrome *b* Sequences of *claudiae*, *fulguritus*, and *minutus*[a]

	Sample ID	1	2	3	4	5
1	*claudiae* 323	—				
2	*claudiae* 324	0.0	—			
3	*claudiae* 330	0.3	0.3	—		
4	*fulguritus* 499	14.0	14.0	13.8	—	
5	*minutus* 1149	8.3	8.3	8.1	15.1	—

[a] Gray lines separate species.

The sister clade to the *minutus* group consists of the remaining species traditionally referred to *Dendrobates*. Fifty-four unambiguous transformations delimit this node, including the origin of even caudal pigmentation in larvae (Character 87, 1 → 2).

Caldwell and Myers (1990) clarified the identity of *quinquevittatus* (removing the unrelated *ventrimaculatus* from its synonymy in the process; see above). They proposed a close relationship between *quinquevittatus* and the clearly heterospecific *castaneoticus*. They did not discuss the relationships of *galactonotus*, but its placement in the *tinctorius* group by Silverstone (1975a) was uncontroversial. The monophyly of *galactonotus*, *castaneoticus*, and *quinquevittatus* was first proposed by Vences et al. (2003a), although these three taxa were unresolved in their topology. In the present study, 105 unambiguous synapomorphies optimize to this node, and Bremer support is 37, leaving little doubt as to the reality of this clade. Nevertheless, the occurrence of *galactonotus* in this clade is unexpected, as its morphology shares little with the diminutive *castaneoticus* and *quinquevittatus*. Pairwise cytochrome *b* distances for these species are shown in table 31.

The next clade is delimited by 37 unambiguous transformations. The first clade included in this group consists of the *histrionicus* group of Myers et al. (1984). The evidence for the monophyly of this group is overwhelming, consisting of 132 unambigously optimized synapomorphies. These include several larval modifications

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TABLE 30
Percent Uncorrected Pairwise Distances Between Cytochrome *b* Sequences of Nominal *ventrimaculatus*[a]

	Sample ID	1	2	3	4	5	6	7
1	Rio Ituxi 376	—						
2	Rio Ituxi 377	0.0	—					
3	Manaus 1310	8.1	8.1	—				
4	Pompeya 374	15.6	15.6	16.4	—			
5	Leticia 1349	14.0	14.0	13.2	11.4	—		
6	Porto Walter 375	17.4	17.4	16.7	16.4	13.2	—	
7	Porto Walter 1311	16.9	16.9	16.1	16.1	12.7	1.0	—

[a] Gray lines separate localities.

(Characters 90, 93, and 94), origin of tadpole transport by female nurse frogs (Character 109, 0 → 1) and larval oophagy (Character 111, 1 → 2), and fusion of the sacrum and vertebra 8 (Character 143, 0 → 1) and vertebrae 2 and 3 (Character 145, 0 → 1).

Myers and Daly (1976b) illustrated and discussed the extensive variation within what they considered to be the single species *histrionicus*, distributed throughout the Pacific lowlands of western Colombia and northwestern Ecuador. In the same paper, they named *lehmanni* Myers and Daly, based primarily on differences in vocalizations, coloration and color pattern, and, especially, the absence of histrionicotoxins from skin alkaloid profiles. Nevertheless, E. Zimmermann (1986:135) claimed that *histrionicus* and *lehmanni* Myers and Daly crosses produced fertile offspring, and Garraffo et al. (2001) showed experimentally that *lehmanni* Myers and Daly efficiently sequesters histrionicotoxins administered in the diet. Based on differences in vocalizations and coloration and color pattern, Lötters et al. (1999) resurrected *sylvaticus* Funkhouser from the synonymy of *histrioncus* for the southernmost populations in southern Colombia and northern Ecuador.

The *histrionicus* samples included here were both collected in Chocó department, Colombia, but are from distant localities and involve different color morphs. Sample 336 was taken along Quebrada Vicordó (locality D of Myers and Daly, 1976b; see their Plate 1C for color morph), whereas sample 498 is from Sierra Mecana (approximately 6°15′N, 77°21′W), north of Bahía Solano; the two localities are separated by >100 km. The *lehmanni* Myers and Daly sample is from the region of the type locality. The sample of *sylvaticus* Funkhouser is from Ecuador. Cytochrome *b* sequences were not available for the GenBank specimens shown in the cladogram.

TABLE 31
Percent Uncorrected Pairwise Distances Between Cytochrome *b* Sequences of *castaneoticus*, *galactonotus*, and *quinquevittatus*[a]

	Sample ID	1	2	3	4	5	6	7	8
1	*castaneoticus* 363	—							
2	*galactonotus* 533 (CR)	18.6	—						
3	*galactonotus* 647	18.6	0.5	—					
4	*quinquevittatus* 368 Rio Ituxi	17.4	15.8	16.4	—				
5	*quinquevittatus* 369 Rio Ituxi	17.4	15.8	16.4	0.0	—			
6	*quinquevittatus* 370 Rio Formoso	17.1	16.1	16.6	0.3	0.3	—		
7	*quinquevittatus* 371 Rio Formoso	17.4	15.8	16.4	0.0	0.0	0.3	—	
8	*quinquevittatus* 1312 Rio Formoso	17.4	15.8	16.4	0.0	0.0	0.3	0.0	—

[a] CR = captive reared. Gray lines separate localities and species.

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TABLE 32
Percent Uncorrected Pairwise Distances Between Cytochrome *b* Sequences of *histrionicus*, *lehmanni* Myers and Daly, and *sylvaticus* Funkhouser[a]

Sample ID	1	2	3	4
1 *histrionicus* 336 Vicordó	—			
2 *histrionicus* 498 Mecana	0.3	—		
3 *lehmanni* 338	5.2	4.9	—	
4 *sylvaticus* 364	5.2	4.9	2.9	—

[a] Gray lines separate species.

TABLE 33
Percent Uncorrected Pairwise Distances Between Cytochrome *b* Sequences of *arboreus*, *pumilio*, *speciosus*, and *vicentei*[a]

Sample ID	1	3	4	5	6
1 *arboreus* 340	—				
3 *pumilio* 367	5.7	—			
4 *pumilio* 1313	4.2	5.5	—		
5 *speciosus* 341	5.5	3.6	4.4	—	
6 *vicentei* 1148	4.9	4.7	3.9	3.6	—

[a] Gray lines separate species.

The cladogram is consistent with the validity of these three species. The two samples of *histrionicus* were recovered as monophyletic; their cytochrome *b* sequences differ from each other in only a single base (0.3%) and are approximately 5% different from both *lehmanni* Myers and Daly and *sylvaticus* Funkhouser (see table 32). Similarly, *sylvaticus* Funkhouser, which had been in the synonymy of *histrionicus* until recently, is more closely related to *lehmanni* Myers and Daly. Although it has never been postulated that these two nominal species may be conspecific to the exclusion of *histrionicus*, that hypothesis is not ruled out by the current results. Their cytochrome *b* sequences are only 2.9% dissimilar, which is less than the distance between the closely related species *bicolor* and *terribilis* (7.0%) and *minutus* and *claudiae* (8.1–8.3%), for example, but is greater than is observed between some specimens of the clearly heterospecific *auratus* and *truncatus* (2.3–3.1%; see below). Regardless of their low degree of pairwise dissimilarity, *lehmanni* Myers and Daly and *sylvaticus* Funkhouser are still diagnosable on the basis of phenotypic evidence (Myers and Daly, 1976b; Lötters et al., 1999) and therefore are valid species.

Also included in this clade are a number of small species allied phenetically to *pumilio*. The systematics of these species has been confounded by the astonishing intra- and interpopulational variation in coloration (e.g., Myers and Daly, 1983). Only *pumilio* is not represented by singletons in the cladogram, and, as such, the monophyly of those species was not tested. Nevertheless, consideration of patristic and pairwise (table 33) distance supports the historical reality of these species.

The sister of the *histrionicus* group is equivalent to Silverstone's (1975a) *tinctorius* group, with the exclusion of *galactonotus* (see above). This clade is individuated by 92 unambiguously optmized synapomorphies. Hoogmoed (1969) described *azureus* from Vier Gebroeders Mountain in southern Sipaliwini, near the Brazilian border. Its resemblance to *tinctorius* was noted in the original description, and Silverstone (1975a) considered it to be closely related to and potentially derived from that species. The extensive variation in *tinctorius* discovered subsequently has only strengthened the suspicion that these two nominal taxa are conspecific. The two samples of *azureus* were obtained from the region of the type locality in Suriname (1330) and in adjacent Brazil (534). One of the *tinctorius* samples is also from near the Tafelberg airstrip, Sipaliwini, Suriname (1327), and the other is from Brazil.

The cladogram indicates that *tinctorius* is paraphyletic with respect to *azureus*. Furthermore, as shown in the pairwise comparisons (table 34), the two *azureus* samples are identical and differ from the Brazilian *tinctorius* sample in only a single nucleotide (0.3%). The pairwise distance between the Brazil and Suriname *tinctorius* is greater than that between it and *azureus*. All of this is consistent with the hypothesis that these samples are conspecific.

Despite the considerable variation in color and color pattern in *auratus*, there are no known problems surrounding the identities of *auratus* and *truncatus* (see table 35). Silverstone (1975a) hypothesized that these two species are closely related, and the

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TABLE 34
Percent Uncorrected Pairwise Distances Between Cytochrome *b* Sequences of *azureus* and *tinctorius*[a]

	Sample ID	1	2	3	4
1	*azureus* 1330	—			
2	*azureus* 534	0.0	—		
3	*tinctorius* 1327	2.6	2.6	—	
4	*tinctorius* 535	0.3	0.3	2.3	—

[a] Gray lines separate species.

available evidence corroborates that claim with a total of 84 unambiguously optimized synapomorphies. Samples of *auratus* are from two localities in Bocas del Toro, Panama (327, 334, 335) and one in Nicaragua (365). One *truncatus* sample was captive raised (1151); the other two were taken in western Colombia.

Summary of Relationships among Dendrobatids

This study resolved the relationships among most of the included terminals. Results are generally consistent with prior findings, especially the species groups proposed by Silverstone (1975a, 1976). At the level of genera, *Allobates* (whether restricted to the *femoralis* group or applied more generally; see below), *Ameerega*, *Dendrobates* (including or excluding *Minyobates*, *Oophaga*, and *Ranitomeya*), *Epipedobates*, *Mannophryne*, *Oophaga*, *Phyllobates*, and *Ranitomeya* were all found to be monophyletic. *Nephelobates* was found to be paraphyletic with respect to *Aromobates nocturnus* and *Colostethus saltuensis*. As expected, the greatest incongruence between generic grouping and phylogeny involves *Colostethus*, which was shown to be vastly nonmonophyletic. Nevertheless, the density of taxon sampling allowed coherent clades to be delimited, which will permit a monophyletic taxonomy to be developed below.

In addition to resolving the relationships among species, this study sheds light on the identities of numerous problematic species. Comparison with topotypic material is required to determine which species are new, and in several cases the lack of locality data for the sequences reported by Santos et al. (2003) makes it difficult to assess species identity (especially in relation to *bocagei*). Nevertheless, consideration of cladistic and patristic distances suggests the 367 dendrobatid terminals included in this analysis represent 156 species. Available evidence clearly delimits two distantly related species conflated under the name *elachyhistus*, corroborating Duellman's (2004) suspicions. The widespread Amazonian taxon *ventrimaculatus* is paraphyletic with respect to *amazonicus*, *duellmani*, *fantasticus*, *reticulatus*, *variabilis*, and an unidentified species reported by Santos et al. (2003), which, in combination with patterns of patristic distances for all data and pairwise distances for cytochrome *b* sequences, suggests this taxon includes five species. Although *femoralis*, *fraterdanieli*, *hahneli*, and *nexipus* were all recovered as monophyletic, pairwise cytochrome *b* distances and patristic distances for all data suggest they may include multiple species (*femoralis*: 8 spp.; *fraterdanieli*: 2 spp.; *hahneli*: 2 spp.; *nexipus*: 2 spp.). Grant and Rodríguez (2001) speculated that *trilineatus*

TABLE 35
Percent Uncorrected Pairwise Distances Between Cytochrome *b* Sequences of *auratus* and *truncatus*[a]

	Sample ID	1	2	3	4	5	6	7
1	*auratus* 327 Panama	—						
2	*auratus* 334 Panama	0.0	—					
3	*auratus* 335 Panama	0.0	0.0	—				
4	*auratus* 365 Nicaragua	0.0	0.0	0.0	—			
5	*truncatus* 1151 (CR)	2.3	2.3	2.3	2.3	—		
6	*truncatus* 1351	3.1	3.1	3.1	3.1	1.3	—	
7	*truncatus* 1352	3.1	3.1	3.1	3.1	1.3	0.0	—

[a] CR = captive reared. Gray lines separate species and localities.

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may be a complex of species, which is borne out by the current analysis; we identify provisionally eight species in the *trilineatus* clade. Similarly, although the diversity of small, cryptically colored Amazonian frogs is greater than the current taxonomy indicates, and the names proposed by Morales (2002 "2000") are available to associate with several of these species, Morales's taxonomy is difficult to apply because it treated some specimens of distantly related species as conspecific and some conspecific specimens as different taxa. Although we have referred populations to Morales's names, this is provisional and topotypic material must be examined to clarify identities. Specimens from Guyana that are mophologically indistinguishable from *degranvillei* are not conspecific with a sample from near the type locality in French Guiana. Among controversial species, our results confirm the independence of *baeobatrachus* and *stepheni*. Our evidence also suggests that *azureus* is nested within, and conspecific with, *tinctorius*.

As a quick heuristic to help identify species, pairwise comparisons of cytochrome *b* sequences proved useful, but they are not a panacea. Focusing on well-delimited, uncontroversial species, intraspecific cytochrome *b* sequence distances ranged from 0.0 to 6.0%. The greatest intraspecific distances were between Nicaraguan and Panamanian samples of *lugubris* (6.0%) and *talamancae* (5.7%). The localities for these pairs of samples are also separated by large geographic distance, but the cytochrome *b* sequences of *auratus* samples from Nicaragua and Panama are identical. Similarly, we expected evidence to indicate that the widespread and phenotypically variable Amazonian species *trivittatus* is composed of multiple species, as was found in *femoralis*; however, *trivittatus* DNA sequences are relatively homogeneous across its distribution, suggesting the existence of a single species. Minimally, these results highlight the pitfalls of generalizing across taxa and suggest caution in interpeting pairwise comparisons alone.

Among closely related species of unproblematic identity, the least interspecific cytochrome *b* distance is 2.3% and 3.9% in the *auratus–truncatus* and *vicentei–pumilio* pairs, respectively. Among putative sister-species pairs, the greatest cytochrome *b* distance is 18.6% between *castaneoticus* and *galactonotus*. Given the degree of morphological divergence between these species, this is unsurprising. However, it is only slightly greater than that observed between the morphologically more similar (but more distantly related) *castaneoticus* and *quinquivittatus* (17.4%). As mentioned above, the Central American species *flotator* and *nubicola* were considered conspecific until recently (Ibáñez and Smith, 1995), yet they are not each other's closest relatives and their pairwise cytochrome *b* distance is 18.4%. Whether these differences in pairwise distances between closely related species are due to incomplete taxon sampling (i.e., they are not as closely related as they were presumed to be) or variation in evolutionary rates is unknown.

A MONOPHYLETIC TAXONOMY

Preliminary Considerations

Evolutionary relationships are the explanatory framework that unifies all areas of biology, and the results of the present study provide a coherent foundation to understand the many fascinating and useful characteristics of dendrobatid frogs. To facilitate understanding and application of the phylogenetic results, we propose a revised taxonomy for dendrobatid frogs that reflects as closely as is presently feasible (see below) current knowledge of phylogeny (figs. 77, 78).

Our adherence to Linnaean nomenclature and the strictures of the Code (ICZN, 1999) is pragmatic and not intended as a complete endorsement. The imposition of Linnaean ranks is arbitrary and artificial, skewing both thought and analysis as they continue to be treated as identifying objectively equivalent entities, despite pleas to the contrary. If scientific language is to accurately reflect understanding of evolutionary relationships, then it is clear that sooner or later Linnaean nomenclature will have to be abandoned or transformed significantly.

The best known alternative is the PhyloCode (e.g., de Queiroz and Gauthier, 1990), which eliminates ranks. However, the PhyloCode also institutes a number of conventions

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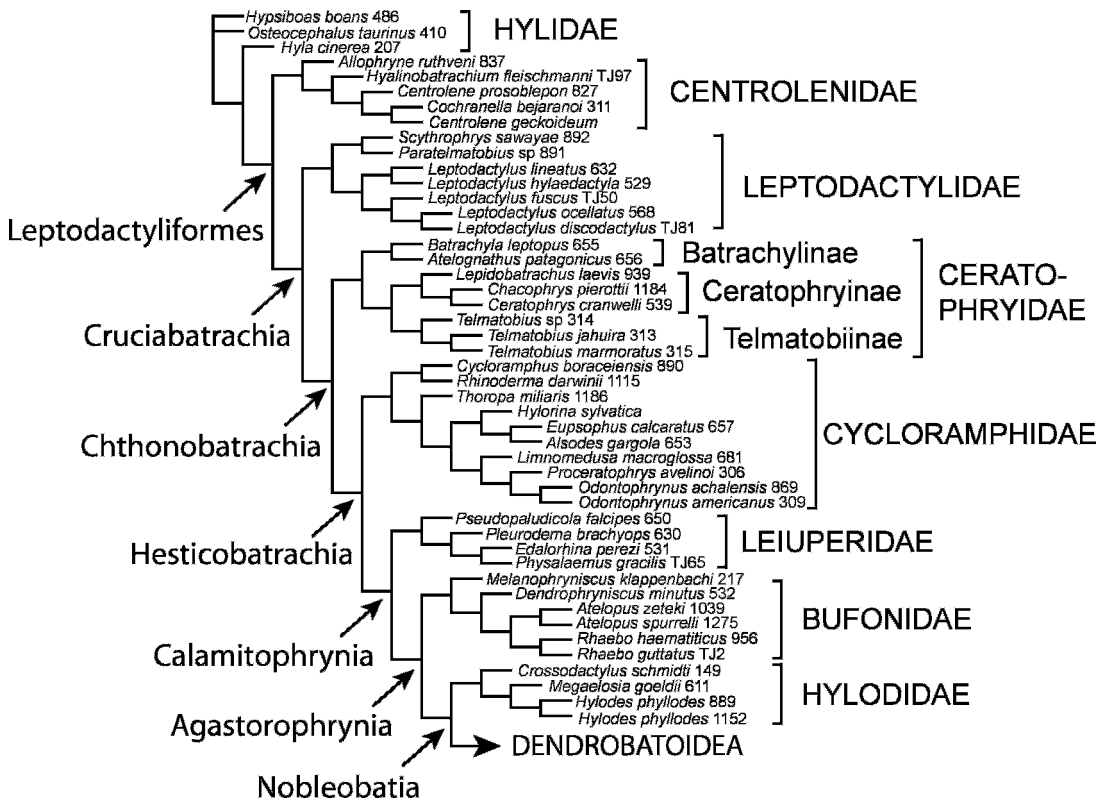

Fig. 77. Graphic summary of the proposed higher-level taxonomy of Athesphatanura.

that would, should they be adopted, surely impede scientific progress, for example, by increasing the frequency with which minor changes in topology would lead to extreme changes in taxonomy (i.e., nomenclatural instability). Consider, for example, that the finding of Darst and Cannatella (2004; see also Faivovich et al., 2005; Frost et al., 2006) that hemiphractines are distant relatives of other hylids makes Ford and Cannatella's (1993) node-based definition of Hylidae apply to all hyloids except brachycephalids (parsimony) or all hyloids (maximum likelihood).

Kluge (2005) recently proposed a novel system to represent phylogeny exactly and eliminate the drawbacks of the Linnaean system without abandoning its strengths (e.g., designation of "types" for bookkeeping purposes, the principle of priority to encourage progress), all or much of which is likely to be implemented (if not endorsed explicitly) simply because it is designed expressly to encourage scientific progress. Indeed, some aspects of his proposal, such as the naming of all clades, may be inevitable by-products of the growth of scientific knowledge, whether the Code is overhauled or not (e.g., by simply shifting ranked names toward the tips, thus pushing the bulk of cladistic structure above the family level where the Code does not apply). Nevertheless, Kluge's proposal has not yet been vetted by the scientific community, and for the immediate need to translate the phylogeny of dendrobatids into a monophyletic taxonomy we continue to apply the existing Code.

Over the past four decades the number of recognized dendrobatid species has exploded from 70 to 247, and there is no indication that discovery of new species in this clade will wane in the foreseeable future. Compared to other vertebrate groups, anuran families are large and cumbersome. Consider, for example, that Frost et al.'s (2006) new taxonomy recognizes only 42 families for approximately 5,000 species of anurans—prior to the Frost

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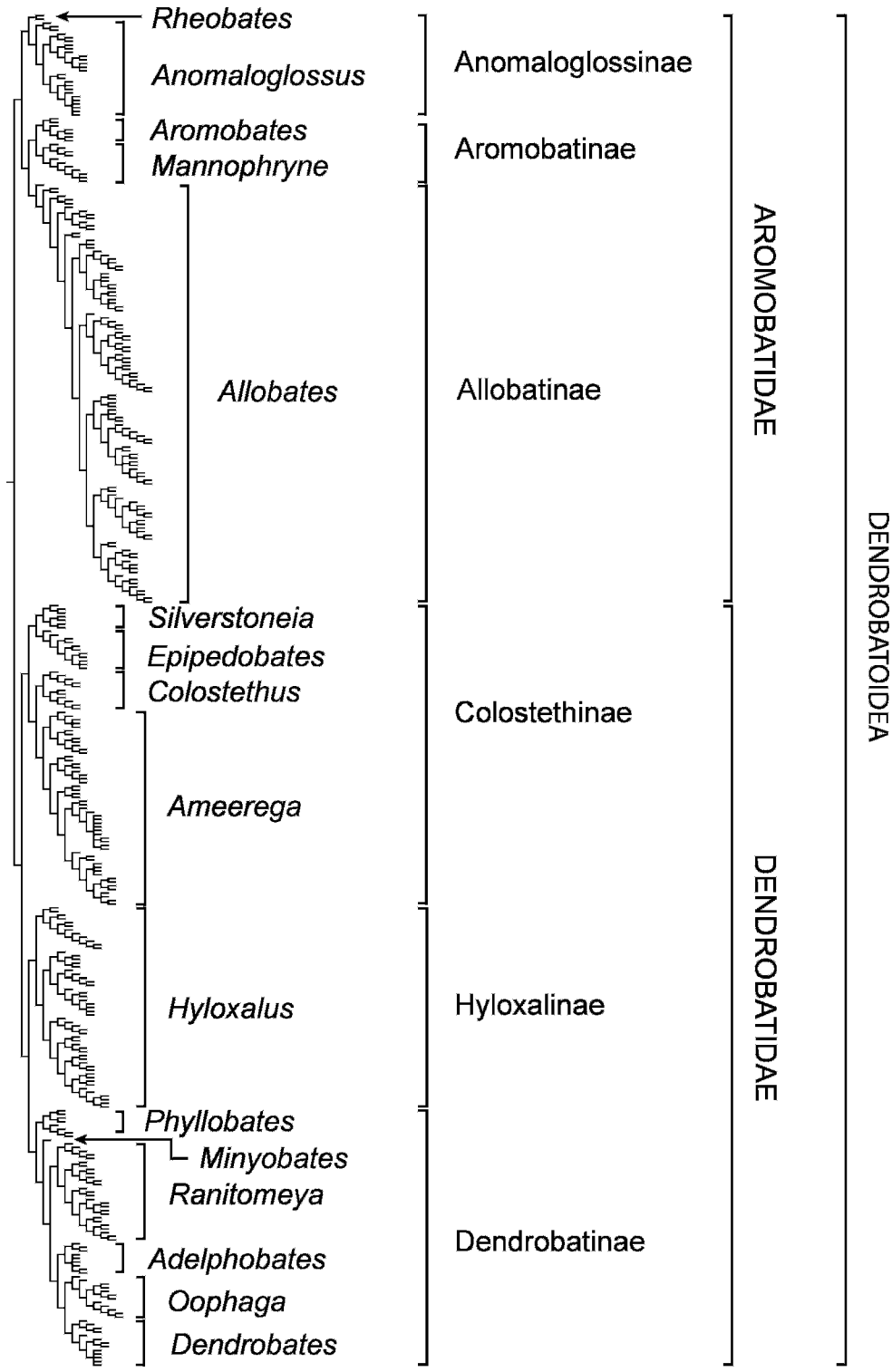

Fig. 78. Graphic summary of the proposed taxonomy of Dendrobatoidea.

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et al. update there were only 33 recognized families of anurans. In comparison, current taxonomy recognizes approximately 220 families of birds to accommodate roughly 10,000 species, 500 families of fishes for 28,000 species, and 130 families for roughly the same number of mammals as there are anurans. Indeed, in all of these groups the orders are approximately equivalent to the families in anuran nomenclature (e.g., there are 26 recognized orders of mammals).

This recognition of few families for frogs is not due to an active decision by the herpetological community but rather tradition and the fact that, as exemplified by dendrobatids, much of the diversity of frogs has been discovered so recently and rapidly (over 45% of recognized amphibian species have been named since 1985; D. R. Frost, unpublished data) without any major revamping of the higher-level taxonomy. This is understandable, given that monophyly is more important than the arbitrary ranking of clades, and by that argument there is no need to elevate the rank of the dendrobatid clade. However, the retention of the old family units also results in an underappreciation of diversity and actually obscures patterns of diversification. Insofar as the purpose of naming clades is to facilitate further research, Linnaean ranks, artificial as they are, are a useful means of carving off chunks of diversity for scientific discussion (if this were not the case, then the optimal Linnaean solution to nonmonophyly would always be accretion, with recognized taxa growing ever larger and obscuring more phylogenetic structure as knowledge increases), and in this sense anuran taxonomy is much less refined than in other vertebrate groups. We therefore elevate the rank of the dendrobatid clade to superfamily (Dendrobatoidea) and propose a new arrangement of families, subfamilies, and genera to better reflect the diversity and phylogeny of this clade.

For taxonomic purposes, we have examined specimens of all but a few species of dendrobatids, but available material of many species was not adequate to permit their inclusion in the phylogenetic analysis (genera and species included are listed below in boldface). We therefore refer them to genera provisionally as both an efficient means of summarizing what is known about those species and as explicit phylogenetic hypotheses to be tested in future studies. To permit provisional reference of species that were not included, we fit names to the cladogram somewhat loosely, that is, names refer to demonstrably monophyletic groups, but much of the finer cladistic structure remains unnamed. This was done as a working compromise between two extreme alternatives.

The two alternatives are (1) to maintain the status quo until knowledge is ''sufficiently complete'' to merit taxonomic revision by allowing all species to be placed with certainty, or (2) to propose a new taxonomy for the species included in this analysis and treat all others as incertae sedis. Alternative (1) is tantamount to a plea for ignorance and is antiscientific. There is no objective basis for determining when any system of scientific knowledge is ''sufficiently complete'' for any purpose. It is a fundamental characteristic of science that future evidence (or discovery operations) may overturn any prior hypothesis, and rejecting current knowledge simply because it may ultimately be wrong would prevent all progress. Alternative (2) is equally unsatisfactory because it effectively hides the evidence that already exists regarding the relationships of those species. New taxonomies build upon prior ones, and those prior ones had some empirical basis, however limited. Finally, provisional placement facilitates content increasing progressive problem shifts (sensu Lakatos, 1978) by increasing the testability of phylogenetic hypotheses (logically, the more species included in the hypotheses, the greater the potential to falsify it) and, further, by facilitating alpha taxonomy and the discovery of new species. For example, in the current system, a new species of *Colostethus* should, in principle, be compared to ca. 120 species ranging from Nicaragua to southeastern Brazil and Bolivia. Most taxonomists are regional specialists and lack the resources to undertake such comparisons, which frequently leads to extensive errors by either referring to different species under the same name or naming species that are not diagnosable in a broader context. A taxonomy that reflects current knowledge of phylogeny will point to appro-

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priate comparisons and thereby greatly facilitate species-level work.

As noted above (Materials and Methods), we included genotypic and phenotypic data for 13 type species (genus name in parentheses): *azureiventris* (*Cryptophyllobates*), *bicolor* (*Phyllobates*), *femoralis* (*Allobates*), *inguinalis* (*Prostherapis*), *nocturnus* (*Aromobates*), *pulchellus* (*Phyllodromus*), *pumilio* (*Oophaga*), *reticulatus* (*Ranitomeya*), *silverstonei* (*Phobobates*), *steyermarki* (*Minyobates*), *tinctorius* (*Dendrobates*), *tricolor* (*Epipedobates*), and *trivittatus* (*Ameerega*). We did not include the type species *alboguttatus* (*Nephelobates*), *fuliginosus* (*Hyloxalus*), *latinasus* (*Colostethus*), or *yustizi* (*Mannophryne*) because adequate data were not available. Nevertheless, we included numerous putatively closely related species and made taxonomic changes accordingly. That is, we treated the sampled species as proxies for the type species in the same way that the sampled species were treated as representative of the complete diversity of dendrobatids. In both cases, further sampling may prove these assumptions to be false, but in the meantime it is better to present a taxonomy derived from a hypothesis of relationships supported by evidence that can form the basis for future testing than to retain the current taxonomy that misrepresents current understanding of phylogeny. In the following accounts, species included in the phylogenetic analysis are in bold.

Unless otherwise noted, only named species are listed in the following accounts. Additional undescribed species of several taxa were included in the phylogenetic analysis, but these are discussed only in the Comment sections. For each named clade we report a summary of the unambiguous transformations (including phenotypic synapomorphies and branch length) and Bremer support. Additionally, generic acounts include a standardized diagnosis designed to allow species to be referred to taxa efficiently following the examination of few, conspicuous, and, insofar as is possible, easily accessible characters, as well as generalities that are taxonomically useful but difficult to individuate as hypotheses of homology. The purpose of these general characterizations is to facilitate rapid identification, and, as such, descriptions are much less precise than in the delimitation and analysis of transformation series. Unambiguous molecular transformations for each named group are given in appendix 8.

The Higher-Level Taxonomy of Athesphatanura Frost et al., 2006

As noted above, the higher-level relationships within Athesphatanura differ from the Frost et al. (2006) hypothesis in two major ways: (1) Leptodactylidae is divided into two distantly related groups, neither of which is the sister of Centrolenidae (i.e., Diphyabatrachia is refuted); one is placed as the sister to all Leptodactyliformes except Centrolenidae, and the other is placed inside Hesticobatrachia as the sister to bufonids, dendrobatids, and hylodines. (2) *Thoropa* (and therefore Thoropidae) move from being the sister of dendrobatids to be nested among cycloramphids, while the hylodines move from being placed with cycloramphids to being the sister of dendrobatoids. Where regulated taxa were concerned, we applied the Code. However, there are different ways in which changes to unregulated taxa can be incorporated, with the opposing strategies focusing on content (i.e., any change in content entails a different phylogenetic hypothesis and, therefore, demands a different name) and nomenclatural stability (i.e., changes in content entail only a reformulation of the existing name and do not necessitate a new name). There are merits to both approaches, and we devised a taxonomy that introduces the fewest new names required to accomodate the new phylogenetic structure and reformulates the remaining groups. Specifically, we propose new names for the additional nodes created by the movement of the leptodactylids, and we reformulate Chthonobatrachia and Hesticobatrachia (which are otherswise unchanged) to include Leiuperidae, and Agastorophrynia to include Hylodidae and exclude *Thoropa*.

The higher-level taxonomy of Athesphatanura is summarized in table 36. The paraphyly of Hylidae in our analysis owes to having rooted on the hylid species *Hypsiboas boans*. Insofar as our results do not otherwise differ from Frost et al. (2006) with regard to

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TABLE 36
The Higher-Level Taxonomy of Athesphatanura Frost et al., 2006

Hylidae Rafinesque, 1815
Leptodactyliformes Frost et al., 2006
  Centrolenidae Taylor, 1951
  Cruciabatrachia **new taxon**
    Leptodactylidae Werner, 1896 (1838)
    Chthonobatrachia Frost et al., 2006
      Ceratophryidae Tschudi, 1838
        Batrachylinae Gallardgo, 1965
        Ceratophryninae Tschudi, 1838
        Telmatobiinae Fitzinger, 1843
      Hesticobatrachia Frost et al., 2006
        Cycloramphidae Bonaparte, 1850
        Calamitophrynia **new taxon**
          Leiuperidae Bonaparte, 1850
          Agastorophrynia Frost et al., 2006
            Bufonidae Gray, 1825
            Nobleobatia **new taxon**
              Hylodidae Günther, 1858
              Dendrobatoidea Cope, 1865

Hylidae or Leptodactyliformes, we omit those taxa from the following accounts.

FAMILY: CENTROLENIDAE TAYLOR, 1951

Centrolenidae Taylor, 1951. Type genus: *Centrolene* Jiménez de la Espada, 1872.
Allophrynidae Goin et al., 1978: 240. Type genus: *Allophryne* Gaige, 1926.

IMMEDIATELY MORE INCLUSIVE TAXON: Leptodactyliformes Frost et al., 2006.

SISTER GROUP: Cruciabatrachia **new taxon**.

CONTENT (4 GENERA): ***Allophryne*** Gaige, 1926; "***Centrolene***" Jiménez de la Espada, 1872; ***Cochranella*** Taylor, 1951; ***Hyalinobatrachium*** Ruiz-Carranza and Lynch, 1991.

CHARACTERIZATION, DIAGNOSIS, AND SUPPORT: Branch length = 39. Bremer support = 15. All unambiguously optimized synapomorphies for this clade are from DNA sequences (see appendix 8). See Frost et al. (2006) for discussion of synapomorphies.

DISTRIBUTION: Tropical southern Mexico to Bolivia, northeastern Argentina, and southeastern Brazil.

COMMENT: Our optimal hypothesis of centrolenid relationships is identical to that of Frost (2006), and we direct the reader to that paper for comments. Our results differ in the placement of Centrolenidae relative to other hyloid lineages. Frost et al. (2006) found Centrolenidae to be grouped with Leptodactylidae, together forming Diphyabatrachia. We did not find support for Diphyabatrachia in the present analysis, and instead found Centrolenidae to be the sister group of a large, predominantly Neotropical radiation, named below.

UNRANKED TAXON: CRUCIABATRACHIA **NEW TAXON**

IMMEDIATELY MORE INCLUSIVE TAXON: Leptodactyliformes Frost et al., 2006.

SISTER GROUP: Centrolenidae Taylor, 1951.

CONTENT: Leptodactylidae Werner, 1896 (1838); Chthonobatrachia Frost et al., 2006.

CHARACTERIZATION, DIAGNOSIS, AND SUPPORT: Branch length = 21. Bremer support = 14. All unambiguously optimized synapomorphies for this clade are from DNA sequences (see appendix 8).

DISTRIBUTION: Cosmopolitan in temperate and tropical areas (but with most species concentrated in the southern hemisphere) except for the Australo-Papuan region, Madagascar, Seychelles, and New Zealand.

ETYMOLOGY: Cruciabatrachia, frogs of the Southern Cross (Crux), referencing the predominantly southern range of this clade.

COMMENT: Following Frost et al. (2006), we include *Somuncuria* in this group provisionally on the basis of the evidence suggested by Lynch (1978), who placed *Somuncuria* as the sister taxon of *Pleurodema*.

FAMILY: LEPTODACTYLIDAE WERNER, 1896 (1838)

Cystignathi Tschudi, 1838. Type genus: *Cystignathus* Wagler, 1830.
Plectromantidae Mivart, 1869, Proc. Zool. Soc. London, 1869: 291. Type genus: *Plectromantis* Peters, 1862.
Adenomeridae Hoffmann, 1878, *In* Bronn (ed.). Type genus: *Adenomera* Steindachner, 1867.
Leptodactylidae Werner, 1896. Type genus: *Leptodactylus* Fitzinger, 1826.

IMMEDIATELY MORE INCLUSIVE TAXON: Cruciabatrachia **new taxon**.

SISTER GROUP: Agastorophrynia Frost et al., 2006.

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CONTENT (4 GENERA): *Hydrolaetare* Gallardo, 1963; ***Leptodactylus*** Fitzinger, 1826; ***Paratelmatobius*** Lutz and Carvalho, 1958; ***Scythrophrys*** Lynch, 1971

CHARACTERIZATION, DIAGNOSIS, AND SUPPORT: Branch length = 42. Bremer support = 14. All unambiguously optimized synapomorphies for this clade are from DNA sequences (see appendix 8).

DISTRIBUTION: Tropical Mexico throughout Central and South America.

COMMENT: Following Frost et al. (2006), we place *Hydrolaetare* in this group because of its presumed close relationship to *Leptodactylus* (Heyer, 1970), although we suggest that this proposition merits further study.

UNRANKED TAXON: CHTHONOBATRACHIA FROST ET AL., 2006

IMMEDIATELY MORE INCLUSIVE TAXON: Cruciabatrachia **new taxon**.

SISTER GROUP: Leptodactylidae Werner, 1896 (1838).

CONTENT: Ceratophryidae Tschudi, 1838; Hesticobatrachia Frost et al., 2006.

CHARACTERIZATION, DIAGNOSIS, AND SUPPORT: Branch length = 27. Bremer support = 14. All unambiguously optimized synapomorphies for this clade are from DNA sequences (see appendix 8). See Frost et al. (2006) for discussion of synapomorphies.

DISTRIBUTION: Cosmopolitan in temperate and tropical areas except for the Australo-Papuan region, Madagascar, Seychelles, and New Zealand.

COMMENT: Our Chthonobatrachia is equivalent to the group proposed by Frost et al. (2006) with the inclusion of Leiuperidae Bonaparte, 1850, which was previously in the synonymy of Leptodactylidae. See Frost et al. (2006) for further comments.

FAMILY: CERATOPHRYIDAE TSCHUDI, 1838

Ceratophrydes Tschudi, 1838: 26. Type genus: *Ceratophrys* Wied-Neuwied, 1824.

IMMEDIATELY MORE INCLUSIVE TAXON: Chthonobatrachia Frost et al., 2006.

SISTER GROUP: Hesticobatrachia Frost et al., 2006.

CONTENT (3 SUBFAMILIES): Batrachylinae Gallardo, 1965; Ceratophryninae Tschudi, 1838; Telmatobiinae Fitzinger, 1843.

CHARACTERIZATION, DIAGNOSIS, AND SUPPORT: Branch length = 30. Bremer support = 19. No phenotypic character-states optimize unambiguously to this node (see appendix 8 for diagostic DNA sequence transformations). See Frost et al. (2006) for discussion of additional synapomorphies.

DISTRIBUTION: Andean and tropical lowland South America from Colombia and Venezuela south to extreme southern Argentina and Chile.

COMMENT: Frost et al. (2006) recognized two subfamilies within Ceratophryidae: Telmatobiinae (for *Telmatobius*) and Ceratophryinae (for the tribes Batrachylini and Ceratophryini). Our results show Ceratophryinae to be paraphyletic with respect to Telmatobiinae. Rather than dissolve all of these groups in the synonymy of Ceratophryidae, below we elevate Batrachylini and Ceratophryini of Frost et al. (2006) to subfamilies.

SUBFAMILY: BATRACHYLINAE GALLARDO, 1965

Batrachylinae Gallardo, 1965: 83. Type genus: *Batrachylus* Bell, 1843.

IMMEDIATELY MORE INCLUSIVE TAXON: Ceratophryidae Tschudi, 1838.

SISTER GROUP: Unnamed group composed of Ceratophryinae Tschudi, 1838; Telmatobiinae Fitzinger, 1843.

CONTENT (2 GENERA): ***Atelognathus*** Lynch, 1978 and ***Batrachyla*** Bell, 1843.

CHARACTERIZATION, DIAGNOSIS, AND SUPPORT: Branch length = 44. Bremer support = 25. All unambiguously optimized synapomorphies for this clade are from DNA sequences (see appendix 8). See Frost et al. (2006) for discussion of synapomorphies.

DISTRIBUTION: Central to extreme southern Argentina and Chile (Patagonia).

COMMENT: This taxon is equal to Batrachylini of Frost et al. (2006).

SUBFAMILY: CERATOPHRYINAE TSCHUDI, 1838

Ceratophrydes Tschudi, 1838: 26. Type genus: *Ceratophrys* Wied-Neuwied, 1824; Stombinae Gallardo, 1965: 82. Type genus: *Stombus* Gravenhorst, 1825.

IMMEDIATELY MORE INCLUSIVE TAXON: Ceratophryidae Tschudi, 1838.

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SISTER GROUP: Telmatobiinae Fitzinger, 1843.

CONTENT (3 GENERA): ***Ceratophrys*** Wied-Neuwied, 1824; ***Chacophrys*** Reig and Limeses, 1963; ***Lepidobatrachus*** Budgett, 1899.

CHARACTERIZATION, DIAGNOSIS, AND SUPPORT: Branch length = 47. Bremer support = 40. All unambiguously optimized synapomorphies for this clade are from DNA sequences (see appendix 8). See Frost et al. (2006) for discussion of synapomorphies.

DISTRIBUTION: Andean and tropical lowlands of South America from Colombia and Venezuela south to extreme southern Argentina and Chile.

COMMENT: This taxon is equal to Ceratophryini of Frost et al. (2006).

SUBFAMILY: TELMATOBIINAE FITZINGER, 1843

Telmatobii Fitzinger, 1843: 31. Type genus: *Telmatobius* Wiegmann, 1834.

IMMEDIATELY MORE INCLUSIVE TAXON: Ceratophryidae Tschudi, 1838.

SISTER GROUP: Ceratophryinae Tschudi, 1838.

CONTENT (1 GENUS): ***Telmatobius*** Wiegmann, 1834.

CHARACTERIZATION, DIAGNOSIS, AND SUPPORT: Branch length = 73. Bremer support = 66. All unambiguously optimized synapomorphies for this clade are from DNA sequences (see appendix 8).

DISTRIBUTION: Andean South America, Ecuador to Chile and Argentina.

COMMENT: This taxon is equal to Telmatobiinae of Frost et al. (2006).

UNRANKED TAXON: HESTICOBATRACHIA FROST ET AL., 2006

IMMEDIATELY MORE INCLUSIVE TAXON: Chthonobatrachia Frost et al., 2006.

SISTER GROUP: Ceratophryidae Tschudi, 1838.

CONTENT: Cycloramphidae Bonaparte, 1850; Calamitophrynia **new taxon**.

CHARACTERIZATION, DIAGNOSIS, AND SUPPORT: Branch length = 26. Bremer support = 14. All unambiguously optimized synapomorphies for this clade are from DNA sequences (see appendix 8). See Frost et al. (2006) for discussion of synapomorphies.

DISTRIBUTION: Cosmopolitan in temperate and tropical areas except for the Australo-Papuan region, Madagascar, Seychelles, and New Zealand.

COMMENT: Our Hesticobatrachia is equivalent to the group proposed by Frost et al. (2006) with the inclusion of Leiuperidae Bonaparte, 1850, which was previously in the synonymy of Leptodactylidae. See Frost et al. (2006) for further comments.

FAMILY: CYCLORAMPHIDAE BONAPARTE, 1850

Cyclorhamphina Bonaparte, 1850. Type genus: *Cycloramphus* Tschudi, 1838.

Rhinodermina Bonaparte, 1850. Type genus: *Rhinoderma* Duméril and Bibron, 1841.

Alsodina Mivart, 1869. Type genus: *Alsodes* Bell, 1843.

Grypiscina Mivart, 1869. Type genus: *Grypiscus* Cope, 1867 "1866".

Odontophrynini Lynch, 1969. Type genus: *Odontophrynus* Reinhardt and Lütken, 1862 "1861". (Odontophrynini subsequently named more formally by Lynch, 1971: 142.)

Thoropidae Frost et al., 2006. Type genus: *Thoropa* Cope, 1865.

IMMEDIATELY MORE INCLUSIVE TAXON: Hesticobatrachia Frost et al., 2006.

SISTER GROUP: Calamitophrynia **new taxon**.

DISTRIBUTION: Southern tropical and temperate South America.

CONTENT (12 GENERA): ***Alsodes*** Bell, 1843; *Crossodactylodes* Cochran, 1938; ***Cycloramphus*** Tschudi, 1838; ***Eupsophus*** Fitzinger, 1843; ***Hylorina*** Bell, 1843; ***Limnomedusa*** Fitzinger, 1843; *Macrogenioglottus* Carvalho, 1946; ***Odontophrynus*** Reinhardt and Lütken, 1862 "1861"; ***Proceratophrys*** Miranda-Ribeiro, 1920; ***Rhinoderma*** Duméril and Bibron, 1841; ***Thoropa*** Cope, 1865; *Zachaenus* Cope, 1866.

CHARACTERIZATION, DIAGNOSIS, AND SUPPORT: Branch length = 32. Bremer support = 8. All unambiguously optimized synapomorphies for this clade are from DNA sequences (see appendix 8). See Frost et al. (2006) for discussion of synapomorphies.

DISTRIBUTION: Southern tropical and temperate South America.

COMMENT: Cycloramphidae, as defined here, differs from Cycloramphidae sensu Frost et al. (2006) in that it excludes

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Hylodinae (see below) and includes *Thoropa* (and therefore Thoropidae). We do not recognize subfamilial divisions within Cycloramphidae. See Frost et al. (2006) for additional discussion.

UNRANKED TAXON: CALAMITOPHRYNIA **NEW TAXON**

IMMEDIATELY MORE INCLUSIVE TAXON: Hesticobatrachia Frost et al., 2006.

SISTER GROUP: Cycloramphidae Bonaparte, 1850.

CONTENT: Leiuperidae Bonaparte, 1850; Agastorophrynia Frost et al., 2006.

CHARACTERIZATION, DIAGNOSIS, AND SUPPORT: Branch length = 27. Bremer support = 20. All unambiguously optimized synapomorphies for this clade are from DNA sequences (see appendix 8).

DISTRIBUTION: Cosmopolitan in temperate and tropical areas except for the Australo-Papuan region, Madagascar, Seychelles, and New Zealand.

ETYMOLOGY: Calamitophrynia, from the Greek calamitas (misfortune), phryne (toad), and suffix ia (having the nature of), referencing the loud calls of so many of the species in this clade.

COMMENT: The placement of Leiuperidae at such cladistic distance from Leptodactylidae was unexpected and contradicts the findings of Frost et al. (2006).

FAMILY: LEIUPERIDAE BONAPARTE, 1850

Leiuperina Bonaparte, 1850. Type genus: *Leiuperus* Duméril and Bibron, 1841.

Paludicolina Mivart, 1869. Type genus: *Paludicola* Wagler, 1830.

Pseudopaludicolinae Gallardo, 1965. Type genus: *Pseudopaludicola* Miranda-Ribeiro, 1926.

IMMEDIATELY MORE INCLUSIVE TAXON: Calamitophrynia **new taxon**.

SISTER GROUP: Agastorophrynia Frost et al., 2006.

CONTENT (7 GENERA): ***Edalorhina*** Jiménez de la Espada, 1871 "1870"; *Engystomops* Jiménezde la Espada, 1872; *Eupemphix* Steindachner, 1863; ***Physalaemus*** Fitzinger, 1826; ***Pleurodema*** Tschudi, 1838; ***Pseudopaludicola*** Miranda-Ribeiro, 1926; *Somuncuria* Lynch, 1978.

CHARACTERIZATION, DIAGNOSIS, AND SUPPORT: Branch length = 36. Bremer support = 23. All unambiguously optimized synapomorphies for this clade are from DNA sequences (see appendix 8).

DISTRIBUTION: Mexico throughout Central and South America.

COMMENT: Following Frost et al. (2006), we include *Somuncuria* in this group provisionally on the basis of the evidence suggested by Lynch (1978), who placed *Somuncuria* as the sister taxon of *Pleurodema*.

UNRANKED TAXON: AGASTOROPHRYNIA FROST ET AL., 2006

IMMEDIATELY MORE INCLUSIVE TAXON: Hesticobatrachia Frost et al., 2006.

SISTER GROUP: Leiuperidae Bonaparte, 1850.

CONTENT: Bufonidae Gray, 1825; Nobleobatia **new taxon**.

CHARACTERIZATION, DIAGNOSIS, AND SUPPORT: Branch length = 22. Bremer support = 5. All unambiguously optimized synapomorphies for this clade are from DNA sequences (see appendix 8). Although the origin of diurnal activity (Character 115) is ambiguous due to incomplete coding of phenotypic characters in the present analysis, it is a likely synapomorphy for Agastorophrynia. *Melanophryniscus*, *Dendrophryniscus*, *Atelopus*, and almost all species of Nobleobatia **new taxon** are diurnal, whereas leiuperids, cycloramphids, ceratophryids, leptodactylids, centrolenids, and hylids are entirely or predominantly nocturnal.

DISTRIBUTION: Cosmopolitan in temperate and tropical areas except for the Australo-Papuan region, Madagascar, Seychelles, and New Zealand.

COMMENT: Agastorophrynia here is equivalent to that of Frost et al. (2006) with the inclusion of their Hylodinae, which is removed from their Cycloramphidae, and the exclusion of Thoropidae, which is found to be a junior synonym of Cycloramphidae.

FAMILY: BUFONIDAE GRAY, 1825

Bufonina Gray, 1825. Type genus: *Bufo* Laurenti, 1768.

Atelopoda Fitzinger, 1843. Type genus: *Atelopus* Duméril and Bibron, 1841.

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Phryniscidae Günther, 1858. Type genus: *Phrynis-cus* Wiegmann, 1834.

Adenomidae Cope, 1861 ''1860''. Type genus: *Adenomus* Cope, 1861.

Dendrophryniscina Jiménezde la Espada, 1871 ''1870''. Type genus: *Dendrophryniscus* Jiménez de la Espada, 1871 ''1870''.

Platosphinae Fejérváry, 1917. Type genus: *Plato-sphus* d'Isle, 1877 (fossil taxon considered to be in this synonymy because *Platosophus* = *Bufo* sensu lato).

Bufavidae Fejérváry, 1920. Type genus: *Bufavus* Portis, 1885 (fossil taxon considered to be in this synonymy because *Bufavus* = *Bufo* sensu lato).

Tornierobatidae Miranda-Ribeiro, 1926. Type genus: *Tornierobates* Miranda-Ribeiro, 1926.

Nectophrynidae Laurent, 1942. Type genus: *Nec-tophryne* Buchholz and Peters, 1875.

Stephopaedini Dubois, 1987 ''1985''. Type genus: *Stephopaedes* Channing, 1978.

IMMEDIATELY MORE INCLUSIVE TAXON: Agastorophrynia Frost et al., 2006.

SISTER GROUP: Nobleobatia **new taxon**.

CONTENT (47 GENERA): *Adenomus* Cope, 1861 ''1860''; *Altiphrynoides* Dubois, 1987 ''1986''; *Amietophrynus* Frost et al., 2006; *Andinophryne* Hoogmoed, 1985; *Anax-yrus* Tschudi, 1845; *Ansonia* Stoliczka, 1870; *Atelophryniscus* McCranie, Wilson, and Williams, 1989; ***Atelopus*** Duméril and Bibron, 1841; *Bufo* Laurenti, 1768; *Bufoides* Pillai and Yazdani, 1973; *Capensibufo* Grandison, 1980; *Chaunus* Wagler, 1828; *Churamiti* Channing and Stanley, 2002; *Cranopsis* Cope, 187 ''1876''; *Crepidophryne* Cope, 1889; ***Dendro-phryniscus*** Jiménez de la Espada, 1871 ''1870''; *Didynamipus* Andersson, 1903; *Dut-taphrynus* Frost et al., 2006; *Epidalea* Cope, 1865; *Frostius* Cannatella, 1986; *Ingerophry-nus* Frost et al., 2006; *Laurentophryne* Tihen, 1960; *Leptophryne* Fitzinger, 1843; ***Melano-phryniscus*** Gallardo, 1961; *Mertensophryne* Tihen, 1960; *Metaphryniscus* Señaris, Ayarzagüena, and Gorzula, 1994; *Nannophryne* Günther, 1870; *Nectophryne* Buchholz and Peters, 1875; ''*Nectophrynoides*'' Noble, 1926; *Nimbaphrynoides* Dubois, 1987 ''1986''; *Or-eophrynella* Boulenger, 1895; *Osornophryne* Ruiz-Carranza and Hernández-Camacho, 1976; *Parapelophryne* Fei, Ye, and Jiang, 2003; *Pedostibes* Günther, 1876 ''1875''; *Pelophryne* Barbour, 1938; *Peltophryne* Fitzinger, 1843; *Phrynoidis* Fitzinger, 1843; *Pseudobufo* Tschudi, 1838; *Pseudepidalea* Frost et al., 2006; ***Rhaebo*** Cope, 1862; *Rhamphophryne* Trueb, 1971; *Rhinella* Fitzinger, 1826; *Schismaderma* Smith, 1849; *True-bella* Graybeal and Cannatella, 1995; *Vandij-kophrynus* Frost et al., 2006; *Werneria* Poche, 1903; ''*Wolterstorffina*'' Mertens, 1939.

CHARACTERIZATION, DIAGNOSIS, AND SUPPORT: Branch length = 78. Bremer support = 37.

Unambiguously optimized phenotypic synapomorphies of this clade are **(1)** origin of spiculate skin texture (Character 0, 1 → 3), **(2)** m. depressor mandibulae origin not extending posterior to the squamosal (Character 73, 1 → 0), **(3)** loss of m. intermandibularis supplementary element (Character 77, 1 → 0), **(4)** origin of median gap in marginal papillae of lower labium of tadpoles (Character 92, 0 → 1), **(5)** epicoracoids overlapping from level between posterior level of procoracoids and anterior ends of coracoids to posterior level of coracoids (Character 120, 1 → 2), **(6)** prezonal element of pectoral girdle (omosternum) absent (Character 123, 1 → 0), **(7)** maxillary teeth absent (Character 139, 1 → 0), **(8)** reduction of chromosome number to 22 (Character 173, 4 → 2). See Frost et al. (2006) for discussion of additional synapomorphies.

DISTRIBUTION: Cosmopolitan in temperate and tropical areas except for the Australo-Papuan region, Madagascar, Seychelles, and New Zealand.

COMMENT: The internal structure of Bufonidae is identical to that of Frost et al. (2006) for the terminals sampled, as is the placement of Bufonidae relative to other groups, the exception being the content of the sister group, named below. See Frost et al. (2006) for further comments and structure within Bufonidae.

UNRANKED TAXON: NOBLEOBATIA **NEW TAXON**

IMMEDIATELY MORE INCLUSIVE TAXON: Calamitophrynia **new taxon**.

SISTER GROUP: Bufonidae Gray, 1825.

CONTENT: Hylodidae Günther, 1858; Dendrobatoidea Cope, 1865.

CHARACTERIZATION, DIAGNOSIS, AND SUPPORT: Branch length = 53. Bremer support = 25.

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Unambiguously optimized phenotypic synapomorphies of this clade are **(1)** origin of paired dorsal digital scutes (Character 1, 0 → 1), **(2)** differentiation of digital discs (Character 6, 0 → 3), **(3)** reduction of postaxial webbing of toe II (Character 39, 3 → 1/2), **(4)** reduction of postaxial webbing of toe III (Character 41, 3 → 2), **(5)** reduction of preaxial webbing of toe IV (Character 42, 3 → 2), **(6)** reduction of postaxial webbing of toe IV (Character 43, 4 → 1), **(7)** reduction of pretaxial webbing of toe V (Character 44, 4 → 1), **(8)** origin of the pale oblique lateral stripe (Character 55, 0 → 1), **(9)** origin of T-shaped terminal phalanges (Character 118, 1 → 0).

DISTRIBUTION: Most of tropical Central and South America and Atlantic forest of Brazil.

ETYMOLOGY: Nobleobatia, formed from Noble (a surname) and batia (from the Greek bates, a walker). We name this taxon in honor of G. K. Noble, who, in 1926, was the first to propose the immediate relationship between the genera now referred to Hylodidae and Dendrobatoidea.

COMMENT: The strongly supported placement of dendrobatids and hylodids as sister taxa corroborates one of the most controversial hypotheses of anuran relationships.

FAMILY: HYLODIDAE GÜNTHER, 1858

Hylodinae Günther, 1858. Type genus: *Hylodes* Fitzinger, 1826.

Elosiidae Miranda-Ribeiro, 1923. Type genus: *Elosia* Tschudi, 1838.

IMMEDIATELY MORE INCLUSIVE TAXON: Nobleobatia **new taxon**.

SISTER GROUP: Dendrobatoidea Cope, 1865.

DISTRIBUTION: Southern tropical and temperate South America.

CONTENT (3 GENERA): ***Crossodactylus*** Duméril and Bibron, 1841; ***Hylodes*** Fitzinger, 1826; ***Megaelosia*** Miranda-Ribeiro, 1923.

CHARACTERIZATION, DIAGNOSIS, AND SUPPORT: Branch length = 113. Bremer support = 74.

Unambiguously optimized phenotypic synapomorphies of this clade are **(1)** origin of preaxial fringe on finger II (Character 13, 0 → 1), **(2)** origin of preaxial fringe on finger III (Character 15, 0 → 1), **(3)** origin of tarsal fringe (Character 30, 0 → 1), **(4)** origin of preaxial fringe on toe I (Character 36, 0 → 1), **(5)** origin of fringe on postaxial fringe on toe V (Character 45, 0 → 1), **(6)** loss of oocyte pigmentation (Character 68, 1 → 0), **(7)** loss of fibers of m. depressor mandibulae originating from the annulus tympanicus (Character 74, 1 → 0), **(8)** origin of paired lateral vocal sacs (Character 76, 1 → 2), **(9)** gain of lateral line stitches (Character 98, 0 → 1).

DISTRIBUTION: The Atlantic forest of Brazil.

COMMENT: Frost et al. (2006) found these genera to form a clade nested within Cycloramphidae, which they referred to as Hylodinae.

SUPERFAMILY: DENDROBATOIDEA COPE, 1865

Phyllobatae Fitzinger, 1843. Type genus: *Phyllobates* Duméril and Bibron, 1841.

Eubaphidae Bonaparte, 1850. Type genus: *Eubaphus* Bonaparte, 1831.

Hysaplesidae Günther, 1858. Type genus: *Hysaplesia* Boie *in* Schlegel, 1826. (Note that this taxon was named as Hylaplesidae, derived from *Hylaplesia*, an incorrent subsequent spelling of *Hysaplesia*.)

Dendrobatidae Cope, 1865. Type genus: *Dendrobates* Wagler, 1830.

IMMEDIATELY MORE INCLUSIVE TAXON: Agastorophrynia Frost et al., 2006.

SISTER GROUP: Hylodidae Günther, 1858.

CONTENT (2 FAMILIES): Dendrobatidae Cope, 1865 and Aromobatidae **new family**.

CHARACTERIZATION, DIAGNOSIS, AND SUPPORT: Branch length = 178. Bremer support = 159.

Unambiguous phenotypic transformations are **(1)** (Character 2, 0 → 1), **(2)** gain of the tarsal keel (Character 28, 0 → 1), (3) origin of the metatarsal fold (Character 46, 0 → 1) **(4)** the "ranid" type insertion of the distal tendon of insertion of the m. semitendinosus (Character 69, 0 → 1), **(5)** gain of the m. semitendinosus binding tendon (Character 70, 0 → 1), **(6)** occurrence of the dorsal flap of the m. depressor mandibulae (Character 72, 0 → 1), **(7)** m. depressor mandibulae overlapping posterodorsal portion of tympanum (Character 75, 0 → 1), **(8)** orientation of

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TABLE 37
The Taxonomy of Dendrobatoidea Cope, 1865

Aromobatidae **new family**
Anomaloglossinae **new subfamily**
Anomaloglossus **new genus**
Rheobates **new genus**
Aromobatinae **new subfamily**
Aromobates Myers, Daly, and Paolillo, 1991
Mannophryne La Marca, 1992
Allobatinae **new subfamily**
Allobates Zimmermann and Zimmermann, 1988
Dendrobatidae Cope, 1865
Colostethinae Cope, 1867
Ameerega Bauer, 1986
Colostethus Cope, 1866
Epipedobates Myers, 1987
Silverstoneia **new genus**
Hyloxalinae **new subfamily**
Hyloxalus Jiménez de la Espada, 1871 "1870"
Dendrobatinae Cope, 1865
Adelphobates **new genus**
Dendrobates Wagler, 1830
Minyobates Myers, 1987
Oophaga Bauer, 1988
Phyllobates Duméril and Bibron, 1841
Ranitomeya Bauer, 1988

the m. intermandibularis supplementary element (Character 78, 0 → 1), **(9)** loss of reproductive amplexus (Character 105, 1 → 0), **(10)** dorsal tadpole transport (Character 109, 0 → 1), **(11)** origin of toe trembling (Character 116, 0 → 1), **(12)** complete fusion of epicoracoids (Character 119, 1/2 → 0), **(13)** nonoverlapping epicoracoids (Character 120, 1 → 0), **(14)** medial ossification of prezonal element (omosternum) of pectoral girdle (Character 127, 0 → 1), **(15)** maxillary teeth nonpedicellate (Character 140, 0 → 1), **(16)** occurrence of the retroarticular process of the mandible (Character 142, 0 → 1), and **(17)** reduction in chromosome number from 26 to 24 (Character 173, 4 → 3).

Additional characteristics useful in diagnosing dendrobatoids are the occurrence of dorsal scutes on the digital tip, shared only with the sister clade Hylodidae (among Neotropical frogs).

DISTRIBUTION: Dendrobatoid frogs occur throughout large parts of Nicaragua, Costa Rica, Panama, Colombia, Ecuador, Peru, Bolivia, Venezuela, Guyana, Suriname, French Guiana, Brazil, and the Lesser Antilles.

COMMENT: As discussed above, the elevation of the dendrobatid clade to superfamily is proposed to allow more information on the phylogeny and biology of the group to be conveyed in the working taxonomy. To maintain rank equivalency, Dubois (1992) recognized Dendrobatoidae as an epifamily (redundant with Dendrobatidae) within the superfamily Ranoidea. Frost et al. (2006) applied Dendrobatoidea to the clade of dendrobatids + *Thoropa* (i.e., Dendrobatidae sensu lato + Thoropidae). In the present analysis *Thoropa* is nested among cycloramphids, and the sister group of dendrobatids is the cycloramphid subfamily Hylodinae (*Crossodactylus*, *Hylodes*, and *Megaelosia*). In recognition of the placement of the hylodine genera outside of Cycloramphidae, we recognize them as a family, Hylodidae Günther, 1858 (see above).

Gross examination reveals fused, nonoverlapping epicoracoid cartilages (i.e., firmisterny in the traditional sense) in dendrobatoids, although histological study has shown this to differ in one species (Noble, 1926; Kaplan, 1995; see also Kaplan, 2004).

THE TAXONOMY OF DENDROBATOIDEA COPE, 1865

Below we propose a formal taxonomy for dendrobatoid frogs. The structure of this taxonomy is outlined in table 37, and the placement of all species is detailed in appendix 1.

FAMILY: AROMOBATIDAE **NEW FAMILY**

Aromobatidae **new family**. Type genus: Aromobates Myers, Daly, and Paolillo, 1991.

IMMEDIATELY MORE INCLUSIVE TAXON: Dendrobatoidea.

SISTER GROUP: Dendrobatidae.

CONTENT (2 SUBFAMILIES): Anomaloglossinae **new subfamily**; Aromobatinae **new subfamily**.

CHARACTERIZATION, DIAGNOSIS, AND SUPPORT: Branch length = 71. Bremer support = 41. No phenotypic character-

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states optimize unambiguously to this node (see appendix 8 for diagostic DNA sequence transformations).

DISTRIBUTION: Central and South America and the Lesser Antilles, with most species occurring on the eastern slopes of the Andes, throughout the Amazon region, and in the Atlantic forest of Brazil.

COMMENT: Insofar as is known, all species of Aromobatidae lack the ability to sequester alkaloids.

SUBFAMILY: ANOMALOGLOSSINAE **NEW SUBFAMILY**

Anomaloglossinae. Type genus: *Anomaloglossus* **new genus**.

IMMEDIATELY MORE INCLUSIVE TAXON: Aromobatidae.

SISTER GROUP: Aromobatinae **new subfamily**.

CONTENT: *Anomaloglossus* **new genus** and *Rheobates* **new genus**.

CHARACTERIZATION, DIAGNOSIS, AND SUPPORT: Branch length = 45. Bremer support = 16.

Unambiguously optimized phenotypic synapomorphies are **(1)** fringe present on preaxial surface of finger II (Character 13, 0 → 1), **(2)** fringe present on preaxial surface of finger III (Character 15, 0 → 1), **(3)** toe disc II moderately expanded (Character 32, 1 → 2), **(4)** fringe on preaxial side of toe I present (Character 36, 0 → 1), **(5)** distal 1.5 phalanges of postaxial side of toe I free of webbing (Character 37, 2 → 3/4), **(6)** fringe present on postaxial side of toe V (Character 45, 0 → 1), **(7)** strong metatarsal fold (Character 46, 1 → 2), **(8)** male abdomen with irregular (clumped) stippling or faint, diffuse spotting (Character 63, 3 → 4).

DISTRIBUTION: Almost exclusively *cis*-Andean, with most species in eastern Amazonia, the Orinoco drainage, and tepui regions. Three species also occur on the Pacific slopes of Colombia and Ecuador.

GENUS: *ANOMALOGLOSSUS* **NEW GENUS**

Anomaloglossus **new genus**. Type species: *Colostethus beebei* Noble, 1923.

IMMEDIATELY MORE INCLUSIVE TAXON: Anomaloglossinae **new subfamily**.

SISTER GROUP: *Rheobates* **new genus**.

CONTENT (19 SPECIES): *Anomaloglossus atopoglossus* (Grant, Humphrey, and Myers, 1997) **new combination**; *A. ayarzaguenai* (La Marca, 1998 "1996") **new combination**; ***A. baeobatrachus*** (Boistel and Massary, 1999 **new combination**; ***A. beebei*** (Noble, 1923) **new combination**; *A.* "*chocoensis*" auctorum (not of Boulenger, 1912; see Grant et al., 1997); ***A. degranvillei*** (Lescure, 1975) **new combination**; *A. guanayensis* (La Marca, 1998 "1996") **new combination**; *A. lacrimosus* (Myers, 1991) **new combination**; *A. murisipanensis* (La Marca, 1998 "1996") **new combination**; *A. parimae* (La Marca, 1998 "1996") **new combination**; *A. parkerae* (Meinhardt and Parmelee, 1996) **new combination**; ***A. praderioi*** (La Marca, 1998 "1996") **new combination**; ***A. roraima*** (La Marca, 1998 "1996") **new combination**; *A. shrevei* (Rivero, 1961) **new combination**; ***A. stepheni*** (Martins, 1989) **new combination**; *A. tamacuarensis* (Myers and Donnelly, 1997) **new combination**; ***A. tepuyensis*** (La Marca, 1998 "1996") **new combination**; *A. triunfo* (Barrio-Amorós, Fuentes, and Rivas, 2004) **new combination**; *A. wothuja* (Barrio-Amorós, Fuentes, and Rivas, 2004) **new combination**.

CHARACTERIZATION, DIAGNOSIS, AND SUPPORT: Branch length = 77. Bremer support = 35.

The only unambiguously optimized phenotypic synapomorphies of this clade is **(1)** the unique and unreversed origin of the median lingual process (Character 79, 0 → 1).

Other characteristics include: (1) Dorsal coloration cryptic, brown or gray; (2) pale oblique lateral stripe present or absent; (3) pale dorsolateral stripe present or absent; (4) pale ventrolateral stripe absent; (5) dorsal skin texture posteriorly granular; (6) toe webbing basal to extensive; (7) third finger of adult males swollen or not; (8) finger I shorter than finger II; (9) finger discs weakly expanded; (10) median lingual process present; (11) larval vent tube usually dextral; (12) larval oral disc shape usually "normal" (not umbelliform), variably reduced in endotrophic species; (13) larval oral disc emarginate (variably reduced in endotrophic species); (14) lipophilic alkaloids absent; (15) chromosome number $2n = 24$ (known in *Anomaloglossus stepheni*); (16) testes unpigmented or medially pigmented; (17) dark throat collar absent.

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DISTRIBUTION: Most species are *cis*-Andean; among these, none occurs west or south of the region of Manaus, and there is a large number of tepui species. Three species also occur on the Pacific slopes of Colombia and Ecuador.

ETYMOLOGY: *Anomaloglossus*, formed from the Greek *anomalos* (irregular, unusual) and *glossa* (tongue), in reference to the unusual tongue bearing the median lingual process. Gender masculine. (This name should not be mistaken for *Anomaloglossa* Percival, 1978, which is a genus of brachiopod.)

COMMENT: *Anomaloglossus* is most simply diagnosed by the synapomorphic occurrence of the median lingual process (Grant et al., 1997). Owing to the shared occurrence of the median lingual process (MLP) in the potential sister taxa specified by the Old World ranoid hypothesis of dendrobatid origins (e.g., Ford and Cannatella, 1993) and its absence in all hyloids, Grant et al. interpreted the MLP as symplesiomorphic in dendrobatids. However, Frost et al. (2006) showed decisively that dendrobatoids are not closely related to Old World ranoids, and their MLP is independently derived.

La Marca (1998 "1996") did not note the presence or absence of the MLP in *A. ayarzaguenai*, *A. guanayensis*, *A. murisipanensis*, or *A. parimae*, and we have not examined these species; as such, their inclusion in this genus is a prediction based on distribution and their resemblance to MLP-possessing species, and it must be confirmed. The presence of the MLP is confirmed for all other species referred to this genus.

Within *Anomaloglossus* there are basically two "flavors" of frogs: small, slender frogs with minimal toe webbing (e.g., *A. stepheni*), and larger, more robust frogs with moderate to extensive toe webbing (e.g., *A. tepuyensis*). The former group is strictly *cis*-Andean, whereas the latter occurs east of the Andes and on the Pacific slopes of Colombia and Ecuador. In the present analysis these two groups are reciprocally monophyletic, but greater taxon sampling is required to thoroughly test this result. Similarly, the *trans*-Andean MLP-possessing species must be included explicitly in phylogenetic analysis to corroborate their placement in *Anomaloglossus*.

GENUS: *RHEOBATES* NEW GENUS

Rheobates **new genus**. Type species: *Phyllobates palmatus* Werner, 1899.

IMMEDIATELY MORE INCLUSIVE TAXON: Anomaloglossinae **new subfamily**.

SISTER GROUP: *Anomaloglossus* **new genus**.

CONTENT (2 SPECIES): ***Rheobates palmatus*** (Werner, 1899) **new combination**; *R. pseudopalmatus* (Rivero and Serna, 2000 "1995") **new combination.**

CHARACTERIZATION, DIAGNOSIS, AND SUPPORT: Branch length = 28. Bremer support = 28.[14] Insofar as this genus is represented by a single species in this analysis, we cannot distinguish between autapomorphies and synapomorphies and therefore do not report the apomorphic states.

Other characteristics include: (1) Dorsal coloration cryptic, brown or gray; (2) pale oblique lateral stripe present or absent, often more conspicuous in juveniles; (3) pale dorsolateral stripe absent; (4) pale ventrolateral stripe absent; (5) dorsal skin texture posteriorly granular; (6) toe webbing extensive; (7) third finger of adult males not swollen; (8) finger I shorter than finger II; (9) finger discs weakly expanded; (10) median lingual process absent; (11) larval vent tube dextral; (12) larval oral disc shape "normal" (not umbelliform); (13) larval oral disc emarginate; (14) lipophilic alkaloids unknown (presumed absent); (15) chromosome number $2n = 24$ (known in *Rheobates palmatus*); (16) testes unpigmented; (17) dark throat collar absent.

DISTRIBUTION: Colombia, eastern amd westerm slopes of the Cordillera Oriental and across the Magdalena valley on the eastern slope of the Cordillera Central. The elevational distribution extends from ca. 400 m to over 2,000 m.

ETYMOLOGY: *Rheobates*, from the Greek rheo (stream, current) and bates (a walker) in reference to the riparian habitat of the type species *R. palmatus*.

[14] The relevance of these values is minimal, given that this clade consists only of two specimens of the same species, but we report them for consistency.

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COMMENT: Phylogenetic analysis showed *Rheobates palmatus* to be the sister taxon of *Anomaloglossus*, from which it differs most strikingly in lacking the median lingual process. Otherwise, this taxon most resembles several extensively webbed species of *Hyloxalus*, from which it differs in having an elongate, robust zygomatic ramus of the squamosal and more extensive toe webbing, and *Colostethus*, from which it differs in lacking the swollen third finger in adult males. It differs from species of *Aromobates* in lacking a pale dorsolateral stripe, and from species of *Mannophryne* in lacking a dark throat collar.

We refer *Rheobates pseudopalmatus* to this genus provisionally based on Rivero and Serna's (2000 "1995") assertion that *R. palmatus* and *R. pseudopalmatus* are sister species. Nevertheless, we caution that the diagnostic characters provided by Rivero and Serna are inadequate to validate their claim and exclude *R. pseudopalmatus* from *Hyloxalus* or *Aromobates*. That said, the diagnostic differences given by Rivero and Serna are also inadequate to distinguish this species from *R. palmatus*, and given that the type locality of Amalfi lies within the known distribution of *R. palmatus* on the eastern slope of the Cordillera Central, it is likely that two taxa are conspecific.

Bernal et al. (2005) recently examined *Rheobates palmatus* on the Amazonian and western flanks of the Cordillera Oriental and reported bioacoustic and genetic evidence of lineage differentiation between populations on either side of the Andes. Should sampling of additional localities corroborate this finding, names are available: *Phyllobates* (*Hypodictyon*) *palmatus* Werner, 1899 was named from Fusagasugá and would therefore apply to the western slope populations, whereas *Hyloxalus granuliventris* Boulenger, 1919 was described from "Bogotá" and, although that is a vague locality, a first reviser could apply the name to the eastern slope populations.

SUBFAMILY: AROMOBATINAE **NEW SUBFAMILY**

Aromobatinae **new subfamily**. Type genus: *Aromobates* Myers, Paolillo, and Daly, 1991.

IMMEDIATELY MORE INCLUSIVE TAXON: Aromobatidae **new family**.

SISTER GROUP: Anomaloglossinae **new subfamily**.

CONTENT (2 GENERA): *Aromobates* and *Mannophryne*.

CHARACTERIZATION, DIAGNOSIS, AND SUPPORT: Branch length = 54. Bremer support = 38. All unambiguously optimized synapomorphies for this clade are from DNA sequences (see appendix 8).

DISTRIBUTION: Mérida Andes of Venezuela and adjacent Cordillera Oriental of Colombia, Cordillera de la Costa, and Peninsula de Paría, Trinidad and Tobago.

COMMENT: *Aromobates* and *Mannophryne* form a morphologically and geographically compact clade.

GENUS: *AROMOBATES* MYERS, PAOLILLO, AND DALY, 1991

Aromobates. Type species *Aromobates nocturnus* Myers, Paolillo, and Daly, 1991 by original designation.

Nephelobates La Marca, 1994. Type species: *Phyllobates alboguttatus* Boulenger, 1903 by original designation.

IMMEDIATELY MORE INCLUSIVE TAXON: Aromobatinae **new subfamily**.

SISTER GROUP: *Mannophryne* La Marca, 1991.

CONTENT (12 SPECIES): *Aromobates alboguttatus* (Boulenger, 1903) **new combination**; *A. capurinensis* (Péfaur, 1993) **new combination**; *A. duranti* (Pefaur, 1985) **new combination**; *A. haydeeae* (Rivero, 1978 "1976") **new combination**; *A. leopardalis* (Rivero, 1980 "1978") **new combination**; *A. mayorgai* (River, 1980 "1978"); *A. meridensis* (Dole and Durant, 1972) **new combination**; ***A. molinarii*** (La Marca, 1985) **new combination**; ***A. nocturnus*** Myers, Paolillo, and Daly, 1991; *A. orostoma* (Rivero, 1978 "1976") **new combination**; ***A. saltuensis*** (Rivero 1980 "1978") **new combination**; *A. serranus* (Péfaur, 1985) **new combination**.

CHARACTERIZATION, DIAGNOSIS, AND SUPPORT: Branch length = 61. Bremer support = 25. All unambiguously optimized synapomorphies for this clade are from DNA sequences.

Other characteristics include: (1) Dorsal coloration cryptic, brown or gray; (2) pale

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oblique lateral stripe present or absent; (3) pale dorsolateral stripe present; (4) pale ventrolateral stripe absent; (5) dorsal skin texture posteriorly granular; (6) toe webbing basal to extensive; (7) third finger of adult males not swollen; (8) finger I shorter than, equal to, or longer than finger II; (9) finger discs weakly to moderately expanded; (10) median lingual process absent; (11) larval vent tube dextral; (12) larval oral disc shape "normal" (not umbelliform); (13) larval oral disc emarginate; (14) lipophilic alkaloids absent; (15) chromosome number $2n = 24$ (known in *Aromobates leopardalis*); (16) testes unpigmented; (17) dark throat collar absent.

DISTRIBUTION: Mérida Andes of Venezuela and adjacent Cordillera Oriental of Colombia.

COMMENT: The inclusion of *A. capurinensis* in this genus is provisional because we have not examined specimens and osteological data (e.g., length of zygomatic ramus) have not been published. Nevertheless, Péfaur's (1993) description called attention to the resemblance of this species to the other species here included in *Aromobates*, and its distribution at approximately 2,400 m in the Mérida Andes lends indirect support to this relationship.

GENUS: *MANNOPHRYNE* LA MARCA, 1991

Mannophryne La Marca, 1992. Type species: *Colostethus yustizi* La Marca, 1989 by original designation.

IMMEDIATELY MORE INCLUSIVE TAXON: Aromobatinae **new subfamily**.

SISTER GROUP: *Aromobates* Myers, Paolillo, and Daly, 1991.

CONTENT (12 SPECIES): *Mannophryne caquetio* Mijares-Urrutia and Arends R., 1999; ***M. collaris*** (Boulenger, 1912); *M. cordilleriana* La Marca, "1994" 1995; ***M. herminae*** (Boettger, 1893); *M. lamarcai* Mijares-Urrutia and Arends R., 1999; *M. larandina* (Yustiz, 1991); *M. neblina* (Test, 1956); *M. oblitterata* (Rivero, 1986 "1984"); *M. olmonae* (Hardy, 1983); *M. riveroi* (Donoso-Barros, 1965 "1964"); ***M. trinitatis*** (Garman, 1887); *M. yustizi* (La Marca, 1989).

CHARACTERIZATION, DIAGNOSIS, AND SUPPORT: Branch length = 72. Bremer support = 40.

Phenotypic synapomorphies that optimize unambiguously to this node are **(1)** presence of a dermal collar (Character 59, $0 \rightarrow 1$) and **(2)** male abdomen color evenly stippled (Character 63, $3 \rightarrow 2$).

Other characteristics include: (1) Dorsal coloration cryptic, brown; (2) pale oblique lateral stripe present; (3) pale dorsolateral stripe present; (4) pale ventrolateral stripe absent; (5) dorsal skin texture posteriorly granular; (6) toe webbing moderate to extensive; (7) third finger of adult males not swollen; (8) finger I shorter than finger II; (9) finger discs narrow to moderately expanded; (10) median lingual process absent; (11) larval vent tube dextral; (12) larval oral disc shape "normal" (not umbelliform); (13) larval oral disc emarginate; (14) lipophilic alkaloids absent; (15) chromosome number $2n = 24$ (known in *Mannophryne herminae*, *M. olmonae*, *M. neblina*, *M. trinitatis*); (16) testes unpigmented; (17) dark throat collar present.

DISTRIBUTION: Andes, Cordillera de la Costa, and Peninsula de París in Venezuela; Trinidad and Tobago.

COMMENT: The content of *Mannophryne* does not change with this study.

SUBFAMILY: ALLOBATINAE **NEW SUBFAMILY**

IMMEDIATELY MORE INCLUSIVE TAXON: Aromobatidae **new family**.

SISTER GROUP: Aromobatinae **new subfamily**.

CONTENT: *Allobates* Zimmermann and Zimmermann, 1988.

CHARACTERIZATION, DIAGNOSIS, AND SUPPORT: Branch length = 56. Bremer support = 33.

Unambiguously optimized phenotypic synapomorphies of this clade are **(1)** finger IV reaching distal half of distal subarticular tubercle of finger III (character 4, $0 \rightarrow 1/2$), **(2)** finger III swollen in adult males (Character 20, $0 \rightarrow 1$), **(3)** webbing absent on postaxial side of toe I (Character 37, $2 \rightarrow 0$), **(4)** webbing absent on preaxial side of toe II (Character 38, $1 \rightarrow 0$), **(5)** webbing absent on postaxial side of toe II (Character 39, $1 \rightarrow 0$), **(6)** webbing absent on preaxial side of toe III (Character 40, $2 \rightarrow 0$), **(7)** pale paracloacal mark present (Character 49, $0 \rightarrow 1$), **(8)** oblique lateral line diffuse (Character 57, $0 \rightarrow 2$), **(9)** male abdomen pale, free or almost free

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of melanophores (Character 63, 3 → 0), **(10)** palatines absent (Character 132, 1 → 0).

DISTRIBUTION: South America and the Lesser Antilles. South American species are *cis*-Andean with two exceptions: (1) *Allobates talamancae* occurs in the Pacific lowlands of Colombia and Ecuador and north through Central America to Nicaragua, (2) its undescribed sister species *A.* "Magdalena" from this study, which occurs in the Magdalena Valley of Colombia. A single species (*A. chalcopis*) occurs in Martinique.

COMMENT: This name is currently redundant with *Allobates*. However, *Allobates* is a large, broadly distributed, and heterogeneous clade. Current knowledge is inadequate to name additional genera and assign species not included explicitly in the present analysis, and the need for a functional taxonomy outweighs the need to name additional clades. Given the rapid accumulation of data over the last few years, we anticipate that the paucity of knowledge will be remedied quickly and this large genus will be partitioned as knowledge of its phylogeny accumulates, making Allobatinae an informative name (for recognized species groups, see Comments for *Allobates*, below). Recognition of Allobatinae is necessitated by the recognition of Aromobatinae for the clade of *Aromobates* and *Mannophryne*.

GENUS: *ALLOBATES* ZIMMERMANN AND ZIMMERMANN, 1988

Allobates Zimmermann and Zimmermann, 1988. Type species *Prostherapis femoralis* Boulenger, 1884, by original designation.

IMMEDIATELY MORE INCLUSIVE TAXON: Aromobatidae **new family**.

SISTER GROUP: Aromobatinae **new subfamily**.

CONTENT (42 SPECIES): ***Allobates alagoanus*** (Bokermann, 1967); *A. alessandroi* (Grant and Rodríguez, 2001) **new combination**; *A. bromelicola* (Test, 1956) **new combination**; ***A. brunneus*** (Cope, 1887) **new combination**; ***A. caeruleodactylus*** (Lima and Caldwell, 2001) **new combination**; *A. capixaba* (Bokermann, 1967) **new combination**; *A. carioca* (Bokermann, 1967) **new combination**; *A. cepedai* (Morales, 2002 "2000") **new combination**; *A. chalcopis* (Kaiser, Coloma, and Gray, 1994) **new combination**; ***A. conspicuus*** (Morales, 2002 "2000") **new combination**; *A. craspedoceps* (Duellman, 2004) **new combination**; *A. crombei* (Morales, 2002 "2000") **new combination**; ***A. femoralis*** (Boulenger, 1883); *A. fratinescus* (Morales, 2002 "2000") **new combination**; *A. fuscellus* (Morales, 2002 "2000") **new combination**; ***A. gasconi*** (Morales, 2002 "2000") **new combination**; *A. goianus* (Bokermann, 1975) **new combination**; ***A. humilis*** (Rivero, 1980 "1978") **new combination**; ***A. insperatus*** (Morales, 2002 "2000") **new combination**; ***A. juanii*** (Morales, 1994) **new combination**; ***A. kingsburyi*** (Boulenger, 1918) **new combination**; *A. mandelorum* (Schmidt, 1932) **new combination**; *A. marchesianus* (Melin, 1941) **new combination**; *A. masniger* (Morales, 2002 "2000") **new combination**; *A. mcdiarmidi* (Reynolds and Foster, 1992) **new combination**; *A. melanolaemus* (Grant and Rodríguez, 2001) **new combination**; *A. myersi* (Pyburn, 1981) **new combination**; ***A. nidicola*** (Caldwell and Lima, 2003) **new combination**; *A. olfersioides* (Lutz, 1925) **new combination**; *A. ornatus* (Morales, 2002 "2000") **new combination**; *A. picachos* (Ardila-Robayo, Acosta-Galvis, and Coloma, 2000 "1999"); *A. pittieri* (La Marca, Manzanilla, and Mijares-Urrutia, 2004) **new combination**; *A. ranoides* (Boulenger, 1918) **new combination**; *A. rufulus* (Gorzula, 1990 "1988"); *A. sanmartini* (Rivero, Langone, and Prigioni, 1986) **new combination**; *A. sumtuosus* (Morales, 2002 "2000") **new combination**; ***A. talamancae*** (Cope, 1875) **new combination**; ***A. trilineatus*** (Boulenger, 1884 "1883") **new combination**; ***A. undulatus*** (Myers and Donnelly, 2001) **new combination**; *A. vanzolinius* (Morales, 2002 "2000") **new combination**; *A. wayuu* (Acosta, Cuentas, and Coloma, 2000 "1999") **new combination**; ***A. zaparo*** (Silverstone, 1976).

CHARACTERIZATION, DIAGNOSIS, AND SUPPORT: As for Allobatinae, above.

Other characteristics include: (1) Dorsal coloration cryptic in most species (brighter in *A. femoralis* group); (2) pale oblique lateral stripe present in most (but not all) species; (3) pale dorsolateral stripe present or absent; (4) pale ventrolateral stripe present or absent; (5) dorsal skin texture posteriorly granular except in *A. femoralis* group, which is strongly granular; (6) toe webbing absent to

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moderate (basal in most species); (7) third finger of adult males swollen or not swollen; (8) finger I longer than finger II in most species (equal or shorter in some); (9) finger discs weakly expanded; (10) median lingual process absent; (11) larval vent tube dextral; (12) larval oral disc shape "normal" (not umbelliform); (13) larval oral disc emarginate; (14) lipophilic alkaloids absent; (15) chromosome number $2n = 24$ (known in *A. femoralis*, A. *olfersioides*, *A. talamancae*) and $2n = 22$ (known in *A. nidicola*, *A. caeruleodactylus*, *A. chalcopis*); (16) testes unpigmented; (17) dark throat collar absent.

DISTRIBUTION: As for Allobatinae, above.

COMMENT: With 42 nominal species, *Allobates* includes nearly half of the species previously referred to the polyphyletic genus *Colostethus*. Although the monophyly of *Allobates* is strongly supported, given the number of species and their morphological, genetic (e.g., chromosome numbers), and behavioral diversity, additional partitioning will likely be required. Although formal recognition at this time is premature because it would leave the remaining species in a paraphyletic group and there are inadequate data to refer all species to particular clades, a restricted *Allobates* may be applied to the *A. femoralis* group. This group is presently composed of only four nominal species (*A. femoralis*, *A. myersi*, *A. zaparo*, and *A. rufulus*—the latter based on minimal evidence), but numerous additional species await description.

FAMILY: DENDROBATIDAE COPE, 1865

IMMEDIATELY MORE INCLUSIVE TAXON: Dendrobatoidea Cope, 1865.

SISTER GROUP: Aromobatidae **new family**.

CONTENT (3 SUBFAMILIES): Colostethinae Cope, 1867; Dendrobatinae Cope, 1865; and Hyloxalinae **new subfamily**.

CHARACTERIZATION, DIAGNOSIS, AND SUPPORT: Branch length = 50. Bremer support = 20.

Unambiguously optimized phenotypic synapomorphies for this clade are **(1)** webbing on the postaxial side of toe I absent (Character 37, $2 \rightarrow 0$), **(2)** webbing on the preaxial side of toe II absent (Character 38, $1/2 \rightarrow 0$), **(3)** webbing on the postaxial side of toe II absent (Character 39, $1/2 \rightarrow 0$), **(4)** webbing on the preaxial side of toe III absent (Character 40, $2/3/4 \rightarrow 0$), and **(5)** palatines absent (Character 132, $1 \rightarrow 0$).

DISTRIBUTION: As for Dendrobatoidea.

COMMENT: For synonymy see Dendrobatoidea, above.

SUBFAMILY: COLOSTETHINAE COPE, 1867

Colostethidae Cope, 1867. Type genus: *Colostethus* Cope, 1866 by monotypy.

IMMEDIATELY MORE INCLUSIVE TAXON: Dendrobatidae Cope, 1865.

SISTER GROUP: Unnamed clade composed of Dendrobatinae Cope, 1865 and Hyloxalinae **new subfamily**.

CONTENT (4 GENERA): *Ameerega* Bauer, 1986; *Colostethus* Cope, 1866; *Epipedobates* Myers, 1987; *Silverstoneia* **new genus**.

CHARACTERIZATION, DIAGNOSIS, AND SUPPORT: Branch length = 89. Bremer support = 20.

Unambiguously optimized phenotypic synapomorphies for this clade are **(1)** finger IV reaching the distal half of the subarticular tubercle of finger III (Character 4, $0 \rightarrow 1$), **(2)** finger I longer than finger II (Character 5, $2 \rightarrow 3$), **(3)** finger III swollen in adult males (Character 20, $0 \rightarrow 1$), **(4)** female crouching in courtship (Character 102, $0 \rightarrow 1$), and **(5)** gain of cephalic amplexus (Character 105, $0 \rightarrow 2$).

DISTRIBUTION: As for Dendrobatidae. *Silverstoneia* and *Epipedobates* are exclusively *trans*-Andean, *Colostethus* is almost exclusively *trans*-Andean (see below), and *Ameerega* is almost exclusively *cis*-Andean.

COMMENT: Mivart's (1869) Calostethina is derived from the subsequent misspelling of *Colostethus* Cope, 1866 and Colostethidae Cope 1867 as *Calostethus* and Calostethidae, respectively, and is therefore not an available name.

GENUS: *AMEEREGA* BAUER, 1986

Ameerega Bauer, 1986. Type species: *Hyla trivittata* Spix, 1824 by original designation.

Phobobates Zimmermann and Zimmermann, 1988. Type species: *Dendrobates silverstonei* Myers and Daly, 1979 by original designation.

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Paruwrobates Bauer, 1994. Type species: *Dendrobates andinus* Myers and Burrowes, 1987 by original designation.

Pseudendrobates Bauer, 1988. Type species: *Dendrobates silverstonei* by original designation.

IMMEDIATELY MORE INCLUSIVE TAXON: Colostethinae Cope, 1867.

SISTER GROUP: *Colostethus* Cope, 1866.

CONTENT (25 SPECIES): *Ameerega andina* (Myers and Burrowes, 1987) **new combination**; ***A. bassleri*** (Melin, 1941); ***A. bilinguis*** (Jungfer, 1989[15]) **new combination**; *A. boliviana* (Boulenger, 1902); ***A. braccata*** (Steindachner, 1864) **new combination**; *A. cainarachi* (Schulte, 1989) **new combination**; *A. erythromos* (Vigle and Miyata, 1980) **new combination**; ***A. flavopicta*** (Lutz, 1925); ***A. hahneli*** (Boulenger, 1883) **new combination**; *A. ingeri* (Cochran and Goin, 1970) **new combination**; *A. labialis* (Cope, 1874) **new combination**; ***A. macero*** (Rodríguez and Myers, 1993) **new combination**; *A. maculata* W. Peters, 1873; ***A. parvula*** (Boulenger, 1882) **new combination**; *A. peruviridis* (Bauer, 1986) **new combination**; ***A. petersi*** (Silverstone, 1976) **new combination**; ***A. picta*** (Tschudi, 1838); *A. planipaleae* (Morales and Velazco, 1998); *A. pongoensis* (Schulte, 1999) **new combination**; ***A. pulchripecta*** (Silverstone, 1976); ***A. rubriventris*** (Lötters, Debold, Henle, Glaw, and Kneller, 1997) **new combination**; ***A. silverstonei*** (Myers and Daly, 1979) **new combination**; *A. simulans* (Myers, Rodriguez, and Icochea, 2000) **new combination**; *A. smaragdina* (Silverstone, 1976); ***A. trivittata*** (Spix, 1824).

CHARACTERIZATION, DIAGNOSIS, AND SUPPORT: Branch length = 131. Bremer support = 103.

Unambiguously optimized phenotypic synapomorphies for this clade include **(1)** granular dorsal skin (Character 0, 1 → 2; unreversed, this being the most conspicuous synapomorphy of this genus), **(2)** female abdomen dark with pale (usually blue) spotting/reticulation/marbling (Character 64, 0 → 3), and **(3)** the ability to sequester lipophilic alkaloids (Character 147, 0 → 1).

Other characteristics include: (1) Dorsal coloration variable (brown, red, bright orange, bright metallic green); (2) pale oblique lateral stripe usually present (often incomplete), absent in *A. silverstonei*; (3) pale dorsolateral stripe absent; (4) pale ventrolateral stripe absent or wavy series of elongate spots; (5) dorsal skin texture strongly granular; (6) toe webbing lacking in most species, at most basal; (7) third finger of adult males swollen in most (but not all) species; (8) finger I equal to finger II in almost all species; (9) finger discs narrow to moderately expanded; (10) median lingual process absent; (11) larval vent tube dextral; (12) larval oral disc shape normal (not umbelliform); (13) larval oral disc emarginate; (14) lipophilic alkaloids present; (15) chromosome number $2n = 24$ (known in *Ameerega flavopicta*, *A. hahneli*, *A. picta*, and *A. trivittata*); (16) testes pigmented in most species (unpigmented in *A. flavopicta* and *A. petersi*); (17) dark throat collar absent.

DISTRIBUTION: This clade is almost entirely *cis*-Andean, the sole exceptions being the presumed sister species *Ameerega andina* and *A. erythromos*, which occur at low to moderate elevations of the Pacific Andean slopes, and *A. maculata*, known only from the Panamanian holotype. Most species occur in lowlands, but some reach as high as ca. 1,400 m.

COMMENT: *Ameerega* is most easily identified by the conspicuously granular dorsal skin texture, consisting of rounded or flattened granules distributed densely and evenly, as was underscored by Jungfer (1989) in his study of the "red-backed granulated" species. In most dendrobatoids, including *Epipedobates*, granules or tubercles are scattered irregularly over the dorsal surfaces, being more distinct and prevalent posteriorly, especially in the sacral region and on the thigh and/or shank, and absent or weaker and sparser anteriorly, and often distinctly elevated and conical. (For detailed discussion and illustrations see Character 0, above.) Other species that possess strongly granular dorsal skin are *Allobates femoralis*, *A. zaparo*, and *D. granuliferus*.

[15]In a recent book on amphibian conservation, Amézquita et al. (2004) explicitly placed *Epipedobates bilinguis* in the synonymy of *Dendrobates ingeri*. However, they offered no evidence for this taxonomic change and did not dispute the differences cited by Jungfer (1989) to distinguish the two species. As such, we continue to recognize both taxa as valid species.

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In content, *Ameerega* is equivalent to the combination of Silverstone's (1976) *pictus* and *trivittatus* groups. Most species previously referred to *Epipedobates* (sensu Myers, 1987) pertain to this group, that is, it is equivalent to *Phyllobates* sensu Silverstone (1975a) following the removal of the *bicolor* and *femoralis* groups.

Vigle and Miyata (1980) described *Ameerega erythromos* as part of Silvertone's (1976) *pictus* group, and Myers and Burrowes (1987) considered *A. andina* to be its sister species. There would be little reason to question the inclusion of these species in *Ameerega* if it were not for their biogeographically anomalous placement west of the Andes, whereas the remainder of the clade is *cis*-Andean (but see also below). The name *Paruwrobates* Bauer, 1994 is available for these species, should they be found not to be nested within *Ameerega*. *Ameerega erythromos* possesses several skin toxins, which suggests it is not closely related to *Hyloxalus azureiventris* (see below). *Ameerega andina* egg clutches are deposited in bromeliads, and presumably tadpoles are transported to phytotelmata, which suggests these species could be part of Dendrobatinae (see below).

Finally, our placement of *Ameerega maculata* in this genus is provisional and deserves further investigation. The species was redescribed by Myers (1982), who removed it from the synonymy of *Dendrobates auratus* where it had been placed by Dunn (1931). Myers (1987) subsequently transferred it to his *Epipedobates*. The species remains known only from the western Panamanian holotype, which has teeth on the maxillary arch, basal webbing between toes II–IV, and a long first finger, like species of *Ameerega*. However, it also possesses a spotted dorsum and smooth skin, thus differing from all known species of *Ameerega*. As noted by Myers (1982; see also Phenotypic Characters, above), skin granulation can be lost in preserved specimens, and insofar as most of the species Myers (1987) placed in *Epipedobates* are here considered *Ameerega*, we transfer this species to that genus as well.

GENUS: *COLOSTETHUS* COPE, 1867

Colostethus Cope, 1867. Type species: *Phyllobates latinasus* by original designation.

Prostherapis Cope, 1868. Type species: *Prostherapis inguinalis* by original designation.

IMMEDIATELY MORE INCLUSIVE TAXON: Colostethinae Cope, 1867.

SISTER GROUP: *Ameerega* Bauer, 1986.

CONTENT (18 SPECIES): *Colostethus agilis* Lynch and Ruiz-Carranza, 1985; *C. alacris* Rivero and Granados-Diaz, 1990 "1989"; *C. brachistriatus* Rivero and Serna, 1986; *C. dysprosium* Rivero and Serna, 2000 "1995"; ***C. fraterdanieli*** Silverstone, 1971; ***C. fugax*** Morales and Schulte, 1993; *C. furviventris* Rivero and Serna, 1991; ***Colostethus imbricolus*** Silverstone, 1975; ***C. inguinalis*** Cope, 1868; *C. jacobuspetersi* Rivero, 1991; *C. mertensi* (Cochran and Goin, 1964); *C. latinasus* (Cope, 1863); *C. lynchi* Grant, 1998; ***C. panamensis*** (Dunn, 1933); ***C. pratti*** (Boulenger, 1899); *C. ruthveni* Kaplan, 1997; *C. thorntoni* (Cochran and Goin, 1970); *C. yaguara* Rivero and Serna, 1991.

CHARACTERIZATION, DIAGNOSIS, AND SUPPORT: Branch length = 37. Bremer support = 14.

Unambiguously optimized phenotypic synapomorphies for this clade are **(1)** toe disc II moderately expanded (Character 32, 1 → 2) and **(2)** male abdomen color pale, free or almost free of melanophores (Character 63, 3 → 0).

Other characteristics include: (1) Dorsal coloration cryptic, brown; (2) pale oblique lateral stripe present (may be broken or incomplete); (3) pale dorsolateral stripe usually absent (present in *C. pratti*); (4) pale ventrolateral stripe present or absent; (5) dorsal skin texture posteriorly granular; (6) toe webbing absent or basal to extensive; (7) third finger of adult males swollen; (8) finger I equal to or longer than finger II; (9) finger discs moderately expanded; (10) median lingual process absent; (11) larval vent tube dextral; (12) larval oral disc shape normal (not umbelliform); (13) larval oral disc emarginate; (14) lipophilic alkaloids absent; (15) chromosome number $2n = 24$ (known in *Colostethus fraterdanieli* and *C. panamensis*); (16) testes entirely pigmented in most species, partially or unpigmented in others; (17) dark throat collar absent.

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DISTRIBUTION: *Colostethus* is a primarily *trans*-Andean clade, extending from eastern Central America to northwestern Ecuador, with most species occurring at cloud forest localities in the western Andes. The only *cis*-Andean species is *C. fugax*, which is known from the eastern slope of the Cordillera Oriental in southern Ecuador, 600–700 m (see Comment).

COMMENT: *Colostethus*, as applied in this revised taxonomy, refers to a morphologically compact group of species. Nevertheless, the type species, *Colostethus latinasus*, was not included in the phylogenetic analysis due to inadequate material, and the name is applied to this clade based on its assumed close relationship to *C. inguinalis* and *C. panamensis* (for comparisons, see Grant, 2004). Among dendrobatids, *Colostethus* differs from all species of *Hyloxalus* in possessing a swollen third finger, and from all species of *Silverstoneia* in larger size (maximum of 22 mm SVL in *Silverstoneia*, greater than 24 mm SVL in *Colostethus*) and possessing a "normal" larval mouth (umbelliform in *Silverstoneia*). Among aromobatids, *Allobates talamancae* is sympatric with several species of *Colostethus* in Pacific Colombia and Ecuador and in Central America. *Allobates talamancae* differs from all species of *Colostethus* in lacking a pale oblique lateral stripe and swelling of finger III in adult males.

The moderately to extensively webbed species *Colostethus agilis*, *C. mertensi*, and *C. thorntoni* are referred to this genus because they (1) have a short zygomatic ramus of the squamosal (thus differing from *Rheobates*), (2) possess a swollen third finger in adult males (thus differing from *Hyloxalus*), (3) lack dorsolateral stripes (thus differing from *Allobates*), and (4) lack a median lingual process (thus differing from *Anomaloglossus*); other genera lack moderate to extensive webbing.

DNA sequence data for *Colostethus fugax* were deposited on GenBank by Santos et al. (2003), who did not provide locality data. Additional samples of this species from a known locality are required to further test the placement of this species from the Amazon slopes in this otherwise *trans*-Andean clade. Nevertheless, it resembles other species of *Colostethus* in possessing a swollen third finger in adult males (unlike *Hyloxalus*) and lacking a dorsolateral stripe (unlike almost all species of *Allobates*).

GENUS: *EPIPEDOBATES* MYERS, 1987

Epipedobates Myers, 1987. Type species: *Prostherapis tricolor* Boulenger, 1899 by original designation.

IMMEDIATELY MORE INCLUSIVE TAXON: Colostethinae Cope, 1867.

SISTER GROUP: *Silverstoneia* **new genus**.

CONTENT (5 SPECIES): ***Epipedobates anthonyi*** (Noble, 1921); ***E. boulengeri*** (Barbour, 1909); ***E. espinosai*** (Funkhouser, 1956); ***E. machalilla*** (Coloma, 1995) **new combination**; ***E. tricolor*** (Boulenger, 1899).

CHARACTERIZATION, DIAGNOSIS, AND SUPPORT: Branch length = 75. Bremer support = 71.

Due to the lack of phenotypic data for the GenBank sample of *E. boulengeri*, all phenotypic transformations that occur at this node are optimization ambiguous. Assuming fast optimization, phenotypic transformations for *Epipedobates* are **(1)** loss of metatarsal fold (Character 46, 1 → 0), **(2)** female throat and chest color dark with pale median longitudinal stripe (Character 62, 0 → 5), and **(3)** female abdomen color dark with discrete pale spotting/reticulation/marbling (Character 64, 0 → 3).

Other characteristics include: (1) Dorsal coloration cryptic, brown; (2) pale oblique lateral stripe present; (3) pale dorsolateral stripe present or absent; (4) pale ventrolateral stripe present or absent; (5) dorsal skin texture smooth or with granules or tubercles scattered irregularly over dorsal surfaces, most distinct and prevalent posteriorly; (6) toe webbing basal; (7) third finger of adult males swollen; (8) finger I longer than finger II; (9) finger discs narrow to moderately expanded; (10) median lingual process absent; (11) larval vent tube dextral; (12) larval oral disc shape "normal" (not umbelliform); (13) larval oral disc emarginate; (14) lipophilic alkaloids present; (15) chromosome number unknown; (16) testes entirely pigmented; (17) dark throat collar absent.

DISTRIBUTION: All species of *Epipedobates* are *trans*-Andean. *Epipedobates boulen-*

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geri, *E. espinosai*, and *E. machalilla* occur in the Pacific lowlands of northern South America. *Epipedobates anthonyi* and *E. tricolor* are montane species, occurring up to 1,800 m on the western versant of the Andes. Following Graham et al. (2004), *E. anthonyi* is applied to populations in central Ecuador, while *E. tricolor* is applied to populations in southern Ecuador and northern Peru (see Comment).

COMMENT: *Epipedobates*, as applied here, is equivalent to the *femoralis* group of Silverstone (1976), with the exclusion of *Phyllobates femoralis* and *Phyllobates zaparo* (both of which are placed in the aromobatid genus *Allobates*; see above).

Silverstone (1976: 29) expressed doubt regarding the identity of some Ecuadorian specimens he referred to *E. boulengeri*, and Lötters et al. (2003b) considered the possibility that a complex of species may be concealed within this nominal taxon. These views seem to be validated by the current study, which found *E. boulengeri* to be nonmonophyletic. However, insofar as Santos et al. (2003) provided no specimen data for the DNA sequence data they deposited on GenBank, it is impossible to address this problem.

For the same reason, it is impossible to address the identity of Santos et al.'s (2003) *Epipedobates* sp. QCAZ16589, although its placement with, and few differences from, *E. espinosai* suggest they may be conspecific.

Graham et al. (2004) generated DNA sequence data for a specimen from the type locality of *E. tricolor* and found that it did not form a clade with samples from further south (although that result was contradicted by alternative, equally parsimonious cladograms). As such, they restricted *E. tricolor* to the northern populations and applied *E. anthonyi* to the southern ones. We follow their usage here, although morphological characters to consistently diagnose the two taxa have yet to be identified.

GENUS: *SILVERSTONEIA* **NEW GENUS**

Silverstoneia **new genus**. Type species: *Phyllobates nubicola* Dunn, 1924.

IMMEDIATELY MORE INCLUSIVE TAXON: Colostethinae Cope, 1867.

SISTER GROUP: *Epipedobates* Myers, 1987.

CONTENT (3 SPECIES): ***Silverstoneia flotator*** (Dunn, 1931) **new combination**; ***S. nubicola*** (Dunn, 1924) **new combination**; *S. erasmios* (Rivero and Serna, "1995" 2000) **new combination**.

CHARACTERIZATION, DIAGNOSIS, AND SUPPORT: Branch length = 46. Bremer support = 14.

Unambiguously optimized phenotypic synapomorphies are **(1)** occurrence of a complete ventrolateral stripe (Character 54, 0 → 2), **(2)** male abdomen color (Character 63, 3 → 0), **(3)** anteriorly pigmented large intestine (Character 66, 0 → 1), umbelliform larval mouth (Character 88, 0 → 1), **(4)** loss of emargination of the oral disc (89, 1 → 0), **(5)** origin of submarginal larval papillae (Character 91, 0 → 1), and **(6)** the loss of posterior keratodont rows in larvae (Character 94, 3 → 0).

Other characteristics include: (1) Dorsal coloration cryptic, brown; (2) pale oblique lateral stripe present; (3) pale dorsolateral stripe usually absent (present in some populations of *S. flotator* in Costa Rica); (4) pale ventrolateral stripe present; (5) dorsal skin texture posteriorly granular; (6) toe webbing basal between toes III and IV; (7) third finger of adult males swollen in named species (not swollen in two undescribed species; see below); (8) finger I longer than finger II; (9) finger discs moderately expanded; (10) median lingual process absent; (11) larval vent tube dextral; (12) larval oral disc shape umbelliform; (13) larval oral disc not emarginate; (14) lipophilic alkaloids absent; (15) chromosome number unknown; (16) testes entirely pigmented; (17) dark throat collar absent.

DISTRIBUTION: Costa Rica to southwestern Colombia (southern Valle del Cauca). Nominal and undescribed species (see below) all occur below 1,600 m.

ETYMOLOGY: *Silverstoneia* (gender feminine) is named in honor of Phillip A. Silverstone for his outstanding contribution to knowledge of dendrobatoid frogs. Silverstone named 11 species of dendrobatoids (all of which are still considered valid), and after 30 years, his superb monographs (Silverstone, 1975a, 1976) remain an essential

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starting point for students of dendrobatoid frogs. Furthermore, Silverstone carried out extensive field studies in South America in the late 1960s and early 1970s, particularly in the Pacific lowlands of Colombia, which have been key to understanding dendrobatoid diversity (e.g., Grant, 2004) and are especially central to discovering the diversity of this genus (see Comment).

COMMENT: These species have long been considered to form a distinct group, the first to recognize it (for *Silverstoneia flotator* and *S. nubicola*) being Dunn (1931) based on the swollen third finger of adult males and the unique larval mouth. At present, *Silverstoneia* contains only three species. However, the descriptions of five additional species (including "*nubicola*-spC" from the present analysis) are currently in manuscript form (T. Grant and C. W. Myers, in progress). All known larvae in this clade have an umbelliform oral disc with submarginal papillae and reduced keratodont rows.

SUBFAMILY: HYLOXALINAE **NEW SUBFAMILY**

IMMEDIATELY MORE INCLUSIVE TAXON: Dendrobatidae Cope, 1865.

SISTER GROUP: Dendrobatinae Wagler, 1865.

CONTENT (1 GENUS): *Hyloxalus* Jiménez de la Espada, 1871 "1870".

CHARACTERIZATION, DIAGNOSIS, AND SUPPORT: Branch length = 52. Bremer support = 35. All unambiguously optimized synapomorphies for this clade are from DNA sequences (see appendix 8).

DISTRIBUTION: Andes and adjacent Amazonian lowlands of South America.

COMMENT: Although this name is currently redundant with *Hyloxalus*, we anticipate that the available names *Cryptophyllobates* and *Phyllodromus* will be resurrected in the near future, making Hyloxalinae an informative name (for species groups, see Comments for *Hyloxalus*, below). Moreover, recognition of Hyloxalinae is necessitated by the recognition of Dendrobatinae for the five genera of brightly colored and highly toxic species.

GENUS: *HYLOXALUS* JIMÉNEZ DE LA ESPADA, 1871 "1870"

Hyloxalus Jiménez de la Espada, 1871 "1870". Type species: *Hyloxalus fuliginosus* Jiménez de la Espada, 1871 "1870" by subsequent designation by Savage (1968).

Phyllodromus Jiménez de la Espada, 1871 "1870". Type species: *Phyllodromus pulchellum* Jiménez de la Espada, 1871 "1870, by monotypy.

Cryptophyllobates Lötters, Jungfer, and Widmer, 2000. Type species: *Phyllobates azureiventris* by original designation.

IMMEDIATELY MORE INCLUSIVE TAXON: Hyloxalinae **new subfamily**.

SISTER GROUP: Dendrobatinae Wagler, 1865.

CONTENT (57 SPECIES): *Hyloxalus abditaurantius* (Silverstone, 1975) **new combination**; *H. aeruginosus* (Duellman, 2004) **new combination**; *H. anthracinus* (Edwards, 1971) **new combination**; *H. argyrogaster* (Morales and Schulte, 1993) **new combination**; ***H. awa*** (Coloma, 1995) **new combination**; ***H. azureiventris*** (Kneller and Henle, 1985) **new combination**; *H. betancuri* (Rivero and Serna, 1991) **new combination**; ***H. bocagei*** Jiménez de la Espada, 1871; *H. borjai* (Rivero and Serna, 2000 "1995") **new combination**; *H. breviquartus* (Rivero and Serna, 1986) **new combination**; *H. cevallosi* (Rivero, 1991) **new combination**; ***H. chlorocraspedus*** (Caldwell, 2005) **new combnation**; *H. chocoensis* Boulenger, 1912; ***H. delatorreae*** (Coloma, 1995) **new combination**; *H. edwardsi* (Lynch, 1982) **new combination**; ***H. elachyhistus*** (Edwards, 1971) **new combination**; *H. eleutherodactylus* (Duellman, 2004) **new combination**; *H. exasperatus* (Duellman and Lynch, 1988) **new combination**; *H. excisus* (Rivero and Serna 2000 "1995") **new combination**; *H. faciopuntulatus* (Rivero, 1991) **new combination**; *H. fallax* (Rivero, 1991) **new combination**; *H. fascianiger* (Grant and Castro-H., 1998) **new combination**; *H. fuliginosus* Jiménez de la Espada, 1871; ***H. idiomelus*** (Rivero, 1991) **new combination**; ***H. infraguttatus*** (Boulenger, 1898) **new combination**; ***H. insulatus*** (Duellman, 2004) **new combination**; *H. lehmanni* (Silverstone, 1971) **new combination**; *H. leucophaeus* (Duellman, 2004) **new combination**; *H. littoralis* (Péfaur, 1984) **new combination**; *H. maculosus* (Rivero, 1991) **new combination**; *H. maquipucuna* (Coloma, 1995) **new combination**; *H. marmoreoventris* (Rivero, 1991) **new combination**; *H. mittermeieri* (Rivero, 1991) **new combination**; *H. mystax* (Duellman and Simmons, 1988) **new combination**; ***H.***

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nexipus (Frost, 1985) **new combination**; *H. parcus* (Rivero, 1991) **new combination**; *H. patitae* (Lötters, Morales, and Proy, 2003) **new combination**; *H. peculiaris* (Rivero, 1991) **new combination**; *H. peruvianus* (Melin, 1941) **new combination**; *H. pinguis* (Rivero and Granados-Diaz, 1990 "1989") **new combination**; ***H. pulchellus*** (Jiménez de la Espada, 1871) **new combination**; ***H. pulcherrimus*** (Duellman, 2004) **new combination**; *H. pumilus* (Rivero, 1991) **new combination**; *H. ramosi* (Silverstone, 1971) **new combination**; *H. ruizi* (Lynch, 1982) **new combination**; *H. saltuarius* (Grant and Ardila-Robayo, 2002) **new combination**; ***H. sauli*** (Edwards, 1974) **new combination**; *H. shuar* (Duellman and Simmons, 1988) **new combination**; *H. sordidatus* (Duellman, 2004); *H. spilotogaster* (Duellman, 2004) **new combination**; ***H. subpunctatus*** (Cope, 1899) **new combination**; ***H. sylvaticus*** (Barbour and Noble, 1920) **new combination**; ***H. toachi*** (Coloma, 1995) **new combination**; *H. utcubambensis* (Morales, 1994) **new combination**; *H. vergeli* Hellmich, 1940; ***H. vertebralis*** (Boulenger, 1899) **new combination**; *H. whymperi* (Boulenger, 1882) **new combination**.

CHARACTERIZATION, DIAGNOSIS, AND SUPPORT: As for Hyloxalinae, above.

Other characteristics include: (1) Dorsal coloration usually cryptic, brown, gray, or black (conspicuous and bright in *H. azureiventris*); (2) pale oblique lateral stripe present; (3) pale dorsolateral stripe absent in most (but not all) species; (4) pale ventrolateral stripe usually absent; (5) dorsal skin texture posteriorly granular; (6) toe webbing varies from absent in most species to basal or extensive in some species; (7) third finger of adult males not swollen; (8) finger I shorter than finger II; (9) finger discs narrow to moderately expanded; (10) median lingual process absent; (11) larval vent tube dextral; (12) larval oral disc shape "normal" (not umbelliform); (13) larval oral disc emarginate; (14) lipophilic alkaloids absent; (15) chromosome number $2n = 24$ (known in *Hyloxalus subpunctatus* and *H. vertebralis*); (16) testes unpigmented in most species (reported as pigmented in *H. toachi* by Coloma, 1995); (17) dark throat collar absent.

DISTRIBUTION: Andean South America.

COMMENT: *Hyloxalus* contains approximately half of the species previously referred to the large, polyphyletic genus *Colostethus* (the other half being referred to the aromobatid genus *Allobates*). *Hyloxalus* is an exclusively Andean radiation, although some species occur in the adjacent foothills.

Unfortunately, available material of the type species, *Hyloxalus fuliginosus*, was inadequate to allow its inclusion in the present analysis, and the name is applied based on the presumed close relationship of that species and *H. bocagei*, that is, *H. bocagei* is treated herein as a proxy for *H. fuliginosus*. In the event that *H. fuliginosus* is found not to be part of this clade, the oldest available name would be *Phyllodromus*, for which the type species is *H. pulchellus*.

Given the number and diversity of species referred to *Hyloxalus*, additional partitioning will be warranted as knowledge of the group increases. We include two previously recognized groups in *Hyloxalus*: (1) The *Hyloxalus ramosi* group is delimited by the unique occurrence of black, apparently glandular tissue on the inner surface of the arm. In addition to the undescribed *H.* "Ibagué", included in the present analysis, we have observed this character-state in *H. anthracinus*, *H. cevallosi*, *H. exasperatus*, *H. fascianiger*, *H. lehmanni*, *H. ramosi*, and *H. saltuarius*. No genus-group name exists for this clade. (2) A group we refer to herein as the *H. azureiventris* group is strongly supported as monophyletic in our analysis, and the external resemblance of the species is undeniable. An unambiguously optimized morphological synapomorphy for the clade is the occurrence of a pale dorsolateral stripe. In addition to *H. azureiventris*, *H. nexipus*, and *H. chlorocraspedus* (all included in the present analysis), this group includes *H. eleutherodactylus* and *H. patitae*. A species sequenced by Santos et al. (2003) is also part of this clade, but its identity remains to be clarified. The genus-group name *Cryptophyllobates* is available for this clade. Formal taxonomic recognition of these clades would render *Hyloxalus* paraphyletic.

SUBFAMILY: DENDROBATINAE COPE, 1865

IMMEDIATELY MORE INCLUSIVE TAXON: Dendrobatidae Cope, 1865.

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SISTER GROUP: Hyloxalinae **new subfamily**.

CONTENT: *Adelphobates* **new genus**; *Dendrobates* Wagler, 1830; *Minyobates* Myers, 1987; *Oophaga* Bauer, 1988; *Phyllobates* Duméril and Bibron, 1941; *Ranitomeya* Bauer, 1988.

CHARACTERIZATION, DIAGNOSIS, AND SUPPORT: Branch length = 63. Bremer support = 20.

Unambiguously optimized phenotypic synapomorphies for this clade are **(1)** dorsal skin texture smooth (Character 0, 1 → 0), **(2)** pale oblique lateral stripe absent (Character 55, 1 → 0), **(3)** iris coloration lacking metallic pigmentation and pupil ring (Character 65, 1 → 0), **(4)** larvae deposited in phytotelmata (Character 111, 0 → 1), and **(5)** the ability to sequester lipophilic alkaloids (Character 147, 0 → 1).

DISTRIBUTION: As for Dendrobatoidea, excluding the Atlantic forest of Brazil and higher elevations of the Andes.

COMMENT: For synonymy see Dendrobatoidea, above.

GENUS: *PHYLLOBATES* DUMÉRIL AND BIBRON, 1841

Phyllobates Duméril and Bibron, 1841. Type species: *Phyllobates bicolor* Duméril and Bibron, 1841 by monotypy.

IMMEDIATELY MORE INCLUSIVE TAXON: Dendrobatinae Cope, 1865.

SISTER GROUP: Unnamed clade composed of *Adelphobates* **new genus**; *Dendrobates* Wagler, 1830; *Minyobates* Myers, 1987; *Oophaga* Bauer, 1988; *Ranitomeya* Bauer, 1988.

CONTENT (5 SPECIES): ***Phyllobates aurotaenia*** (Boulenger, 1913); ***P. bicolor*** Duméril and Bibron, 1841; ***P. lugubris*** (Schmidt, 1857); ***P. terribilis*** Myers, Daly, and Malkin, 1978; and ***P. vittatus*** (Cope, 1893).

CHARACTERIZATION, DIAGNOSIS, AND SUPPORT: Branch length = 146. Bremer support = 132.

Unambiguously optimized phenotypic synapomorphies of this clade are **(1)** finger I longer than finger II (Character 5, 2 → 3) and **(2)** the uniquely derived ability to sequester batrachotoxin (Character 148, 0 → 1).

Other characteristics include: (1) Dorsal coloration bright, composed of either shiny black with bright yellow, orange, or green dorsolateral stripes or solid bright yellow, orange or green; (2) pale oblique lateral stripe absent; (3) pale dorsolateral stripe present in all juveniles, lost ontogenetically in *P. bicolor* and *P. terribilis*; (4) pale ventrolateral stripe absent in most, a wavy series of elongate spots in *P. vittatus*; (5) dorsal skin texture smooth; (6) toe webbing absent; (7) third finger of adult males not swollen; (8) finger I longer than finger II; (9) finger discs narrow to moderately expanded; (10) median lingual process absent; (11) larval vent tube dextral; (12) larval oral disc shape "normal" (not umbelliform); (13) lipophilic alkaloids present; (14) larval oral disc emarginate; (15) chromosome number $2n = 24$ (known in *Phyllobates lugubris*); (16) testes unpigmented; (17) dark throat collar absent.

DISTRIBUTION: *Phyllobates* is an exclusively *trans*-Andean group with species occurring from Costa Rica through the Chocó region of southwestern Colombia up to a maximum elevation of approximately 1500 m.

COMMENT: *Phyllobates* in the present taxonomy is unchanged from that proposed by Myers et al. (1978).

GENUS: *MINYOBATES* MYERS, 1987

Minyobates Myers, 1987. Type species: *Dendrobates steyermarki* Rivero, 1971 by original designation.

IMMEDIATELY MORE INCLUSIVE TAXON: Dendrobatinae Cope, 1865.

SISTER GROUP: Unnamed clade composed of *Adelphobates* **new genus**; *Dendrobates* Wagler, 1830; *Oophaga* Bauer, 1994; *Ranitomeya* Bauer, 1988.

CONTENT (1 SPECIES): ***Minyobates steyermarki*** (Rivero, 1971).

CHARACTERIZATION, DIAGNOSIS, AND SUPPORT: Branch length = 39.

Other characteristics include: (1) Dorsal coloration conspicuous, bright; (2) pale oblique lateral stripe absent; (3) pale dorsolateral stripe absent; (4) pale ventrolateral stripe absent; (5) dorsal skin texture smooth; (6) toe webbing absent; (7) third finger of adult males not swollen; (8) finger I longer than

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finger II; (9) finger discs II–IV weakly expanded; (10) median lingual process absent; (11) larval vent tube dextral or medial; (12) larval oral disc shape "normal" (not umbelliform); (13) larval oral disc emarginate; (14) lipophilic alkaloids present; (15) chromosome number unknown; (16) testes color polymorphic; (17) dark throat collar absent.

DISTRIBUTION: *Minyobates steyermarki* is known only from Cerro Yapacana, Venezuela.

COMMENT: The placement of *Minyobates steyermarki* is poorly supported, as indicated by the low Bremer values of associated nodes. During the course of the analysis its placement alternated between being sister to all dendrobatines except *Phyllobates*—as in our optimal solutions and the findings reported by Vences et al. (2003a)—and sister to all species referred to *Ranitomeya* (see below) in near-optimal solutions. Recognizing *Minyobates* as a monotypic genus is consistent with both of those solutions and expedient in that it does not require additional taxa to be named.

GENUS: *RANITOMEYA* BAUER, 1988

Ranitomeya Bauer, 1988. Type species: *Dendrobates reticulatus* Boulenger, 1884 "1883" by original designation.

IMMEDIATELY MORE INCLUSIVE TAXON: Dendrobatinae Cope, 1865.

SISTER GROUP: Unnamed clade composed of *Adelphobates* **new genus**; *Dendrobates* Wagler, 1830; *Oophaga* Bauer, 1994.

CONTENT (24 SPECIES): *Ranitomeya abdita* (Myers and Daly, 1976) **new combination**; *R. altobueyensis* (Silverstone, 1975) **new combination**; ***R. amazonica*** (Schulte, 1999) **new combination**; ***R. biolat*** (Morales, 1992) **new combination**; *R. bombetes* (Myers and Daly, 1980) **new combination**; ***R. claudiae*** (Jungfer, Lötters, and Jorgens, 2000) **new combination**; *R. duellmani* (Schulte, 1999) **new combination**; ***R. fantastica*** (Boulenger, 1884 "1883"); *R. flavovittata* (Schulte, 1999) **new combination**; ***R. fulgurita*** (Silverstone, 1975) **new combination**; *R. ignea* (Melin, 1941) **new combination**; ***R. imitator*** (Schulte, 1986) **new combination**; *R. intermedia* (Schulte, 1999) **new combination**; *R. lamasi* (Morales, 1992) **new combination**; ***R. minuta*** (Shreve, 1935) **new combination**; *R. opisthomelas* (Boulenger, 1899) **new combination**; *R. reticulata* (Boulenger, 1884 "1883"); *R. rubrocephala* (Schulte, 1999); *R. sirensis* (Aichinger, 1991) **new combination**; ***R. vanzolinii*** (Myers, 1982) **new combination**; ***R. variabilis*** (Zimmermann and Zimmermann, 1988); ***R. ventrimaculata*** (Shreve, 1935) **new combination**; *R. viridis* (Myers and Daly, 1976) **new combination**; *R. virolinensis* (Ruiz-Carranza and Ramírez-Pinilla, 1992) **new combination**.

CHARACTERIZATION, DIAGNOSIS, AND SUPPORT: Branch length = 83. Bremer support = 13.

The sole unambiguously optimized phenotypic synapomorphy for this clade is **(1)** the greatly reduced length of finger I (Character 5, 1 → 0).

Other characteristics include: (1) Dorsal coloration conspicuous, bright; (2) pale oblique lateral stripe absent; (3) pale dorsolateral stripe absent in most species; (4) pale ventrolateral stripe absent; (5) dorsal skin texture smooth; (6) toe webbing absent; (7) third finger of adult males not swollen; (8) finger I shorter than finger II; (9) finger discs II–IV greatly expanded in most species; (10) median lingual process absent; (11) larval vent tube dextral or medial; (12) larval oral disc shape "normal" (not umbelliform); (13) larval oral disc emarginate; (14) lipophilic alkaloids present; (15) chromosome number $2n = 20$ (known in *Ranitomeya vanzolinii*); (16) testes pigmented in most species (polymorphic in *R. imitator*); (17) dark throat collar absent.

DISTRIBUTION: As for Dendrobatinae, above.

COMMENT: *Ranitomeya* is equivalent to Silverstone's (1975a) *minutus* group with the removal of *steyermarki* and *quinquevittatus* sensu stricto. Within *Ranitomeya* we recovered a monophyletic radiation equivalent to *Minyobates* sensu Myers (1987) minus *steyermarki* (the type species of *Minyobates*). This clade is found in Central America and the Colombian Chocó and is absent from the Amazon basin and eastern slope of the Cordillera Oriental. The sister clade to that radiation is an exclusively Amazonian group. We recommend referring to these clades as

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the *minutus* and *ventrimaculatus* groups, respectively, pending further study of the placement of *steyermarki* and the Andean species.

GENUS: *ADELPHOBATES* NEW GENUS

Adelphobates **new genus**. Type species: *Dendrobates castaneoticus* Caldwell and Myers, 1990.

IMMEDIATELY MORE INCLUSIVE TAXON: Dendrobatinae Cope, 1865.

SISTER GROUP: Unnamed clade composed of *Dendrobates* Wagler, 1830; *Oophaga* Bauer, 1994

CONTENT (4 SPECIES): *Adelphobates captivus* (Myers, 1982) **new combination**; ***A. castaneoticus*** (Caldwell and Myers, 1990) **new combination**; ***A. galactonotus*** (Steindachner, 1864) **new combination**; ***A. quinquevittatus*** (Steindachner, 1864) **new combination**.

CHARACTERIZATION, DIAGNOSIS, AND SUPPORT: Branch length = 105. Bremer support = 37. All unambiguously optimized synapomorphies for this clade are from DNA sequences (see appendix 8).

Other characteristics include: (1) Dorsal coloration conspicuous, bright; (2) pale oblique lateral stripe absent or present; (3) pale dorsolateral stripe absent or present; (4) pale ventrolateral stripe absent or present; (5) dorsal skin texture smooth; (6) toe webbing absent; (7) third finger of adult males not swollen; (8) finger I shorter than finger II; (9) finger discs of fingers II–IV greatly expanded; (10) median lingual process absent; (11) larval vent tube medial; (12) larval oral disc shape "normal" (not umbelliform); (13) larval oral disc emarginate; (14) lipophilic alkaloids present; (15) chromosome number unknown; (16) testes unpigmented in *Adelphobates castaneoticus* and *A. galactonotus*, pigmented in *A. quinquevittatus*; (17) dark throat collar absent.

DISTRIBUTION: Amazonia.

ETYMOLOGY: *Adelphobates*, from the Greek adelphos (twin, brother) and bates (a walker). Gender masculine. We take great pleasure in proposing this name in honor of Charles W. Myers and John W. Daly. Through an ambitious field and laboratory research program that began nearly four decades ago and remains active, the Myers and Daly collaboration has led to an unprecedented increase in scientific knowledge of dendrobatoid frogs. Although they pursued independent investigations, their names have become synonymous with this group, and it is only fitting that the contribution of these scientific "brothers" be commemorated by this generic name.

COMMENT: *Adelphobates galactonotus* was previously considered to be a species of the *tinctorius* species group (e.g., Silverstone, 1975a), and the remaining species were placed in what is herein called *Ranitomeya*. Caldwell and Myers (1990) considered *A. castaneoticus* and *A. quinquevittatus* to be sister species; however, in addition to the extensive support from DNA sequence evidence for the proposed relationships, *A. castaneoticus* and *A. galactonotus* share the loss of testis pigmentation. We include *Adelphobates captivus* in this genus instead of *Ranitomeya* on the basis of its distinctive dorsal pattern of elongate spots, found also in *A. castaneoticus* but not known in any species of *Ranitomeya*.

GENUS: *OOPHAGA* BAUER, 1994

Oophaga Bauer, 1988. Type species: *Dendrobates pumilio* Schmidt, 1857 by original designation.

IMMEDIATELY MORE INCLUSIVE TAXON: Dendrobatinae Cope, 1865.

SISTER GROUP: *Dendrobates* Wagler, 1830.

CONTENT (9 SPECIES): ***Oophaga arborea*** (Myers, Daly, and Martínez, 1984); ***O. granulifera*** (Taylor, 1958); ***O. histrionica*** (Berthold, 1845); ***O. lehmanni*** (Myers and Daly, 1976); *O. occultator* (Myers and Daly, 1976); ***O. pumilio*** (Schmidt, 1857); ***O. speciosa*** (Schmidt, 1857); ***O. sylvatica*** (Funkhouser, 1956); ***O. vicentei*** (Jungfer, Weygoldt, and Juraske, 1996) **new combination**.

CHARACTERIZATION, DIAGNOSIS, AND SUPPORT: Branch length = 132. Bremer support = 114.

Unambiguously optimized phenotypic synapomorphies of this clade are **(1)** larval marginal papillae enlarged (Character 90, 0 → 1), **(2)** occurrence of a single anterior larval tooth keratodont (Character 93, 2 → 1), **(3)** single posterior larval tooth keratodont (Character 94, 3 → 1), **(4)** the chirp call (Character 99, 0 → 1); **(5)** cloacal touching

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during courtship/oviposition (Character 106, 0 → 1), **(6)** female nurse frog (Character 110, 0 → 1), **(7)** omosternum entirely cartilaginous (Character 127, 1 → 0), **(8)** anterior projection of suprascapula heavily calcified (Character 128, 0 → 1), **(9)** sacrum and vertebra 8 fused (Character 144, 0 → 1), **(10)** vertebrae 2 and 3 fused (Character 146, 0 → 1).

Other characteristics include: (1) Dorsal coloration conspicuous, bright; (2) pale oblique lateral stripe absent; (3) pale dorsolateral stripe absent; (4) pale ventrolateral stripe absent; (5) dorsal skin texture smooth in all but *O. granulifera*, in which it is strongly granular; (6) toe webbing absent; (7) third finger of adult males not swollen; (8) finger I shorter than finger II; (9) finger discs moderately expanded; (10) median lingual process absent; (11) larval vent tube medial; (12) larval oral disc shape "normal" (not umbelliform); (13) larval oral disc not emarginate; (14) lipophilic alkaloids present; (15) chromosome number $2n = 20$ (known in *Oophaga granulifera*, *O. pumilio*, and *O. sylvatica*); (16) testes pigmented (entirely in most; medially in *O. sylvatica*); (17) dark throat collar absent.

DISTRIBUTION: Nicaragua through the Colombian Chocó to northern Ecuador at elevations below 1,200 m.

COMMENT: *Oophaga* is identical to the *histrionicus* group of Myers et al. (1984), with the addition of newly discovered taxa. This is one of the most conspicuous and well-known clades within Dendrobatoidea, thanks to its chirp call, tadpole morphology, and reproductive behavior.

GENUS: *DENDROBATES* WAGLER, 1830

Hysaplesia Boie *in* Schlegel, 1826. Type species: *Calamata punctatus* Schneider, 1799 by subsequent designation by Stejneger, 1937.

Dendrobates Wagler, 1830. Type species: *Rana tinctoria* Cuvier, 1797 by subsequent designation by Diméril and Bibron, 1841.

Eubaphus Bonaparte, 1832. Type species: *Rana tinctoria* Shaw 1802, by monotypy.

Dendromedusa Gistel, 1848. Replacement name for *Hylaplesia* Boie, 1827 (an incorrect subsequent spelling of *Hysaplesia*).

IMMEDIATELY MORE INCLUSIVE TAXON: Dendrobatinae Cope, 1865.

SISTER GROUP: *Oophaga* Bauer, 1988.

CONTENT (6 SPECIES): ***Dendrobates auratus*** Girard, 1855; ***Dendrobates azureus*** Hoogmoed, 1969; ***Dendrobates leucomelas*** Steindachner, 1864; *Dendrobates nubeculosus* Jungfer and Böhme, 2004; ***Dendrobates tinctorius*** (Cuvier, 1797); ***Dendrobates truncatus*** (Cope, 1861).

CHARACTERIZATION, DIAGNOSIS, AND SUPPORT: Branch length = 92. Bremer support = 79. All unambiguously optimized synapomorphies for this clade are from DNA sequences (see appendix 8).

Other characteristics include: (1) Dorsal coloration conspicuous, bright; (2) pale oblique lateral stripe absent; (3) pale dorsolateral stripe absent in most species (present in *D. truncatus*); (4) pale ventrolateral stripe absent; (5) dorsal skin texture smooth; (6) toe webbing absent; (7) third finger of adult males not swollen; (8) finger I shorter than finger II; (9) finger discs moderately to greatly expanded; (10) median lingual process absent; (11) larval vent tube medial; (12) larval oral disc shape "normal" (not umbelliform); (13) larval oral disc emarginate; (14) lipophilic alkaloids present; (15) chromosome number $2n = 18$ (known in *Dendrobates auratus* and *D. truncatus*); (16) testes pigmented; (17) dark throat collar absent.

DISTRIBUTION: As for Dendrobatinae, above.

COMMENT: This greatly restricted *Dendrobates* clade is equivalent to the combination of Silverstone's (1975a) *Dendrobates tinctorius* group (minus *galactonotus*) and *Dendrobates auratus* group. See Savage et al. (in press) for nomenclatural notes on *Dendrobates*.

We include *Dendrobates azureus* as a valid species. However, Wollenberg et al. (2006) argue for its synonymy with *D. tinctorius*, which is also supported by our results (see above).

INCERTAE SEDIS AND NOMINA DUBIA

Of the 304 taxa that were named as or subsequently transferred into the current Dendrobatoidea, five are of dubious status. The identity of *Phyllobates peruensis* Steindachner, 1867 has been uncertain for well

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over a century. Boulenger (1882: 194) suspected it may be a species of *Hylodes*, and Silverstone (1976: 6) questioned whether it was a dendrobatid. The holotype does not exist at the Vienna Natural History Museum (F. Tiedemann, in litt. 10/10/02), and the description is inadequate to relate any known population to this name. We therefore consider this taxon to be nomen dubium.

The second species is *Prostherapis dunni* Rivero, 1961. La Marca (2004) redescribed the species, and we refer the reader to that paper for a complete account. La Marca clarified that, contrary to previous accounts, the species does not possess a collar (and is therefore not referable to *Mannophryne*) and appears to be confined to the central part of the Venezuelan Coastal Range. The feet are extensively webbed, the zygomatic ramus is elongate and robust, and the tongue lacks the median lingual process (T. Grant, personal obs.). Given these character-states and geographic distribution, it seems most likely that *Prostherapis dunni* is a species of *Aromobates*. However, we are unable to rule out the possibility that it is a species of *Rheobates*, also an aromobatid, given that *R. palmatus* also shares these character-states. Insofar as we have no further insights to offer into the systematics of *Prostherapis dunni*, we follow La Marca (2004: 24) in concluding that "[i]ts phylogenetic relationships remain enigmatic" and refer it only to Aromobatidae, incerta sedis.

The third species is *Dendrobates mysteriosus* Myers, 1982. Myers (1982) placed this species in the *captivus* group with *Adelphobates captivus*, stating that "[t]he large pale spots on either the dorsal or especially the ventral surface of the thigh may provide a necessary synapomorphy in support of such a relationship." Schulte (1990) concluded that it is not related to *A. captivus* (as *Dendrobates*) or any part of the *quinquevittatus* group (sensu Silverstone, 1975a, presumably) and is instead related to *Oophaga* (as the *Dendrobates histrionicus* group). He based this conclusion on shared size, absence of omosternum, occurrence of round spots on a dark background, similar reproductive behavior, an elevated number of small ova, and an apparently (no audiospectrographic data were presented) similar fundamental frequency of the call. None of these characters is unique to the *Oophaga*, and several other reported character-states conflict with this relationship (e.g., larval mouth parts). As such, given the current evidence, we consider *Dendrobates mystersiosus* to be Dendrobatinae, incerta sedis.

The fourth species is *Colostethus ramirezi* Rivero and Serna, 2000 "1995". Rivero and Serna (2000 "1995": 50) described this species from the northwestern Colombian Andes as "medium sized, surely referable to either group IV or IX" (translated freely from the Spanish), species of which are placed in the dendrobatid genera *Colostethus*, *Hyloxalus*, and *Silverstoneia* in the current taxonomy. The data reported by Rivero and Serna (2000 "1995") do not permit the species to be allocated defensibly to any of these genera, and we therefore consider it to be Dendrobatidae, incerta sedis.

Finally, *Colostethus poecilonotus* Rivero, 1991 is known only from the type locality at 500 m in the Peruvian department of Amazonas. Rivero (1991a) described this species as "probably belonging to Group IX", species of which are placed in *Anomaloglossus*, *Colostethus*, and (mostly) *Hyloxalus* in the current taxonomy. This species lacks the median lingual process (which excludes it from *Anomaloglossus*), but evidence is lacking to place it in either *Colostethus* or *Hyloxalus*. Likewise, there is no evidence to indicate that this is not a species of *Allobates*. As such, we consider this species to be Dendrobatoidea, incerta sedis.

DISCUSSION: CHARACTER EVOLUTION

The novel knowledge claims that emerge from phylogenetic analysis have implications beyond the immediate problems of systematics. By providing a causally relevant framework of reference, knowledge of phylogeny imposes meaningful structure on otherwise disparate biological data from unrelated fields of biology, which often leads to unanticipated insights and identifies novel problems for further investigation. It is this potential for cross-discipline unification that makes phylogenetic systematics a fundamen-

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tal part of an ampliative, progressive research program.

In this section, we analyze the implications of the phylogeny of Dendrobatoidea for the evolution of several characters and character systems. Although this does not entail phylogenetic analysis in the strict sense of cladogram searching, our approach remains decidedly phylogenetic. Rather than search for statistical correlations to explain biological variation in terms of its adaptive value, functional significance, or selective pressures (e.g., Summers and Earn, 1999; Caldwell and de Araújo, 2004), we explain it in terms of its evolutionary origins.

The following analysis of character evolution should be interpreted in light of two caveats: First, the analysis necessarily assumes the veracity and completeness of reported observations. For the most part this is not likely to be problematic. Data were taken either from personal observations, field notes and photographs, or published sources that were vetted by peer review. However, increased sampling may lead to alternative scorings. For example, nurse frog sex is usually known from one or a few observations, but detection of biparental transport requires multiple observations, by definition. Second, there are extensive missing data for several of the characters we analyze below, and, although the most parsimonious optimization often allows unambiguous retrodiction of unknown states, it is possible that future discoveries will overturn some retrodictions and favor alternative evolutionary explanations. Unless otherwise stated, only unambiguous optimizations are considered. There is no defensible basis for choosing between fast (accelerated) and slow (delayed) optimizations, making any evolutionary inference drawn from such optimizations untenable.

As noted above, many aspects of the natural history of dendrobatoids have been studied. Here we focus on adult habitat selection and reproductive biology, including parental care, larval habitat, and larval diet. Parental care in dendrobatoids involves at least three distinct components, each of which may be undertaken by one or both parents: clutch attendance, tadpole transport, and oocyte provision for larval consumption. Few data on clutch attendance are available (but were coded nonetheless as Character 109), and we therefore focus only on tadpole transport and provision of oocytes for larval consumption, the latter in the context of larval diet.

In terms of species diversity, the most thorough comparative study of dendrobatoid reproductive biology to date is that of Summers and McKeon (2004). However, the phylogeny used in that study was a composite "derived from several of the recent molecular phylogenetic analyses" (p. 56). The means of resolving conflict among those studies was not specified. Furthermore, species not included in any of those analyses were placed in the cladogram based on their assumed position (e.g., *Aromobates nocturnus*, *Dendrobates mysteriosus*). Additionally, as mentioned above (Phenotypic Characters), some character-states were misattributed by Summers and McKeon (2004), which has implications for the evolutionary scenarios they proposed.

Adult Habitat Selection

The traditional view inherited from Noble (1926) is that dendrobatoids evolved progressively from more aquatic to more terrestrial species. This was also manifest in the phylogeny proposed by Myers et al. (1991), in which the fully aquatic *Aromobates nocturnus* was sister to all other dendrobatids, which, in turn, were divided into the riparian "*Hyloxalus* sensu stricto" and more terrestrial "*Colostethus* sensu stricto" and aposematic taxa. Adult association with water was coded here as Character 114.

The ancestral state for Dendrobatoidea is ambiguous in our analysis. However, the ancestral state for Dendrobatidae optimizes unambiguously as terrestrial (i.e., independent of bodies of water, adults reaching 30 m or more into the forest), with no fewer than six independent origins of riparian habitat preference (i.e., adults occurring along streams or pools, extending no further than 3 m from the water's edge) and one subsequent origin of terrestriality (in *Hyloxalus toachi*; see Coloma, 1995: 54).

Among aromobatids the situation is less clear. Under slow optimization the ancestral

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state is riparian, with five independent origins of terrestriality and one subsequent return to a riparian lifestyle. Under fast optimization the ancestral state is terrestrial, with five independent origins of riparian habitat preference and one reversal to terrestriality. Nevertheless, it is clear that rather than being the primitive state for dendrobatoids (as proposed by Myers et al., 1991), the fully aquatic behavior of *Aromobates nocturnus* is unambiguously derived.

It is also clear that neither clade evolved through a simple progression from a more aquatic lifestyle to a more terrestrial one, and the pattern that emerges is complex. Nevertheless, adult association with water is conserved phylogenetically, with a retention index of 0.71. In some cases, the transition is accompanied by morphological transformations that are presumably associated with the degree of association with water, such as the gain or loss of webbing (e.g., *Hyloxalus bocagei*, *H. nexipus*, *Rheobates palmatus*, and *Anomaloglossus tepuyensis* all possess extensive toe webbing). However, although there are no extensively webbed species coded as independent of water, species with intermediate webbing may be terrestrial (e.g., *Colostethus fraterdanieli*, with basal webbing between toes II and III) or riparian (e.g., *Hyloxalus insulatus*, with the same degree of webbing between toes II and III).

Reproductive Amplexus

Cephalic reproductive amplexus has long been considered a synapomorphy of Dendrobatoidea, with the absence in numerous dendrobatids explained as a derived loss within the clade (e.g., Duellman and Trueb, 1986; Myers and Ford, 1986; Myers et al., 1991; Haas, 2003). Although data are lacking for many species, our results indicate unambiguously that axillary amplexus was lost (Character 105, $1 \rightarrow 0$) in the most recent common ancestor of Dendrobatoidea, with cephalic amplexus derived independently (Character 105, $0 \rightarrow 2$) in *Anomaloglossus* (either in the common ancestor of the genus or within the genus; data are only available for *A. beebei*), the most recent common ancestor of Colostethinae, and *Minyobates steyermarki*. This reversal of the polarity of this character in dendrobatoids necessitates a fundamental rethinking of the evolution of amplexus in Dendrobatoidea. For example, rather than the cephalic grasping that occurs during wrestling and courtship being a vestigial remnant of the ancestral cephalic reproductive amplexus (e.g., Myers et al., 1991), our results suggest this behavior may be a first, intermediate step toward cephalic reproductive amplexus.

Sex of Nurse Frogs

Previous studies have claimed dorsal tadpole transport as a synapomorphy of Dendrobatoidea (e.g., Myers, 1987; Weygoldt, 1987), which is corroborated unambiguously in the present study. Moreover, the two included dendrobatoids known to lack dorsal transport (*Allobates nidicola* and *Anomaloglossus stepheni*; both aromobatids) lost it independently, as discussed in greater detail below in the context of larval endotrophy.

Tadpole transport by male nurse frogs is also the unambiguously primitive state for dendrobatoids, with transport by female nurse frogs and biparental transport having evolved repeatedly. Among aromobatids, transport exclusively by female nurse frogs evolved only in *Allobates talamancae*. Tadpole transport remains unknown in the undescribed sister species of *A. talamancae* (*A.* "Magdalena"), but no other aromobatid is known to have exclusively female nurse frogs.

Biparental transport evolved independently in the ancestor of the *Allobates femoralis* complex and *A. trilineatus*, although the particulars of each case are unclear. First, tadpole transport is unknown in *A. zaparo*. Second, we coded all specimens presumed to be "*Allobates femoralis*" on morphological grounds as having biparental transport. However, this is based on reports by Silverstone (1976: 31) of female nurse frogs from Peru and Suriname, Lescure (1976a: 487, 1976b) of male nurse frogs from French Guiana, and Aichinger (1991) of male nurse frogs from Peru (explicit reports of both sexes are by Weygoldt, 1987 and Caldwell and de Araújo, 2005). In light of the evidence that *A. femoralis* is a complex of species it is possible that at least some of these species may have

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nurse frogs of a single sex. Nevertheless, Caldwell and de Araújo (2005) reported nurse frogs of both sexes for this species at a single locality (Rio Curuá-Una, Brazil), and there is no evidence to suggest more than one species is involved. Observations of biparental transport in *A. trilineatus* also occurred at a single locality (Panguana, Peru; Aichinger, 1991), and, whether or not this is viewed as a complex of species, there is no evidence that more than one *trilineatus* complex species occurs there. Larval transport is unknown in the closest relatives of *A. trilineatus*, but *A. insperatus* has exclusively male transport.

Among dendrobatids, transport by exclusively female nurse frogs evolved two or three times: once or twice in *Colostethus* and once in the ancestor of *Oophaga*. Among species of *Colostethus*, *C. panamensis* and *C. pratti* possess female nurse frogs, whereas *C. fraterdanieli* and the undescribed species *C.* "*pratti*-like" are known only to have male nurse frogs. The ambiguity is due to the unknown states of *C. imbricolus* and, in particular, *C. inguinalis* (note that prior reports of *C. inguinalis* transport apply to *C. panamensis*; Grant, 2004). Finding that *C. inguinalis* has male nurse frogs would entail independent origins of female nurse frogs in *C. panamensis* and *C. pratti*; finding that *C. inguinalis* has female nurse frogs would imply a single origin of female nurse frogs, with a reversal to male nurse frogs in *C.* "*pratti*-like".

Female larval transport optimizes unambiguously as homologous in all species of *Oophaga*. In this clade, the shift to female transport was accompanied by the production of maternal oocytes for larval consumption (see Character 112). The adaptive significance, if any, of this correlation is unknown, but the independent evolution of female nurse frogs in lineages that lack larval oophagy demonstrates that the relation is not necessary biologically. It should also be noted that larval use of phytotelmata (Character 111) arose in the common ancestor of Dendrobatinae and is therefore not coupled with female transport (or oophagy; see below).

As in Aromobatidae, biparental transport appears to have evolved multiple times in Dendrobatidae. Coloma (1995:20) reported a male nurse frog for *Hyloxalus awa*, but Mudrack's (1969) detailed observations of the breeding behavior of *H. awa* (as *Phyllobates* sp.) in captivity showed that either sex may transport tadpoles.[16] *Ameerega hahneli* and *A. petersi* are closely related species, but biparental care (reported for *A. hahneli* [as *Epipedobates pictus*] by Aichinger, 1991 [see also Haddad and Martins, 1994:291; Kok, 2000:13] and *A. petersi* by Silverstone, 1976:38) optimizes unambiguously as independently evolved.

Larval Habitat and Diet

Three habitats are exploited by larval dendrobatoids (Character 111). The primitive state for dendrobatoids is for larvae to occupy ground level pools or streams, as is typical of most anurans. Larval use of phytotelmata (i.e., phytotelm breeding) evolved three times: twice in aromobatids and once in dendrobatids. Among aromobatids, phytotelm breeding was reported for *Anomaloglossus beebei* by Bourne et al. (2001). In the present study, we also found that its sister species *A. roraima* is a phytotelm breeder. Adults and tadpoles of *A. roraima* were collected from tank bromeliads near the type locality, and tadpole identification was accomplished by analysis of DNA sequences. The cytochrome *b* sequences of the three specimens sampled (two adults, one tadpole) differ in only 1–3 bp (0.3–0.8% uncorrected pairwise distance). Larval habitat is unknown for all close relatives of *A. beebei* and *A. roraima*. As such, it is unclear if phytotelm breeding is homologous in just these two species or a more inclusive clade.

The second origin of larval use of phytotelmata in aromobatids occurred in *Allobates femoralis*, as reported by Caldwell and de Araújo (2004). Nevertheless, in this species,

[16] Weygoldt (1987: 55) disputed Mudrack's (1969) claim of biparental care in *Hyloxalus awa* (as *Colostethus* sp.), stating that it "may be a captivity artifact because under crowded conditions many frogs occasionally attempt to sit on or close to eggs". However, that does not address Mudrack's observation that both males and females actually transport tadpoles. We therefore accept Mudrack's report at face value.

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phytotelm breeding is most likely opportunistic, that is, ground-level phytotelmata are probably exploited like any other ground-level body of water and not targeted preferentially. This species is not known to exploit aboveground phytotelmata. (Caldwell and de Araújo also mentioned finding "*Colostethus*" [probably *Allobates*] larvae in ground-level phytotelmata, but they did not identify the species.)

Among dendrobatids, available evidence indicates that phytotelm breeding evolved only once, in the most recent common ancestor of Dendrobatinae (*Phyllobates* + *Minyobates* + *Ranitomeya* + *Adelphobates* + *Oophaga* + *Dendrobates*). Within that clade, *Dendrobates leucomelas* reevolved the larval use of ground-level streams and pools, and *D. auratus* and *D. truncatus* evolved a generalist strategy whereby they transport larvae to aboveground phytotelmata or ground-level water bodies.

Larval oophagy (i.e., larval consumption of nutritive eggs provided by the mother; Character 112) evolved independently in phytotelm breeders of Dendrobatidae and Aromobatidae. In *Oophaga*, females perform all parental care and deposit nutritive oocytes for larval consumption without any involvement of the male. Brust (1993) and Pramuk and Hiler (1999) demonstrated the obligate oophagy of *O. pumilio* larvae, and it is likely that this is the case for the remainder of the clade as well. Insofar as is known, this has not evolved in Aromobatidae.

Nevertheless, in both Aromobatidae and Dendrobatidae a form of biparental care has evolved in which courtship culminates in the female depositing oocytes directly into the water for larval consumption, that is, male involvement in courtship is required to stimulate the female to release oocytes (Character 113). This cooperative behavior was first reported for the dendrobatines *Ranitomeya reticulatus* (Kneller, 1982; Zimmermann and Zimmermann, 1984), *R. vanzolinii* (Caldwell, 1997; Caldwell and de Oliveira, 1999) and *R. ventrimaculatus* (Zimmermann and Zimmermann, 1988, as *quinquevittatus*; note that exclusively male care was observed in Peruvian *R. ventrimaculatus* by Summers et al., 1999b, further supporting Caldwell and Myers's, 1990, conjecture that this is a complex of cryptic species) and more recently for the aromobatid *Anomaloglossus beebei* (Bourne et al., 2001). Even in these cases of biparental care, oocytes are not fertilized and are deposited directly into the water (and not on the dry surfaces above water), which indicates that they are deposited solely for larval consumption and not merely as a biproduct of repeated mating. This reproductive mode therefore differs from larval oophagy in *Osteocephalus* (Hylidae), in which parents mate repeatedly at the same sites and freshly laid eggs are either consumed by older siblings or survive through competition to metamorphosis (Jungfer and Weygoldt, 1999; see also Haddad et al., 2005, in regard to *Aplastodiscus perviridis*). However, the oophagy resembles that of the foam-nest breeder *Leptodactylus fallax*, in which maternal provisioning of nutritive oocytes is unaccompanied by the male (Gibson and Buley, 2004).

According to available data, nidicolous larvae evolved at least twice in Aromobatidae and never in Dendrobatidae. *Anomaloglossus stepheni* (Juncá et al., 1994; Juncá, 1996, 1998) and *Allobates nidicola* are not closely related. *Anomaloglossus degranvillei* is also endotrophic, but this species is exoviviparous (Altig and Johnston, 1989), that is, tadpoles develop while being transported by the male nurse frog (see review by Caldwell and Lima, 2003). *Allobates chalcopis* is also endotrophic (Kaiser and Altig, 1994) and is predicted to be exoviviparous (Juncá et al., 1994). The phylogenetic placement of *A. chalcopis* is somewhat unclear in that it was not included explicitly in the present study. Nevertheless, it lacks the median lingual process, which suggests it is not closely related to *Anomaloglossus stepheni*, and the fact that it is endotrophic and has $2n = 22$ chromosomes suggests it may be closely related to *A. nidicola* (see A Monophyletic Taxonomy, above, for further discussion of this species).

As coded for the present analysis, endotrophy optimizes unambiguously as the primitive state for the nonwebbed clade of *Anomaloglossus*. Nevertheless, this must be interpreted in light of (1) the extensive missing data and (2) the fact that we coded observed specimens of *A. "degranvillei"* from Guyana according to reproductive observa-

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tions made on *A. degranvillei* sensu stricto from French Guiana. As discussed above, these are likely different species. In that case, and assuming that *A. ''degranvillei''* is not endotrophic, endotrophy would optimize as homologous in the less inclusive clade that includes *A. stepheni*. In either case, current evidence indicates at least two independent origins of endotrophy in aromobatid frogs (depending on the exact placement of *Allobates chalcopis*). Further investigation will be required to determine if the independent origins of endotrophy are accompanied by different developmental modifications as well. Detailed developmental data exist for only a few anurans (reviewed by Thibaudeau and Altig, 1999; Callery et al., 2001; Desnitskiy, 2004) and are entirely lacking for aromobatids.

As noted by Juncá et al. (1994) and Caldwell and Lima, (2003), the timing modifications that produced endotrophic larvae differ. The exoviviparous larvae of *Anomaloglossus degranvillei* lack the keratinized jaw sheath, oral disc, and spiracle, whereas nidicolous larvae of the closely related *A. stepheni* lack the keratinized jaw sheath and oral disc but possess a spiracle. The inverse occurs in *Allobates*, in which the presumably exoviviparous larvae of *Allobates chalcopis* have a complete larval morpholgy and the nidicolous larvae of *Allobates nidicola* possess an unkeratinized lower jaw and lack the oral disc and spiracle.

The close phylogenetic relationship between *Anomaloglossus degranvillei* and *A. stepheni* to *A. beebei* draws attention to a previously unappreciated relationship between endotrophy and oophagy. Conceptually, endotrophy and oophagy are different physiological and behavioral means to the same end: the female's reproductive biology is altered to provide additional nutrients for larval development, either through pre-oviposition enrichment of the oocyte or post-oviposition provision of nutritive oocytes. This observation that oophagy and endotrophy are in this sense adaptationally equivalent raises more questions than answers. As mentioned above, the unambiguous optimization of endotrophy as the primitive state for this clade may be an artifact of taxonomy. Nevertheless, assuming that relationship to be true implies that oophagous species evolved from an endotrophic ancestor. Data are unavailable on the relative metabolic costs of production of normal-sized oocytes for larval consumption versus expansion of the nutritive endoderm, but they will be essential to understanding the trade-offs involved in these transformations.

Further, in terms of reproductive success, under what conditions would natural selection favor one or the other strategy? Summers and Earn (1999) analyzed the conditions under which entirely female care (including provision of nutritive oocytes) would be favored, but the relative costs and benefits of endotrophy have not been considered in this context. Summers and Earn suggested that the transition from all male to all female care may have been driven in part by males suffering a cost of lost mating opportunities due to investment in parental care. Male investment in parental care is not appreciably less, and may actually be greater, in nidicolous species (Juncá, 1996) than other dendrobatoids, the difference being that males guard clutches throughout development in nidicolous species, which lengthens the duration of male investment, but must transport tadpoles to water in nonnidicolous species, which is also costly and may increase the risk of predation (potentially through decreased locomotor performance [but see Downie et al., 2005] or increased exposure and lack of known escape routes) and loss of territory (Cummins and Swan, 1995). The potential exists for tadpole transport to be a cost to male foraging, but in *Mannophryne trinitatis* male nurse frogs do not appear to forage less than calling males (Downie et al., 2005). The fact that the male remains in (and therefore does not risk losing) his territory and continues to vocalize and mate successfully (Juncá, 1996) lends support to Summers and Earn's model, with the subtle clarification that it is not the paternal investment that matters per se, but the cost it entails in terms of lost mating opportunities.

SUMMARY AND CONCLUSIONS

DNA sequences totaling approximately 6,100 bp ($\bar{x}$ = 3,740 bp per terminal; total dataset ≈1.55 million bp) were generated for

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five mitochondrial and six nuclear loci, and 174 phenotypic characters were individuated from adult and larval morphology, alkaloid profiles, and behavior. The complete dataset included 414 terminals: 367 terminals of 156 ingroup species, and 47 outgroup terminals. Direct optimization parsimony analysis resulted in a 25,872 most parsimonious solutions of 46,520 transformations, with all conflict restricted to conspecific terminals. Dendrobatids were recovered as a monophyletic group, identified in the new taxonomy as Dendrobatoidea Cope, 1865, and the sister group was found to consist of *Crossodactylus* Duméril and Bibron, 1841, *Hylodes* Fitzinger, 1826, and *Megaelosia* Miranda-Ribeiro, 1923, recognized herein as Hylodidae Günther, 1858. The latter finding disagrees with the results of Frost et al. (2006) but is based on greatly increased character sampling for immediately relevant terminals and included a large sample of taxa from the Frost et al. study. Additional changes to outgroup taxonomy are: proposal of Cruciabatrachia **new taxon** for the sister group of Centrolenidae Taylor, 1951; elevation of the tribes Batrachylini and Ceratophrynini to subfamilies (Batrachylinae Gallardo, 1965 and Ceratophryinae Tschudi, 1838); proposal of Calamitophrynia **new taxon** for the sister group of Cycloramphidae (including Thoropidae Frost et al., 2006), resurrection of Leiuperidae Bonaparte, 1850 for several genera referred previously to Leptodactylidae Werner, 1896 (1938); and proposal of Nobleobatia **new taxon** for the clade composed of Hylodidae Günther, 1858 and Dendrobatoidea Cope, 1865.

As expected, *Colostethus* Cope, 1866 was found to be violently polyphyletic, and we proposed a new monophyletic taxonomy. The sampled dendrobatoids were distributed approximately symmetrically in two clades: Aromobatidae **new family** and Dendrobatidae Cope, 1865. Insofar as is known, all aromobatids are nontoxic. Within Aromobatidae, a diverse clade of species that possess the median lingual process was discovered and named *Anomaloglossus* **n.gen**. All included species of *Anomaloglossus* occur east of the Andes, but three species (*A. atopoglossus* Grant, Humphrey, and Myers, 1997; *A.* "*chocoensis*" auctorum [not *Hyloxalus chocoensis* Boulenger, 1912; see Grant et al., 1997]), and *A. lacrimosus* Myers, 1991), are distributed in the Pacific slopes and lowlands of Colombia and Ecuador. Several species of *Anomaloglossus* possess highly derived reproductive biology, including nidicolous and exoviviparous endotrophic larvae, phytotelm breeding, and the biparental production of nutritive oocytes for larval consumption. The sister of that genus is *Rheobates* **n. gen.** from the eastern and central Andes of Colombia. The inclusive *Anomaloglossus* + *Rheobates* clade was named Anomaloglossinae **new subfamily**.

Colostethus saltuensis Rivero 1980 "1978" and *Aromobates nocturnus* Myers, Daly, and Paolillo, 1991, the latter being the type species of *Aromobates* Myers, Daly, and Paolillo, 1991, were found to be nested within a clade of species referred previously to *Nephelobates* La Marca, 1994. Consequently, *Nephelobates* is a junior synonym of *Aromobates*. *Mannophryne* La Marca, 1992, whose status has been controversial, was found to be monophyletic. The *Aromobates* + *Mannophryne* clade was recognized as Aromobatinae **new subfamily**. Aromobatinae is distributed primarily in the Andes of Venezuela, with minor incursions into adjacent Colombia and a few lowland species that also extend to Trinidad.

The remaining species of aromobatids form a large, predominantly *cis*-Andean radiation referred to the existing name *Allobates* Zimmermann and Zimmermann, 1988. Within this clade is a complex of superficially similar species traditionally placed in Silverstone's (1976) *femoralis* group (or directly in *A. femoralis* Boulenger, 1883), including *A. femoralis*, *A. zaparo* Silverstone, 1976, *A. myersi* Pyburn, 1981, and *A. rufulus* Gorzula, 1990 "1988". Also in this clade are roughly half of the species formerly referred to *Colostethus*, including *Allobates nidicola* Caldwell and Lima, 2003 and *A. chalcopis* Kaiser, Coloma, and Gray, 1994, which possess nidicolous and exoviviparous endotrophic larvae, respectively. Given the diversity of species in this clade (in terms of the number of species and their morphological, behavioral, and reproductive variation), it is likely that further progress will allow additional clades in this group to be recognized

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formally and for *Allobates* to be restricted to the *femoralis* group. We therefore propose the name Allobatinae **new subfamily** for this clade.

All poisonous species of dendrobatoids are restricted to Dendrobatidae Cope, 1865. Numerous conspicuous clades occur in this clade, many of which can be referred to available names. Colostethinae Cope, 1868 includes four genera. *Silverstoneia* **n.gen.** is named for the *nubicola* group of species, a clade of three nominal and at least five as yet undescribed species (one of which was included in our analysis) with highly modified larvae. The sister group of *Silverstoneia* is *Epipedobates* Myers, 1987, which is here applied to the species related to *E. tricolor*. This clade includes the toxic species *E. tricolor* and *E. anthonyi*. Darst et al. (2005) reported *E. boulengeri* as lacking alkaloids, and we coded this species accordingly, but we suggest that result deserves further invesigation, either through additional sampling of wild populations or controlled feeding experiments. Likewise, the toxicity of *E. machalilla* has yet to be investigated.

The sister group of those genera includes *Colostethus* Cope, 1866 and *Ameerega* Bauer, 1986. *Colostethus* in our restricted sense is a moderate-sized clade (18 recognized species) from the Andes of Colombia and Ecuador, the inter-Andean valleys of Colombia, and a single species (*C. fugax* Morales and Schulte, 1993) known from the Amazon slope of the Ecuadorean Andes. No species of *Colostethus* is known to sequester lipophilic alkaloids, but *C. panamensis* (Dunn, 1933) possesses tetrodotoxin (Daly et al., 1994b). Parental care varies among species of *Colostethus*; *C. pratti* (Boulenger, 1899) and *C. panamensis* have female nurse frogs, whereas *C. fraterdanieli* Silverstone, 1971 and the undescribed species referred to as C. "*pratti*-like" have male nurse frogs.

Ameerega consists of most of the species referred to *Epipedobates* recently and *Phyllobates* Duméril and Bibron, 1841 sensu Silverstone (1976) before that. The bulk of this radiation is *cis*-Andean, with only *A. andina* (Myers and Burrowes, 1987) and *A. erythromos* (Vigle and Miyata, 1980) known on the Pacific slopes of Colombia and Ecuador, respectively, and *A. maculata* (W. Peters, 1873) from Panama. Although we did not include these western species in the phylogenetic analysis, we allied them with this clade on the basis of their previous placement in the *pictus* group and *Epipedobates*, respectively. Insofar as is known, all species of *Ameerega* sequester lipophilic alkaloids.

Hyloxalus Jiménez de la Espada, 1871 "1870" is applied to a large clade of nontoxic, primarily (but not exclusively) Andean species, including approximately half of the species referred previously to *Colostethus* (with most others referred to *Allobates*, above). Available names included in the synonymy of *Hyloxalus* are *Cryptophyllobates* Lötters, Jungfer, and Widmer, 2000 and *Phyllodromus* Jiménez de la Espada, 1871 "1870". The type species of both of these genera were included in the analysis, and both fall out in strongly supported clades. The clade that would be referred to *Cryptophyllobates* is morphologically conspicuous, and referring species not analyzed explicitly (such as *H. eleutherodactylus* [Duellman, 2004]) is unproblematic. However, owing to its placement as sister to the clade that includes the type species of *Phyllodromus* (*Phyllodromus pulchellum* Jiménez de la Espada, 1871 "1870"), recognition of *Cryptophyllobates* would require that species not analyzed explicitly be allocated to either *Hyloxalus* or *Phyllodromus*, which is not feasible at present.

The remaining clade consists of the five genera most widely recognized as dart-poison frogs. All of these species are toxic and most place larvae in phytotelmata. Given the distinctiveness of this clade and its importance in many areas of biology, we recognize it as Dendrobatinae Cope, 1865. As such, we proposed Hyoxalinae **new subfamily** for the sister group, that is, *Hyloxalus*. This solution is not entirely satisfactory because it produces a redundant name. Nevertheless, as discussed above, available genus-group names exist within *Hyloxalus* and at least two conspicuous clades are known, and we expect the formal nomenclatural recognition of additional clades as knowledge of dendrobatid phylogeny increases.

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Phyllobates Duméril and Bibron, 1841 is identical to the group proposed by Myers et al. (1978) and is here recovered as the sister group of the remaining dendrobatines. We recognize the sister of the next less-inclusive clade as the monotypic genus *Minyobates* Myers, 1987 for *M. steyermarki* (Rivero, 1971). Support for the placement of this species is weak, owing primarily to the small amount of available DNA sequence data (see Vences et al., 2003a), but its recognition as a monotypic genus is expedient in that it does not require that more names be proposed.

Ranitomeya Bauer, 1986 includes most of the diminutive species included in Silverstone's (1975a) *minutus* group prior to the placement by Myers (1987) of several of those species in *Minyobates* Myers, 1987 (additional species otherwise referable to Silverstone's *minutus* group are not related to these species; see below). *Ranitomeya* includes two conspicuous clades: a *trans*-Andean/Central American clade and a strictly Amazonian *cis*-Andean clade; we refer to these clades as the *minutus* and *ventrimaculatus* groups, respectively.

Oophaga Bauer, 1988 is applied to the *histrionicus* group of Myers et al. (1984). These species have unique vocalizations and exhibit all-female parental care, including female tadpole transport and the production of nutritive oocytes solely for the purpose of feeding larvae.

Adelphobates **n.gen.** was proposed for the clade containing *A. castaneoticus* (Caldwell and Myers, 1990), *A. quinquevittatus* (Steindachner, 1864), *A. galactonotus* (Steindachner, 1864), and (provisionally) *A. captivus* (Myers, 1982). The close relationships between *A. castaneoticus* and *A. quinquevittatus* were expected, but the placement of *A. galactonotus* here is somewhat heterodox in that it alone was previously referred to the *tinctorius* group of Silverstone (1975a). Nevertheless, this result was also obtained by Vences et al. (2003a), and, insofar as morphology for this species was included in the present analysis, there is no empirical basis to challenge its placement. Finally, *Dendrobates* Wagler, 1830 was applied to the remainder of the *tinctorius* group of Silverstone (1975a).

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APPENDIX 1
Chronology of Available Species Names Proposed or Currently in Dendrobatoidea, with Original, Current, and Proposed Generic Placement

Name	Authorship	Status	Original genus	Current genus[a]	Revised taxonomy
tinctorius	Cuvier, 1797		*Rana*	*Dendrobates*	*Dendrobates*
nigerrima	Spix, 1824	*trivittatus*	*Hyla*	—	—
trivittata	Spix, 1824		*Hyla*	*Epipedobates*	*Ameerega*
picta	Tschudi, 1838		*Hylaplesia*	*Epipedobates*	*Ameerega*
bicolor	Duméril & Bibron, 1841		*Phyllobates*	*Phyllobates*	*Phyllobates*
obscurus	Dumeril & Bibron, 1841	*trivittatus*	*Dendrobates*	—	—
histrionicus	Berthold, 1845		*Dendrobates*	*Dendrobates*	*Oophaga*
lateralis	Guichenot, 1848	*Batrachyla taeniata*	*Dendrobates*	*Batrachyla* (Ceratophryidae)	*Batrachyla* (Ceratophryidae)
inhambanensis	Bianconi, 1849	*Phrynomantis bifasciatus*	*Dendrobates*	*Phrynomantis* (Microhylidae)	*Phrynomantis* (Microhylidae)
auratus	Girard, 1855		*Dendrobates*	*Dendrobates*	*Dendrobates*
lugubris	O. Schmidt, 1857		*Dendrobates*	*Phyllobates*	*Phyllobates*
pumilio	O. Schmidt, 1857		*Dendrobates*	*Dendrobates*	*Oophaga*
speciosus	O. Schmidt, 1857		*Dendrobates*	*Dendrobates*	*Oophaga*
latimaculatus	Günther, 1859 "1858"	*auratus*	*Dendrobates*	—	—
truncatus	Cope, 1861		*Phyllobates*	*Dendrobates*	*Dendrobates*
limbatus	Cope, 1862		*Phyllobates*	"*Euhyas*" (Brachycephalidae)	"*Euhyas*" (Brachycephalidae)
glandulosus	Fitzinger, 1863	*Physalaemus olfersi*	*Phyllobates*	*Physalaemus* (Leptodactylidae)	*Physalaemus* (Leiuperidae)
latinasus	Cope, 1863		*Phyllobates*	*Colostethus*	*Colostethus*
braccatus	Steindachner, 1864		*Dendrobates*	*Epipedobates*	*Ameerega*
cocteaui	Steindachner, 1864	*histrionicus*	*Dendrobates*	—	—
daudini	Steindachner, 1864	*tinctorius*	*Dendrobates*	—	—
eucnemis	Steindachner, 1864	*pictus*	*Dendrobates*	—	—
galactonotus	Steindachner, 1864		*Dendrobates*	*Dendrobates*	*Adelphobates*
leucomelas	Steindachner, 1864		*Dendrobates*	*Dendrobates*	*Dendrobates*
quinquevittatus	Steindachner, 1864		*Dendrobates*	*Dendrobates*	*Adelphobates*
ridens	Cope, 1866		*Phyllobates*	"*Eleutherodactylus*" (Brachycephalidae)	"*Eleutherodactylus*" (Brachycephalidae)
peruensis	Steindachner, 1867	nomen dubium	*Phyllobates*	nomen dubium	nomen dubium
typographus	Keferstein, 1867	*pumilio*	*Dendrobates*	—	—
inguinalis	Cope, 1868		*Prostherapis*	*Colostethus*	*Colostethus*
chocoensis	Posada Arango, 1869	*bicolor*	*Phyllobates*	—	—
verruculatus	W. Peters, 1870		*Phyllobates*	*Syrrhophus* (Brachycephalidae)	*Syrrhophus* (Brachycephalidae)
bocagei	Jiménez de la Espada, 1871		*Hyloxalus*	*Colostethus*	*Hyloxalus*
fuliginosus	Jiménez de la Espada, 1871		*Hyloxalus*	*Colostethus*	*Hyloxalus*
pulchellum	Jiménez de la Espada, 1871		*Phyllodromus*	*Colostethus*	*Hyloxalus*
betsileo	Grandidier, 1872		*Dendrobates*	*Mantella* (Mantellidae)	*Mantella* (Mantellidae)
madagascariensis	Grandidier, 1872		*Dendrobates*	*Mantella* (Mantellidae)	*Mantella* (Mantellidae)
chalceus	W. Peters, 1873		*Phyllobates*	"*Eleutherodactylus*" (Brachycephalidae)	"*Eleutherodactylus*" (Brachycephalidae)
maculatus	W. Peters, 1873		*Dendrobates*	*Epipedobates*	*Ameerega*
ignitus	Cope, 1874	*pumilio*	*Dendrobates*	—	—
labialis	Cope, 1874		*Dendrobates*	*Epipedobates*	*Ameerega*

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Name	Authorship	Status	Original genus	Current genus[a]	Revised taxonomy
hylaeformis	Cope, 1875		*Phyllobates*	"*Eleutherodactylus*" Brachycephalidae	"*Eleutherodactylus*" Brachycephalidae
talamancae	Cope, 1875		*Dendrobates*	*Colostethus*	*Allobates*
cystignathoides	Cope, 1877		*Phyllobates*	*Syrrhophus* (Brachycephalidae)	*Syrrhophus* (Brachycephalidae)
ebenaui	Boettger, 1880	*Mantella betsileo*	*Dendrobates*	*Mantella* (Mantellidae)	*Mantella* (Mantellidae)
parvulus	Boulenger, 1882		*Dendrobates*	*Epipedobates*	*Ameerega*
whymperi	Boulenger, 1882		*Prostherapis*	*Colostethus*	*Hyloxalus*
femoralis	Boulenger, 1883		*Prostherapis*	*Epipedobates*	*Allobates*
hahneli	Boulenger, 1883		*Dendrobates*	*Epipedobates*	*Ameerega*
fantasticus	Boulenger, 1884 "1883"		*Dendrobates*	*Dendrobates*	*Ranitomeya*
reticulatus	Boulenger, 1884 "1883"		*Dendrobates*	*Dendrobates*	*Ranitomeya*
trilineatus	Boulenger, 1884 "1883"		*Phyllobates*	*Colostethus*	*Allobates*
braccatus	Cope, 1887	*braccatus* Steindachner, 1864	*Dendrobates*	—	—
brunneus	Cope, 1887		*Prostherapis*	*Colostethus*	*Allobates*
trinitatis	Garman, 1887		*Phyllobates*	*Mannophryne*	*Mannophryne*
herminae	Boettger, 1893		*Prostherapis*	*Mannophryne*	*Mannophryne*
vittatus	Cope, 1893		*Dendrobates*	*Phyllobates*	*Phyllobates*
infraguttatus	Boulenger, 1898		*Phyllobates*	*Colostethus*	*Hyloxalus*
opisthomelas	Boulenger, 1899		*Dendrobates*	*Minyobates*	*Ranitomeya*
palmatus	Werner, 1899		*Phyllobates*	*Colostethus*	*Rheobates*
pratti	Boulenger, 1899		*Phyllobates*	*Colostethus*	*Colostethus*
subpunctatus	Cope, 1899		*Prostherapis*	*Colostethus*	*Hyloxalus*
tricolor	Boulenger, 1899		*Prostherapis*	*Epipedobates*	*Epipedobates*
variabilis	Werner, 1899	*subpunctatus*	*Prostherapis*	—	—
vertebralis	Boulengeri, 1899		*Phyllodromus*	*Colostethus*	*Hyloxalus*
amoenus	Werner, 1901	*auratus*	*Dendrobates*	—	—
bolivianus	Boulenger, 1902		*Prostherapis*	*Epipedobates*	*Ameerega*
alboguttatus	Boulenger, 1903		*Phyllobates*	*Nephelobates*	*Aromobates*
festae	Peracca, 1904	*parvulus*	*Prostherapis*	—	—
flavopicta	A. Lutz, 1925		*Hylaplesia*	*Epipedobates*	*Ameerega*
femoralis	Barbour, 1905	*boulengeri*	*Prostherapis*	—	—
equatorialis	Barbour, 1908	*Eleutherodactylus unistrigatus*	*Prostherapis*	"*Eleutherodactylus*" (Brachycephalidae)	"*Eleutherodactylus*" (Brachycephalidae)
boulengeri	Barbour, 1909		*Prostherapis*	*Epipedobates*	*Epipedobates*
chocoensis	Boulenger, 1912		*Hylixalus*	*Colostethus*	*Hyloxalus*
collaris	Boulenger, 1912		*Hylixalus*	*Mannophryne*	*Mannophryne*
huigrae	Fowler, 1913	"*Eleutherodactylus*" *diastema*	*Hyloxalus*	"*Eleutherodactylus*" (Brachycephalidae)	"*Eleutherodactylus*" (Brachycephalidae)
aurotaenia	Boulenger, 1914 "1913"		*Dendrobates*	*Phyllobates*	*Phyllobates*
coctaei	Boulenger, 1914 "1913"	*histrionicus*	*Dendrobates*	—	—
paraensis	Boulenger, 1914 "1913"	*galactonotus*	*Dendrobates*	—	—
walkeri	Ruthven, 1915		*Geobatrachus*	*Geobatrachus* (Brachycephalidae)	*Geobatrachus* (Brachycephalidae)
tarsalis	Werner, 1916	*subpunctatus*	*Prostherapis*	—	—
kingsburyi	Boulenger, 1918		*Phyllobates*	*Colostethus*	*Allobates*
ranoides	Boulenger, 1918		*Dendrobates*	*Colostethus*	*Allobates*
granuliventris	Boulenger, 1919	*palmatus*	*Hylixalus*	—	—
sylvaticus	Barbour & Noble, 1920		*Phyllobates*	*Colostethus*	*Hyloxalus*
anthonyi	Noble, 1921		*Phyllobates*	*Epipedobates*	*Epipedobates*
beatriciae	Barbour & Dunn, 1921	*lugubris*	*Phyllobates*	—	—
beebei	Noble, 1923		*Hyloxalus*	*Colostethus*	*Anomaloglossus*
nubicola	Dunn, 1924		*Phyllobates*	*Colostethus*	*Silverstoneia*

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Name	Authorship	Status	Original genus	Current genus[a]	Revised taxonomy
nigriventris	A. Lutz, 1925		*Hylaplesia*	"*Eleutherodactylus*" (Brachycephalidae)	"*Eleutherodactylus*" (Brachycephalidae)
olfersioides	A. Lutz, 1925		*Eupemfix*	*Colostethus*	*Allobates*
tetravittatus	Miranda Ribeiro, 1926	*trivittatus*	*Dendrobates*	—	—
brasiliensis	Witte, 1930	*Crossodactylus gaudichaudi*	*Phyllobates*	*Crossodactylus* (Hylodidae)	*Crossodactylus* (Hylodidae)
flotator	Dunn, 1931		*Phyllobates*	*Colostethus*	*Silverstoneia*
mandelorum	Schmidt, 1932		*Phyllobates*	*Colostethus*	*Allobates*
panamensis	Dunn, 1933		*Hyloxalus*	*Colostethus*	*Colostethus*
minutus	Shreve, 1935		*Dendrobates*	*Minyobates*	*Ranitomeya*
ventrimaculatus	Shreve, 1935		*Dendrobates*	*Dendrobates*	*Ranitomeya*
shrevei	Dunn, 1940	*minutus*	*Dendrobates*	—	—
vergeli	Hellmich, 1940		*Hyloxalus*	*Colostethus*	*Hyloxalus*
bassleri	Melin, 1941		*Dendrobates*	*Epipedobates*	*Ameerega*
igneus	Melin, 1941		*Dendrobates*	*Dendrobates*	*Ranitomeya*
marchesianus	Melin, 1941		*Phyllobates*	*Colostethus*	*Allobates*
peruvianus	Melin, 1941		*Phyllobates*	*Colostethus*	*Hyloxalus*
intermedius	Andersson, 1945	*kingsburyi*	*Phyllobates*	—	—
riocasangae	Andersson, 1945	*pulchellus*	*Phyllobates*	—	—
taeniatus	Andersson, 1945	*pulchellus*	*Phyllobates*	—	—
galindoi	Trapido, 1953	*pumilio*	*Dendrobates*	—	—
bromelicola	Test, 1956		*Phyllobates*	*Colostethus*	*Allobates*
confluens	Funkhouser, 1956	*histrionicus*	*Dendrobates*	—	—
espinosai	Funkhouser, 1956		*Phyllobates*	*Epipedobates*	*Epipedobates*
neblina	Test, 1956		*Prostherapis*	*Mannophryne*	*Mannophryne*
sylvaticus	Funkhouser, 1956		*Dendrobates*	*Dendrobates*	*Oophaga*
granuliferus	Taylor, 1958		*Dendrobates*	*Dendrobates*	*Oophaga*
machadoi	Bokermann, 1958	*tinctorius*	*Dendrobates*	—	—
dunni	Rivero, 1961		*Prostherapis*	*Colostethus*	Aromobatidae *incerta sedis*
shrevei	Rivero, 1961		*Prostherapis*	*Colostethus*	*Anomaloglossus*
mertensi	Cochran & Goin, 1964		*Phyllobates*	*Colostethus*	*Colostethus*
guayanensis	Heatwole et al., 1965	*pictus*	*Phyllobates*	—	—
riveroi	Donoso-Barros, 1965 "1964"		*Prostherapis*	*Mannophryne*	*Mannophryne*
alagoanus	Bokermann, 1967		*Phyllobates*	*Colostethus*	*Allobates*
capixaba	Bokermann, 1967		*Phyllobates*	*Colostethus*	*Allobates*
carioca	Bokermann, 1967		*Phyllobates*	*Colostethus*	*Allobates*
azureus	Hoogmoed, 1969		*Dendrobates*	*Dendrobates*	*Dendrobates*
ingeri	Cochran & Goin, 1970		*Dendrobates*	*Epipedobates*	*Ameerega*
thorntoni	Cochran & Goin, 1970		*Phyllobates*	*Colostethus*	*Colostethus*
walesi	Cochran & Goin, 1970	*subpunctatus*	*Phyllobates*	—	—
anthracinus	Edwards, 1971		*Colostethus*	*Colostethus*	*Hyloxalus*
elachyhistus	Edwards, 1971		*Colostethus*	*Colostethus*	*Hyloxalus*
fraterdanieli	Silverstone, 1971		*Colostethus*	*Colostethus*	*Colostethus*
lehmanni	Silverstone, 1971		*Colostethus*	*Colostethus*	*Hyloxalus*
ramosi	Silverstone, 1971		*Colostethus*	*Colostethus*	*Hyloxalus*
steyermarki	Rivero, 1971		*Dendrobates*	*Minyobates*	*Minyobates*
meridensis	Dole & Durant, 1972		*Colostethus*	*Nephelobates*	*Aromobates*
sauli	Edwards, 1974		*Colostethus*	*Colostethus*	*Hyloxalus*
abditaurantius	Silverstone, 1975		*Colostethus*	*Colostethus*	*Hyloxalus*
altobueyensis	Silverstone, 1975		*Dendrobates*	*Minyobates*	*Ranitomeya*
degranvillei	Lescure, 1975		*Colostethus*	*Colostethus*	*Anomaloglossus*
fulguritus	Silverstone, 1975		*Dendrobates*	*Minyobates*	*Ranitomeya*
goianus	Bokermann, 1975		*Colostethus*	*Colostethus*	*Allobates*
imbricolus	Silverstone, 1975		*Colostethus*	*Colostethus*	*Colostethus*

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Name	Authorship	Status	Original genus	Current genus[a]	Revised taxonomy
abditus	Myers & Daly, 1976		*Dendrobates*	*Minyobates*	*Ranitomeya*
lehmanni	Myers & Daly, 1976		*Dendrobates*	*Dendrobates*	*Oophaga*
occultator	Myers & Daly, 1976		*Dendrobates*	*Dendrobates*	*Oophaga*
petersi	Silverstone, 1976		*Phyllobates*	*Epipedobates*	*Ameerega*
pulchripectis	Silverstone, 1976		*Phyllobates*	*Epipedobates*	*Ameerega*
smaragdinus	Silverstone, 1976		*Phyllobates*	*Epipedobates*	*Ameerega*
viridis	Myers & Daly, 1976		*Dendrobates*	*Minyobates*	*Ranitomeya*
zaparo	Silverstone, 1976		*Phyllobates*	*Epipedobates*	*Allobates*
haydeeae	Rivero, 1978 "1976"		*Colostethus*	*Nephelobates*	*Aromobates*
orostoma	Rivero, 1978 "1976"		*Colostethus*	*Nephelobates*	*Aromobates*
terribilis	Myers et al., 1978		*Phyllobates*	*Phyllobates*	*Phyllobates*
silverstonei	Myers & Daly, 1979		*Dendrobates*	*Epipedobates*	*Ameerega*
bombetes	Myers & Daly, 1980		*Dendrobates*	*Minyobates*	*Ranitomeya*
erythromos	Vigle & Miyata, 1980		*Dendrobates*	*Epipedobates*	*Ameerega*
humilis	Rivero 1980 "1978"		*Colostethus*	*Colostethus*	*Allobates*
inflexus	Rivero, 1980 "1978"	*alboguttatus*	*Colostethus*	—	—
leopardalis	Rivero, 1980 "1978"		*Colostethus*	*Nephelobates*	*Aromobates*
mayorgai	River, 1980 "1978"		*Colostethus*	*Nephelobates*	*Aromobates*
saltuensis	Rivero 1980 "1978"		*Colostethus*	*Colostethus*	*Aromobates*
myersi	Pyburn, 1981		*Dendrobates*	*Epipedobates*	*Allobates*
andinus	Myers & Burrowes, 1987		*Dendrobates*	*Epipedobates*	*Ameerega*
captivus	Myers, 1982		*Dendrobates*	*Dendrobates*	*Adelphobates*
edwardsi	Lynch, 1982		*Colostethus*	*Colostethus*	*Hyloxalus*
mysteriosus	Myers, 1982		*Dendrobates*	*Dendrobates*	Dendrobatinae *incerta sedis*
ruizi	Lynch, 1982		*Colostethus*	*Colostethus*	*Hyloxalus*
syntomopus	Lynch & Ruiz-Carranza, 1982		*Atopophrynus*	*Atopophrynus* (Brachycephalidae)	*Atopophrynus* (Brachycephalidae)
vanzolinii	Myers, 1982		*Dendrobates*	*Dendrobates*	*Ranitomeya*
olmonae	Hardy, 1983		*Colostethus*	*Mannophryne*	*Mannophryne*
arboreus	Myers et al., 1984		*Dendrobates*	*Dendrobates*	*Oophaga*
littoralis	Pefaur, 1984		*Colostethus*	*Colostethus*	*Hyloxalus*
agilis	Lynch & Ruiz-Carranza, 1985		*Colostethus*	*Colostethus*	*Colostethus*
azureiventris	Kneller & Henle, 1985		*Phyllobates*	*Cryptophyllobates*	*Hyloxalus*
duranti	Pefaur, 1985		*Colostethus*	*Nephelobates*	*Aromobates*
guatopoensis	Dixon & Rivero Blanco, 1985	*oblitteratus*	*Colostethus*	—	—
molinarii	La Marca, 1985		*Colostethus*	*Nephelobates*	*Aromobates*
serranus	Pefaur, 1985		*Colostethus*	*Nephelobates*	*Aromobates*
brachistriatus	Rivero & Serna, 1986		*Colostethus*	*Colostethus*	*Colostethus*
breviquartus	Rivero & Serna, 1986		*Colostethus*	*Colostethus*	*Hyloxalus*
imitator	Schulte, 1986		*Dendrobates*	*Dendrobates*	*Ranitomeya*
nexipus	Frost, 1986		*Colostethus*	*Colostethus*	*Hyloxalus*
oblitterata	Rivero, 1986 "1984"		*Colostethus*	*Mannophryne*	*Mannophryne*
peruviridis	Bauer, 1986		*Ameerega*	*Epipedobates*	*Ameerega*
sanmartini	Rivero, Langone, & Prigioni, 1986		*Colostethus*	*Colostethus*	*Allobates*
exasperatus	Duellman & Lynch, 1988		*Colostethus*	*Colostethus*	*Hyloxalus*
mystax	Duellman & Simmons, 1988		*Colostethus*	*Colostethus*	*Hyloxalus*
shuar	Duellman & Simmons, 1988		*Colostethus*	*Colostethus*	*Hyloxalus*
variabilis	Zimmermann & Zimmermann, 1988		*Dendrobates*	*Dendrobates*	*Ranitomeya*
ardens	Jungfer, 1989	*cainarachi*	*Epipedobates*	—	—
bilinguis	Jungfer, 1989		*Epipedobates*	*Epipedobates*	*Ameerega*
cainarachi	Schulte, 1989		*Epipedobates*	*Epipedobates*	*Ameerega*

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stepheni	Martins, 1989		*Colostethus*	*Colostethus*	*Anomaloglossus*
yustizi	La Marca, 1989		*Colostethus*	*Mannophryne*	*Mannophryne*
alacris	Rivero & Granados-Diaz, 1990 "1989"		*Colostethus*	*Colostethus*	*Colostethus*
castaneoticus	Caldwell & Myers, 1990		*Dendrobates*	*Dendrobates*	*Adelphobates*
pinguis	Rivero, Granados-Dias, 1990 "1989"		*Colostethus*	*Colostethus*	*Hyloxalus*
rufulus	Gorzula, 1990 "1988"		*Dendrobates*	*Epipedobates*	*Allobates*
betancuri	Rivero & Serna, 1991		*Colostethus*	*Colostethus*	*Hyloxalus*
cevallosi	Rivero, 1991		*Colostethus*	*Colostethus*	*Hyloxalus*
citreicola	Rivero, 1991b	*nexipus*	*Colostethus*	—	—
faciopunctulatus	Rivero, 1991a		*Colostethus*	*Colostethus*	*Hyloxalus*
fallax	Rivero, 1991b		*Colostethus*	*Colostethus*	*Hyloxalus*
furviventris	Rivero & Serna, 1991		*Colostethus*	*Colostethus*	*Colostethus*
idiomelus	Rivero, 1991a		*Colostethus*	*Colostethus*	*Hyloxalus*
jacobuspetersi	Rivero, 1991		*Colostethus*	*Colostethus*	*Colostethus*
lacrimosus	Myers, 1991		*Colostethus*	*Colostethus*	*Anomaloglossus*
larandina	Yustiz, 1991		*Colostethus*	*Mannophryne*	*Mannophryne*
maculosus	Rivero, 1991		*Colostethus*	*Colostethus*	*Hyloxalus*
marmoreoventris	Rivero, 1991b		*Colostethus*	*Colostethus*	*Hyloxalus*
mittermieri	Rivero, 1991		*Colostethus*	*Colostethus*	*Hyloxalus*
nocturnus	Myers et al., 1991		*Aromobates*	*Aromobates*	*Aromobates*
paradoxus	Rivero, 1991	*tricolor*	*Colostethus*	—	—
parcus	Rivero, 1991b		*Colostethus*	*Colostethus*	*Hyloxalus*
peculiaris	Rivero, 1991		*Colostethus*	*Colostethus*	*Hyloxalus*
poecilonotus	Rivero, 1991a		*Colostethus*	*Colostethus*	Dendrobatoidea *incerta sedis*
pumilus	Rivero, 1991b		*Colostethus*	*Colostethus*	*Hyloxalus*
sirensis	Aichinger, 1991		*Dendrobates*	*Dendrobates*	*Ranitomeya*
tergogranularis	Rivero, 1991	*pulchellus*	*Colostethus*	—	—
torrenticola	Rivero, 1991	*jacobuspetersi*	*Colostethus*	—	—
yaguara	Rivero & Serna, 1991		*Colostethus*	*Colostethus*	*Colostethus*
biolat	Morales, 1992		*Dendrobates*	*Dendrobates*	*Ranitomeya*
lamasi	Morales, 1992		*Dendrobates*	*Dendrobates*	*Ranitomeya*
mcdiarmidi	Reynolds & Foster, 1992		*Colostethus*	*Colostethus*	*Allobates*
virolinensis	Ruiz-Carranza & Ramírez-Pinilla, 1992		*Minyobates*	*Minyobates*	*Ranitomeya*
argyrogaster	Morales & Schulte, 1993		*Colostethus*	*Colostethus*	*Hyloxalus*
capurinensis	Pefaur, 1993		*Colostethus*	*Colostethus*	*Aromobates*
fugax	Morales & Schulte, 1993		*Colostethus*	*Colostethus*	*Colostethus*
macero	Rodríguez & Myers, 1993		*Epipedobates*	*Epipedobates*	*Ameerega*
chalcopis	Kaiser et al., 1994		*Colostethus*	*Colostethus*	*Allobates*
juanii	Morales, 1994		*Colostethus*	*Colostethus*	*Allobates*
utcubambensis	Morales, 1994		*Colostethus*	*Colostethus*	*Hyloxalus*
awa	Coloma, 1995		*Colostethus*	*Colostethus*	*Hyloxalus*
cordilleriana	La Marca, 1995 "1994"		*Mannophryne*	*Mannophryne*	*Mannophryne*
delatorreae	Coloma, 1995		*Colostethus*	*Colostethus*	*Hyloxalus*
machalilla	Coloma, 1995		*Colostethus*	*Colostethus*	*Epipedobates*
maquipucuna	Coloma, 1995		*Colostethus*	*Colostethus*	*Hyloxalus*
toachi	Coloma, 1995		*Colostethus*	*Colostethus*	*Hyloxalus*
parkerae	Meinhardt & Parmelee, 1996		*Colostethus*	*Colostethus*	*Anomaloglossus*
vicentei	Jungfer et al., 1996		*Dendrobates*	*Dendrobates*	*Oophaga*
atopoglossus	Grant et al., 1997		*Colostethus*	*Colostethus*	*Anomaloglossus*
ayarzaguenai	La Marca, 1997 "1996"		*Colostethus*	*Colostethus*	*Anomaloglossus*

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Name	Authorship	Status	Original genus	Current genus[a]	Revised taxonomy
guanayensis	La Marca, 1997 "1996"		*Colostethus*	*Colostethus*	*Anomaloglossus*
murisipanesis	La Marca, 1997 "1996"		*Colostethus*	*Colostethus*	*Anomaloglossus*
parimae	La Marca, 1997 "1996"		*Colostethus*	*Colostethus*	*Anomaloglossus*
praderioi	La Marca, 1997 "1996"		*Colostethus*	*Colostethus*	*Anomaloglossus*
roraima	La Marca, 1997 "1996"		*Colostethus*	*Colostethus*	*Anomaloglossus*
rubriventris	Lötters et al., 1997		*Epipedobates*	*Epipedobates*	*Ameerega*
ruthveni	Kaplan, 1997		*Colostethus*	*Colostethus*	*Colostethus*
tamacuarensis	Myers & Donnelly, 1997		*Colostethus*	*Colostethus*	*Anomaloglossus*
tepuyensis	La Marca, 1997 "1996"		*Colostethus*	*Colostethus*	*Anomaloglossus*
fascianiger	Grant & Castro, 1998		*Colostethus*	*Colostethus*	*Hyloxalus*
lynchi	Grant, 1998		*Colostethus*	*Colostethus*	*Colostethus*
planipaleae	Morales & Velazco, 1998		*Epipedobates*	*Epipedobates*	*Ameerega*
amazonicus	Schulte, 1999		*Dendrobates*	*Dendrobates*	*Ranitomeya*
baeobatrachus	Boistel & de Massary, 1999		*Colostethus*	*Colostethus*	*Anomaloglossus*
caquetio	Mijares-Urrutia & Arends R., 1999		*Mannophryne*	*Mannophryne*	*Mannophryne*
duellmani	Schulte, 1999		*Dendorbates*	*Dendrobates*	*Ranitomeya*
flavovittatus	Schulte, 1999		*Dendrobates*	*Dendrobates*	*Ranitomeya*
intermedius	Schulte, 1999		*Dendrobates*	*Dendrobates*	*Ranitomeya*
lamarcai	Mijares-Urrutia & Arends R., 1999		*Mannophryne*	*Mannophryne*	*Mannophryne*
pongoensis	Schulte, 1999		*Epipedobates*	*Epipedobates*	*Ameerega*
rubrocephalus	Schulte, 1999		*Dendrobates*	*Dendrobates*	*Ranitomeya*
yurimaguensis	Schulte, 1999	*imitator*	*Dendrobates*	—	—
borjai	Rivero & Serna, 2000 "1995"		*Colostethus*	*Colostethus*	*Hyloxalus*
cacerensis	Rivero & Serna, 2000 "1995"	*inguinalis*	*Colostethus*	—	—
claudiae	Junger et al., 2000		*Dendrobates*	*Dendrobates*	*Ranitomeya*
dysprosium	Rivero & Serna, 2000 "1995"		*Colostethus*	*Colostethus*	*Colostethus*
erasmios	Rivero & Serna, 2000 "1995"		*Colostethus*	*Colostethus*	*Silverstoneia*
excisus	Rivero & Serna, 2000 "1995"		*Colostethus*	*Colostethus*	*Hyloxalus*
picachos	Ardila-Robayo et al., 2000 "1999"		*Colostethus*	*Colostethus*	*Allobates*
pseudopalmatus	Rivero & Serna, 2000 "1995"		*Colostethus*	*Colostethus*	*Rheobates*
ramirezi	Rivero & Serna, 2000 "1995"		*Colostethus*	*Colostethus*	Dendrobatidae *incerta sedis*
simulans	Myers et al., 2000		*Epipedobates*	*Epipedobates*	*Ameerega*
wayuu	Acosta et al., 2000 "1999"		*Colostethus*	*Colostethus*	*Allobates*
alessandroi	Grant & Rodríguez, 2001		*Colostethus*	*Colostethus*	*Allobates*
caeruleodactylus	Lima & Caldwell, 2001		*Colostethus*	*Colostethus*	*Allobates*
melanolaemus	Grant & Rodríguez, 2001		*Colostethus*	*Colostethus*	*Allobates*
undulatus	Myers & Donnelly, 2001		*Colostethus*	*Colostethus*	*Allobates*
saltuarius	Grant & Ardila-Robayo, 2002		*Colostethus*	*Colostethus*	*Hyloxalus*
cepedai	Morales, 2002 "2000"		*Colostethus*	*Colostethus*	*Allobates*
conspicuus	Morales, 2002 "2000"		*Colostethus*	*Colostethus*	*Allobates*
crombiei	Morales, 2002 "2000"		*Colostethus*	*Colostethus*	*Allobates*
fratisenescus	Morales, 2002 "2000"		*Colostethus*	*Colostethus*	*Allobates*
fuscellus	Morales, 2002 "2000"		*Colostethus*	*Colostethus*	*Allobates*
gasconi	Morales, 2002 "2000"		*Colostethus*	*Colostethus*	*Allobates*
insperatus	Morales, 2002 "2000"		*Colostethus*	*Colostethus*	*Allobates*
masniger	Morales, 2002 "2000"		*Colostethus*	*Colostethus*	*Allobates*
ornatus	Morales, 2002 "2000"		*Colostethus*	*Colostethus*	*Allobates*
sumtuosus	Morales, 2002 "2000"		*Colostethus*	*Colostethus*	*Allobates*
vanzolinius	Morales, 2002 "2000"		*Colostethus*	*Colostethus*	*Allobates*

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Name	Authorship	Status	Original genus	Current genus[a]	Revised taxonomy
nidicola	Caldwell & Lima, 2003		*Colostethus*	*Colostethus*	*Allobates*
patitae	Lötters et al., 2003		*Colostethus*	*Colostethus*	*Hyloxalus*
aeruginosus	Duellman, 2004		*Colostethus*	*Colostethus*	*Hyloxalus*
craspedoceps	Duellman, 2004		*Colostethus*	*Colostethus*	*Allobates*
eleutherodactylus	Duellman, 2004		*Colostethus*	*Colostethus*	*Hyloxalus*
insulatus	Duellman, 2004		*Colostethus*	*Colostethus*	*Hyloxalus*
leucophaeus	Duellman, 2004		*Colostethus*	*Colostethus*	*Hyloxalus*
pulcherrimus	Duellman, 2004		*Colostethus*	*Colostethus*	*Hyloxalus*
sordidatus	Duellman, 2004		*Colostethus*	*Colostethus*	*Hyloxalus*
spilotogaster	Duellman, 2004		*Colostethus*	*Colostethus*	*Hyloxalus*
nubeculosus	Jungfer & Böhme, 2004		*Dendrobates*	*Dendrobates*	*Dendrobates*
pittieri	La Marca et al., 2004		*Colostethus*	*Colostethus*	*Allobates*
triunfo	Barrio-Amorós et al., 2005		*Colostethus*	*Colostethus*	*Anomaloglossus*
wothuja	Barrio-Amorós et al., 2005		*Colostethus*	*Colostethus*	*Anomaloglossus*
chlorocraspedus	Caldwell, 2005		*Cryptophyllobates*	*Cryptophyllobates*	*Hyloxalus*

[a] As discussed in Materials and Methods, there is no universally accepted "current" taxonomy of dendrobatoid frogs, and this category is intended only to provide a general reference for the proposed changes. Nondendrobatoid taxonomy follows Frost et al. (2006).

APPENDIX 2
Chronology of Available Dendrobatoid Genus-Group Names

Name	Authorship	Type species
Hysaplesia	Boie, 1826	*Rana tinctoria*
Dendrobates	Wagler, 1830	*Rana tinctoria*
Phyllobates	Duméril and Bibron, 1841	*Phyllobates bicolor*
Eubaphus	Bonaparte, 1850	*Rana tinctoria*
Colostethus	Cope, 1866	*Phyllobates latinasus*
Prostherapis	Cope, 1868	*Prostherapis inguinalis*
Phyllodromus	Jiménez de la Espada, 1871"1870"	*Phyllodromus pulchellum*
Hyloxalus	Jiménez de la Espada, 1871 "1870"	*Hyloxalus fuliginosus*
Ameerega	Bauer, 1986	*Hyla trivittata*
Minyobates	Myers, 1987	*Dendrobates steyermarki*
Epipedobates	Myers, 1987	*Prostherapis tricolor*
Phobobates	Zimmermann and Zimmermann, 1988	*Dendrobates silverstonei*
Allobates	Zimmermann and Zimmermann, 1988	*Prostherapis femoralis*
Pseudendrobates	Bauer, 1988	*Dendrobates silverstonei*
Ranitomeya	Bauer, 1988	*Dendrobates reticulatus*
Oophaga	Bauer, 1988	*Dendrobates pumilio*
Aromobates	Myers, Paolillo, and Daly, 1991	*Aromobates nocturnus*
Mannophryne	La Marca, 1992	*Colostethus yustizi*
Nephelobates	La Marca, 1994	*Phyllobates alboguttatus*
Paruwrobates	Bauer, 1994	*Dendrobates andinus*
Cryptophyllobates	Lötters, Jungfer, and Widmer, 2000	*Phyllobates azureiventris*
Adelphobates	**new genus**	*Dendrobates castaneoticus*
Anomaloglossus	**new genus**	*Hyloxalus beebei*
Rheobates	**new genus**	*Phyllobates palmatus*
Silverstoneia	**new genus**	*Phyllobates nubicola*

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APPENDIX 3
Chronology of Dendrobatoid Family-Group Names

Name	Authorship
Phyllobatae	Fitzinger, 1843
Eubaphidae	Bonaparte, 1850
Eubaphina	Bonaparte, 1850
Hylaplesidae	Günther, 1858
Hylaplesina	Günther, 1858
Dendrobatidae	Cope, 1865
Colostethidae	Cope, 1867
Hylaplesiina	Günther, 1868
Calostethina	Mivart, 1869
Hylaplesiidae	Cope, 1875
Phyllobatidae	Parker, 1933
Allobatinae	**new subfamily**
Anomaloglossinae	**new subfamily**
Aromobatidae	**new family**
Aromobatinae	**new subfamily**
Hyloxalinae	**new subfamily**

APPENDIX 4
Numbers and References for Sequences Obtained from GenBank

Accession numbers, length (in base pairs; bp), and publication reference for GenBank sequences included in this study.

GenBank identification	GenBank number	Locus	Length (bp)	Reference
Colostethus awa	AY364544	12S, $tRNA^{val}$, 16S	2445	Santos et al., 2003
Colostethus baeobatrachus	AY263231	16S	535	Vences et al., 2003a
Colostethus bocagei	AY364545	12S, $tRNA^{val}$, 16S	2435	Santos et al., 2003
Colostethus degranvillei	AY263260	16S	506	Vences et al., 2003a
Colostethus degranvillei	AY263234	16S	542	Vences et al., 2003a
Colostethus degranvillei	AY263213	12S	371	Vences et al., 2003a
Colostethus elachyhistus	AY364546	12S, $tRNA^{val}$, 16S	2440	Santos et al., 2003
Colostethus fugax	AY364547	12S, $tRNA^{val}$, 16S	2442	Santos et al., 2003
Colostethus humilis	AJ430673	16S	544	La Marca et al., 2002
Colostethus infraguttatus	AY326028	12S, $tRNA^{val}$, 16S	2418	Darst and Cannatella, 2004
Colostethus infraguttatus	AY364548	12S, $tRNA^{val}$, 16S	2433	Santos et al., 2003
Colostethus insperatus	AY364557	12S, $tRNA^{val}$, 16S	2434	Santos et al., 2003
Colostethus kingsburyi	AY364550	12S, $tRNA^{val}$, 16S	2457	Santos et al., 2003
Colostethus kingsburyi	AY364549	12S, $tRNA^{val}$, 16S	2446	Santos et al., 2003
Colostethus machalilla	AY364551	12S, $tRNA^{val}$, 16S	2444	Santos et al., 2003
Colostethus maculosus	AY364552	12S, $tRNA^{val}$, 16S	2436	Santos et al., 2003
Colostethus nexipus	AY364553	12S, $tRNA^{val}$, 16S	2444	Santos et al., 2003
Colostethus palmatus	AY263228	16S	478	Vences et al., 2003a
Colostethus pratti	AY263238	16S	499	Vences et al., 2003a
Colostethus pulchellus	AY364554	12S, $tRNA^{val}$, 16S	2443	Santos et al., 2003
Colostethus sauli	AY364555	12S, $tRNA^{val}$, 16S	2445	Santos et al., 2003
Colostethus sp MNHN1995-9454	AY263236	16S	546	Vences et al., 2003a

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GenBank identification	GenBank number	Locus	Length (bp)	Reference
Colostethus sp QCAZ16490	AY364556	12S, $tRNA^{val}$, 16S	2443	Santos et al., 2003
Colostethus sp QCAZ16503	AY364560	12S, $tRNA^{val}$, 16S	2486	Santos et al., 2003
Colostethus sp QCAZ16504	AY364559	12S, $tRNA^{val}$, 16S	2443	Santos et al., 2003
Colostethus sp QCAZ16511	AY364558	12S, $tRNA^{val}$, 16S	2442	Santos et al., 2003
Colostethus sp QCAZ16609	AY364561	12S, $tRNA^{val}$, 16S	2436	Santos et al., 2003
Colostethus stepheni	AY263237	16S	487	Vences et al., 2003a
Colostethus subpunctatus	AY263242	16S	448	Vences et al., 2003a
Colostethus toachi	AY364563	12S, $tRNA^{val}$, 16S	2444	Santos et al., 2003
Colostethus vertebralis	AY364564	12S, $tRNA^{val}$, 16S	2435	Santos et al., 2003
Dendrobates amazonicus	AF482800	cytochrome *b*	268	Symula et al., 2003
Dendrobates amazonicus	AF482785	16S	463	Symula et al., 2003
Dendrobates amazonicus	AF482770	12S	280	Symula et al., 2003
Dendrobates auratus	AY364370	16S	571	Biju and Bossuyt, 2003
Dendrobates auratus	AY364349	12S, $tRNA^{val}$, 16S	748	Biju and Bossuyt, 2003
Dendrobates auratus	AY364395	rhodopsin	316	Biju and Bossuyt, 2003
Dendrobates biolat	AF482809	cytochrome *b*	268	Symula et al., 2003
Dendrobates biolat	AF482794	16S	506	Symula et al., 2003
Dendrobates biolat	AF482779	12S	311	Symula et al., 2003
Dendrobates duellmani	AY364566	12S, $tRNA^{val}$, 16S	2456	Santos et al., 2003
Dendrobates fantasticus	AF128624	cytochrome *b*	284	Clough and Summers, 2000
Dendrobates fantasticus	AF128623	12S	361	Clough and Summers, 2000
Dendrobates fantasticus	AF128622	16S	522	Clough and Summers, 2000
Dendrobates fantasticus DfTY26b	AF412503	cytochrome *b*	272	Symula et al., 2003
Dendrobates fantasticus DfTY26b	AF412475	16S	409	Symula et al., 2003
Dendrobates fantasticus DfTY26b	AF412447	12S	282	Symula et al., 2003
Dendrobates imitator	AF124118	16S	560	Vences et al., 2000
Dendrobates imitator	AY263217	12S	354	Vences et al., 2003a
Dendrobates imitator	AY263267	16S	492	Vences et al., 2003a
Dendrobates imitator DiTY26b	AF412518	cytochrome *b*	282	Symula et al., 2003
Dendrobates imitator DiTY26b	AF412490	16S	406	Symula et al., 2003
Dendrobates imitator DiTY26b	AF412462	12S	282	Symula et al., 2003
Dendrobates lamasi	AF482808	cytochrome *b*	268	Symula et al., 2003
Dendrobates lamasi	AF482793	16S	499	Symula et al., 2003
Dendrobates lamasi	AF482778	12S	311	Symula et al., 2003
Dendrobates quinquevittatus	AY263253	16S	575	Vences et al., 2003a
Dendrobates sp. QCAZ16558	AY364568	12S, $tRNA^{val}$, 16S	2459	Santos et al., 2003
Dendrobates steyermarki	AY263244	16S	547	Vences et al., 2003a
Dendrobates sylvaticus	AY364569	12S, $tRNA^{val}$, 16S	2449	Santos et al., 2003
Dendrobates variabilis	AF412463	12S	282	Symula et al., 2003
Dendrobates variabilis	AY263249	16S	575	Vences et al., 2003a
Dendrobates ventrimaculatus (French Guiana)	AY263248	16S		Vences et al., 2003a
Epipedobates anthonyi QCAZ16591 (sensu Graham et al., 2004)	AY364576	12S, $tRNA^{val}$, 16S	2443	Santos et al., 2003
Epipedobates azureiventris	AY263255	16S	511	Vences et al., 2003a
Epipedobates azureiventris	AF124124	16S	542	Vences et al., 2000
Epipedobates azureiventris	AF128562	cytochrome *b*	283	Clough and Summers, 2000
Epipedobates azureiventris	AF128561	12S	277	Clough and Summers, 2000
Epipedobates azureiventris	AF128560	16S	516	Clough and Summers, 2000

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GenBank identification	GenBank number	Locus	Length (bp)	Reference
Epipedobates bassleri	AF128565	cytochrome *b*	275	Clough and Summers, 2000
Epipedobates bassleri	AF128564	12S	358	Clough and Summers, 2000
Epipedobates bassleri	AF128563	16S	519	Clough and Summers, 2000
Epipedobates bilinguis	AY364571	12S, $tRNA^{val}$, 16S	2430	Santos et al., 2003
Epipedobates bilinguis	AF128559	cytochrome *b*	272	Clough and Summers, 2000
Epipedobates boulengeri	AY364572	12S, $tRNA^{val}$, 16S	2440	Santos et al., 2003
Epipedobates boulengeri	AF128556	cytochrome *b*	278	Clough and Summers, 2000
Epipedobates hahneli (Bolivia)	AF282246	16S	421	Lötters and Vences, 2000
Epipedobates hahneli QCAZ13325	AY364573	12S, $tRNA^{val}$, 16S	2437	Santos et al., 2003
Epipedobates parvulus QCAZ16583	AY364574	12S, $tRNA^{val}$, 16S	2438	Santos et al., 2003
Epipedobates pictus (sensu stricto)	AF124126	16S	555	Vences et al., 2000
Epipedobates rubriventris	AF282247	16S	566	Lötters and Vences, 2000
Epipedobates sp. QCAZ16589	AY364575	12S, $tRNA^{val}$, 16S	2436	Santos et al., 2003
Epipedobates tricolor (sensu Graham et al. 2004)	AY395961	12S, $tRNA^{val}$, 16S	2393	Graham et al., 2004
Epipedobates zaparo QCAZ16601	AY364578	12S, $tRNA^{val}$, 16S	2432	Santos et al. 2003
Epipedobates zaparo QCAZ16604	AY364579	12S, $tRNA^{val}$, 16S	2433	Santos et al. 2003
Mannophryne collaris	AJ430675	16S	534	La Marca et al., 2002
Mannophryne herminae	AY263269	16S	506	Vences et al., 2003a
Mannophryne herminae	AY263219	12S	358	Vences et al., 2003a
Mannophryne herminae	AJ430676	16S	538	La Marca et al., 2002
Mannophryne sp. ULABG 4453	AY263221	16S	535	Vences et al., 2003a
Mannophryne sp. ULABG 4458	AY263224	16S	538	Vences et al., 2003a
Mannophryne sp. ULABG 4465	AY263222	16S	535	Vences et al., 2003a
Mannophryne sp. ULABG 4481	AY263223	16S	535	Vences et al., 2003a
Nephelobates molinarii	AY263263	16S	505	Vences et al., 2003a
Nephelobates molinarii	AY263216	12S	368	Vences et al., 2003a
Nephelobates molinarii	AJ430678	16S	546	La Marca et al., 2002
Nephelobates sp. ULABG 4445	AY263229	16S	540	Vences et al., 2003a
Nephelobates sp. ULABG 4496	AJ430677	16S	543	La Marca et al., 2002
Phyllobates vittatus	AY263265	16S	473	Vences et al., 2003a
Phyllobates vittatus	AF124134	16S	556	Vences et al., 2000
Phyllobates vittatus	AF128582	cytochrome *b*	284	Clough and Summers, 2000
Phyllobates vittatus	AF128581	12S	360	Clough and Summers, 2000
Phyllobates vittatus	AF128580	16S	517	Clough and Summers, 2000

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APPENDIX 5

Tissue and Sequence Data

Below we give the species identification (as treated in the text and figs. 70–76), sample identification number (Sample ID), source (voucher or tissue identification number or, if unavailable, collector or breeder), locality, GenBank accession number for each locus, and total number of base pairs (bp) for each terminal sequenced for Faivovich et al. (2004), Frost et al. (2006), or the present study. Sequences previously submitted to GenBank are given in bold (see appendix 4 for additional sequences obtained from GenBank). See Materials and Methods for collection abbreviations. Locus abbreviations: 28S (large nuclear ribosomal subunit), COI (cytochrome *c* oxidase I), cytb (cytochrome *b*), H1 (mitochondrial H-strand transcription unit 1), H3 (histone H3), RAG1 (recombination activating gene 1), rhodopsin (rhodopsin exon 1), and SIA (seventh in absentia).

Species	Sample ID	Source	Locality	Cytochrome *b*	H1	COI	Rhodopsin	Histone H3	Tyrosinase	RAG 1	SIA	28S	Total bp
alagoanus	538	MRT 6031	Brazil: Bahia: São José da Vitória, Fazenda Unacau, 15°09′S 39°18′W	DQ502557	DQ502126	DQ502833	DQ503232	DQ502342			DQ503093		4485
Allophryne ruthveni	837	MAD 1512	Guyana: Kabocali camp, 101 m, 4°17.10′N 58°30.56′W		**AY843564**		**AY844538**				**AY844766**		2422
Alsodes gargola	653	MACN 37942	Argentina: Neuquén: Aluminé, stream 10 km W Primeros Pinos		**AY843565**		**AY844539**	**DQ284118**			**AY844767**	**AY844197**	4212
anthonyi	838	RG	No data (captive bred)	DQ502584	DQ502151	DQ502853		DQ502355		DQ503354	DQ503104		4620
anthonyi	1290	AMCC 125660	Ecuador: El Oro: 7 km W Pasajo in banana/cacao		DQ502215								608
arboreus	340	CWM 18636	Panama: Chiriquí: Continental divide above upper Quebrada de Arenam 1120 m	DQ502467	DQ502036	DQ502763	DQ503197	DQ502306		DQ503312	DQ503060	DQ502959	5714
Atelognathus patagonicus	656	MACN 37905	Argentina: Neuquén: Catan Lil, Laguna del Burro		**AY843571**		**AY844545**		**AY844027**		**AY844773**	**AY844203**	4409
Atelopus spurrelli	1275	MHNUC 273	Colombia: Chocó: Bahía Solano, Quebrada Tebada, 160 m, 06°28.786′N 77°20.678′W		DQ502200	DQ502895				DQ503380			3509
Atelopus zeteki	1039	UMFS 11492	Captive bred, Detroit Zoo (parental stock from Panama: Las Filipinas, near Sora, 8°39.99′N 80°0.249′W)		**DQ283252**	DQ502857							2177
auratus Nicaragua	365	OMNH 33270	Nicaragua: Río San Juán: Near Isla de Diamante (ca. 15 km SE El Castillo on Río San Juán), 10°56′N 84°18′W	DQ502491	DQ502060	DQ502782							3471
auratus Panama	327	USNM 313818	Panama: Bocas del Toro: Laguna de Tierra Oscura, 3.7 km S of Tiger Key	**AY843803**	**AY843581**	DQ502751	**AY844554**	**DQ284072**	**AY844032**	DQ503304	**AY844781**	**AY844211**	6238

Species	Sample ID	Source	Locality	Cytochrome *b*	H1	COI	Rhodopsin	Histone H3	Tyrosinase	RAG 1	SIA	28S	Total bp
auratus Panama	334	CWM 17698(A)	Panama: Bocas del Toro: North side Isla Pastores	DQ502461	DQ502030	DQ502758							3471
auratus Panama	335	CWM 17698(B)	Panama: Bocas del Toro: North side Isla Pastores	DQ502462	DQ502031	DQ502759							3471
aurotaenia	840	RG	No data (captive bred)	DQ502586	DQ502153	DQ502855		DQ502356		DQ503356	DQ503106		4618
"Ayanganna"	607	ROM 39639	Guyana: Mt. Ayanganna, northeast plateau, 1490–1550 m, 5°24′N 59°57′W	DQ502560	DQ502129	DQ502836	DQ503235	DQ502345	DQ503163	DQ503344	DQ503096	DQ502993	6230
azureus	534	MRT 5089	Brazil (no other data)	DQ502553	DQ502122	DQ502829	DQ503228	DQ502338		DQ503338	DQ503089	DQ502989	5702
azureus	1330	BPN 977	Suriname: Sipaliwini: forest island on W slope of Vier Gebroders Mts., Sipaliwini savannah, 2°1.4′N 55°57.41′W	DQ502683	DQ502251	DQ502921		DQ502386		DQ503388	DQ503135	DQ503031	5386
baeobatrachus	14	PK-437-1	French Guiana: Pic Matécho, 3°44′53″N 3°2′19″W	DQ502405	DQ501980	DQ502706							3448
baeobatrachus	42	PK-437-2	French Guiana: Pic Matécho, 3°44′53″N 3°2′19″W	DQ502406	DQ501981	DQ502707		DQ502275					3779
baeobatrachus	43	PK-437-3	French Guiana: Pic Matécho, 3°44′53″N 3°2′19″W	DQ502407	DQ501982	DQ502708							3448
baeobatrachus	44	PK-737-4	French Guiana: Pic Matécho, 3°44′53″N 3°2′19″W	DQ502408	DQ501983	DQ502709		DQ502276		DQ503281	DQ503037	DQ502936	5367
Batrachyla leptopus	655	MACN 38008	Argentina: Chubut: Cushamen, Lago Puelo		**AY843572**		**AY844546**	**DQ284119**	**AY844028**		**AY844774**	**AY844204**	4727
beebei	605	ROM 39631	Guyana: Mount Ayanganna, northeast plateau, 1490–1550 m, 5°24′N 59°57′W	DQ502558	DQ502127	DQ502834	DQ503233	DQ502343		DQ503342	DQ503094	DQ502991	5695
beebei	608	ROM 39632	Guyana: Mount Ayanganna, northeast plateau, 1490–1550 m, 5°24′N 59°57′W	DQ502561	DQ502130	DQ502837		DQ502346					3781
bicolor	1233	MB	No data (captive bred)	DQ502617	DQ502181	DQ502884		DQ502377		DQ503377		DQ503019	4989
bilinguis	378	OMNH 34125	Ecuador: Sucumbíos: Estacíon Cientifica de Universidad Católica near Reserva Faunística Cuyabeno, 220 m, 0°0′S 76°10′W	DQ502504	DQ502073								2793

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Species	Sample ID	Source	Locality	Cytochrome *b*	H1	COI	Rhodopsin	Histone H3	Tyrosinase	RAG 1	SIA	28S	Total bp
bilinguis	401	OMNH 34127	Ecuador: Sucumbíos: Estacíon Cientifica de Universidad Católica near Reserva Faunística Cuyabeno, 220 m, 0°0′S 76°10′W	DQ502527	DQ502095		DQ503216	DQ502326	DQ503157		DQ503078	DQ502978	5141
bilinguis	1303	OMNH 34126	Ecuador: Sucumbíos: Estacíon Cientifica de Universidad Católica near Reserva Faunística Cuyabeno, 220 m, 0°0′S 76°10′W		DQ502225								2411
bocagei	343	OMNH 34070	Ecuador: Sucumbíos: Dantas Trail near Reserva Faunística Cuyabeno, 220 m, 0°0′S 76°10′W	DQ502469	DQ502038	DQ502764	DQ503199	DQ502308		DQ503314	DQ503062	DQ502961	5700
bocagei	344	LSUMZ 12908	Ecuador: Sucumbíos: Dantas Trail near Reserva Faunística Cuyabeno, 220 m, 0°0′S 76°10′W	DQ502470	DQ502039	DQ502765							3462
bocagei	345	LSUMZ 12909	Ecuador: Sucumbíos: Dantas Trail near Reserva Faunística Cuyabeno, 220 m, 0°0′S 76°10′W	DQ502471	DQ502040	DQ502766							3462
bocagei	1267	OMNH 34072	Ecuador: Sucumbíos: Dantas Trail near Reserva Faunística Cuyabeno, 220 m, 0°0′S 76°10′W	DQ502628	DQ502192	DQ502890							3460
boulengeri	280	UMMZ 227952	Pet trade, imported from Ecuador	DQ502447	**DQ283037**	DQ502742	**DQ283768**	**DQ284063**	**DQ282902**	DQ503301	**DQ282653**	**DQ283461**	6239
braccatus	537	MRT 5603	Brazil: Mato Grosso: APM Manso, 15°27′S 58°44′W	DQ502556	DQ502125	DQ502832	DQ503231	DQ502341	DQ503161	DQ503341	DQ503092		5467
"Brownsberg"	1328	UTA A56469	Suriname: Brokopondo: Brownsberg Nature Park	DQ502681	DQ502249	DQ502919	DQ503267	DQ502385			DQ503134	DQ503029	5251
brunneus	352	OMNH 34473	Brazil: Pará: 101 km S and 15 km E Santarém (near Rio Curuá-una), 3°9′S 54°50′W	DQ502478	DQ502047								2795
brunneus	612	MPEG 11923	Brazil: Pará: 101 km S and 15 km E Santarém (near Rio Curuá-una), 3°9′S 54°50′W	DQ502564	DQ502132		DQ503237	DQ502348		DQ503347	DQ503098	DQ502994	5049
brunneus	613	OMNH 34460	Brazil: Pará: 101 km S and 15 km E Santarém (near Rio Curuá-una), 3°9′S 54°50′W	DQ502565	DQ502133	DQ502840							3454
brunneus	1264	MPEG 11921	Brazil: Pará: 101 km S and 15 km E Santarém (near Rio Curuá-una), 3°9′S 54°50′W	DQ502625	DQ502189								2795

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Species	Sample ID	Source	Locality	Cytochrome *b*	H1	COI	Rhodopsin	Histone H3	Tyrosinase	RAG 1	SIA	28S	Total bp
brunneus	1271	OMNH 34472	Brazil: Pará: 101 km S and 15 km E Santarém (near Rio Curuá-una), 3°9′S 54°50′W	DQ502632	DQ502196								2794
brunneus	1278	OMNH 34468	Brazil: Pará: 101 km S and 15 km E Santarém (near Rio Curuá-una), 3°9′S 54°50′W	DQ502638	DQ502203								2795
brunneus	1280	OMNH 34461	Brazil: Pará: 101 km S and 15 km E Santarém (near Rio Curuá-una), 3°9′S 54°50′W	DQ502640	DQ502205								2795
brunneus	1281	OMNH 34471	Brazil: Pará: 101 km S and 15 km E Santarém (near Rio Curuá-una), 3°9′S 54°50′W	DQ502641	DQ502206								2796
brunneus	1286	OMNH 34474	Brazil: Pará: 101 km S and 15 km E Santarém (near Rio Curuá-una), 3°9′S 54°50′W	DQ502646	DQ502211								2797
brunneus	1294	OMNH 34470	Brazil: Pará: 101 km S and 15 km E Santarém (near Rio Curuá-una), 3°9′S 54°50′W	DQ502650	DQ502216								2796
brunneus	1316	OMNH 34469	Brazil: Pará: 101 km S and 15 km E Santarém (near Rio Curuá-una), 3°9′S 54°50′W	DQ502670	DQ502238	DQ502910							3454
caeruleodactylus	406	MPEG 13809	Brazil: Amazonas: Castanho: ca. 40 km S Manaus, at km 12 on road to Autazes, 3°37′10.4″S 59°86′78.4″W	DQ502532	DQ502100	DQ502814	DQ503218	DQ502328		DQ503329	DQ503080		4929
caeruleodactylus	621	OMNH 37410	Brazil: Amazonas: Castanho: ca. 40 km S Manaus, at km 12 on road to Autazes, 3°37′10.4″S 59°86′78.4″W	DQ502573	DQ502141	DQ502845							3453
caeruleodactylus	1261	MPEG 13808	Brazil: Amazonas: Castanho: ca. 40 km S Manaus, at km 12 on road to Autazes, 3°37′10.4″S 59°86′78.4″W	DQ502622	DQ502186	DQ502887							3453
caeruleodactylus	1287	OMNH 37411	Brazil: Amazonas: Castanho: ca. 40 km S Manaus, at km 12 on road to Autazes, 3°37′10.4″S 59°86′78.4″W	DQ502647	DQ502212	DQ502899							3453

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Species	Sample ID	Source	Locality	Cytochrome *b*	H1	COI	Rhodopsin	Histone H3	Tyrosinase	RAG 1	SIA	28S	Total bp
castaneoticus	363	OMNH 34517	Brazil: Pará: 101 km S and 15 km E Santarém (near Rio Curuá-una), 3°9′S 54°50′W	DQ502489	DQ502058	DQ502780	DQ503202	DQ502311				DQ502964	4884
Centrolene prosoblepon	827	SIUC 7053	Panama: Coclé: El Copé, Parque Nacional General de División "Omar Torrijos Herrera"		**AY843574**						**AY844776**	**AY844206**	3872
Ceratophrys cranwelli	539	JF 929	Argentina: Santa Fe: Vera, "Las Gamas"		**AY843575**		**AY843797**					**AY844207**	3470
Chacophrys pierottii	1184	AMNH A168435	No data (pet trade)		**DQ283328**								2422
chlorocraspedus	383	OMNH 36170	Brazil: Acre: Porto Walter, 8°15′31.2″S 72°46′37.1″W	DQ502509	DQ502078	DQ502798	DQ503210	DQ502320		DQ503323	DQ503072	DQ502973	5713
chlorocraspedus	385	MPEG 13853	Brazil: Amazonas: Castanho: ca. 40 km S Manaus, at km 12 on road to Autazes, 3°37′10.4″S 59°86′78.4″W	DQ502511	DQ502080	DQ502800	DQ503212	DQ502322	DQ503153	DQ503325	DQ503074	DQ502975	6245
chlorocraspedus	623	OMNH 36169	Brazil: Acre: Porto Walter, 8°15′31.2″S 72°46′37.1″W	DQ502575	DQ502143	DQ502846							3463
chlorocraspedus	624	MPEG 12511	Brazil: Acre: Porto Walter, 8°15′31.2″S 72°46′37.1″W	DQ502576	DQ502144	DQ502847							3463
chlorocraspedus	1235	MPEG 12505	Brazil: Acre: Porto Walter, 8°15′31.2″S 72°46′37.1″W	DQ502618	DQ502182	DQ502885	DQ503260	DQ502378		DQ503378	DQ503124	DQ503020	5712
claudiae	323	USNM-FS 59979	Panama: Bocas del Toro: S end Isla Popa, 1 km E Sumwood Channel	DQ502452	DQ502024	DQ502747							3467
claudiae	324	USNM-FS 59980	Panama: Bocas del Toro: S end Isla Popa, 1 km E Sumwood Channel	DQ502453	**DQ283042**	DQ502748	**DQ283772**	**DQ284071**		DQ503303	**DQ282654**	**DQ283462**	5703
claudiae	330	USNM-FS 51785	Panama: Bocas del Toro: Isla Colon, Ilsa Colon, La Gruta	DQ502457	DQ502027	DQ502754				DQ503307	DQ503056	DQ502956	5058

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Species	Sample ID	Source	Locality	Cytochrome *b*	H1	COI	Rhodopsin	Histone H3	Tyrosinase	RAG 1	SIA	28S	Total bp
Cochranella bejaranoi	311	NK A 5292	Bolivia: Santa Cruz: Caballero: San Juán Cantón, Amboró, National Park, near San Juán del Portrero on Río Cerro Bravo, 1800–2100 m, near 17°50′08″S 64°23′23″W		**AY843576**		**AY844372**	**DQ284066**	**AY844029**	**AY844372**	**AY844777**	**AY844208**	4731
conspicuus	614	MPEG 12321	Brazil: Acre: Porto Walter, 8°15′31.2″S 72°46′37.1″W	DQ502566	DQ502134	DQ502841	DQ503238	DQ502349		DQ503348	DQ503099	DQ502995	5705
conspicuus	615	OMNH 35997	Brazil: Acre: Porto Walter, 8°15′31.2″S 72°46′37.1″W	DQ502567	DQ502135	DQ502842							3448
Crossodactylus schmidti	149	MLPA 1414	Argentina: Misiones: Aristobulo del Valle, Balneario Cuñapirú	**AY843801**	**AY843579**	DQ502738	**AY844552**	**DQ284050**	**AY844031**	DQ503298	**AY844780**	**AY844210**	6235
"Curuá-Una"	353	OMNH 34498	Brazil: Pará: 101 km S and 15 km E Santarém (near Rio Curuá-una), 3°9′S 54°50′W	DQ502479	DQ502048	DQ502773							3455
"Curuá-Una"	354	MPEG 11961	Brazil: Pará: 101 km S and 15 km E Santarém (near Rio Curuá-una), 3°9′S 54°50′W	DQ502480	DQ502049	DQ502774							3456
"Curuá-Una"	517	MJH 3973	Brazil: Pará: Rio Curuá-una	DQ502542	DQ502110	DQ502820							3455
"Curuá-Una"	1260	OMNH 34496	Brazil: Pará: 101 km S and 15 km E Santarém (near Rio Curuá-una), 3°9′S 54°50′W	DQ502621	DQ502185	DQ502886							3456
"Curuá-Una"	1268	OMNH 34497	Brazil: Pará: 101 km S and 15 km E Santarém (near Rio Curuá-una), 3°9′S 54°50′W	DQ502629	DQ502193	DQ502891							3455
"Curuá-Una"	351	LSUMZ 15176	Brazil: Pará: 101 km S and 15 km E Santarém (near Rio Curuá-una), 3°9′S 54°50′W	DQ502477	DQ502046	DQ502772	DQ503201	DQ502310		DQ503316	DQ503064	DQ502963	5712
"Cuyabeno"	346	OMNH 34086	Ecuador: Sucumbíos: Estación Científica de Universidad Católica near Reserva Faunística Cuyabeno, 220 m, 0°0′S 76°10′W	DQ502472	DQ502041	DQ502767	DQ503200	DQ502309		DQ503315	DQ503063	DQ502962	5706
"Cuyabeno"	347	LSUMZ 12969	Ecuador: Sucumbíos: Palmas Rojas Trail near Estación Científica de Universidad Católica, 220 m, 0°0′S 76°10′W	DQ502473	DQ502042	DQ502768							3446
"Cuyabeno"	348	LSUMZ 12970	Ecuador: Sucumbíos: Palmas Rojas Trail near Estación Científica de Universidad Católica, 220 m, 0°0′S 76°10′W	DQ502474	DQ502043	DQ502769							3447

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Species	Sample ID	Source	Locality	Cytochrome *b*	H1	COI	Rhodopsin	Histone H3	Tyrosinase	RAG 1	SIA	28S	Total bp
"Cuyabeno"	349	LSUMZ 12971	Ecuador: Sucumbíos: Reserva Faunística Cuyabeno, 220 m, 0°0′S 76°10′W	DQ502475	DQ502044	DQ502770							3448
"Cuyabeno"	350	LSUMZ 12972	Ecuador: Sucumbíos: Reserva Faunística Cuyabeno, 220 m, 0°0′S 76°10′W	DQ502476	DQ502045	DQ502771							3447
"Cuyabeno"	402	LSUMZ 12938	Ecuador: Sucumbíos: Estación Cientifica de Universidad Católica near Reserva Faunística Cuyabeno, 220 m, 0°0′S 76°10′W	DQ502528	DQ502096	DQ502812							3445
"Cuyabeno"	403	LSUMZ 12950	Ecuador: Sucumbíos: Dantas Trail near Reserva Faunística Cuyabeno, 220 m, 0°0′S 76°10′W	DQ502529	DQ502097	DQ502813							3448
"Cuyabeno"	1262	OMNH 34085	Ecuador: Sucumbíos: Estación Científica de Universidad Católica near Reserva Faunística Cuyabeno, 220 m, 0°0′S 76°10′W	DQ502623	DQ502187	DQ502888							3449
"Cuyabeno"	1270	LSUMZ 12936	Ecuador: Sucumbíos: Estación Cientifica de Universidad Católica near Reserva Faunística Cuyabeno, 220 m, 0°0′S 76°10′W	DQ502631	DQ502195	DQ502893							3447
"Cuyabeno"	1283	OMNH 34079	Ecuador: Sucumbíos: Estación Científica de Universidad Católica near Reserva Faunística Cuyabeno, 220 m, 0°0′S 76°10′W	DQ502643	DQ502208	DQ502897							3447
"Cuyabeno"	1317	LSUMZ 12948	Ecuador: Sucumbíos: Estación Científica de Universidad Católica near Reserva Faunística Cuyabeno, 220 m, 0°0′S 76°10′W	DQ502671	DQ502239	DQ502911							3447
Cycloramphus boraceiensis	890	CFBH 5757	Brazil: São Paulo: Picinguaba: Ubatuba	DQ502588	**DQ283097**	DQ502856	**DQ283813**	**DQ284147**	**DQ282924**	DQ503357	**DQ282675**	**DQ283498**	6222
degranvillei Guyana	278	GB	Guyana: Merume Mountains	DQ502445	DQ502019	DQ502740	DQ503188	DQ502296			DQ503051	DQ502951	5260
degranvillei Guyana	279	GB	Guyana: Merume Mountains	DQ502446	DQ502020	DQ502741	DQ503189	DQ502297		DQ503300	DQ503052	DQ502952	5695

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Species	Sample ID	Source	Locality	Cytochrome *b*	H1	COI	Rhodopsin	Histone H3	Tyrosinase	RAG 1	SIA	28S	Total bp
degranvillei Guyana	1336	CPI 10209	Guyana: Mazaruni-Potoro: Mt. Roraima, 1075 m	DQ502689	DQ502257								2800
delatorreae	71	KU 220621	Ecuador: Charchi: 26.9 to 27.3 km E Maldonado on road to Tulcán	DQ502409	DQ501984	DQ502710		DQ502277	DQ503140	DQ503282	DQ503038		5150
Dendrophryniscus minutus	532	MJH 7095	Peru: Huánuco: Río Llullapichis, Panguana	**AY843804**	DQ502120	DQ502828	**AY844555**	**DQ284096**		DQ503337			4535
Edalorhina perezi	531	MJH 7082	Peru: Huánuco: Río Llullapichis, Panguana		**AY843585**		**AY844558**	**DQ284095**			**AY844764**	**DQ283474**	4201
elachyhistus Cajamarca	105	KU 212522	Peru: Cajamarca, Chota, 4 km W Llama, 2500 m	DQ502417	DQ501992		DQ503181	DQ502284		DQ503288		DQ502941	4637
elachyhistus Cajamarca	106	KU 212523	Peru: Cajamarca, Chota, 4 km W Llama, 2500 m	DQ502418	DQ501993								2798
elachyhistus Cajamarca	107	KU 212524	Peru: Cajamarca, Chota, 4 km W Llama, 2500 m	DQ502419	DQ501994								2799
elachyhistus Piura	108	KU 219749	Peru: Piura: 8.5 km W Canchaque	DQ502420	DQ501995		DQ503182	DQ502285		DQ503289		DQ502942	4640
elachyhistus Piura	114	KU 212514	Peru: Piura: Ayacaba, ca. Ayacaba, 2750 m	DQ502425	DQ502000		DQ503185	DQ502288		DQ503291	DQ503046	DQ502945	5037
elachyhistus Piura	115	KU 212515	Peru: Piura: Ayacaba, ca. Ayacaba, 2750 m	DQ502426	DQ502001			DQ502289		DQ503292	DQ503047	DQ502946	4721
elachyhistus Piura	116	KU 212516	Peru: Piura: Ayacaba, ca. Ayacaba, 2750 m	DQ502427	DQ502002	DQ502722							3461
elachyhistus Piura	117	KU 212517	Peru: Piura: Ayacaba, ca. Ayacaba, 2750 m	DQ502428	DQ502003	DQ502723							3461
espinosai	1139	AMCC 125662	Ecuador: Pichincha: Santo Domingo de los Colorados, bypass road	DQ502594	DQ502158, DQ502159	DQ502862							2985
Eupsophus calcaratus	657	MACN 37980	Argentina: Neuquén: Huiliches: Termas de Epulafquen	**AY843808**	**AY843587**	DQ502852	**AY844560**	**DQ284120**	**AY844036**		**AY844786**	**AY844214**	5796
femoralis Curuá-Una	395	OMNH 34568	Brazil: Pará: 101 km S and 15 km E Santarém (near Rio Curuá-Una), 3°9′S 54°50′W	DQ502521	DQ502089								2790
femoralis Curuá-Una	396	OMNH 34572	Brazil: Pará: 101 km S and 15 km E Santarém (near Rio Curuá-Una), 3°9′S 54°50′W	DQ502522	DQ502090	DQ502809							3448
femoralis Curuá-Una	1298	MPEG 12021	Brazil: Pará: 101 km S and 15 km E Santarém (near Rio Curuá-Una), 3°9′S 54°50′W	DQ502654	DQ502220								2819

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Species	Sample ID	Source	Locality	Cytochrome *b*	H1	COI	Rhodopsin	Histone H3	Tyrosinase	RAG 1	SIA	28S	Total bp
femoralis Cusco Amazónico	78	KU 215179	Peru: Madre de Dios: Cusco Amazónico, 15 km E Puerto Maldonado, 200 m	DQ502415	DQ501990	DQ502716	DQ503180	DQ502283					4097
femoralis Cusco Amazónico	128	KU 215177	Peru: Madre de Dios: Cusco Amazónico, 15 km E Puerto Maldonado, 200 m	DQ502439	DQ502014	DQ502733							3452
femoralis Cusco Amazónico	129	KU 215180	Peru: Madre de Dios: Cusco Amazónico, 15 km E Puerto Maldonado, 200 m	DQ502440	DQ502015	DQ502734							3455
femoralis Cuyabeno	399	OMNH 34102	Ecuador: Sucumbíos: Estación Científica de Universidad Católica near Reserva Faunística Cuyabeno, 220 m, 0°0′S 76°10′W	DQ502525	DQ502093								2792
femoralis Cuyabeno	400	OMNH 34104	Ecuador: Sucumbíos: Estación Científica de Universidad Católica near Reserva Faunística Cuyabeno, 220 m, 0°0′S 76°10′W	DQ502526	DQ502094								2791
femoralis Cuyabeno	1306	LSUMZ 12798	Ecuador: Sucumbíos: Estación Científica de Universidad Católica near Reserva Faunística Cuyabeno, 220 m, 0°0′S 76°10′W	DQ502661	DQ502228								2792
femoralis Panguana	526	MJH 7354	Peru: Huánuco: Río Llullapichis, Panguana	DQ502549	DQ502117								2793
femoralis PortoWalter	397	OMNH 36066	Brazil: Acre: Porto Walter, 8°15′31.2″S 72°46′37.1″W	DQ502523	DQ502091	DQ502810							3455
femoralis PortoWalter	398	OMNH 36070	Brazil: Acre: Porto Walter, 8°15′31.2″S 72°46′37.1″W	DQ502524	DQ502092	DQ502811	DQ503215	DQ502325	DQ503156	DQ503327	DQ503077		5460
femoralis PortoWalter	1309	OMNH 36073	Brazil: Acre: Porto Walter, 9°34′38.9″S 72°46′37.1″W	DQ502664	DQ502231	DQ502904							3450
femoralis Reserva Ducke	520	MJH 3976	Brazil: Amazonas: Reserva Florestal Adolfo Ducke	DQ502545	DQ502113								2790
femoralis RioFormoso	393	MPEG 13415	Brazil: Rondônia: Parque Estadual Guajará-Mirim, 10°19′17.2″S 64°33′47.9″W	DQ502519	DQ502088	DQ502808							3447
femoralis RioFormoso	394	LSUMZ 17552	Brazil: Rondônia: Parque Estadual Guajará-Mirim, 10°19′17.2″S 64°33′47.9″W	DQ502520	**DQ283045**		**DQ283774**	**DQ284074**		DQ503326	**DQ282657**	**DQ283465**	5047

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femoralis Suriname	1325	UTA A56478	Suriname: Sipaliwini: in the vicinity of Kayser airstrip, 3°5.7′N 56°28.3′W	DQ502678	DQ502246	DQ502916	DQ503264	DQ502383		DQ503385	DQ503131		4956
flavopictus	536	MZUSP 111790	Brazil: Tocantins: Paraná, 12°36′N 47°52′W	DQ502555	DQ502124	DQ502831	DQ503230	DQ502340	DQ503160	DQ503340	DQ503091		5464
flotator	1143	SIUC 7657	Panama: Coclé: El Copé, Parque Nacional General de División "Omar Torrijos Herrera"	DQ502597	DQ502162	DQ502864	DQ503246	DQ502361		DQ503360		DQ503001	5312
flotator	1145	SIUC 7664	Panama: Coclé: El Copé, Parque Nacional General de División "Omar Torrijos Herrera"	DQ502599	DQ502164	DQ502866	DQ503248	DQ502363		DQ503362			4534
fraterdanieli Caldas	1230	ARA	Colombia: Caldas: Cordillera Central, W slope, 2400 m	DQ502615	DQ502179	DQ502882	DQ503259	DQ502375		DQ503375		DQ503017	5310
fraterdanieli Cauca	1226	MHNUC 360	Colombia: Cauca: Popayán, Hacienda La Paz, 2°28.704′N 76°36.257′W	DQ502611	DQ502175	DQ502878	DQ503256	DQ502372		DQ503371		DQ503013	5304
fraterdanieli Cauca	1227	MHNUC 361	Colombia: Cauca: Popayán, Hacienda La Paz, 2°28.704′N 76°36.257′W	DQ502612	DQ502176	DQ502879	DQ503257	DQ502373		DQ503372		DQ503014	5305
fraterdanieli Cauca	1228	MHNUC 364	Colombia: Cauca: Popayán, Hacienda La Paz, 2°28.704′N 76°36.257′W	DQ502613	DQ502177	DQ502880	DQ503258	DQ502374		DQ503373		DQ503015	5304
fulguritus	499	MHNUC 340	Colombia: Chocó: Bahía Solano, Sierra Mecana, 260 m, 6°15.508′N 77°21.336′W	DQ502538	DQ502106	DQ502817	DQ503222	DQ502332	DQ503158	DQ503333	DQ503084	DQ502983	6234
galactonotus	533	MRT 5088	Brazil: locality unknown	DQ502552	DQ502121		DQ503227	DQ502337			DQ503088	DQ502988	4628
galactonotus	647	RG	No data (captive bred)	DQ502583	DQ502150								2823
gasconi	357	MPEG 13003	Brazil: Amazonas: Rio Ituxi: Scheffer Madeireira, 8°28′45.8″S 65°42′59.6″W	DQ502483	DQ502052	DQ502777							3460
gasconi	358	MPEG 12993	Brazil: Amazonas: Rio Ituxi: Scheffer Madeireira, 8°28′45.8″S 65°42′59.6″W	DQ502484	DQ502053								2802
gasconi	1277	OMNH 36637	Brazil: Amazonas: Rio Ituxi: Scheffer Madeireira, 8°28′45.8″S 65°42′59.6″W	DQ502637	DQ502202	DQ502896							3461

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gasconi	1284	OMNH 36636	Brazil: Amazonas: Rio Ituxi: Scheffer Madeireira, 8°28′45.8″S 65°42′59.6″W	DQ502644	DQ502209	DQ502898							3460
granuliferus	339	CWM 19044	Costa Rica: Puntarenas: About 6 km airline E Palmar Norte, stream draining into Rio Granada de Terraba	DQ502466	DQ502035	DQ502762	DQ503196	DQ502305		DQ503311	DQ503059	DQ502958	5703
hahneli Cusco Amazónico	79	KU 215183	Peru: Madre de Dios: Cusco Amazónico, 15 km E Puerto Maldonado, 200 m	DQ502416	DQ501991	DQ502717							3456
hahneli Cusco Amazónico	109	KU 215185	Peru: Madre de Dios: Cusco Amazónico, 15 km E Puerto Maldonado, 200 m	DQ502421	DQ501996	DQ502718	DQ503183	DQ502286	DQ503142		DQ503044	DQ502943	5806
hahneli Cusco Amazónico	110	KU 215184	Peru: Madre de Dios: Cusco Amazónico, 15 km E Puerto Maldonado, 200 m	DQ502422	DQ501997	DQ502719							3462
hahneli Leticia	1354	ICN 50410	Colombia: Amazonas: Leticia, Lago Yahuarcaca	DQ502701	DQ502270	DQ502932	DQ503276	DQ502400	DQ503174				4634
hahneli Manaus	386	OMNH 37443	Brazil: Amazonas: Castanho: ca. 40 km S Manaus, at km 12 on road to Autazes, 3°37′10.4″S 59°86′78.4″W	DQ502512	DQ502081	DQ502801							3457
hahneli Manaus	391	MPEG 13849	Brazil: Amazonas: Castanho: ca. 40 km S Manaus, at km 12 on road to Autazes, 3°37′10.4″S 59°86′78.4″W	DQ502517	DQ502086	DQ502806							3456
hahneli Manaus	392	OMNH 37444	Brazil: Amazonas: Castanho: ca. 40 km S Manaus, at km 12 on road to Autazes, 3°37′10.4″S 59°86′78.4″W	DQ502518	DQ502087	DQ502807	DQ503214	DQ502324	DQ503155		DQ503076	DQ502977	5806
hahneli Manaus	1304	MPEG 13844	Brazil: Amazonas: Castanho: ca. 40 km S Manaus, at km 12 on road to Autazes, 3°37′10.4″S 59°86′78.4″W	DQ502659	DQ502226	DQ502902							3456
hahneli PortoWalter	382	OMNH 36088	Brazil: Acre: Porto Walter, 8°15′31.2″S 72°46′37.1″W	DQ502508	DQ502077	DQ502797	DQ503209	DQ502319	DQ503151		DQ503071	DQ502972	5799
hahneli PortoWalter	388	MPEG 12420	Brazil: Acre: Porto Walter, 8°15′31.2″S 72°46′37.1″W	DQ502514	DQ502083	DQ502803	DQ503213	DQ502323	DQ503154		DQ503075	DQ502976	5800
hahneli PortoWalter	389	OMNH 36092	Brazil: Acre: Porto Walter, 8°15′31.2″S 72°46′37.1″W	DQ502515	DQ502084	DQ502804							3460

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Species	Sample ID	Source	Locality	Cytochrome *b*	H1	COI	Rhodopsin	Histone H3	Tyrosinase	RAG 1	SIA	28S	Total bp
hahneli PortoWalter	390	OMNH 36090	Brazil: Acre: Porto Walter, 8°15′31.2″S 72°46′37.1″W	DQ502516	DQ502085	DQ502805							3456
herminae	1141	CWM	Venezuela: Trujillo: about 2 km (airline) W La Peña, 1920 m	DQ502595	DQ502160								2315
histrionicus	336	AMNH A122232	Colombia: Chocó: Quebrada Vicordó, upstream from Noanamá	DQ502463	DQ502032	DQ502760							3473
histrionicus	498	MHNUC 344	Colombia: Chocó: Bahía Solano, Sierra Mecana, 330 m, 6°15.581′N 77°21.105′W	DQ502537	DQ502105	DQ502816	DQ503221	DQ502331		DQ503332	DQ503083	DQ502982	5707
Hyalinobatrachium fleischmanni	TJ97	JAC 21365	Mexico: Oaxaca: San José Pacífico-Candelaria Loxicha Hwy, 480m		**DQ283453**		**DQ284043**					**DQ283756**	3804
Hyla cinerea	207	MVZ 145385	USA: Texas: Travis Co.: Austin, municipal golf course	**AY843846**	**AY549327**		**AY844597**	**DQ284057**	**AY844063**		**AY844816**	**AY844241**	5557
Hylodes phyllodes	889	CFBH-T 249	Brazil: São Paulo: Picinguaba: Ubatuba	DQ502587	**DQ283096**		**DQ283812**	**DQ284146**	**DQ282923**		**DQ282674**		4378
Hylodes phyllodes	1152	MCL 00015	Brazil (no additional data)	DQ502606	DQ502171	DQ502873	DQ503253	DQ502368		DQ503367	DQ503119	DQ503009	5722
Hypsiboas boans	486	RWM 17746	Venezuela: Amazonas: Caño Agua Blanca, 3.5 km SE Neblina base camp on Río Baria		**AY843610**		**AY844588**	**DQ284086**	**AY844055**		**AY844809**	**AY844231**	4747
"Ibagué"	1225	MUJ 3564	Colombia: Tolima: Ibagué, El Totumo, finca La Magnolia, Quebrada El Cural, 1047 m	DQ502610	DQ502174	DQ502877	DQ503255			DQ503370		DQ503012	4967
"Ibagué"	1345	ARA 2520	Colombia: Cundimamarca: La Mesa, finca Tacarcuna, km 3 vía Chachipay, 1300 m	DQ502693	DQ502261	DQ502924	DQ503270	DQ502394	DQ503171	DQ503396			5073
"Ibagué"	1347	MAR 105	Colombia: Tolima: Ibagué, El Totumo, finca La Magnolia, Quebrada El Cural, 1047 m	DQ502695	DQ502264	DQ502926				DQ503397			3415
idiomelus	77	KU 211885	Peru: Amazonas: Bongara, Pomachochas, 2150 m	DQ502414	DQ501989	DQ502715	DQ503179	DQ502282		DQ503287	DQ503043	DQ502940	5693

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idiomelus	120	KU 211908	Peru: San Martin: Rioja, E slope Abra Pardo de Miguel, 2180 m	DQ502431	DQ502006	DQ502726		DQ502291		DQ503294	DQ503048	DQ502948	5693
idiomelus	121	KU 211109	Peru: San Martin: Rioja, E slope Abra Pardo de Miguel, 2180 m	DQ502432	DQ502007	DQ502727		DQ502292		DQ503295	DQ503049		4623
idiomelus	122	KU 211110	Peru: San Martin: Rioja, E slope Abra Pardo de Miguel, 2180 m	DQ502433	DQ502008	DQ502728							3460
idiomelus	126	KU 211886	Peru: Amazonas: Pomachochas, 2150 m	DQ502437	DQ502012			DQ502294		DQ503297			3565
imbricolus	1229	MHNUC 257	Colombia: Chocó: Bahía Solano, near Quebrada Nabugá, 15 m, 06°21.680′N 77°20.432′W	DQ502614	DQ502178	DQ502881				DQ503374	DQ503122	DQ503016	5065
inguinalis	1348	MUJ 3247	Colombia: Caldas: La Dorada: San Roque, Reserva Natural Privada Riomanso, 255 m, 5°40′N 74°47′W	DQ502696	DQ502265	DQ502927		DQ502395		DQ503398			4230
insulatus	124	KU 211877	Peru: Amazonas: 6 km W Pedro Ruiz Gallo, 1260 m	DQ502435	DQ502010	DQ502730		DQ502293		DQ503296		DQ502949	4978
insulatus	125	KU 211878	Peru: Amazonas: 6 km W Pedro Ruiz Gallo, 1260 m	DQ502436	DQ502011	DQ502731							3457
juanii	1357	ARA 2394	Colombia: Meta: Villavicencio, Pozo Azul, 560 m	DQ502702	DQ502271	DQ502933	DQ503277	DQ502401		DQ503403			4534
lehmanni Myers and Daly	338	CWM 19050	Colombia: Valle del Cauca: General region of type locality	DQ502465	DQ502034	DQ502761	DQ503195	DQ502304		DQ503310	DQ503058	DQ502957	5709
Lepidobatrachus laevis	939	AMNH A168407	No data (pet trade)		**DQ283152**		**DQ283851**	**DQ284191**			**DQ282707**	**DQ283543**	4194
Leptodactylus discodactylus	TJ81	RDS	Ecuador (no other data)		**DQ283433**		**DQ284033**	**DQ284410**			**DQ282887**	**DQ283742**	4205
Leptodactylus fuscus	TJ50	AMNH A139088	Guyana: Southern Rupununi savanna, Aishalton (on Kubabawau Creek), 150 m, 2°28′31″N 59°19′16″W		**DQ283404**		**DQ284015**	**DQ284385**			**DQ282862**	**DQ283716**	4745
Leptodactylus hylaedactyla	529	MJH 3669	Peru: Huánuco: Río Llullapichis, Panguana		**DQ283063**		**DQ283790**	**DQ284093**					3064

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Leptodactylus lineatus	632	AMNH A166426	Guyana: Berebice River camp at ca. 18 mi (linear) SW Kwakwani (ca 2 mi downriver from Kurundi River confluence), 200 ft, 5°5′6″N 58°14′14″W		**AY843690**		**AY844683**	**DQ284112**	**AY844129**			**AY844303**	4349
Leptodactylus ocellatus	568	MACN 38648	Argentina: Buenos Aires: Escobar, Loma Verde, Establecimiento "Los Cipreses"		**AY843688**		**AY844681**	**DQ284104**				**AY844302**	3810
leucomelas	645	RG	No data (captive bred)	DQ502581	DQ502149	DQ502850	DQ503242	DQ502354		DQ503353	DQ503103		4948
Limnomedusa macroglossa	681	MACN 38641	Argentina: Misiones: Aristobulo del Valle: Balneario Cuñapirú		**AY843689**		**AY844682**	**DQ284127**	**AY844128**				3595
lugubris Nicaragua	366	OMNH 33325	Nicaragua: Río San Juán: Near Isla de Diamante (ca. 15 km SE El Castillo on Río San Juán), 10°56′N 84°18′W	DQ502492	DQ502061	DQ502783							3453
lugubris Panama	329	USNM-FS 195116	Panama: Bocas del Toro: S end of Isla Popa, 1 km E Sumwood Channel	DQ502456	**DQ283043**	DQ502753	DQ503193	DQ502302		DQ503306	**DQ282655**	**DQ283463**	5303
macero	1133	LR 742	Peru: Madre de Dios: Parque Nacional del Manu	DQ502591	DQ502155			DQ502358	DQ503167		DQ503108	DQ502997	4823
machalilla	73	KU 220631	Ecuador: Manabi: 38 km NW El Carmen, ca road to Pedernales	DQ502410	DQ501985	DQ502711	DQ503175	DQ502278		DQ503283	DQ503039	DQ502937	5708
machalilla	132	KU 220632	Ecuador: Manabi: 38 km NW El Carmen, ca. road to Pedernales	DQ502443	DQ502018	DQ502737							3461
"Magdalena"	1358	MUJ 3520	Colombia: Caldas: La Dorada: San Roque, Reserva Natural Privada Riomanso, 280 m, 5°40′N 74°46′W	DQ502703	DQ502272	DQ502934	DQ503278	DQ502402		DQ503404			4530
"Manaus1"	405	MPEG 13826	Brazil: Amazonas: Castanho: ca. 40 km S Manaus, at km 12 on road to Autazes, 3°37′10.4″S 59°86′78.4″W	DQ502531	DQ502099		DQ503217	DQ502327		DQ503328	DQ503079	DQ502979	5052

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Species	Sample ID	Source	Locality	Cytochrome *b*	H1	COI	Rhodopsin	Histone H3	Tyrosinase	RAG 1	SIA	28S	Total bp
"Manaus1"	620	MPEG 13829	Brazil: Amazonas: Castanho: ca. 40 km S Manaus, at km 12 on road to Autazes, 3°37′10.4″S 59°86′78.4″W	DQ502572	DQ502140								2793
"Manaus1"	1318	MPEG13827	Brazil: Amazonas: Castanho: ca. 40 km S Manaus, at km 12 on road to Autazes, 3°37′10.4″S 59°86′78.4″W	DQ502672	DQ502240								2792
Mannophryne sp	1322	WES 1034	Venezuela: Estado Monagas: Quebrada que fluye hacia la Cueva del Guacharo (altura te la debo pero esta alrededor de los 1400 m), cerca de Caripe	DQ502675	DQ502243	DQ502913	DQ503263	DQ502380		DQ503382	DQ503128	DQ503024	5708
Mannophryne sp	1323	WES 1035	Venezuela: Estado Monagas: Quebrada que fluye hacia la Cueva del Guacharo (altura te la debo pero esta alrededor de los 1400 m), cerca de Caripe	DQ502676	DQ502244	DQ502914		DQ502381		DQ503383	DQ503129	DQ503025	5394
Mannophryne sp	1324	WES 1036	Venezuela: Estado Monagas: Quebrada que fluye hacia la Cueva del Guacharo (altura te la debo pero esta alrededor de los 1400 m), cerca de Caripe	DQ502677	DQ502245	DQ502915		DQ502382		DQ503384	DQ503130	DQ503026	5394
Megaelosia goeldii	611	MZUSP 95879	Brazil: Rio de Janeiro: Teresópolis: Rio Beija Flor, 910 m, 22°24′S 42°69′W	DQ502563	**DQ283072**	DQ502839	**DQ283797**	**DQ284109**	**DQ282911**	DQ503346			5069
Melanophryniscus klappenbachi	217	BB 216	Argentina: Chaco: Proximidades de Resistencia	DQ502444	**AY843699**	DQ502739	**DQ283765**	**DQ284060**		DQ503299	**AY844899**	**AY844306**	5689
minutus	1149	KRL 790	Panama: Coclé: El Copé, Parque Nacional General de División "Omar Torrijos Herrera"	DQ502603	DQ502168	DQ502870	DQ503251	DQ502366		DQ503365	DQ503116	DQ503006	5717
"Neblina species"	379	AMCC 106112	Venezuela: Amazonas: Rio Negro: Neblina Base Camp on Rio Mawarinuma, 140 m, 0°50′N 66°10′W	DQ502505	DQ502074	DQ502795	DQ503207	DQ502317	DQ503149	DQ503321	DQ503069	DQ502970	6222

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"Neblina species"	380	AMCC 106118	Venezuela: Amazonas: Rio Negro: Neblina Base Camp on Rio Mawarinuma, 140 m, 0°50′N 66°10′W	DQ502506	DQ502075	DQ502796							3436
Nephelobates sp	1321	WES 626	Venezuela: Estado Trujillo: Carretera Humocaro Bajo-Agua de Obispos, 2400 m	DQ502674	DQ502242			DQ502379		DQ503381	DQ503127	DQ503023	4730
nexipus	75	KU 211806	Peru: San Martin: Cataratas Ahuashiyacu, 14 km NE Tarapoto, 730 m	DQ502412	DQ501987	DQ502713	DQ503177	DQ502280		DQ503285	DQ503041	DQ502939	5720
nexipus	123	KU 212486	Peru: San Martin: 6 km ESE Shapaja, 300 m	DQ502434	DQ502009	DQ502729							3456
nexipus	130	KU 211807	Peru: San Martin: Cataratas Ahuashiyacu, 14 km NE Tarapoto, 730 m	DQ502441	DQ502016	DQ502735							3457
nexipus	131	KU 211808	Peru: San Martin: Cataratas Ahuashiyacu, 14 km NE Tarapoto, 730 m	DQ502442	DQ502017	DQ502736							3458
nidicola	407	MPEG 13821	Brazil: Amazonas: Castanho: ca. 40 km S Manaus, at km 12 on road to Autazes, 3°37′10.4″S 59°86′78.4″W	DQ502533	DQ502101		DQ503219	DQ502329		DQ503330	DQ503081	DQ502980	5019
nidicola	622	MPEG 13820	Brazil: Amazonas: Castanho: ca. 40 km S Manaus, at km 12 on road to Autazes, 3°37′10.4″S 59°86′78.4″W	DQ502574	DQ502142		DQ503241	DQ502353		DQ503352	DQ503102		4245
nidicola	1285	MPEG 13819	Brazil: Amazonas: Castanho: ca. 40 km S Manaus, at km 12 on road to Autazes, 3°37′10.4″S 59°86′78.4″W	DQ502645	DQ502210								2768
nocturnus	1132	AMNH A130041	Venezuela:Trujillo: About 2 km (airline) ESE Agua de Obispos, 2250 m, 94°2′N 70°5′W	DQ502590	DQ502154	DQ502859	DQ503243	DQ502357			DQ503107	DQ502996	5270
nocturnus	1134	AMNH A130042	Venezuela:Trujillo: About 2 km (airline) ESE Agua de Obispos, 2250 m, 94°2′N 70°5′W	DQ502592	DQ502156	DQ502860		DQ502359			DQ503109	DQ502998	4954

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Species	Sample ID	Source	Locality	Cytochrome *b*	H1	COI	Rhodopsin	Histone H3	Tyrosinase	RAG 1	SIA	28S	Total bp
nubicola	1142	SIUC 7652	Panama: Coclé: El Copé, Parque Nacional General de División "Omar Torrijos Herrera"	DQ502596	DQ502161	DQ502863	DQ503245			DQ503359	DQ503111	DQ503000	5387
nubicola	1146	SIUC 7663	Panama: Coclé: El Copé, Parque Nacional General de División "Omar Torrijos Herrera"	DQ502600	DQ502165	DQ502867	DQ503249				DQ503113	DQ503003	4950
"*nubicola*-spC"	496	MHNUC 320	Colombia: Chocó: Bahía Solano, Quebrada Tebada, 165 m, 06°28.924′N 77°20.682W	DQ502535	DQ502103		DQ503220	DQ502330		DQ503331			3878
"*nubicola*-spC"	497	MHNUC 321	Colombia: Chocó: Bahía Solano, Quebrada Tebada, 165 m, 06°28.924′N 77°20.682W	DQ502536	DQ502104						DQ503082	DQ502981	3972
Odontophrynus achalensis	869	ZSM 733/2000; BB 1324	Argentina: Córdoba: Pampa de Achala; Argentina: Córdoba: proximity of Pampilla, near Parador El Cóndor		**DQ283247, DQ283248**		**DQ283918**	**DQ284273**			**DQ282773**	**DQ283611**	4244
Odontophrynus americanus	309	JF 1946	Argentina: Buenos Aires: Escobar: Loma Verde, E "Los Cipreses"		**AY843704**		**AY844695**				**AY844901**	**AY844309**	3914
Osteocephalus taurinus	410	AMNH A131254	Venezuela: Amazonas: Neblina base camp on Rio Mawarinuma (= Río Baria), 140 M		**AY843709**		**AY844700**	**DQ284075**	**AY844140**		**AY844905**	**AY844313**	4735
palmatus	1346	MUJ 5003	Colombia: Cundimamarca: La Mesa, finca Tacarcuna, km 3 vía Chachipay, 1300 m	DQ502694	DQ502262, DQ502263	DQ502925	DQ503271		DQ503172				3885
panamensis	1150	SIUC 7666	Panama: Coclé: El Copé, Parque Nacional General de División "Omar Torrijos Herrera"	DQ502604	DQ502169	DQ502871					DQ503117	DQ503007	4625
panamensis	1223	CH 5546	Panama: Darién: Caná	DQ502608	DQ502172	DQ502875		DQ502370		DQ503368	DQ503120	DQ503010	5393
Paratelmatobius sp	891	CFBH-T 240	Brazil: Paraná: Piraquara		**DQ283098**		**DQ283814**	**DQ284148**	**DQ282925**		**DQ282676**	**DQ283499**	4195
"PEG-M1"	359	OMNH 37004	Brazil: Rondônia: Parque Estadual Guajará-Mirim, 10°19′17.2″S 64°33′47.9″W	DQ502485	DQ502054	DQ502778							3454
"PEG-M1"	616	LSUMZ 17601	Brazil: Rondônia: Parque Estadual Guajará-Mirim, 10°19′17.2″S 64°33′47.9″W	DQ502568	DQ502136	DQ502843		DQ502350		DQ503349	DQ503100		4616

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"PEG-M1"	1288	MPEG 13397	Brazil: Rondônia: Parque Estadual Guajará-Mirim, 10°19′17.2″S 64°33′47.9″W	DQ502648	DQ502213	DQ502900							3456
"PEG-M2"	617	OMNH 36958	Brazil: Rondônia: Parque Estadual Guajará-Mirim, 10°19′17.2″S 64°33′47.9″W	DQ502569	DQ502137		DQ503239	DQ502351		DQ503350	DQ503101		4266
"PEG-M2"	618	MPEG 13349	Brazil: Rondônia: Parque Estadual Guajará-Mirim, 10°19′17.2″S 64°33′47.9″W	DQ502570	DQ502138								2790
"PEG-M2"	1237	OMNH 36959	Brazil: Rondônia: Parque Estadual Guajará-Mirim, 10°19′17.2″S 64°33′47.9″W	DQ502620	DQ502184		DQ503262		DQ503169	DQ503379	DQ503126	DQ503022	5246
"PEG-M2"	1276	OMNH 36985	Brazil: Rondônia: Parque Estadual Guajará-Mirim, 10°19′17.2″S 64°33′47.9″W	DQ502636	DQ502201								2790
"PEG-M2"	1282	MPEG 13375	Brazil: Rondônia: Parque Estadual Guajará-Mirim, 10°19′17.2″S 64°33′47.9″W	DQ502642	DQ502207								2790
"PEG-M2"	1289	OMNH 36993	Brazil: Rondônia: Parque Estadual Guajará-Mirim, 10°19′17.2″S 64°33′47.9″W	DQ502649	DQ502214								2790
"PEG-M3"	360	OMNH 36988	Brazil: Rondônia: Parque Estadual Guajará-Mirim, 10°19′17.2″S 64°33′47.9″W	DQ502486	DQ502055	DQ502779							3456
"PEG-M3"	619	MPEG 13386	Brazil: Rondônia: Parque Estadual Guajará-Mirim, 10°19′17.2″S 64°33′47.9″W	DQ502571	DQ502139	DQ502844	DQ503240	DQ502352	DQ503164	DQ503351			5073
"PEG-M3"	1263	MPEG 13388	Brazil: Rondônia: Parque Estadual Guajará-Mirim, 10°19′17.2″S 64°33′47.9″W	DQ502624	DQ502188								2798
"PEG-M3"	1266	MPEG 13385	Brazil: Rondônia: Parque Estadual Guajará-Mirim, 10°19′17.2″S 64°33′47.9″W	DQ502627	DQ502191								2798
"PEG-M3"	1272	MPEG 13389	Brazil: Rondônia: Parque Estadual Guajará-Mirim, 10°19′17.2″S 64°33′47.9″W	DQ502633	DQ502197								2798
"PEG-M3"	1274	MPEG 13384	Brazil: Rondônia: Parque Estadual Guajará-Mirim, 10°19′17.2″S 64°33′47.9″W	DQ502635	DQ502199								2797
"PEG-M3"	1279	MPEG 13394	Brazil: Rondônia: Parque Estadual Guajará-Mirim, 10°19′17.2″S 64°33′47.9″W	DQ502639	DQ502204								2796

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"PEG-M3"	1295	MPEG 13387	Brazil: Rondônia: Parque Estadual Guajará-Mirim, 10°19′17.2″S 64°33′47.9″W	DQ502651	DQ502217								2798
"PEG-M3"	1296	MPEG 13393	Brazil: Rondônia: Parque Estadual Guajará-Mirim, 10°19′17.2″S 64°33′47.9″W	DQ502652	DQ502218								2798
"PEG-M3"	1319	MPEG 13383	Brazil: Rondônia: Parque Estadual Guajará-Mirim, 10°19′17.2″S 64°33′47.9″W	DQ502673	DQ502241	DQ502912							3456
petersi	522	MJH 7041	Peru: Huánuco: Río Llullapichis, Panguana	DQ502546	DQ502114	DQ502823							3454
petersi	525	MJH 3715	Peru: Humboldt	DQ502548	DQ502116	DQ502825	DQ503225	DQ502335	DQ503159	DQ503335	DQ503087	DQ502986	6236
Physalaemus gracilis	TJ65	RdS 788	Uruguay: Flores		**DQ283417**		**DQ284022**				**DQ282875**	**DQ283728**	3889
pictus Guyana	1331	BPN 1074	Guyana: Mazaruni-Potaro: Kartabo Pt. (confluence of Cyuni & Mazaruni Rivers)	DQ502684	DQ502252	DQ502922		DQ502387				DQ503032	4553
Pleurodema brachyops	630	AMNH A139118	Guyana: Southern Rupununi Savanna, Aishalton (on Kubabawau Creek), 150 m, 2°28′31″N 59°19′16″W		**AY843733**		**AY844721**				**AY844926**		3470
"Porto-Walter1"	381	MPEG 12482	Brazil: Acre: Porto Walter, 8°15′31.2″S 72°46′37.1″W	DQ502507	DQ502076		DQ503208	DQ502318	DQ503150	DQ503322	DQ503070	DQ502971	5573
"Porto-Walter1"	625	OMNH 36153	Brazil: Acre: Porto Walter, 8°15′31.2″S 72°46′37.1″W	DQ502577	DQ502145								2795
"PortoWalter1"	626	OMNH 36148	Brazil: Acre: Porto Walter, 8°15′31.2″S 72°46′37.1″W	DQ502578	DQ502146								2794
"PortoWalter1"	1236	OMNH 36152	Brazil: Acre: Porto Walter, 8°15′31.2″S 72°46′37.1″W	DQ502619	DQ502183		DQ503261		DQ503168		DQ503125	DQ503021	4813
"PortoWalter1"	1299	OMNH 36147	Brazil: Acre: Porto Walter, 8°15′31.2″S 72°46′37.1″W	DQ502655	DQ502221								2794
"PortoWalter1"	1300	MPEG 12480	Brazil: Acre: Porto Walter, 8°15′31.2″S 72°46′37.1″W	DQ502656	DQ502222								2795
"PortoWalter1"	1301	MPEG 12486	Brazil: Acre: Porto Walter, 8°15′31.2″S 72°46′37.1″W	DQ502657	DQ502223								2794
"PortoWalter1"	1302	MPEG 12488	Brazil: Acre: Porto Walter, 8°15′31.2″S 72°46′37.1″W	DQ502658	DQ502224								2794
"PortoWalter1"	1307	OMNH 36149	Brazil: Acre: Porto Walter, 8°15′31.2″S 72°46′37.1″W	DQ502662	DQ502229								2794
"PortoWalter1"	1308	OMNH 36151	Brazil: Acre: Porto Walter, 8°15′31.2″S 72°46′37.1″W	DQ502663	DQ502230								2794
"PortoWalter2"	355	MPEG 12356	Brazil: Acre: Porto Walter, 8°15′31.2″S 72°46′37.1″W	DQ502481	DQ502050	DQ502775							3455

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Species	Sample ID	Source	Locality	Cytochrome *b*	H1	COI	Rhodopsin	Histone H3	Tyrosinase	RAG 1	SIA	28S	Total bp
"PortoWalter2"	356	MPEG 12359	Brazil: Acre: Porto Walter, 8°15′31.2″S 72°46′37.1″W	DQ502482	DQ502051	DQ502776							3455
"PortoWalter2"	1265	MPEG 12360	Brazil: Acre: Porto Walter, 8°15′31.2″S 72°46′37.1″W	DQ502626	DQ502190	DQ502889							3455
"PortoWalter2"	1269	OMNH 36027	Brazil: Acre: Porto Walter, 8°15′31.2″S 72°46′37.1″W	DQ502630	DQ502194	DQ502892							3455
"PortoWalter2"	1273	OMNH 36026	Brazil: Acre: Porto Walter, 8°15′31.2″S 72°46′37.1″W	DQ502634	DQ502198	DQ502894							3456
praderioi	1334	CPI 10198	Guyana: Mazaruni-Potoro: Mt. Roraima, 1310 m	DQ502687	DQ502255					DQ503391		DQ503035	3996
praderioi	1335	CPI 10208	Guyana: Mazaruni-Potoro: Mt. Roraima, 1310 m	DQ502688	DQ502256	DQ502923		DQ502390		DQ503392	DQ503137	DQ503036	5377
pratti	1144	SIUC 7658	Panama: Coclé: El Copé, Parque Nacional General de División "Omar Torrijos Herrera"	DQ502598	DQ502163	DQ502865	DQ503247	DQ502362		DQ503361	DQ503112	DQ503002	5700
"pratti-like"	1224	CH 5524	Panama: Darién: Caná	DQ502609	DQ502173	DQ502876	DQ503254	DQ502371		DQ503369	DQ503121	DQ503011	5702
Procerato-phrys avelinoi	306	JF 1947	Argentina: Misiones: Guarani: San Vicente, Campo Anexo INTA "Cuartel Río Victoria"		**DQ283038, DQ283039**		**DQ283769**		**DQ282903**				3262
Pseudopalu-dicola falcipes	650	MACN 38647	Argentina: Corrientes: Yapeyu		**AY843741**		**AY844728**	**DQ284117**	**AY844168**		**AY844930**		3593
pulcherrimus	118	KU 211947	Peru: Cajamarca, immediate vicinity of Cutervo, 2620 m, 06°22′S 78°49′W	DQ502429	DQ502004	DQ502724	DQ503186	DQ502290	DQ503143	DQ503293		DQ502947	5840
pulcherrimus	119	KU 211948	Peru: Cajamarca, immediate vicinity of Cutervo, 2620 m, 06°22′S 78°49′W	DQ502430	DQ502005	DQ502725							3456
pulchripectus	337	CWM 19053	Brazil: Amapá: Serra do Navio, 0°59′N 50°03′W	DQ502464	DQ502033		DQ503194	DQ502303	DQ503147	DQ503309	DQ503057		4808
pumilio	367	OMNH 33297	Nicaragua: Río San Juán: Near Isla de Diamante (ca. 15 km SE El Castillo on Río San Juán), 10°56′N 84°18′W	DQ502493	DQ502062	DQ502784							3475
pumilio	1313	OMNH 33299	Nicaragua: Río San Juán: Near Isla de Diamante (ca. 15 km SE El Castillo on Río San Juán), 10°56′N 84°18′W	DQ502668	DQ502235	DQ502907							3472

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pumilio	1315	OMNH 33300	Nicaragua: Río San Juán: Near Isla de Diamante (ca. 15 km SE El Castillo on Río San Juán), 10°56′N 84°18′W		DQ502237	DQ502909							3087
quinquevittatus RioFormoso	370	OMNH 37013	Brazil: Rondônia: Parque Estadual Guajará-Mirim, 10°19′17.2″S 64°33′47.9″W	DQ502496	DQ502065	DQ502787							3480
quinquevittatus RioFormoso	371	OMNH 37016	Brazil: Rondônia: Parque Estadual Guajará-Mirim, 10°19′17.2″S 64°33′47.9″W	DQ502497	DQ502066	DQ502788							3480
quinque-vittatus RioItuxi	368	OMNH 36665	Brazil: Amazonas: Rio Ituxi: Scheffer Madeireira, 8°28′45.8″S 65°42′59.6″W	DQ502494	DQ502063	DQ502785	DQ503203	DQ502313			DQ503066	DQ502966	5285
quinquevittatus RioItuxi	369	MPEG 13035	Brazil: Amazonas: Rio Ituxi: Scheffer Madeireira, 8°28′45.8″S 65°42′59.6″W	DQ502495	DQ502064	DQ502786							3483
quinquevittatus RioItuxi	1312	MPEG 13034	Brazil: Amazonas: Rio Ituxi: Scheffer Madeireira, 8°28′45.8″S 65°42′59.6″W	DQ502667	DQ502234	DQ502906							3482
ReservaDucke	524	MJH 3988	Brazil: Amazonas: Reserva Florestal Adolfo Ducke	DQ502547	DQ502115	DQ502824							3452
reticulatus	528	MJH 3754	Peru: Loreto: Alpahuayo	DQ502551	DQ502119	DQ502827	DQ503226	DQ502336		DQ503336		DQ502987	5306
Rhaebo guttatus	TJ2	AMNH A141058	Guyana: Dubulay Ranch on Berbice River, 200 ft, 5°40′55″N 57°51′32″W		**DQ283375**		**DQ283994**	**DQ284361**				**DQ283693**	3824
Rhaebo haematiticus	956	SIUC 7059	Panama: Coclé: El Copé, Parque Nacional General de División "Omar Torrijos Herrera"		**DQ283167**		**DQ283861**	**DQ284205**			**DQ282720**	**DQ283557**	4221
Rhinoderma darwinii	1115	IZUA 3504	Chile: X Región: Valdivia, Reserva Forestal de Oncol	DQ502589	**DQ283324**	DQ502858	**DQ283963**	**DQ284320**			**DQ282813**	**DQ283654**	5246
"RioItuxi"	404	MPEG 12978	Brazil: Amazonas: Rio Ituxi: Scheffer Madeireira, 8°28′45.8″S 65°42′59.6″W	DQ502530	DQ502098								2792
roraima	1337	CPI 10216	Guyana: Mazaruni-Potoro: Mt. Roraima, 1860–2350 m	DQ502690	DQ502258			DQ502391		DQ503393			3557

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roraima	1338	CPI 10217	Guyana: Mazaruni-Potoro: Mt. Roraima, 1860–2350 m	DQ502691	DQ502259			DQ502392		DQ503394	DQ503138		3954
roraima	1339	Tadpole (untagged)	Guyana: Mazaruni-Potoro: Mt. Roraima, 1860–2350 m	DQ502692	DQ502260		DQ503269	DQ502393		DQ503395	DQ503139		4275
saltuensis	1360	MUJ 3726	Colombia: Boyacá: Cubará, Fátima, Quebrada Gralanday, 1560 m	DQ502705	DQ502274	DQ502935	DQ503280	DQ502404		DQ503406			4543
"SãoFrancisco"	516	MJH 3909	Brazil: Amazonas: Facenda São Francisco, 2 km N km 49 on Manaus-Manacapuru road	DQ502541	DQ502109								2795
Scythrophrys sawayae	892	CFBH 6072	Brazil: Paraná: Piraquara		**DQ283099**		**DQ283815**	**DQ284149**	**DQ282926**			**DQ283500**	4338
silverstonei	646	RG	No data (captive bred)	DQ502582	**DQ283073**	DQ502851	**DQ283798**	**DQ284116**	DQ503165		**DQ282663**	**DQ283479**	5037
speciosus	341	CWM 17826(D)	Panama: Chiriquí: Continental divide above upper Quebrada de Arenam 1250–1400 m	DQ502468	DQ502037		DQ503198	DQ502307		DQ503313	DQ503061	DQ502960	5055
stepheni	514	MJH 3928	Brazil: Amazonas: Reserva Florestal Adolfo Ducke	DQ502539	DQ502107	DQ502818	DQ503223	DQ502333		DQ503334	DQ503085	DQ502984	5691
stepheni	515	MJH 3950	Brazil: Amazonas: Reserva Florestal Adolfo Ducke	DQ502540	DQ502108	DQ502819							3455
subpunctatus	1359	MUJ 5212	Colombia: Bogotá, D.C., campus of Universidad Nacional de Colombia	DQ502704	DQ502273		DQ503279	DQ502403		DQ503405			3889
sylvaticus Barbour and Noble	76	KU 219756	Peru: Piura: Ayacaba, 12.7 km E El Tambo, 2820 m	DQ502413	DQ501988	DQ502714	DQ503178	DQ502281	DQ503141	DQ503286	DQ503042		5463
sylvaticus Barbour and Noble	113	KU 219757	Peru: Piura: Ayacaba, 12.7 km E El Tambo, 2820 m	DQ502424	DQ501999	DQ502721							3455
sylvaticus Funkhouser	364	LSUMZ 14730	Ecuador: Santo Domingo	DQ502490	DQ502059	DQ502781		DQ502312		DQ503317	DQ503065	DQ502965	5395
"Tafelberg"	1326	UTA A55758	Suriname: Sipaliwini: ca. 4.0 km N of Tafelberg airstrip	DQ502679	DQ502247	DQ502917	DQ503265			DQ503386	DQ503132	DQ503027	4478

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talamancae Nicaragua	361	OMNH 33236	Nicaragua: Río San Juán: Near Isla de Diamante (ca. 15 km SE El Castillo on Río San Juán), 10°56′N 84°18′W	DQ502487	DQ502056								2792
talamancae Nicaragua	362	OMNH 33237	Nicaragua: Río San Juán: Near Isla de Diamante (ca. 15 km SE El Castillo on Río San Juán), 10°56′N 84°18′W	DQ502488	DQ502057								2794
talamancae Nicaragua	408	OMNH 33238	Nicaragua: Río San Juán: Near Isla de Diamante (ca. 15 km SE El Castillo on Río San Juán), 10°56′N 84°18′W	DQ502534	DQ502102	DQ502815							3449
talamancae Panama	325	USNM-FS 52055	Panama: Bocas del Toro: Cayo Nancy	**AY843799**	**AY843577**	DQ502749	**AY844550**	DQ502300		**AY844373**	**AY844778**	DQ502954	5701
talamancae Panama	326	USNM-FS 59757	Panama: Bocas del Toro: S end of Isla Popa, 1 km E Sumwood Channel	DQ502454	DQ502025	DQ502750							3450
talamancae Panama	1147	SIUC 7667	Panama: Coclé: El Copé, Parque Nacional General de División ‘‘Omar Torrijos Herrera’’	DQ502601	DQ502166	DQ502868	DQ503250	DQ502364		DQ503363	DQ503114	DQ503004	5704
Telmatobius jahuira	313	AMNH A165110	Bolivia: La Paz: Bautista Saavedra: Charazani Canton, Stream 4, 15°7′49″S 68°53′17″W	DQ502448	**DQ283040**	DQ502743	**DQ283770**						3787
Telmatobius marmoratus	315	AMNH A165114	Bolivia: La Paz: Bautista Saavedra: Charazani Canton, stream 2700–2750 m, 15°7′49″S 68°53′17″W		**AY843769**		**AY844757**	**DQ284068**			**AY844952**	**AY844355**	4193
Telmatobius sp	314	AMNH A165130	Bolivia: La Paz: Bautista Saavedra: Charazani Canton, stream 4, 15°7′49″S 68°53′17″W		**DQ283041**		**DQ283771**	**DQ284067**					3070
tepuyensis	606	ROM 39637	Guyana: Mount Ayanganna, northeast plateau, 1490 m, 5°24′N 59°57′W	DQ502559	DQ502128	DQ502835	DQ503234	DQ502344	DQ503162	DQ503343	DQ503095	DQ502992	6228
terribilis	1135	AMNH A118566	Colombia: Cauca: Quebrada Guanguí, 0.5 km above Rio Patia (upper Saija drainage), 100–200 m	DQ502593	DQ502157	DQ502861	DQ503244	DQ502360		DQ503358	DQ503110	DQ502999	5706

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terribilis	1232	MB	No data (captive bred)	DQ502616	DQ502180	DQ502883		DQ502376		DQ503376	DQ503123	DQ503018	5388
''Thomasing''	1332	UTA A56709	Guyana: Mazaruni-Potaro: Mt. Thomasing (~2 km N Imbaimadai) 5°44′22.8″N 60°17′51.3″W	DQ502685	DQ502253			DQ502388		DQ503389		DQ503033	4326
''Thomasing''	1333	UTA A56710	Guyana: Mazaruni-Potaro: Mt. Thomasing (~2 km N Imbaimadai) 5°44′22.8″N 60°17′51.3″W	DQ502686	DQ502254			DQ502389		DQ503390	DQ503136	DQ503034	4722
Thoropa miliaris	1186	CFBH 3239	Brazil: São Paulo: Picinguaba: Ubatuba	DQ502607	**DQ283331**	DQ502874		DQ502369					3796
tinctorius	535	MRT 5087	Brazil: locality unknown	DQ502554	DQ502123	DQ502830	DQ503229	DQ502339		DQ503339	DQ503090	DQ502990	5702
tinctorius	1327	UTA A56495	Suriname: Sipaliwini: ca. 1.0 km N of Tafelberg airstrip	DQ502680	DQ502248	DQ502918	DQ503266	DQ502384		DQ503387	DQ503133	DQ503028	5702
trilineatus	74	KU 215172	Peru: Madre de Dios: Cusco Amazónico, 15 km E Puerto Maldonado, 200 m	DQ502411	DQ501986	DQ502712	DQ503176	DQ502279		DQ503284	DQ503040	DQ502938	5713
trilineatus	112	KU 215175	Peru: Madre de Dios: Cusco Amazónico, 15 km E Puerto Maldonado, 200 m	DQ502423	DQ501998	DQ502720	DQ503184	DQ502287		DQ503290	DQ503045	DQ502944	5712
trilineatus	527	MJH 7477	Peru: Huánuco: Río Llullapichis, Panguana	DQ502550	DQ502118	DQ502826							3457
trinitatis	609	MVZ 199828	Trinidad and Tobago: Nariva Parish: Charuma Ward, Tamana Cave	DQ502562	DQ502131	DQ502838	DQ503236	DQ502347		DQ503345	DQ503097		4928
trivittatus Balbina	519	MJH 3907	Brazil: Amazonas: Base 2 island in reservoir of Uatuma river, 8 km NW represa de Balbina	DQ502544	DQ502112	DQ502822							3456
trivittatus Leticia	1350	ICN 50437	Colombia: Amazonas: Leticia, Km 11 (Leticia-Tarapacá)	DQ502698	DQ502267	DQ502929	DQ503273	DQ502397	DQ503173	DQ503400			5066
trivittatus Manaus	627	OMNH 37455	Brazil: Amazonas: Castanho: ca. 40 km S Manaus, at km 12 on road to Autazes, 3°37′10.4″S 59°86′78.4″W	DQ502579	DQ502147	DQ502848							3458

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trivittatus Manaus	628	OMNH 37453	Brazil: Amazonas: Castanho: ca. 40 km S Manaus, at km 12 on road to Autazes, 3°37′10.4″S 59°86′78.4″W	DQ502580	DQ502148	DQ502849							3458
trivittatus Panguana	518	MJH 7483	Peru: Huánuco: Río Llullapichis, Panguana	DQ502543	DQ502111	DQ502821	DQ503224	DQ502334			DQ503086	DQ502985	5267
trivittatus Port Walter	1297	MPEG 12447	Brazil: Acre: Porto Walter, 8°15′31.2″S 72°46′37.1″W	DQ502653	DQ502219	DQ502901							3456
trivittatus Port Walter	1305	MPEG 12468	Brazil: Acre: Porto Walter, 8°15′31.2″S 72°46′37.1″W	DQ502660	DQ502227	DQ502903							3454
trivittatus Porto Walter	384	MPEG 12504	Brazil: Acre: Porto Walter, 8°15′31.2″S, 72°46′37.1″W	DQ502510	DQ502079	DQ502799	DQ503211	DQ502321	DQ503152	DQ503324	DQ503073	DQ502974	6237
trivittatus Porto Walter	387	MPEG 12450	Brazil: Acre: Porto Walter, 8°15′31.2″S 72°46′37.1″W	DQ502513	DQ502082	DQ502802							3456
trivittatus Suriname	1329	BPN 910	Suriname: Para: Paramaribo-Apura road	DQ502682	DQ502250	DQ502920	DQ503268		DQ503170			DQ503030	5075
trivittatus Tambopata	319	USNM 268846	Peru: Madre de Dios: Puerto Maldonado: Explorer's Inn, 30 km (airline) SSW of Tambopata Reserve	DQ502449	DQ502021	DQ502744	DQ503190	DQ502298	DQ503145		DQ503053		5029
trivittatus Tambopata	322	USNM 269052	Peru: Madre de Dios: Puerto Maldonado: Explorer's Inn, 30 km (airline) SSW of Tambopata Reserve	DQ502451	DQ502023	DQ502746	DQ503191	DQ502299	DQ503146	DQ503302	DQ503054	DQ502953	6234
truncatus	1151	RG	No data (captive bred)	DQ502605	DQ502170	DQ502872	DQ503252	DQ502367		DQ503366	DQ503118	DQ503008	5712
truncatus	1351	ICN 48474	Colombia: Córdoba: Pueblonuevo, hacienda Praga	DQ502699	DQ502268	DQ502930	DQ503274	DQ502398		DQ503401			4550
truncatus	1352	ICN 48477	Colombia: Córdoba: Pueblonuevo, finca Embajada	DQ502700	DQ502269	DQ502931	DQ503275	DQ502399		DQ503402			4550
undulatus	331	AMNH A159141	Venezuela: Amazonas: Cerro Yutajé, 1700 m, 5°46′N 66°8′W	DQ502458	DQ502028	DQ502755							3449
undulatus	332	AMNH A159139	Venezuela: Amazonas: Cerro Yutajé, 1700 m, 5°46′N 66°8′W	DQ502459	**DQ283044**	DQ502756	**DQ283773**	**DQ284073**		DQ503308	**DQ282656**	**DQ283464**	5702

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undulatus	333	AMNH A159140	Venezuela: Amazonas: Cerro Yutajé, 1700 m, 5°46′N 66°8′W	DQ502460	DQ502029	DQ502757							3451
vanzolinii	372	OMNH 36035	Brazil: Acre: Porto Walter, 8°15′31.2″S 72°46′37.1″W	DQ502498	DQ502067	DQ502789	DQ503204	DQ502314		DQ503318	DQ503067	DQ502967	5708
vanzolinii	373	OMNH 36037	Brazil: Acre: Porto Walter, 8°15′31.2″S 72°46′37.1″W	DQ502499	DQ502068	DQ502790							3472
vanzolinii	1314	OMNH 36036	Brazil: Acre: Porto Walter, 8°15′31.2″S 72°46′37.1″W	DQ502669	DQ502236	DQ502908							3471
ventrimaculatus Leticia	1349	JDL 24489	Colombia: Amazonas: Leticia, Km 11 (Leticia-Tarapacá)	DQ502697	DQ502266	DQ502928	DQ503272	DQ502396		DQ503399			4547
ventrimaculatus Manaus	1310	OMNH 37440	Brazil: Amazonas: Castanho: ca. 40 km S Manaus, at km 12 on road to Autazes, 3°37′10.4″S 59°86′78.4″W	DQ502665	DQ502232	DQ502905							3466
ventrimaculatus Pompeya	374	OMNH 34091	Ecuador: Sucumbíos: Estación Científica de Universidad Católica near Reserva Faunística Cuyabeno, 220 m, 0°0′S 76°10′W	DQ502500	DQ502069	DQ502791	DQ503205	DQ502315		DQ503319		DQ502968	5307
ventrimaculatus Porto Walter	375	MPEG 12394	Brazil: Acre: Porto Walter, 8°15′31.2″S 72°46′37.1″W	DQ502501	DQ502070	DQ502792							3466
ventrimaculatus Porto Walter	1311	OMNH 36062	Brazil: Acre: Porto Walter, 8°15′31.2″S 72°46′37.1″W	DQ502666	DQ502233								2810
ventrimaculatus Rio Ituxi	376	OMNH 36666	Brazil: Amazonas: Rio Ituxi: Scheffer Madeireira, 8°28′45.8″S 65°42′59.6″W	DQ502502	DQ502071	DQ502793	DQ503206	DQ502316	DQ503148	DQ503320	DQ503068	DQ502969	6232
ventrimaculatus Rio Ituxi	377	OMNH 36667	Brazil: Amazonas: Rio Ituxi: Scheffer Madeireira, 8°28′45.8″S 65°42′59.6″W	DQ502503	DQ502072	DQ502794							3468
vicentei	1148	KRL 789	Panama: Coclé: El Copé, Parque Nacional General de División "Omar Torrijos Herrera"	DQ502602	DQ502167	DQ502869		DQ502365		DQ503364	DQ503115	DQ503005	5406
vittatus	839	RG	No data (captive bred)	DQ502585	DQ502152	DQ502854			DQ503166	DQ503355	DQ503105		4821

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Species	Sample ID	Source	Locality	Cytochrome *b*	H1	COI	Rhodopsin	Histone H3	Tyrosinase	RAG 1	SIA	28S	Total bp
zaparo	321	USNM 546404	Ecuador: Pastaza: Coca, 130 km S of Nuevo Golandrina, on trail W toward Rio Curaray, 300 m, 1°07′S 76°57′W	DQ502450	DQ502022	DQ502745							3452
zaparo	328	USNM 546405	Ecuador: Pastaza: Coca, 130 km S of Nuevo Golandrina, on trail W toward Rio Curaray, 300 m, 1°07′S 76°57′W	DQ502455	DQ502026	DQ502752	DQ503192	DQ502301		DQ503305	DQ503055	DQ502955	5713
"*zaparo*"	127	KU 221841	Peru: Loreto: San Jacinto, 175 m	DQ502438	DQ502013	DQ502732	DQ503187	DQ502295	DQ503144		DQ503050	DQ502950	5801

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APPENDIX 6
SPECIMENS EXAMINED

The following list of specimens examined includes material used explicitly to score the character states reported in appendix 7. The extensive material examined in the course of species identification and transformation series individuation is not listed. Species are listed following the new taxonomy proposed above. See Materials and Methods for collection abbreviations.

OUTGROUP TAXA

Atelopus spurrelli: COLOMBIA: **Chocó**: Quesada River, Atrato River, AMNH 13597–98. Puerto Utría, AMNH 50983–84. Serranía de Baudó, northern base Alto del Buey, Quebrada Mutatá, 200 m, AMNH 102065–68.

Atelopus zeteki: PANAMA: El Valle, AMNH 44687–91. Probably El Valle region, AMNH 45995–96. **Coclé**: El Valle de Antón, 2000 ft, AMNH 55533–43. N side of El Valle de Anton, AMNH 83920–22. **Panamá**: Laguna [probably 9 km E El Valle], AMNH 55544.

Crossodactylus schmidti: ARGENTINA: **Misiones**: Aristobulo del Valle, Balneario Cuñapirú, JF 832, 850.

Cycloramphus boraceiensis: BRAZIL: **São Paulo**: Boracéia, AMNH 54546.

Cycloramphus fuliginosus: BRAZIL: **Rio de Janeiro**: Rio de Janeiro, Tijuca, KU 92789 (C&S).

Dendrophryniscus minutus: ECUADOR: **Morona-Santiago**: 320 m, 2°40′S 77°42′W, Cusuime, Río Cusuime [60 km airline SE Macas], AMNH 93804–72.

Eupsophus roseus: CHILE: Cerro Caracol, Cordillera de la Costa, Concepción, 25–137 m, AMNH 13979. Corral, AMNH 22102, 22126, 23988, 22104 (skeleton). Ancud, Chiloe Island, AMNH 22142, 22151. Valdivia, AMNH 23959. Valdivia, Bosque San Martín, KU 207501 (C&S).

Hylodes phyllodes: BRAZIL: **São Paulo**: Serra do Mar, Estacão Biologica de Boracéia, 850 m, AMNH 103850–95,103945–46 (larvae).

Megaelosia goeldii: BRAZIL: **Rio de Janeiro**: Petropolis, AMNH 70249. Near SE edge Teresópolis, 950 m, AMNH 103947–53.

Melanophryniscus stelzneri: ARGENTINA: **Córdoba**: Achiras, AMNH 51883–92. **San Luis**: Sierras of San Luis, 1000 m, AMNH 76121–23, 77710 (skeleton).

Rhinoderma darwinii: CHILE: Concepción, AMNH 7567. Arauco, AMNH 14441–45, 37848–50. Valdivia, AMNH 37813–14. Isla Maullín, 41°35′S 73°W, AMNH 45331. Received from Concepción Zoo, AMNH 58082–91.

Telmatobius jahuira: BOLIVIA: **La Paz**: Bautista Saavedra, Charazani Cantón, Stream 4, 15°7′49″S 68°53′17″W, AMNH 165110.

Thoropa lutzi: BRAZIL: **Rio de Janeiro**: Rio de Janeiro, Sumare, KU92850 (C&S).

Thoropa miliaris: BRAZIL: **Rio de Janeiro**: AMNH 36275–76. Rio de Janeiro, AMNH 509. Voita de Almoço, Serra do Itatiaya, AMNH 17043–46, 17048–49, 17059. Mountains near Rio de Janeiro, AMNH 20251–52, 20254. Teresópolis, AMNH 20861, 70141. Teresópolis, Parque Nacional da Serra dos Órgãos, 2700 ft, AMNH 52186.

AROMOBATIDAE

Allobates femoralis: COLOMBIA: **Putumayo**: Santa Rosa de Sucumbíos (Kofan Indian Village), upper Río San Miguel, AMNH 116149. Ca. 10 km (airline) S Mocoa, AMNH 85258 (C&S), 85260 (C&S). BRAZIL: **Amapá**: Serra do Navio, 100–200 m, 0°59′N 50°3′W, AMNH 140633–49. GUYANA: Iwokrama, Cowfly Camp, AMNH 164053. Iwokrama, cutline, AMNH 164054. PERU: **Loreto**: 3 km NE Pebas on Río Amazonas, 3°8′S 71°49′W, AMNH 103581 (C&S). SURINAME: **Brokopondo**: 65 km airline SSE Paramaribo on Afobaka Rd., AMNH 87680. **Saramacca**: Raleigh Cataracts, Coppename River, AMNH 87681–86. **Marowijne**: Loë Creek, Camp Hofwijks VIII, 56 km (airline) SSW Oelemari, AMNH 90930–32.

Allobates insperatus: ECUADOR: **Napo**: Santa Cecilia, 340 m, KU 109310 (C&S), 149663–90, 149691 (C&S), 149692–70, 149671 (C&S), 149672–707. Río Yasuni, 150 km upstream from Río Napo, KU 175165, 175168–69. Dureno, 320 m, KU 175485. Limoncocha, 243 m, KU 182124.

Allobates juanii: COLOMBIA: **Cundinamarca**: Medina, vereda Choapal, 6–7 km NNW Medina, 580–630 m, ICN 15644–45. **Meta**: Acacias, Portachuelo (crest of divide between Guayabetal and Acacias, ca. 1500 m), ICN 5097 (C&S). Cubarral, El Dorado, ICN 39494–95.

Allobates kingsburyi: PERU: Chanchamayo, AMNH 42282–83, 43604, 43606. ECUADOR: Mapoto, 1300 m, UMMZ 89063–64. **Pastaza**: Abitagua Napo-Pastaza, 1200 m, UMMZ 90373 (3 specimens), 90374 (8 specimens), 90375, 217617 (C&S). Napo-Pastaza Mera Oriente, 1000 m, UMMZ 90376. Near Mera Oriente, UMMZ 90377 (2 specimens).

Allobates "Magdalena": COLOMBIA: **Caldas**: La Dorada: San Roque: Reserva Natural Privada Riomanso, 280 m, 5°40′N 74°46′W, MUJ 3519–34, 3544. **Santander**: Cimitarra: Los Indios: El Triángulo, Finca Las Camelias, 240 m, MUJ 2900, 2917. Puerto Araujo, Hacienda El Manantial, 180 m MUJ 2927–28.

Allobates "Neblina species": VENEZUELA: **Amazonas**: Río Negro: Neblina Base Camp on Río Mawarinuma, 140 m, 0°50′N 66°10′W, AMNH 118650–64, 118667 (C&S), 118669 (C&S), 118670, 118673 (larvae), 118674–83, 118684 (C&S), 118685–86, 118687 (C&S), 118688–90.

Allobates olfersioides: BRAZIL: **Rio de Janeiro**: Guanabara, Tijuca, AMNH 72445–47, UMMZ 127922 (3 specimens), UMMZ 217618 (C&S), KU 93161 (C&S).

Allobates talamancae: COLOMBIA: **Valle del Cauca**: Buenaventura, Bajo Calima, MUJ 808 (+ larvae). **Risaralda**: Pueblo Rico, Santa Cecilia y alrededores, ICN 47972. COSTA RICA: **Puntarenas**: Osa Peninsula, Corcovado National Park, about

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6 km E Sirena Biological Station on Trail to Los Patos Ranger Station, UMMZ 193379 (C&S). PANAMA: **Bocas del Toro**: east slope of Cerro Miramar, (ca. 1.5 km S of Miramar), AMNH 113893–901. Isla Bastimentos, AMNH 118380–81 (C&S). Isla Bastimentos, hills W Short Cut, 3.1 km SE Toro Point, AMNH 124225–33. South side Cayo de Agua, AMNH 124234–39 (+ uncataloged carcasses).

Allobates trilineatus: PERU: **Madre de Dios**: Parque Nacional del Manu, Cocha Cashu Biological Station, 11°51′S 71°19′W, 380 m, AMNH 153038–39. Puerto Maldonado, 280 m, USNM 343061.

Allobates undulatus: VENEZUELA: **Amazonas**: Cerro Yutajé, 1750 m, 5°46′S 66°8′W, AMNH 159118–40, 159141–42 (C&S).

Allobates zaparo: ECUADOR: AMNH 52881–82 (C&S). **Morona-Santiago**: Ashuara village on Río Macuma, ca. 10 km above Río Morona [ca. 83 km ESE Macas], 300 m, AMNH, 94562–68. **Pastaza**: Coca, 130 km S of Nueva Golandrina, on trail W toward Río Curaray, 300 m, 1°07′S 76°57′W, USNM 546404–405.

Anomaloglossus ''Ayanganna'': GUYANA: Mt. Ayanganna, northeast plateau, 1490–1550 m, 5°24′N 59°57′W, ROM 39639.

Anomaloglossus baeobatrachus: BRAZIL: **Amapá**: Serra do Navio, AMNH 140650–73, AMNH 140674 (larvae). FRENCH GUIANA: Saül, Mantagne Belvédère, 3°37′N 53°12′W, IRSNB-KBIN 12662, 12976, 12977.

Anomaloglossus beebei: GUYANA: near Kaieteur Falls, AMNH 18683. Kaieteur National Park, 5°118N 59°298W, UMMZ 218880, 221371–74. Mt. Ayanganna, northeast plateau, 1490–1550 m, 5°24′N 59°57′W, ROM 39629–32.

Anomaloglossus ''Brownsberg'': SURINAME: **Brokopondo**: Brownsberg Nature Park, UTA 56469.

Anomaloglossus degranvillei: SURINAME: **Marowijn**: Central Lely Mountains, headwaters of Djoeka Creek (Suralco Camp V), 620 m, AMNH 90871–76, 90878–92.

Anomaloglossus praderioi: GUYANA: **Mazaruni-Potoro**: Mt. Roraima, 1310 m, CPI 10198–205, 101207–208.

Anomaloglossus roraima: GUYANA: **Mazaruni-Potoro**: Mt. Roraima, 1860–2350 m, CPI 10212–17 (+ untagged larvae).

Anomaloglossus stepheni: BRAZIL: **Amazonas**: Ducke Reserve, 150 m, KU 129988–130008. Ducke Reserve, KU 130009–14. Sudam Floral Reserve, 74 km E Santarem, KU 129987, 130144–45.

Anomaloglossus ''Tafelberg'': SURINAME: **Sipaliwini**: ca. 4.0 km N of Tafelberg airstrip, UTA 55758.

Anomaloglossus tepuyensis: GUYANA: Mt. Ayanganna, northeast plateau, 1490 m, 5°24′N 59°57′W, ROM 39637. VENEZUELA: **Bolívar**: Auyantepui, Camp 1, 1700 m, 5°51′N 62°32′W, AMNH 164817–22. Auyantepui Camp 3, 1850 m, 5°538N 62°388W, AMNH 164823. Auyantepui Camp 4, 1600 m, 5°58′N 62°33′W, AMNH 168424–33.

Anomaloglossus ''Thomasing'': GUYANA: **Mazaruni-Potaro**: Mt. Thomasing (~2 km N Imbaimadai) 5°44′22.8″N 60°17′51.3″W, UTA 56708–10.

Aromobates molinarii: VENEZUELA: **Mérida**: Cascada de Bailadores, 1800 m, UMMZ 176207 (C&S), 176208–11, 176220, 176222.

Aromobates nocturnus: VENEZUELA: **Trujillo**: about 2 km (airline) ESE Agua de Obispos, 2250 m, 9°42′N 70°05′W, AMNH 129940 (C&S), 130006–13, 130014 (C&S), 130016–21, 130026–33, 130036–38, 130041 (C&S), 130047 (skeleton).

Aromobates saltuensis: COLOMBIA: **Norte de Santander**: Bucarsica, ICN 42512–16, 33587.

Aromobates sp.: VENEZUELA: **Trujillo**: about 2 km (airline) ESE Agua de Obispos, 2250 m, 9°42′N 70°05′W, AMNH 129958–74.

Mannophryne collaris: VENEZUELA: near Mérida, Río Albirregas, AMNH 10512–16. Merida, UMMZ 217615 (C&S). **Trujillo**: Between Niquito and La Columna, USNM 291062–64.

Mannoprhyne herminae: VENEZUELA: **Aragua**: Rancho Grande, near Maracay, AMNH 70761–87, 116941–977, 116978–79 (larvae). Parque Nacional Henri Pittier, Rancho Grande, below toma del agua, 1100 m, USNM 259176 (larvae). Río Ocumare, 110 m, UMMZ 210143–44 (C&S). **Carabobo**: San Esteban, UMMZ 139774–75 (larvae).

Mannophryne trinitatis: TRINIDAD AND TOBAGO: **Trinidad**: Arima Valley, Spring Hill Estate, on trail to Guacharo Cave, USNM 166302–04. St. George, Maracas, on trail to Maracas waterfall, USNM 166305–37. St. George, Mount El Tucuche, USNM 166338–42. 7 mi N Arima, 800 ft, UMMZ 167465 (C&S), 167469, 167471, 167474. Northern Range, ca. 8 km (airline) N Arima, 560 m, AMNH 118384 (C&S), 118389 (C&S).

Rheobates palmatus: COLOMBIA: Magdalena, UMMZ 149232, 149233 (skeletons). **Cundinamarca**: Anolaima, AMNH 13472. Honda [data ambiguous, possibly from Páramo del Verjón, E of Bogotà], AMNH 20359–63. Páramo del Verjón, E of Bogotá, AMNH 20364–65, 20367–69. Formeque, 20409–18. Choachi, AMNH 20425–33, 20436–37. Aguadita, AMNH 22610–15. Ca. 25 mi N Villavicencio, UTA 8028–32, 39725. **Meta**: Serranía de la Macarena, UTA 4929. Los Micos (16 km S San Juán), ca. 4 hours S of this location at Cañon Joel, UTA 39711. Caño Cristalina, 8.0 hours S Los Micos, UTA 39712. Ca. 30 km WSW Vista Hermosa, Caño Sardinita, UTA 39713, 39715–23, 39737, 39738–40 (larvae). Ca. 32 km WSW Vista Hermosa, Caño Sardinita, UTA 39714. Sierra de La Macarena, ca. 30 km WSW Vista Hermosa, UTA 39724. **Santander**: Virolín, 2500 m, MUJ 5003. **Tolima**: 20.3 mi WNW Cajamarca [on way from Cali to Bogotá], UTA 39728–29.

DENDROBATIDAE

Ameerega bassleri: PERU: **San Martín**: Cainarachi, AMNH 42313. Pachiza, Río Huallaga, AMNH 42327, 42333, 43402 (C&S). Chasuta, AMNH 42867, 42944.

Ameerega bilinguis: COLOMBIA: **Putumayo**: ca. 10 km (airline) S Mocoa, 700–800 m, AMNH 85200–208, 85210–14, 85215 (C&S), 85216, 85219 (C&S), 85221 (C&S), 85224, 85226–27.

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Ameerega braccatus: BRAZIL: **Mato Grosso**: Estação Ecológica Serra das Araras, USNM 505750 (larvae).

Ameerega flavopicta: BRAZIL: **Goiás**: Minacu: Upper Tocantins River, Serra da Mesa, 13°50′13″S 48°19′28″W, AMNH 158104–05. **Minas Gerais**: Jaboticatubas, Serra do Cipo, km 114, AMNH 88642. Santana do Riacho, USNM 505751 (larvae).

Ameerega hahneli: PERU: **Loreto**: Yagua Indian Village, headwaters of Río Loretoyacu [100+ km NW Leticia], AMNH 96185–96. 5 rd km NE Previsto, near Boqueron del Padre Abad, upper Río Aguaytía, 500 m, AMNH 118421 (C&S). BRAZIL: **Amazonas**: Igarapé Belém, near Rio Solimões, ca. (70 km E Leticia), AMNH 96751–54. Presidente Figueiredo, USNM 505752 (larvae). COLOMBIA: **Amazonas**: Leticia, boca a Los Lagos (Yahuarcaca), ICN 53105 (larvae).

Ameerega macero: PERU: Madre de Dios: West side Río Manu across from Cocha Cashu Biological Station, Parque Nacional del Manu, ca. 380 m, 11°55′S 71°1′W, AMNH 129473–74, 133205, 133207 (larvae), 134159–63.

Ameerega petersi: PERU: **Junín**: Valle de Perene, 1200m, AMNH 17257. Otica, Río Tambo, AMNH 111000. **San Martín**: Achinamisa (Río Huallaga), AMNH 42179, 42505–07, 42546. Chasuta (Río Huallaga), AMNH 42790, 42945. **Huánuco**: Monte Alegre, Río Pachitea, AMNH 43016 (C&S).

Ameerega pulchripectus: BRAZIL: **Amapá**: Serra do Navio, AMNH 137280–137293.

Ameerega picta: BOLIVIA: Buenavista, AMNH 22637–38. **Santa Cruz**: Buenavista, 500 m, AMNH 33959, 34075, 39562–63. 4.5 km N 1.5 km E Cerro Amboró, Río Pitasama, 620 m, 17°45′S 63°40′W, AMNH 153546. 3 km N 13.5 km W San Rafael de Amboro, Río Saguayo, 400 m, AMNH 153547–49. **Beni**: Río Benicito, Chacabo, AMNH 70151. Río Mamor' ca. 4 km below Santa Cruz, 11°10′S, AMNH 79196–211. 45 km N of Yacuma, 400 m, 14°42′S 67°4′W, AMNH 153550–51. 6 km W of Casarabe, 400 m, AMNH 153552–73. Prov. Ballivian, Lago Del Gringo, 10 km N of Puerto Salinas, 1 km from Beni River, 14°108S 67°408W, UMMZ 184099 (C&S).

Ameerega rubriventris: PERU: **Ucayali**: El Boquerón del Padre Abad, edge of road connecting Tingo María and Pucallpa, ca. 1000 m, AMNH 168494–97.

Ameerega silverstonei: PERU: **Huánuco**: about 30 km NE Tingo María, Cordillera Azul, [= 5 km by road SW high point (1640 m) on Tingo María-Pucallpa Rd], 1330 m, AMNH 91845–46, 91847 (C&S), 91848 (C&S), 91849 (C&S), 91851, 94803–05.

Ameerega trivittata: PERU: Cachiyacu (East of Balsapuerto), AMNH 42576. **Madre de Dios**: 30 km (airline) SSW of Puerto Maldonado, Tambopata Reserve, Explorer's Inn, 280 m, 12°50′S 69°17′W, USNM 268845–47. **San Martín**: Achinamisa, AMNH 42183–84, 42539–43, 42545, 43204. SURINAME: Jodensavanne, Kamp 8, AMNH 77450. **Brokopondo**: Brownsberg Nature Park, near Mazaroni Top, ca. 450 m, AMNH 118431 (C&S) **Marowijne**: Central Lely Mountains, headwaters of Djoeka Creek (Suralco Camp V), 620 m, AMNH 90916–22, 90977–78. Airstrip, Lely Mountains, 680 m, AMNH 90923–29, 90979. **Saramacca**: Raleigh Cataracts, Coppename River, 50 m, AMNH 118428 (C&S).

Colostethus fraterdanieli: COLOMBIA: **Antioquia**: ca. 10 km airline [17 km by rd] NW of Bolívar on Quibdó road, 2050 m, AMNH 104361–68. **Caldas**: 5.5–6 km by rd southeastward Villa María, 2320 m, AMNH 104375–92, 104399 (male + larvae), 104400 (male + larvae), 104401 (male + larvae). 13 km by rd southeastward Villa Maria, 2400 m, AMNH 104397.

Colostethus fugax: ECUADOR: **Pastaza**: Cabeceras del Río Bobonaza, 2250 ft., USNM 282831.

Colostethus imbricolus: COLOMBIA: **Chocó**: Serranía de Baudó, N slope Alto del Buey, 970 m, AMNH 102082. Serranía de Baudó, northern base Alto del Buey, Quebrada Mutatá, 200 m, AMNH 102083–85.

Colostethus inguinalis: COLOMBIA: **Caldas**: La Dorada, San Roque, Reserva Natural Privada Riomanso, 255 m, 5° 40′78″N 74° 47′78″W, MUJ 3247. **Chocó**: River Truandó, USNM 4349. Upper Río Napipí, 45 min by canoe below mouth of Río Merendó (tributary of Río Napipí), ca. 60–90 m, LACM 42325–42332; trail between Río Merendó and Cerro Los Hermanos, LACM 42333; upper Río Napipí, forested hills near river on left bank, 45 min by canoe below mouth of Río Merendó, 60–200 m, LACM 42334–42340, 43955; upper Río Napipí, forested hills near river on right bank, LACM 42341–42344; upper Río Opogadó, ca. 1 hr 45 min by canoe above mouth of Río Merendó, LACM 42345–42490. Camino de Yupe, LACM 72009–10.

Colostethus panamensis: COLOMBIA: **Chocó**: Parque Nacional Natural Los Katios, IAvH [INDAN] 3337–3370, 6206, 6208–6209. PANAMA: **Coclé**: Continental Divide N El Copé, 600–800 m, 80°368W, AMNH 98317 (female + larvae), 98318 (female + larvae). El Valle, Río Antón, ± 650 m, AMNH 87293 (females + larvae). **Veraguas**: 6–12 km N Santa Fe N of Altopiedra and Agricultural School in montane area called Buenos Aires, UMMZ 167459 (C&S).

Colostethus pratti: COLOMBIA: **Risaralda**: Pueblo Rico, Santa Cecilia y alrededores, ICN 47973–74, 47976, 47978. PANAMA: **Coclé**: 12 km N El Copé, continental divide at sawmill, UMMZ 167503 (C&S). **Darién**: Río Jaque, 1.5 km above Río Imamadó, AMNH 118364 (C&S), 118365–67, 118369–370, 118371 (C&S). **Veraguas**: 5–6 mi NW (via road) Santa Fe (Pacific drainage), 1700–2000 ft, AMNH 108339. Cerro Delgadito, 2–4 mi W Santa Fe, ca 4000 ft, AMNH 162528. 6–12 km N Santa Fe N of Altopiedra and Agricultural School in mt area called Buenas Aires, UMMZ 167460. 6–12 km N Santa Fe N of Altopiedra and Agricultural School in mt area called Buenas Aires, 3000–3500 ft, UMMZ 167506, 167512, 167514–15.

Colostethus "*pratti*-like": PANAMA: **Darién**: Caná, CH4052–47, 4650, 4702–03, 5524–25, 5598 (larvae), 5601–02.

Dendrobates auratus: COSTA RICA: **Puntarenas**: 8 km ENE Palmar Norte, AMNH 118524 (C&S). PANAMA: **Bocas del Toro**: 8.9 km (airline) WSW Chiriquí Grande, 100 m, AMNH 113904. 4.9 km (airline) WSW Chiriquí Grande, 60 m, AMNH 113905–06. East slopes Cerro Miramar (ca. 1.5 km S of Miramar), 340 m, AMNH 113907–12. **Coclé**:

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Continental divide N El Copé' 700 m, AMNH 97874. Continental divide N El Copé' 600–800 m, AMNH 98325–40. East shoulder Cerro Caracol (above El Valle de Antón), 870 m, AMNH 114588. **Panamá**: Isla Tobago, AMNH 118528 (C&S) (+20 uncataloged skinned carcasses).

Dendrobates azureus: SURINAME: **Nickerie**: Sipaliwini Savannah, AMNH 88626–88631 (+ uncataloged AMNH specimens).

Dendrobates leucomelas: BRAZIL: **Roraima**: Serra do Tepequ'm, 500–600 m, 3°458N 61°458W, AMNH 137308 (larvae), 137309–11. VENEZUELA: **Amazonas**: Río Pescado, Mt. Duida Region, 325 ft, AMNH 23179. Río Pescado, foothills camp, 750 ft, AMNH 23202, 23206. Caño Pescado, AMNH 23235. **Bolívar**: Mt. Auyan-tepui, 460 m, AMNH 46045–47, 46051. San Felix, edge of Río Orinoco, AMNH 75789. Guri Dam, ca. 300 m, AMNH 81455. El Manteco, AMNH 90203–04. Canaima Falls (near Auyan Tepui), AMNH 90998.

Dendrobates tinctorius: GUYANA: Shudikar-Wan, AMNH 49301–28. BRAZIL: **Amapá**: Serra do Navio, 100–200 m, AMNH 140675. Serra do Navio, ca. 100 m, AMNH 140676–87. Serra do Navio, KU 93147 (C&S).

Dendrobates truncatus: COLOMBIA: **Antioquia**: Santa Rosa de Oso, 2640 m [doubtful locality], AMNH 38820–21. Medellín, AMNH 39087. **Cundinamarca**: Fusagasugá, AMNH 40309–12. **Caldas**: La Dorada, San Roque, Reserva Natural Privada Riomanso, 255 m, 5° 40′78″N 74° 47′78″W, MUJ 3088 (larvae). **Cesar**: El Roncón, ca. 10–12 km E Becerril (foothills of Sierra de Perijá), 250–280 m, AMNH 84381–83. **Huila**: Neiva, Tamarindo, Alto La Tribuna, Reserva Hocol, 570 m, 3°4′N 75°22.38W, MUJ 3607. **Tolima**: Shore of Río Gualí, 1–2 km above Mariquita, 530 m, AMNH 85229–36, 118401 (C&S), 118403 (C&S). **Magdalena**: Sierra Nevada de Santa Marta, El Pueblito, Parque Nacional Tayrona, 230–290 m, AMNH 88578–79.

Epipedobates anthonyi: ECUADOR: **Azuay**: ca. 10 km (airline) W Santa Isabel, Río Jubones drainage, 1490 m, AMNH 104903–17. **El Oro**: 10 km SE Machala, 20 m, AMNH 118499 (C&S), 118502 (C&S).

Epipedobates boulengeri: COLOMBIA: **Cauca**: Isla Gorgona, USNM 145248 (larvae), 145249–252, 145253 (C&S), 145254–300 (topotypes), AMNH 50970–72 (topotypes).

Epipedobates espinosai: ECUADOR: **Pichincha**: Río Baba, 5–10 km SSW Santo Domingo de los Colorados, 500 m, AMNH 89668–87, 118411 (C&S), 118417 (C&S). Santo Domingo de los Colorados, Bypass Road, AMNH 162663. Centro Científico Río Palenque, 170 m, AMNH 104869–98, 162662. Ca. 2 km S Santo Domingo de los Colorados AMNH 162664.

Epipedobates machalilla: ECUADOR: Chimbo, BMNH 1898.3.1.4–7. **Guayas**: 3 km N Naranjal, 30 m, AMNH 89525–36, 89537 (male with 19 tadpoles). **Manabí**: 38 km NW El Carmen, ca. road to Pedernales KU 220631–33.

Epipedobates tricolor: ECUADOR: Bolivar-Cotopaxi border, ca. 7 km (airline) SSW of El Corazón, AMNH 104946–54. **Cotopaxi**: 11 km E (by road) Moraspungo, USNM 286082–83.

Hyloxalus awa: ECUADOR: **Pichincha**: ca. 15 km SE Santo Domingo de los Colorados, at Tinalandia, 800 m, AMNH 111541–44. 8 km SE Santo Domingo de los Colorados, Hacienda Delta, UMMZ 217614 (C&S).

Hyloxalus azureiventris: PERU: **San Martín**: Achinamisa, AMNH 42186.

Hyloxalus bocagei: ECUADOR: **Napo**: Río Oyacachi at Quito-Lago Agrio Road, about 20 km NNE Baeza, 1550 m, AMNH 89570–71. **Morona-Santiago**: Cusuime, Río Cusuime [60 km airline SE Macas], 320 m, AMNH 94043–73. **Pastaza**: Hills N of Mera, 78°88W, 1°268S UMMZ 182465 (C&S).

Hyloxalus delatorreae: **Carchi**: 14 km (airline) SE Maldonado, 2500 m, KU 182197. 18.5 km E Maldonado, ca. Maldonado-Tulcan rd, 2420 m, KU 220618.

Hyloxalus elachyhistus: ECUADOR: Río Linoma, AMNH 16262–303, 16305–13, 16315, 16317, 16321. **Loja**: 2150 m, KU 120543 (C&S).

Hyloxalus "Ibague": COLOMBIA: **Cundinamarca**: La Mesa, Sector de la gran vía, Finca Tacarcuna, 3km vía Cahipay, 1200 m. ARA 2343–45, 2347–57, 2443–44. Ibagué, El Totumo, Finca La Magnolia, quebrada El Cural, 1047 m, MUJ 3545–48, 3551–3553, (+ untagged larvae, to be deposited at MUJ).

Hyloxalus infraguttatus: COLOMBIA: **Nariño**: 4 km NW Junín, 1170 m, AMNH 85031 (male + larvae). ECUADOR: **Azuay**: About 16 km (airline) W Santa Isabel, Río Jubones drainage, 1000 m, AMNH 89563–65, 91824. Ca. 10 km (airline) W Santa Isabel, Río Jubones drainage, 1490 m, AMNH 104846–48. Río Minas, 8 km (airline) W of Santa Isabel, Río Jubones drainage, 1440 m, AMNH 104849. Ca. 9 km (airline) E Pasaje, 100 m, AMNH 104041–45. **El Oro**: about 20 km (airline) E Pasaje, 240 m, AMNH 91823, 104838–40.

Hyloxalus nexipus: PERU: **Amazonas**: S of Aintami entse on the Río Cenepa, 4°28′S 78°10′W, USNM 317147–53. Vicinity of San Antonio, on the Río Cenepa, 4°30′S 78°10′W, USNM 317154–60, USNM 317609 (larvae). Vicinity of Sua, on the Río Cenepa, 4°32′S 78°11′W, USNM 317161–63. Huampami, Quebrada Sasa, on the Río Cenepa, 210 m, 4°28′S 78°10′W, USNM 317164–72. Shimpunts, vicinity of, on the lower Río Alto Cenepa (tributary of the Río Cenepa), 4°25′S 78°12′W, USNM 317173–74. Paagat, on the lower Río Alto Cenepa (tributary of the Río Cenepa), 4°25′S 78°12′W, USNM 317175. Vicinity of Kagka, at the confluence of Río Kagka and Río Comaina (tributary of the Río Cenepa), 4°27′S 78°13′W, USNM 317176. Vicinity of Tseasim, on the upper Río Huampami (tributary of the Río Cenepa), 4°23′S 78°10′W, USNM 3171777–79. Vicinity of Shaim, on the Río Alto Comaina (tributary of the Río Cenepa), 4°15′S 78°22′W, USNM 317180–85.

Hyloxalus pulchellus: COLOMBIA: **Putumayo**: 4 km (airline) SE San Francisco, 2320 m, AMNH 85018–21. ECUADOR: **Napo**: Río Azuela, Quito-Lago Agrio Road, eastern base Volcán Reventador, 1700 m, AMNH 89538 (C&S).

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Hyloxalus sauli: COLOMBIA: **Putumayo**: ca. 10 km (airline) S Mocoa, 700–800 m, AMNH 85029. ECUADOR: **Napo**: Río Nachiyacu S of Venecia, 77°42′W, 1°7′S UMMZ 182477(C&S), 182478–79. Río Cotopino, UMMZ 195745.

Hyloxalus subpunctatus: COLOMBIA: **Boyacá**: Chita, El Arbolito, carretera Chita-La Salina, ICN 3990. Duitama, Páramo de la Rusia, ICN 4468. Duitama, Páramo de La Rusia, km 19–21 carretera Duitama-Charalá, 3650 m, ICN 26963. Pajarito, hacienda Comijoque, 2015 m, ICN 7196, 7235, 7237. Susacón, Páramo Guantiva, km 3–4 via Onzaga, 3170 m, ICN 10361. Ramiriqui, km 11–12 carretera Ramiriquí-Zetaquirá, 3060m, ICN 11020. Ventaquemada, vereda El Boquerón, Páramo Albarracín, 3120m, ICN 11044. Páramo de Pisba, ICN 31699. **Cundinamarca**: Bogotá, Ciudad Universitaria (Universidad Nacional), ICN 27024, 45777 (larvae). Bogotá, near Monserrate, 3000 m, UMMZ 221158–59 (C&S). Usme, Laguna Chisacá, 3700m, ICN 11868, 45779 (larvae). Bogotá, Universidad de Los Andes, 2500 m, ICN 33686, 45778 (larvae). Guasca, ICN 35672, 45780 (larvae).

Hyloxalus sylvaticus: PERU: summit Cordillera between Chanchaque and Huancabamba, 3100 m, KU 138071–79. 29.3 km SW Huancabamba, 3010 m, KU 181667–73. 31 km SW Huancabamba, 3080 m, KU 181674–79. SW slope Abra de Porculla, 1850 m, KU 164093 (C&S).

Hyloxalus toachi: ECUADOR: **Pichincha**: Río Baba, 5–10 km SSW Santo Domingo de los Colorados, 500 m, AMNH 89550–61, 89562 (male + larvae). Ca. 15 km SE Santo Domingo de los Colorados, at Tinalandia, 800 m, AMNH 111539–40.

Hyloxalus vertebralis: ECUADOR: Cinincay, 8300 ft, AMNH 17458, 17604–08, 140977–141011. **Azuay**: Cuenca, 8365 ft, USNM 282308–16, 282352–58. **Cañar**: about 8 km SE Cañar, Pan-Amer Hwy, 3000 m, AMNH 89569 (male + larvae). Cuenca, 2540 m, KU 120633–34 (C&S). **Chimborazo**: Chunchi El Tambo Road 20 km N of Gun Junction ca. 9600 ft, UMMZ 217621 (C&S).

Adelphobates castaneoticus: BRAZIL: **Pará**: near Cachoeira Juruá, Rio Xingu, 3°22′S 51°51′W, AMNH 133451–55 (paratypes).

Adelphobates galactonotus: BRAZIL: **Pará**: Cachoeira do Limão, Rio Tapajós, AMNH 128232–33.

Adelphobates quinquevittatus: BRAZIL: **Rondônia**: Alto Paraiso, AMNH 124068–71, 124072 (larvae).

Oophaga arborea: PANAMA: **Bocas del Toro and Chiriquí**: ca. 7 km airline W of Chiriquí Grande, 20 m (bocas del Toro), and continental divide (Chiriquí), AMNH 116771–80 (paratypes). **Chiriquí**: continental divide above upper Quebrada de Arena, 1120 m, 82°12′31″W, AMNH 116725–60 (paratopotypes), 116761–68 (C&S; paratopotypes). Continental divide above upper Quebrada de Arena, 1200–1300 m, 82°13′W, AMNH 116769–70 (paratypes).

Oophaga granulifera: COSTA RICA: 4.5 km W Rincon de Osa, 40 m, KU 110223 (C&S). **Puntarenas**: about 6 km airline E Palmar Norte, stream draining into Río Grande de Terruba, AMNH 134069, 134071–81, 118408–409. 8 km ENE Palmer Norte, 90 m, AMNH 86631.

Oophaga histrionica: COLOMBIA: **Chocó**: West bank of lower Río San Juán at Pangala, ca. 40 km (by boat) N Palestina, AMNH 88242–82. **Risaralda**: ca. 7 km (airline) SE Santa Cecilia, upper Río San Juán, 500–600 m, AMNH 118458 (C&S), 118461–62 (C&S).

Oophaga lehmanni: COLOMBIA: **Valle del Cauca**: ca. 13 km W Dagua, Río Anchicayá drainage, 850–1200 m, AMNH 88154–95 (topoparatypes), 88231–34 (C&S; topoparatypes), 118435–37, 118438 (C&S), 118439, 118441, 118442 (C&S), 118443–45.

Oophaga pumilio: PANAMA: **Bocas del Toro**: Isla Bastimentos, near Bastimentos, AMNH 102256–63. East end Isla Escudo de Veraguas, AMNH 118510 (C&S). Isla Bastimentos AMNH 118514 (C&S). 7.1 km (airline) WSW Chiriquí Grande, 70–100 m, AMNH 161952 (larvae). (+ several hundred uncataloged skinned carcasses from Bocas del Toro at AMNH.)

Oophaga speciosa: PANAMA: **Chiriquí**: Continental divide above upper Quebrada de Arena, 1140–1410 m, 82°13′40″W, AMNH 124279–321. Continental divide above upper Quebrada de Arena, 1300 m, 82°13′40″W, AMNH 124322–31. Continental divide above upper Quebrada de Arena, 1250–1400 m, 82°13′40″W, AMNH 124332–34, 118447 (C&S), 118454 (C&S). Continental divide above upper Quebrada de Arena, 1250–1410 m, 82°13′40″W, AMNH 124335–48, 124349 (larvae). Continental divide above upper Quebrada de Arena, 1250–1410 m, 82°13′30″W, AMNH 161120, 161122–23.

Oophaga sylvatica: COLOMBIA: **Nariño**: Guayacana, 500 m, AMNH 85048–158, 86635–40. ECUADOR: **Pichincha**: Río Baba, 5–10 km SSW Santo Domingo de los Colorados, 500 m, AMNH 89589–601. About 10 mi S of Santo Domingo de los Colorados, in banana plantation, AMNH 88225–26 (C&S).

Oophaga vicentei: PANAMA: **Coclé**: Continental Divide N El Copé, 600–800 m, AMNH 98344–50, 98351–53 (C&S), 98354 (larvae). East shoulder Cerro Caracol (above El Valle de Antón), 870 m, AMNH 114583–84, 114586, 114587 (C&S).

Minyobates steyermarki: VENEZUELA: **Amazonas**: SW sector Cerro Yapacana, 900 m, AMNH 100760–99, 118579 (C&S), 118572 (C&S), 118575–76 (C&S), 118581 (C&S).

Phyllobates aurotaenia: COLOMBIA: **Chocó**: 2 km above Playa de Oro, Río San Juán, 210 m, AMNH 85238–45. Vicinity of Playa de Oro, upper Río San Juán, ca. 200 m, AMNH 85246 (male + larvae), 85247 (male + larvae), 85248 (male + larvae), 85249 (male + larvae), 87167 (male + larvae) AMNH 87168 (male + larvae), 161108 (C&S), 161109–111.

Phyllobates bicolor: COLOMBIA: **Risaralda**: about 7 km (airline) SE Santa Cecilia, mountain side above north bank Río San Juán, 500–600 m, AMNH 98209–236, 98256 (C&S).

Phyllobates lugubris: PANAMA: **Bocas del Toro**: ca. 5 km W Almirante, 30–40 m, AMNH 86642 (male + larvae). Río Changuinola, near Quebrada El Guabo, 16 km airline W Almirante, 200 m, AMNH 107237 (larva from AMNH 107231). East slope Cerro Miramar (ca. 1.5 km S of Miramar), 340 m, AMNH 113936. Península Valiente, near Punta Valiente, 1–5 m, AMNH 113937. Northwest side Isla San

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Cristóbal, 5–10 m, AMNH 113938–39. North side Isla Pastores, 5–15 m, AMNH 113940. Mainland ca. 1 km (airline) NNW Isla Split Hill, 20–30 m, AMNH 113941–43. Mainland ca. 1 km (airline) NNW Isla Split Hill, 20–30 m, AMNH 124350–53, 55–56. Ca. 5 km W Almirante, 40 m, AMNH 118554 (C&S), 118557 (C&S).

Phyllobates terribilis: COLOMBIA: **Cauca**: Quebrada Guanguí, about 0.5 km above junction with Río Patia, in upper Río Saija drainage, 100–200 m, AMNH 86319–24 (C&S; paratopotypes), 118563 (skeleton; paratopotype), 125831–35 (C&S). Captive bred, lab-reared F1 from paratopotypic parents (AMNH A118562-67, A125826-830 series), AMNH 162738–43.

Phyllobates vittatus: Western Zoological Supply (received by John W. Daly, National Institutes of Health), AMNH 114041. COSTA RICA: **Puntarenas**: 8 km ENE Palmar Norte, 90 m, AMNH 82257, 86643–45, 118542–45 (C&S), 118546, 118547–50 (C&S), 118551.

Ranitomeya biolat: PERU: **Cuzco**: San Martin-3, ca. 5 km N of the Camisea River, 474 m, USNM 537557–58. Cashiriari-3, S of the Camisea River, 690 m, USNM 537559–565. **Madre de Dios**: Parque Nacional del Manu, Cocha Cashu Biological Station, ca. 380 m, AMNH 143908. Pakitza, Reserve Zone, Manu National Park, ca. 57 km (airline) NW of mouth of Río Manu, on Río Manu, 350 m, USNM 342882 (larvae).

Ranitomeya claudiae: PANAMA: **Bocas del Toro**: Isla Colón, near La Gruta, AMNH 102307–68, 103514–23 (C&S). Isla Colón, about 2.5 km airline N La Gruta, 40 m, AMNH 124255–65.

Ranitomeya fulgurita: PANAMA: **Panamá**: km 12.8 on El Llano-Cartí Rd, 290 m, AMNH 89435–37. Km 14.6 on El Llano-Cartí Rd, 370 m, AMNH 89438–47, 89448–53 (C&S).

Ranitomeya imitator: PERU: **San Martín**: Km 33, Carretera Tarapoto-Yurimagaus, Valle del Río Cainarache, 500–650 m, AMNH 127991–99, 128003–06, 162723–27, KU 209412–13 (C&S). Km 48, road to Yurimaguas from Tarapoto AMNH 162728–30. Km 10 road to Chamilla from Tarapoto, AMNH 162731–32.

Ranitomeya minuta: PANAMA: **Panamá**: Cerro Campana, 2800 ft, AMNH 59660–62. Cerro Campana, 900–950 m, AMNH 84896–900. S slope Cerro Campana, 900–950 m, AMNH 87310. Km 14.6 on El Llano-Cartí Rd, 370 m, AMNH 89426–32. Cerro Campana, 800 m, AMNH 118132.

Ranitomeya reticulata: PERU: **Loreto**: 3 km airline SSW Mishana, on Río Nanay, 150 m, AMNH 103619–30, 103638–73; AMNH 103676 (C&S), 103680–81 (C&S).

Ranitomeya vanzolinii: BRAZIL: **Acre**: Porto Walter, Rio Juruá, 8°16′S 72°46′W, AMNH 108332 (paratopotype). PERU: **Loreto**: mouth of Río Sepahua (Río Urubamba), AMNH 43597–98.

Ranitomeya ventrimaculata: COLOMBIA: **Amazonas**: Leticia, Km 7 (Leticia-Tarapacá), ICN 47609. Leticia, Km 9 (Leticia-Tarapacá), ICN 47330–32, 47334–35. Leticia, km 11 (Leticia-Tarapacá), ICN 53027 (larvae), 53034 (larvae). PERU: **Loreto**: 3 km NE Pebas on Río Amazonas, 100 m, 103603–04 (C&S).

Silverstoneia flotator: PANAMA: **Colcé**: El Valle de Antón, 2000 ft, AMNH 55509, 116781–83. El Valle, Río Anton, ±650 m, AMNH 87300–01, 124210–15. Continental Divide N El Copé' 98323. Km 13.4 on El Llano-Cartí Rd, 300 m, AMNH 104229 (larvae). Barro Colorado Island, KU 77678 (C&S).

Silverstoneia nubicola: PANAMA: **Chiriquí**: upper Río Chiriquí, Fortuna Dam Site, 1000 m, AMNH 94846–48, 94849 (larvae). Upper Río Chiriquí, near mouth Río Hornito, 1020 m, AMNH 114574–77. Río Frijoles, UMMZ 145585 (C&S).Continental divide above upper Quebrada de Arena, 1660–1270 m, AMNH 124249.

Silverstoneia ''*nubicola*-spC'': COLOMBIA: **Chocó**: Serranía de Baudó, northern base Alto del Buey, Quebrada Mutatá, 200 m, AMNH 102092–95. Bahía Solano, Quebrada Tebada, 165 m, 06°28.924′N 77°20.682′W, MHNUC 320–21.

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APPENDIX 7
PHENOTYPIC DATA

Phenotypic data are reported here in FASTA format. The dataset may be downloaded from http://research.amnh.org/herpetology/downloads.html as a Hennig 86 matrix. Inapplicable characters are shown with a dash (-); uncoded characters (missing data) are shown with a question mark (?).

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braccatus
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castaneoticus
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collaris
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espinosai
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fantasticus
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femoralis
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fugax
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fulguritus
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kingsburyi
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??-
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??????????????????????????????????1011001001000000000000
00???
petersi
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1?0110001011001001000000000000???
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0000-1001110000[45]3331021110111111 10-------10100
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0100001011100101010000001 11000??3
praderioi
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????????????????????????????21?????????????????????????????
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quinquevittatus
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speciosus
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stepheni
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steyermarki
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sylvaticus Barbour and Noble
11010?1?????????????0-00-0101?0??????????????0000400000010[01]0000001?0????????1??0-------10100023201????????1000-11?1000001??010?501010000110100000????????????????????????
sylvaticus Funkhouser
0101011122200000000000-00-0101300111100000000000000[123]00000--000[35][34][13][13]002111011111110-------???????????1?????????????21?1000010----1040000 12110-011101101110111101010010100000 1?1
talamancae
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tepuyensis
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toachi
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truncatus
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undulatus
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vanzolinii
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ventrimaculatus
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vertebralis
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vicentei
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vittatus
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zaparo
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APPENDIX 8

Diagnostic DNA Sequence Transformations for Named Clades

Below we report all unambiguous DNA sequence transformations to diagnose the named clades addressed in the monophyletic taxonomy presented above; unambiguous morphological transformations are reported in the text. Insertions and deletions are depicted by gap states (-). Locus abbreviations: 28S (large nuclear ribosomal subunit), COI (cytochrome *c* oxidase I), cytb (cytochrome *b*), H1 (mitochondrial H-strand transcription unit 1), H3 (histone H3), RAG1 (recombination activating gene 1), rhodopsin (rhodopsin exon 1), SIA (seventh in absentia), and tyr (tyrosinase). Other abbreviations: Anc (ancestral state), Des (descendant state), frag. (DNA sequence fragment), Pos (aligned position).

Taxon/Locus	Pos	Anc	Des
Centrolenidae			
H1 frag. 2	150	T	C
H1 frag. 2	174	T	C
H1 frag. 2	196	T	C
H1 frag. 2	316	T	C
H1 frag. 2	545	A	T
H1 frag. 2	707	T	A
H1 frag. 3	110	T	C
H1 frag. 3	177	A	C
H1 frag. 3	251	A	G
H1 frag. 4	14	T	A
H1 frag. 4	130	A	C
H1 frag. 5	42	A	G
H1 frag. 6	34	T	C
H1 frag. 6	36	T	C
H1 frag. 6	61	—	C
H1 frag. 6	187	—	T
H1 frag. 6	279	T	A
H1 frag. 6	287	T	C
H1 frag. 6	295	—	C
H1 frag. 6	328	A	C
H1 frag. 6	359	T	C
H1 frag. 6	386	T	C
H1 frag. 6	446	T	C
H1 frag. 6	472	—	C
H1 frag. 6	525	A	T
H1 frag. 6	572	A	C
H1 frag. 8	224	T	C
H1 frag. 8	592	T	G
H1 frag. 9	70	A	G
H1 frag. 9	75	T	A
H1 frag. 9	158	T	—
H1 frag. 9	191	A	T
H1 frag. 9	200	—	A
H1 frag. 10	37	T	C
H1 frag. 12	104	G	A
H1 frag. 12	446	T	A
H1 frag. 13	121	—	A
H1 frag. 13	195	T	A
H1 frag. 15	9	A	G
Cruciabatrachia			
H3	286	G	A
H1 frag. 2	31	—	C
H1 frag. 2	399	C	T
H1 frag. 2	576	G	A
H1 frag. 2	577	A	G
H1 frag. 3	118	C	—
H1 frag. 5	73	A	T
H1 frag. 6	128	A	T
H1 frag. 8	532	T	A
H1 frag. 8	577	C	T
H1 frag. 9	299	—	T
H1 frag. 9	371	A	T
H1 frag. 10	99	C	T
H1 frag. 12	225	C	A
H1 frag. 13	80	A	T
H1 frag. 13	180	A	T
rhodopsin	106	A	G
rhodopsin	296	T	C
rhodopsin	299	T	C
tyr frag. 1	9	T	C
tyr frag. 2	188	C	T
Leptodactylidae			
28S frag. 1	510	T	A
H3	169	G	T
H1 frag. 2	444	A	G
H1 frag. 2	496	T	A
H1 frag. 2	507	C	A
H1 frag. 2	541	T	C
H1 frag. 2	581	C	A
H1 frag. 2	681	—	C
H1 frag. 2	697	A	C
H1 frag. 3	182	A	T
H1 frag. 3	185	C	—
H1 frag. 3	190	T	A
H1 frag. 4	128	A	T
H1 frag. 4	191	A	C
H1 frag. 4	204	T	A
H1 frag. 5	38	A	T
H1 frag. 6	44	T	C
H1 frag. 6	213	—	T
H1 frag. 6	214	—	T
H1 frag. 6	422	G	A
H1 frag. 8	41	A	T
H1 frag. 8	116	A	C
H1 frag. 8	247	A	T
H1 frag. 8	263	A	T
H1 frag. 8	531	—	A
H1 frag. 9	48	A	C
H1 frag. 9	91	T	A
H1 frag. 9	115	T	A
H1 frag. 9	238	T	C
H1 frag. 10	238	A	—
H1 frag. 12	263	—	T
H1 frag. 12	378	T	—
H1 frag. 12	408	A	C
H1 frag. 13	32	A	G
H1 frag. 13	78	—	C
H1 frag. 13	203	T	C
H1 frag. 13	284	T	C
rhodopsin	135	—	T
tyr frag. 1	71	T	C
tyr frag. 1	179	G	C
tyr frag. 2	59	C	T
tyr frag. 2	149	C	T
Chthonobatrachia			
H3	175	T	G
H1 frag. 2	409	T	A
H1 frag. 2	492	C	T
H1 frag. 3	56	A	C
H1 frag. 3	129	A	T
H1 frag. 4	35	A	T
H1 frag. 4	206	C	T
H1 frag. 6	157	A	T
H1 frag. 6	446	T	A
H1 frag. 6	471	—	T
H1 frag. 8	188	A	G
H1 frag. 8	555	C	T
H1 frag. 9	96	C	T
H1 frag. 9	125	C	T
H1 frag. 9	160	A	C
H1 frag. 9	355	A	C
H1 frag. 9	378	C	T
H1 frag. 10	3	C	T
H1 frag. 12	112	C	T
H1 frag. 12	249	C	T
H1 frag. 12	387	C	T
H1 frag. 13	158	C	A
rhodopsin	10	G	A
SIA frag. 1	189	A	G
SIA frag. 2	12	T	C
tyr frag. 1	151	T	C
tyr frag. 2	110	T	C
Ceratophryidae			
28S frag. 1	181	C	—
28S frag. 1	385	C	—
28S frag. 1	596	C	T
28S frag. 1	606	C	A
H3	290	G	C
H1 frag. 2	316	T	C
H1 frag. 2	447	G	A
H1 frag. 2	489	—	A
H1 frag. 2	526	C	T
H1 frag. 3	123	C	T
H1 frag. 4	52	C	T
H1 frag. 6	116	C	T
H1 frag. 6	218	A	T
H1 frag. 6	241	—	T
H1 frag. 6	256	—	T
H1 frag. 8	283	—	A
H1 frag. 8	538	T	A
H1 frag. 8	565	T	G
H1 frag. 8	593	—	A
H1 frag. 8	595	—	C
H1 frag. 9	79	A	G
H1 frag. 9	103	A	T
H1 frag. 9	109	A	T
H1 frag. 9	191	A	C
H1 frag. 10	18	T	A
H1 frag. 12	109	A	T
H1 frag. 12	110	A	T
H1 frag. 12	187	T	A
H1 frag. 12	280	—	A
H1 frag. 12	401	—	C
Batrachylinae			
28S frag. 1	238	G	C
28S frag. 1	387	C	G
28S frag. 1	402	—	C

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Taxon/Locus	Pos	Anc	Des
28S frag. 1	567	—	C
28S frag. 1	598	—	A
28S frag. 1	610	C	A
28S frag. 1	617	C	A
H1 frag. 2	421	—	C
H1 frag. 2	496	T	A
H1 frag. 2	563	T	C
H1 frag. 2	615	A	C
H1 frag. 3	10	G	A
H1 frag. 6	79	A	T
H1 frag. 6	157	T	C
H1 frag. 6	170	—	T
H1 frag. 6	438	T	C
H1 frag. 6	474	A	T
H1 frag. 6	524	A	T
H1 frag. 6	570	T	A
H1 frag. 7	7	C	A
H1 frag. 8	45	T	A
H1 frag. 8	259	C	T
H1 frag. 8	530	—	T
H1 frag. 8	587	T	A
H1 frag. 9	70	A	G
H1 frag. 9	148	—	C
H1 frag. 9	158	T	C
H1 frag. 9	172	A	C
H1 frag. 9	264	A	T
H1 frag. 10	2	C	A
H1 frag. 10	70	C	T
H1 frag. 10	262	A	T
H1 frag. 12	17	G	A
H1 frag. 12	377	—	C
H1 frag. 12	411	T	—
H1 frag. 12	425	T	C
H1 frag. 13	14	C	A
rhodopsin	96	C	T
rhodopsin	98	T	A
rhodopsin	185	C	G
rhodopsin	271	C	G
rhodopsin	299	C	G
SIA frag. 1	3	T	C
SIA frag. 2	54	C	T
Ceratophryinae			
28S frag. 1	182	C	—
28S frag. 1	241	—	T
28S frag. 1	386	—	T
28S frag. 1	418	A	—
28S frag. 1	419	T	C
28S frag. 1	478	G	A
28S frag. 1	596	T	—
28S frag. 1	606	A	—
28S frag. 1	657	—	C
H1 frag. 1	24	A	G
H1 frag. 2	90	A	G
H1 frag. 2	254	A	T
H1 frag. 2	314	—	C
H1 frag. 2	321	T	C
H1 frag. 2	497	T	A
H1 frag. 2	632	A	C
H1 frag. 2	707	T	C
H1 frag. 3	129	T	A
H1 frag. 4	145	T	A
H1 frag. 4	191	A	C
H1 frag. 6	20	T	C
H1 frag. 6	218	T	—
H1 frag. 6	267	—	C
H1 frag. 6	328	A	C
H1 frag. 6	352	T	A
H1 frag. 6	445	A	T
H1 frag. 6	469	T	A
H1 frag. 6	506	A	G
H1 frag. 7	10	T	C
H1 frag. 8	52	A	C
H1 frag. 8	206	A	T
H1 frag. 8	215	A	T
H1 frag. 8	297	A	C
H1 frag. 8	319	C	T
H1 frag. 8	420	T	C
H1 frag. 9	149	C	A
H1 frag. 9	198	T	A
H1 frag. 9	238	T	C
H1 frag. 9	264	A	G
H1 frag. 9	265	T	A
H1 frag. 10	1	C	T
H1 frag. 10	18	A	C
H1 frag. 10	96	C	A
H1 frag. 12	221	A	T
H1 frag. 15	9	A	G
H1 frag. 15	26	T	C
rhodopsin	124	T	C
Telmatobiinae			
H3	6	A	G
H3	102	C	T
H3	123	—	C
H3	127	T	—
H3	314	C	T
H1 frag. 2	390	A	C
H1 frag. 2	492	T	C
H1 frag. 3	184	A	T
H1 frag. 3	307	C	T
H1 frag. 4	137	A	T
H1 frag. 5	73	T	C
H1 frag. 6	141	T	C
H1 frag. 6	241	T	C
H1 frag. 6	270	C	T
H1 frag. 6	319	—	G
H1 frag. 6	377	A	C
H1 frag. 6	449	T	C
H1 frag. 6	471	T	C
H1 frag. 6	565	G	A
H1 frag. 6	574	C	T
H1 frag. 6	578	C	T
H1 frag. 7	37	A	C
H1 frag. 8	107	C	T
H1 frag. 8	160	T	A
H1 frag. 8	167	A	G
H1 frag. 8	177	A	G
H1 frag. 8	197	T	C
H1 frag. 8	233	A	T
H1 frag. 8	253	A	T
H1 frag. 8	328	T	C
H1 frag. 8	364	T	C
H1 frag. 8	369	C	T
H1 frag. 8	422	A	C
H1 frag. 8	451	A	T
H1 frag. 8	454	A	C
H1 frag. 8	532	A	C
H1 frag. 8	577	T	A
H1 frag. 9	26	T	A
H1 frag. 9	160	C	A
H1 frag. 9	213	G	T
H1 frag. 9	242	T	A
H1 frag. 9	248	A	G
H1 frag. 9	286	A	C
H1 frag. 9	313	A	T
H1 frag. 9	371	T	A
H1 frag. 9	378	T	C
H1 frag. 9	383	T	C
H1 frag. 9	384	G	A
H1 frag. 9	407	C	A
H1 frag. 10	26	A	T
H1 frag. 10	37	T	C
H1 frag. 10	51	T	A
H1 frag. 10	127	C	T
H1 frag. 11	14	T	C
H1 frag. 11	16	C	A
H1 frag. 12	69	A	G
H1 frag. 12	101	G	T
H1 frag. 12	151	A	G
H1 frag. 12	160	T	A
H1 frag. 12	235	T	C
H1 frag. 12	249	T	A
H1 frag. 12	408	A	T
H1 frag. 12	461	A	T
H1 frag. 12	463	T	C
H1 frag. 13	20	A	T
H1 frag. 13	49	—	C
H1 frag. 13	88	C	T
H1 frag. 13	97	T	A
H1 frag. 13	180	T	A
H1 frag. 13	190	T	C
H1 frag. 13	203	T	C
H1 frag. 13	204	T	C
rhodopsin	308	T	A
Hesticobatrachia			
28S frag. 1	325	—	G
28S frag. 1	350	—	C
28S frag. 1	603	—	C
cytb frag. 2	34	C	A
cytb frag. 2	47	A	C
cytb frag. 2	159	T	C
cytb frag. 2	190	G	A
cytb frag. 2	223	C	T
cytb frag. 3	11	C	A
H1 frag. 2	707	T	C
H1 frag. 3	308	C	T
H1 frag. 6	31	G	A
H1 frag. 6	232	T	C
H1 frag. 6	328	A	T
H1 frag. 8	319	C	A
H1 frag. 8	369	C	T
H1 frag. 8	527	C	T
H1 frag. 9	213	G	T
H1 frag. 9	286	A	T
H1 frag. 10	1	C	T
H1 frag. 10	108	A	T
H1 frag. 12	113	A	T
H1 frag. 12	408	A	T
H1 frag. 13	102	—	A
H1 frag. 13	223	A	T
rhodopsin	263	G	C
Cycloramphidae			
28S frag. 1	224	—	T
28S frag. 1	276	—	T
28S frag. 1	317	—	G
28S frag. 1	319	—	G
28S frag. 1	359	—	G
28S frag. 1	361	—	T
28S frag. 1	397	—	G
COI frag. 1	108	A	T
cytb frag. 2	41	C	T
cytb frag. 2	147	C	T
cytb frag. 2	180	T	A
cytb frag. 2	252	C	T
H3	15	A	C
H1 frag. 2	492	T	A
H1 frag. 2	579	—	A
H1 frag. 6	19	C	T
H1 frag. 6	100	—	C
H1 frag. 6	247	—	A
H1 frag. 6	248	—	A
H1 frag. 6	476	T	A
H1 frag. 8	259	C	A
H1 frag. 8	565	T	A
H1 frag. 12	184	T	—
H1 frag. 12	213	T	A
H1 frag. 12	274	—	C
H1 frag. 13	80	T	—
H1 frag. 13	88	C	A
H1 frag. 13	220	—	A
rhodopsin	168	A	G
rhodopsin	271	C	G
tyr frag. 2	197	T	C
tyr frag. 2	275	C	T
Calamitophrynia			

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Taxon/Locus	Pos	Anc	Des
28S frag. 1	571	—	T
28S frag. 1	578	—	C
28S frag. 1	584	—	C
28S frag. 1	587	—	C
28S frag. 1	588	—	C
28S frag. 1	624	—	G
28S frag. 1	626	—	G
28S frag. 1	633	—	G
28S frag. 1	634	—	G
28S frag. 1	636	—	G
H1 frag. 2	150	T	C
H1 frag. 2	374	T	C
H1 frag. 2	423	A	T
H1 frag. 2	545	A	T
H1 frag. 2	581	C	A
H1 frag. 3	207	C	T
H1 frag. 6	195	—	C
H1 frag. 6	469	T	A
H1 frag. 8	206	A	—
H1 frag. 8	208	A	—
H1 frag. 10	55	A	T
H1 frag. 10	71	C	T
H1 frag. 10	96	C	—
H1 frag. 13	67	G	A
H1 frag. 13	180	T	A
rhodopsin	87	A	G
rhodopsin	116	T	C
Leiuperidae			
H3	6	A	G
H3	136	C	T
H3	175	G	T
H3	199	G	A
H1 frag. 2	632	A	T
H1 frag. 3	56	C	A
H1 frag. 3	110	T	C
H1 frag. 3	250	A	G
H1 frag. 3	251	A	G
H1 frag. 4	135	A	T
H1 frag. 4	204	T	A
H1 frag. 6	141	T	A
H1 frag. 6	314	—	C
H1 frag. 6	422	G	—
H1 frag. 6	445	A	T
H1 frag. 8	116	A	C
H1 frag. 8	155	G	A
H1 frag. 8	188	G	T
H1 frag. 8	224	T	C
H1 frag. 8	278	A	T
H1 frag. 8	281	T	C
H1 frag. 8	313	A	T
H1 frag. 8	399	A	T
H1 frag. 8	592	T	C
H1 frag. 8	601	A	G
H1 frag. 9	208	—	T
H1 frag. 9	283	T	A
H1 frag. 9	371	T	A
H1 frag. 10	23	—	G
H1 frag. 10	26	A	T
H1 frag. 10	47	—	A
H1 frag. 12	160	T	C
H1 frag. 12	378	T	C
H1 frag. 13	22	T	C
H1 frag. 13	160	A	C
H1 frag. 13	204	T	C
Agastorophrynia			
28S frag. 1	214	C	—
28S frag. 1	305	G	—
28S frag. 1	385	C	G
28S frag. 1	589	—	G
28S frag. 1	628	—	C
H1 frag. 1	24	A	G
H1 frag. 2	399	T	A
H1 frag. 2	424	A	—
H1 frag. 3	15	A	T
H1 frag. 3	255	G	A
H1 frag. 4	172	T	A
H1 frag. 6	181	G	—
H1 frag. 6	290	A	—
H1 frag. 6	315	T	C
H1 frag. 6	538	A	T
H1 frag. 9	160	C	—
H1 frag. 10	3	T	C
H1 frag. 10	78	—	C
H1 frag. 11	14	T	A
H1 frag. 12	285	C	A
rhodopsin	54	A	G
rhodopsin	299	C	G
Bufonidae			
28S frag. 1	181	C	—
28S frag. 1	192	G	A
28S frag. 1	381	G	C
28S frag. 1	413	A	C
28S frag. 1	492	—	T
28S frag. 1	499	—	C
28S frag. 1	597	C	G
COI frag. 1	47	A	C
COI frag. 1	123	T	C
COI frag. 1	258	C	T
COI frag. 1	299	C	T
COI frag. 1	326	A	T
COI frag. 2	209	T	A
COI frag. 2	235	T	C
COI frag. 2	284	C	T
cytb frag. 1	9	C	A
cytb frag. 1	10	G	C
cytb frag. 1	13	C	A
cytb frag. 2	56	T	C
cytb frag. 2	95	C	T
cytb frag. 2	116	C	T
cytb frag. 2	168	T	C
cytb frag. 2	239	C	T
cytb frag. 2	242	T	C
cytb frag. 3	14	C	T
H3	114	A	C
H3	130	G	A
H1 frag. 1	69	A	C
H1 frag. 2	27	T	—
H1 frag. 2	319	T	C
H1 frag. 2	542	T	C
H1 frag. 2	682	C	T
H1 frag. 2	695	C	T
H1 frag. 3	92	C	A
H1 frag. 3	300	G	A
H1 frag. 3	307	C	A
H1 frag. 3	327	C	T
H1 frag. 6	16	A	G
H1 frag. 6	33	T	C
H1 frag. 6	125	—	A
H1 frag. 6	232	C	A
H1 frag. 6	371	C	T
H1 frag. 6	521	T	A
H1 frag. 6	535	T	C
H1 frag. 7	36	T	A
H1 frag. 8	15	C	T
H1 frag. 8	39	T	A
H1 frag. 8	45	T	C
H1 frag. 8	120	G	A
H1 frag. 8	200	—	A
H1 frag. 8	282	—	A
H1 frag. 8	344	A	T
H1 frag. 8	556	—	A
H1 frag. 9	185	A	C
H1 frag. 9	204	—	T
H1 frag. 9	342	A	C
H1 frag. 12	185	—	A
H1 frag. 12	304	—	T
H1 frag. 13	112	T	A
RAG1 frag. 1	181	G	A
RAG1 frag. 2	76	C	T
rhodopsin	39	A	G
rhodopsin	85	A	C
rhodopsin	182	A	G
rhodopsin	188	A	G
rhodopsin	221	G	C
rhodopsin	230	T	C
SIA frag. 1	57	C	G
SIA frag. 2	30	T	C
SIA frag. 2	99	G	C
Nobleobatia			
28S frag. 1	193	—	T
28S frag. 1	199	—	C
28S frag. 1	225	C	G
28S frag. 1	561	—	C
28S frag. 1	562	—	C
28S frag. 1	592	—	C
28S frag. 1	593	—	T
28S frag. 1	605	—	G
28S frag. 1	611	—	G
28S frag. 1	623	—	G
28S frag. 1	637	—	C
COI frag. 1	132	T	C
COI frag. 1	153	T	A
COI frag. 1	216	C	T
COI frag. 1	307	T	C
COI frag. 2	10	T	A
COI frag. 2	98	T	A
COI frag. 2	278	T	C
cytb frag. 2	113	T	C
cytb frag. 2	125	C	T
H3	277	C	T
H1 frag. 2	90	A	—
H1 frag. 2	138	G	A
H1 frag. 2	492	T	C
H1 frag. 2	697	A	T
H1 frag. 3	248	G	A
H1 frag. 6	195	C	T
H1 frag. 6	240	C	T
H1 frag. 6	462	T	A
H1 frag. 9	62	T	C
H1 frag. 9	75	T	C
H1 frag. 9	103	A	T
H1 frag. 9	176	—	C
H1 frag. 9	191	A	T
H1 frag. 9	387	A	C
H1 frag. 10	99	T	C
H1 frag. 12	149	A	—
H1 frag. 12	191	—	C
H1 frag. 12	253	A	T
H1 frag. 12	311	A	C
H1 frag. 13	21	A	T
H1 frag. 13	102	A	—
H1 frag. 13	223	T	A
rhodopsin	291	G	A
Hylodidae			
28S frag. 1	192	G	C
28S frag. 1	202	—	A
28S frag. 1	223	C	—
28S frag. 1	413	A	G
28S frag. 1	495	—	C
28S frag. 1	497	—	A
28S frag. 1	498	—	A
28S frag. 1	528	C	G
28S frag. 1	556	—	G
28S frag. 1	570	C	G
28S frag. 1	571	T	A
28S frag. 1	579	—	T
28S frag. 1	591	G	T
28S frag. 1	606	C	G
28S frag. 1	625	—	C
28S frag. 1	634	G	C
28S frag. 1	636	G	C
28S frag. 1	638	—	A
28S frag. 1	639	—	A
28S frag. 1	661	G	C
28S frag. 2	69	A	G
28S frag. 2	164	—	A
COI frag. 1	74	A	C
COI frag. 1	84	T	C

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COI frag. 1	279	T	G
COI frag. 2	198	T	C
COI frag. 2	200	A	T
COI frag. 2	318	A	G
COI frag. 2	345	C	T
cytb frag. 1	10	G	T
cytb frag. 1	13	C	T
cytb frag. 1	56	C	T
cytb frag. 2	87	G	A
cytb frag. 2	178	C	T
H3	69	C	G
H3	84	G	C
H3	193	G	C
H3	253	C	T
H1 frag. 1	12	G	A
H1 frag. 1	24	G	—
H1 frag. 2	374	C	T
H1 frag. 2	409	A	C
H1 frag. 2	508	C	A
H1 frag. 2	574	C	T
H1 frag. 2	581	A	C
H1 frag. 3	217	A	G
H1 frag. 3	308	T	C
H1 frag. 4	137	A	T
H1 frag. 4	144	A	C
H1 frag. 4	194	A	T
H1 frag. 4	206	T	A
H1 frag. 5	63	—	T
H1 frag. 6	203	A	C
H1 frag. 6	255	—	C
H1 frag. 6	478	A	T
H1 frag. 6	504	A	—
H1 frag. 6	596	G	A
H1 frag. 7	13	A	C
H1 frag. 8	79	G	A
H1 frag. 8	199	—	C
H1 frag. 8	345	—	G
H1 frag. 8	377	A	T
H1 frag. 8	532	A	T
H1 frag. 8	612	A	T
H1 frag. 9	147	T	A
H1 frag. 9	328	G	T
H1 frag. 9	357	C	T
H1 frag. 10	55	T	A
H1 frag. 10	95	A	C
H1 frag. 10	108	T	A
H1 frag. 10	238	A	C
H1 frag. 11	14	A	C
H1 frag. 12	108	A	T
H1 frag. 12	221	A	T
H1 frag. 12	362	A	T
H1 frag. 12	399	A	T
H1 frag. 15	16	C	T
RAG1 frag. 1	51	T	C
RAG1 frag. 1	127	A	T
RAG1 frag. 2	106	C	T
RAG1 frag. 2	133	T	C
RAG1 frag. 2	175	T	C
rhodopsin	0	A	G
rhodopsin	39	A	C
rhodopsin	60	T	C
rhodopsin	124	T	C
rhodopsin	185	C	G
rhodopsin	191	A	G
rhodopsin	195	T	C
rhodopsin	299	G	T
SIA frag. 2	54	C	A
SIA frag. 2	57	C	T
SIA frag. 2	69	C	T
tyr frag. 1	19	T	A
tyr frag. 1	41	T	C
tyr frag. 1	74	T	C
tyr frag. 1	103	A	G
tyr frag. 1	113	C	T
tyr frag. 1	210	T	C
tyr frag. 2	164	T	G
tyr frag. 2	178	G	C
tyr frag. 2	188	T	C
tyr frag. 2	213	C	T
tyr frag. 2	275	C	T
Dendrobatoidea			
28S frag. 1	139	C	A
28S frag. 1	140	A	C
28S frag. 1	219	—	T
28S frag. 1	238	G	C
28S frag. 1	356	—	G
28S frag. 1	408	—	A
28S frag. 1	410	C	A
28S frag. 1	485	C	T
28S frag. 1	538	—	A
28S frag. 1	560	G	C
28S frag. 1	566	G	C
28S frag. 1	594	—	A
28S frag. 1	595	—	C
28S frag. 1	648	C	—
28S frag. 1	649	C	G
28S frag. 2	67	A	C
COI frag. 1	63	C	T
COI frag. 1	108	A	T
COI frag. 1	150	T	C
COI frag. 1	181	A	C
COI frag. 2	44	C	T
COI frag. 2	53	C	A
COI frag. 2	130	T	C
COI frag. 2	131	T	C
cytb frag. 1	11	T	C
cytb frag. 1	12	A	C
cytb frag. 1	33	A	T
cytb frag. 1	61	T	A
cytb frag. 1	63	A	C
cytb frag. 1	68	T	G
cytb frag. 2	34	A	C
cytb frag. 2	41	C	T
cytb frag. 2	59	C	T
cytb frag. 2	126	T	C
cytb frag. 2	128	A	T
cytb frag. 2	174	T	C
cytb frag. 2	216	C	T
cytb frag. 2	248	T	A
cytb frag. 2	256	C	T
H3	175	G	T
H1 frag. 1	41	C	T
H1 frag. 2	58	C	A
H1 frag. 2	148	T	C
H1 frag. 2	149	A	T
H1 frag. 2	173	A	C
H1 frag. 2	195	A	G
H1 frag. 2	232	G	C
H1 frag. 2	316	T	C
H1 frag. 2	432	A	C
H1 frag. 2	488	—	A
H1 frag. 2	496	T	C
H1 frag. 2	545	T	A
H1 frag. 2	572	G	A
H1 frag. 2	613	C	T
H1 frag. 2	618	C	T
H1 frag. 3	177	A	—
H1 frag. 3	182	A	—
H1 frag. 3	184	A	—
H1 frag. 3	185	C	—
H1 frag. 3	208	C	T
H1 frag. 3	214	A	T
H1 frag. 3	219	C	A
H1 frag. 3	242	G	A
H1 frag. 4	30	C	T
H1 frag. 4	103	T	C
H1 frag. 4	116	A	T
H1 frag. 4	130	A	C
H1 frag. 6	123	T	C
H1 frag. 6	141	T	C
H1 frag. 6	225	-	C
H1 frag. 6	297	A	T
H1 frag. 6	311	A	T
H1 frag. 6	336	T	C
H1 frag. 6	422	G	A
H1 frag. 6	445	A	T
H1 frag. 7	37	A	T
H1 frag. 8	13	A	G
H1 frag. 8	25	C	T
H1 frag. 8	88	C	A
H1 frag. 8	141	A	G
H1 frag. 8	148	A	T
H1 frag. 8	169	C	T
H1 frag. 8	230	A	—
H1 frag. 8	233	A	—
H1 frag. 8	263	A	—
H1 frag. 8	265	A	—
H1 frag. 8	281	T	—
H1 frag. 8	366	G	A
H1 frag. 8	422	A	C
H1 frag. 8	451	A	T
H1 frag. 8	541	A	T
H1 frag. 8	577	T	A
H1 frag. 8	609	A	G
H1 frag. 9	26	T	A
H1 frag. 9	31	—	C
H1 frag. 9	55	A	—
H1 frag. 9	70	A	—
H1 frag. 9	128	—	A
H1 frag. 9	193	—	C
H1 frag. 9	245	T	C
H1 frag. 9	258	T	A
H1 frag. 9	262	T	C
H1 frag. 9	299	T	A
H1 frag. 9	395	A	C
H1 frag. 10	4	A	—
H1 frag. 10	8	G	T
H1 frag. 10	83	C	T
H1 frag. 10	145	C	T
H1 frag. 10	196	A	G
H1 frag. 10	247	A	T
H1 frag. 12	38	A	C
H1 frag. 12	46	G	A
H1 frag. 12	49	T	C
H1 frag. 12	159	A	C
H1 frag. 12	167	C	—
H1 frag. 12	174	T	—
H1 frag. 12	176	G	A
H1 frag. 12	349	A	C
H1 frag. 12	430	T	A
H1 frag. 12	455	A	T
H1 frag. 12	461	A	C
H1 frag. 13	33	C	T
H1 frag. 13	34	A	G
H1 frag. 13	124	A	C
RAG1 frag. 1	4	A	C
RAG1 frag. 1	7	T	G
RAG1 frag. 1	21	A	C
RAG1 frag. 1	60	C	T
RAG1 frag. 1	79	T	C
RAG1 frag. 1	108	C	T
RAG1 frag. 1	128	C	G
RAG1 frag. 1	138	A	C
RAG1 frag. 1	175	A	C
RAG1 frag. 2	128	A	C
RAG1 frag. 2	136	G	A
RAG1 frag. 2	163	A	G
rhodopsin	48	A	C
rhodopsin	54	G	T
rhodopsin	87	G	A
rhodopsin	116	C	T
rhodopsin	240	G	A
rhodopsin	308	T	G
SIA frag. 1	18	T	C
SIA frag. 1	33	A	G
SIA frag. 1	39	T	C
SIA frag. 2	75	A	G
tyr frag. 1	9	C	T

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Taxon/Locus	Pos	Anc	Des
tyr frag. 1	11	C	A
tyr frag. 1	27	C	T
tyr frag. 1	29	T	A
tyr frag. 1	44	T	C
tyr frag. 1	71	T	A
tyr frag. 1	73	C	T
tyr frag. 1	192	A	G
tyr frag. 1	201	C	T
tyr frag. 1	214	G	A
tyr frag. 2	11	G	C
tyr frag. 2	22	C	G
tyr frag. 2	32	G	C
tyr frag. 2	41	C	G
tyr frag. 2	209	C	A
Aromobatidae			
28S frag. 1	297	—	C
COI frag. 1	25	G	C
COI frag. 1	194	A	C
COI frag. 2	81	C	T
COI frag. 2	210	G	A
cytb frag. 2	171	T	C
cytb frag. 2	242	T	C
cytb frag. 3	26	A	C
H1 frag. 2	290	C	—
H1 frag. 2	297	T	A
H1 frag. 2	298	G	A
H1 frag. 2	449	T	C
H1 frag. 2	555	A	C
H1 frag. 3	56	C	A
H1 frag. 3	244	A	T
H1 frag. 3	320	C	A
H1 frag. 4	107	—	T
H1 frag. 4	227	C	T
H1 frag. 5	38	A	G
H1 frag. 5	45	G	A
H1 frag. 5	91	C	T
H1 frag. 6	13	A	T
H1 frag. 6	19	C	T
H1 frag. 6	38	T	C
H1 frag. 6	49	A	C
H1 frag. 6	158	—	A
H1 frag. 6	223	—	C
H1 frag. 6	361	T	A
H1 frag. 6	416	T	A
H1 frag. 6	471	T	A
H1 frag. 6	485	C	T
H1 frag. 6	527	—	C
H1 frag. 6	572	A	C
H1 frag. 7	42	T	C
H1 frag. 8	52	A	C
H1 frag. 8	146	C	T
H1 frag. 8	147	A	T
H1 frag. 8	384	A	T
H1 frag. 8	420	T	C
H1 frag. 8	463	T	—
H1 frag. 8	532	A	C
H1 frag. 8	568	A	T
H1 frag. 9	125	T	A
H1 frag. 9	129	—	C
H1 frag. 9	202	A	C
H1 frag. 9	238	T	C
H1 frag. 9	259	G	A
H1 frag. 9	346	A	C
H1 frag. 9	371	T	A
H1 frag. 9	382	G	C
H1 frag. 10	3	C	T
H1 frag. 10	54	A	C
H1 frag. 10	95	A	T
H1 frag. 10	183	T	C
H1 frag. 10	262	A	C
H1 frag. 10	266	T	C
H1 frag. 12	8	T	C
H1 frag. 12	76	G	T
H1 frag. 12	191	C	G
H1 frag. 12	311	C	T
H1 frag. 12	425	T	A
RAG1 frag. 2	61	G	A
RAG1 frag. 2	160	C	T
RAG1 frag. 2	169	A	G
rhodopsin	72	G	A
SIA frag. 1	12	T	G
SIA frag. 2	51	T	C
SIA frag. 2	72	T	C
tyr frag. 2	177	A	C
tyr frag. 2	182	T	C
tyr frag. 2	206	A	G
Anomaloglossinae			
COI frag. 1	18	A	C
COI frag. 1	74	A	T
COI frag. 1	197	T	C
COI frag. 1	225	T	C
COI frag. 1	288	A	T
COI frag. 2	206	T	C
COI frag. 2	209	T	C
cytb frag. 1	83	T	C
cytb frag. 1	92	T	C
cytb frag. 2	1	A	T
cytb frag. 2	10	C	T
cytb frag. 2	53	C	T
cytb frag. 2	128	T	C
cytb frag. 2	202	C	T
cytb frag. 3	14	C	A
H1 frag. 2	447	G	A
H1 frag. 2	526	C	T
H1 frag. 2	697	T	C
H1 frag. 5	94	T	C
H1 frag. 6	133	T	C
H1 frag. 6	197	—	A
H1 frag. 8	215	A	T
H1 frag. 8	543	A	G
H1 frag. 8	577	A	C
H1 frag. 9	109	A	T
H1 frag. 9	131	T	C
H1 frag. 9	286	T	C
H1 frag. 9	395	C	T
H1 frag. 9	396	A	T
H1 frag. 10	2	C	T
H1 frag. 10	11	—	C
H1 frag. 10	14	T	C
H1 frag. 12	430	A	C
H1 frag. 13	80	A	G
H1 frag. 13	223	A	T
H1 frag. 13	274	C	T
H1 frag. 14	3	G	A
Anomaloglossus			
COI frag. 1	11	C	T
COI frag. 1	59	C	T
COI frag. 1	147	T	A
COI frag. 1	171	T	C
COI frag. 1	228	A	C
COI frag. 1	320	T	A
COI frag. 2	10	A	C
COI frag. 2	122	T	C
COI frag. 2	244	C	A
COI frag. 2	270	C	T
COI frag. 2	285	C	T
COI frag. 2	351	C	T
cytb frag. 1	15	A	C
cytb frag. 1	33	T	A
cytb frag. 1	48	A	C
cytb frag. 2	26	A	C
cytb frag. 2	135	C	A
cytb frag. 2	136	T	C
cytb frag. 2	150	C	A
cytb frag. 2	168	T	C
H1 frag. 2	11	T	A
H1 frag. 2	113	—	A
H1 frag. 2	117	T	C
H1 frag. 2	172	A	C
H1 frag. 2	232	C	T
H1 frag. 2	241	T	C
H1 frag. 2	359	—	C
H1 frag. 2	390	A	C
H1 frag. 2	451	A	T
H1 frag. 2	476	T	C
H1 frag. 2	545	A	C
H1 frag. 6	328	T	C
H1 frag. 6	372	T	C
H1 frag. 6	446	C	T
H1 frag. 6	450	—	C
H1 frag. 6	463	A	T
H1 frag. 6	469	A	C
H1 frag. 6	474	A	T
H1 frag. 8	41	T	C
H1 frag. 8	113	T	A
H1 frag. 8	166	A	C
H1 frag. 8	170	T	C
H1 frag. 8	241	T	A
H1 frag. 8	344	A	C
H1 frag. 8	365	A	G
H1 frag. 8	527	T	C
H1 frag. 8	587	T	A
H1 frag. 9	161	—	C
H1 frag. 9	284	T	A
H1 frag. 10	79	—	T
H1 frag. 10	108	T	C
H1 frag. 10	250	—	A
H1 frag. 12	349	C	A
H1 frag. 12	378	T	C
H1 frag. 12	434	A	C
H1 frag. 13	33	T	C
H1 frag. 13	67	A	—
H1 frag. 13	103	—	A
H1 frag. 13	112	T	A
H1 frag. 13	138	T	C
H1 frag. 13	154	G	A
H1 frag. 13	182	C	T
H1 frag. 13	185	C	T
H1 frag. 13	192	A	C
H1 frag. 13	197	G	A
rhodopsin	103	C	T
rhodopsin	170	C	A
tyr frag. 1	32	A	G
tyr frag. 1	134	T	C
tyr frag. 1	179	G	C
tyr frag. 1	228	G	A
tyr frag. 2	86	G	A
tyr frag. 2	87	C	A
tyr frag. 2	89	T	G
tyr frag. 2	144	A	C
tyr frag. 2	262	A	G
Rheobates			
H1 frag. 12	34	T	C
H1 frag. 12	66	T	C
H1 frag. 12	67	C	T
H1 frag. 12	108	A	T
H1 frag. 12	160	T	C
H1 frag. 12	181	C	T
H1 frag. 12	261	—	A
H1 frag. 12	265	T	A
H1 frag. 12	305	—	C
H1 frag. 12	306	—	T
H1 frag. 12	341	—	T
H1 frag. 12	342	—	T
H1 frag. 12	362	A	G
H1 frag. 12	415	T	C
H1 frag. 12	465	A	T
H1 frag. 13	22	T	C
H1 frag. 13	32	A	T
H1 frag. 13	57	—	T
H1 frag. 13	58	—	T
H1 frag. 13	148	C	—
H1 frag. 13	165	G	A
H1 frag. 13	167	T	C
H1 frag. 13	173	C	T
H1 frag. 13	203	T	C
H1 frag. 13	204	A	C
H1 frag. 13	206	A	C

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Taxon/Locus	Pos	Anc	Des
H1 frag. 15	1	T	C
H1 frag. 16	11	A	G
Aromobatinae			
COI frag. 1	53	C	T
COI frag. 2	1	C	T
COI frag. 2	10	A	T
COI frag. 2	154	C	T
COI frag. 2	206	T	A
cytb frag. 1	13	C	A
cytb frag. 1	15	A	T
cytb frag. 1	27	C	T
cytb frag. 2	19	C	T
cytb frag. 2	41	T	C
cytb frag. 2	86	T	A
cytb frag. 2	174	C	T
cytb frag. 2	233	A	T
H3	302	C	A
H3	314	C	T
H1 frag. 2	211	A	T
H1 frag. 2	236	A	T
H1 frag. 2	369	—	T
H1 frag. 2	476	T	C
H1 frag. 2	545	A	T
H1 frag. 3	207	T	—
H1 frag. 3	255	A	G
H1 frag. 3	322	C	T
H1 frag. 3	324	A	T
H1 frag. 4	30	T	C
H1 frag. 4	32	G	A
H1 frag. 6	47	A	C
H1 frag. 6	116	C	T
H1 frag. 6	123	C	A
H1 frag. 6	162	—	T
H1 frag. 6	277	—	T
H1 frag. 6	371	C	T
H1 frag. 6	412	C	T
H1 frag. 6	538	T	C
H1 frag. 8	12	A	G
H1 frag. 8	123	T	C
H1 frag. 8	220	—	C
H1 frag. 8	352	—	T
H1 frag. 8	353	—	T
H1 frag. 8	541	T	A
H1 frag. 8	612	A	T
H1 frag. 9	65	T	A
H1 frag. 9	156	—	T
H1 frag. 9	185	A	—
H1 frag. 9	247	A	T
H1 frag. 9	345	G	A
H1 frag. 10	53	—	T
H1 frag. 10	92	—	C
H1 frag. 10	254	A	T
H1 frag. 11	16	T	A
H1 frag. 12	52	T	C
H1 frag. 12	108	A	T
H1 frag. 13	117	—	A
SIA frag. 2	81	A	G
Aromobates			
28S frag. 1	325	G	—
cytb frag. 1	51	C	A
cytb frag. 1	63	C	T
cytb frag. 1	80	C	T
cytb frag. 2	53	C	T
cytb frag. 2	135	C	T
cytb frag. 2	137	C	A
cytb frag. 2	150	C	A
cytb frag. 2	253	C	T
H1 frag. 2	11	T	C
H1 frag. 2	107	C	T
H1 frag. 2	117	T	A
H1 frag. 2	127	C	T
H1 frag. 2	206	A	T
H1 frag. 2	510	A	C
H1 frag. 2	522	T	C
H1 frag. 3	281	T	A
H1 frag. 4	52	C	T
H1 frag. 4	113	A	T
H1 frag. 4	152	T	A
H1 frag. 4	191	A	C
H1 frag. 6	128	T	A
H1 frag. 6	161	—	T
H1 frag. 6	352	T	A
H1 frag. 6	394	A	T
H1 frag. 6	448	—	T
H1 frag. 6	506	A	G
H1 frag. 6	598	T	C
H1 frag. 7	7	C	T
H1 frag. 8	29	G	A
H1 frag. 8	52	C	T
H1 frag. 8	85	C	T
H1 frag. 8	90	C	T
H1 frag. 8	415	A	T
H1 frag. 8	538	C	A
H1 frag. 9	149	C	T
H1 frag. 9	248	C	T
H1 frag. 9	282	T	—
H1 frag. 9	287	—	A
H1 frag. 9	312	A	G
H1 frag. 9	371	A	T
H1 frag. 9	387	C	A
H1 frag. 9	395	C	T
H1 frag. 10	91	A	C
H1 frag. 10	156	A	T
H1 frag. 12	46	A	G
H1 frag. 12	169	A	T
H1 frag. 12	172	A	T
H1 frag. 12	253	C	A
H1 frag. 12	282	—	T
H1 frag. 12	380	—	C
H1 frag. 13	36	T	A
H1 frag. 13	165	G	A
H1 frag. 13	173	C	T
H1 frag. 13	190	C	T
H1 frag. 15	20	C	A
RAG1 frag. 1	78	T	C
SIA frag. 1	54	T	C
SIA frag. 1	180	A	G
SIA frag. 2	72	C	T
SIA frag. 2	204	T	G
Mannophryne			
cytb frag. 1	6	C	T
cytb frag. 1	92	T	A
cytb frag. 2	17	G	A
cytb frag. 2	18	C	T
H1 frag. 3	92	C	A
H1 frag. 3	124	T	C
H1 frag. 3	248	A	G
H1 frag. 4	21	A	C
H1 frag. 4	28	C	T
H1 frag. 4	34	G	A
H1 frag. 4	37	G	A
H1 frag. 4	41	T	C
H1 frag. 4	43	T	G
H1 frag. 4	143	A	C
H1 frag. 5	45	A	T
H1 frag. 6	23	G	T
H1 frag. 6	43	C	G
H1 frag. 6	44	T	C
H1 frag. 6	45	A	C
H1 frag. 6	141	C	—
H1 frag. 6	147	C	T
H1 frag. 6	189	A	T
H1 frag. 6	195	T	C
H1 frag. 6	287	T	C
H1 frag. 6	336	C	A
H1 frag. 6	393	T	G
H1 frag. 6	408	A	C
H1 frag. 6	462	A	T
H1 frag. 6	463	A	T
H1 frag. 6	469	A	C
H1 frag. 6	527	C	T
H1 frag. 6	552	G	C
H1 frag. 7	1	C	T
H1 frag. 7	45	A	G
H1 frag. 8	259	C	T
H1 frag. 8	277	—	C
H1 frag. 8	527	T	—
H1 frag. 8	543	A	C
H1 frag. 8	555	T	G
H1 frag. 8	568	T	C
H1 frag. 9	30	A	T
H1 frag. 9	109	A	—
H1 frag. 9	125	A	G
H1 frag. 9	202	C	T
H1 frag. 9	209	C	A
H1 frag. 9	382	C	T
H1 frag. 9	384	G	T
H1 frag. 9	408	T	A
H1 frag. 10	17	A	C
H1 frag. 10	32	G	T
H1 frag. 10	37	C	T
H1 frag. 10	48	A	—
H1 frag. 10	72	C	T
H1 frag. 10	99	C	T
H1 frag. 10	194	T	C
H1 frag. 10	228	T	C
H1 frag. 10	247	T	A
H1 frag. 10	259	A	C
H1 frag. 12	34	T	C
H1 frag. 12	51	A	G
H1 frag. 12	159	C	T
H1 frag. 12	168	—	T
H1 frag. 12	295	T	—
H1 frag. 12	311	T	A
H1 frag. 12	357	A	—
H1 frag. 12	362	A	—
H1 frag. 13	20	A	C
H1 frag. 13	26	A	T
H1 frag. 13	88	C	T
H1 frag. 13	124	C	T
Allobatinae/*Allobates*			
COI frag. 1	108	T	C
COI frag. 1	279	T	A
COI frag. 2	227	T	A
COI frag. 2	315	A	T
COI frag. 2	318	A	C
COI frag. 2	329	G	A
cytb frag. 2	135	C	A
cytb frag. 2	216	T	C
H1 frag. 2	220	C	T
H1 frag. 2	317	T	C
H1 frag. 2	399	A	T
H1 frag. 2	423	T	C
H1 frag. 2	466	T	C
H1 frag. 2	541	T	C
H1 frag. 2	682	C	—
H1 frag. 3	200	T	C
H1 frag. 3	309	A	—
H1 frag. 4	184	T	A
H1 frag. 6	157	T	A
H1 frag. 6	218	A	C
H1 frag. 6	328	T	C
H1 frag. 6	359	T	C
H1 frag. 6	364	A	C
H1 frag. 6	394	A	C
H1 frag. 6	511	A	C
H1 frag. 8	148	T	A
H1 frag. 8	272	—	T
H1 frag. 8	527	T	A
H1 frag. 9	129	C	T
H1 frag. 9	381	A	C
H1 frag. 10	145	T	A
H1 frag. 12	169	A	G
H1 frag. 12	184	T	C
H1 frag. 12	249	T	A
H1 frag. 12	349	C	—
H1 frag. 12	391	A	—
H1 frag. 12	436	G	T

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Taxon/Locus	Pos	Anc	Des
H1 frag. 12	446	T	C
H1 frag. 12	448	T	C
H1 frag. 12	458	T	C
H1 frag. 15	29	A	C
rhodopsin	33	G	A
rhodopsin	302	G	A
SIA frag. 1	12	G	A
SIA frag. 1	57	C	G
SIA frag. 2	60	C	T
Dendrobatidae			
28S frag. 1	345	G	C
28S frag. 1	547	—	T
28S frag. 1	550	—	T
28S frag. 1	551	—	T
COI frag. 1	94	C	G
COI frag. 1	234	T	A
COI frag. 2	138	T	C
H3	75	C	T
H3	196	A	G
H1 frag. 2	16	—	C
H1 frag. 2	17	A	T
H1 frag. 2	127	C	T
H1 frag. 2	196	T	C
H1 frag. 2	292	—	T
H1 frag. 2	390	A	T
H1 frag. 2	414	C	A
H1 frag. 4	178	A	C
H1 frag. 4	191	A	T
H1 frag. 4	204	T	A
H1 frag. 4	206	T	C
H1 frag. 6	31	A	G
H1 frag. 6	359	T	C
H1 frag. 8	166	A	T
H1 frag. 8	167	A	G
H1 frag. 8	224	T	A
H1 frag. 8	270	A	T
H1 frag. 9	120	A	T
H1 frag. 9	134	—	A
H1 frag. 9	153	—	T
H1 frag. 9	185	A	—
H1 frag. 9	322	C	T
H1 frag. 9	408	T	C
H1 frag. 10	15	—	A
H1 frag. 12	74	G	A
H1 frag. 12	188	—	G
H1 frag. 12	198	—	T
H1 frag. 12	208	—	T
H1 frag. 12	249	T	C
H1 frag. 12	454	G	A
H1 frag. 13	206	A	C
H1 frag. 13	272	C	T
tyr frag. 1	57	A	C
tyr frag. 1	151	C	T
tyr frag. 2	17	A	G
tyr frag. 2	254	A	G
Colostethinae			
28S frag. 1	226	—	T
28S frag. 1	312	—	G
28S frag. 1	313	—	G
COI frag. 1	98	T	—
COI frag. 1	102	—	A
COI frag. 1	270	T	C
COI frag. 1	307	C	A
COI frag. 2	83	A	T
COI frag. 2	132	C	T
COI frag. 2	209	T	A
COI frag. 2	244	C	T
COI frag. 2	287	A	T
COI frag. 2	348	A	C
cytb frag. 1	27	C	T
cytb frag. 1	42	C	T
cytb frag. 2	262	C	T
cytb frag. 3	8	T	C
H3	51	C	T
H3	187	C	T
H1 frag. 2	15	A	T
H1 frag. 2	137	A	T
H1 frag. 2	212	C	T
H1 frag. 2	397	C	A
H1 frag. 2	507	C	A
H1 frag. 3	116	A	T
H1 frag. 3	279	A	C
H1 frag. 3	308	T	—
H1 frag. 4	35	A	C
H1 frag. 4	41	T	A
H1 frag. 4	46	T	A
H1 frag. 4	181	A	T
H1 frag. 5	34	A	T
H1 frag. 6	51	C	T
H1 frag. 6	134	—	C
H1 frag. 6	225	C	T
H1 frag. 6	244	T	C
H1 frag. 6	270	C	A
H1 frag. 6	318	—	T
H1 frag. 6	338	—	T
H1 frag. 6	449	T	C
H1 frag. 6	470	A	C
H1 frag. 6	496	G	A
H1 frag. 6	596	G	A
H1 frag. 7	48	C	T
H1 frag. 8	14	G	A
H1 frag. 8	22	C	T
H1 frag. 8	121	C	T
H1 frag. 8	189	—	C
H1 frag. 8	344	A	T
H1 frag. 8	405	T	A
H1 frag. 8	545	—	C
H1 frag. 9	231	T	A
H1 frag. 9	382	G	A
H1 frag. 9	383	T	C
H1 frag. 10	14	T	A
H1 frag. 10	262	A	T
H1 frag. 11	14	A	T
H1 frag. 12	52	T	C
H1 frag. 12	110	A	T
H1 frag. 12	279	A	T
H1 frag. 12	329	—	C
H1 frag. 12	362	A	G
H1 frag. 12	368	A	C
H1 frag. 12	442	—	T
H1 frag. 13	20	A	T
H1 frag. 13	71	A	G
H1 frag. 13	171	A	T
RAG1 frag. 1	21	C	T
RAG1 frag. 1	42	G	A
RAG1 frag. 1	57	A	G
RAG1 frag. 1	138	C	T
RAG1 frag. 1	148	G	A
RAG1 frag. 1	153	C	T
RAG1 frag. 2	178	C	T
RAG1 frag. 2	199	C	T
SIA frag. 1	102	C	T
tyr frag. 1	113	C	T
tyr frag. 1	184	A	G
tyr frag. 1	202	A	C
tyr frag. 2	86	G	T
tyr frag. 2	99	A	G
tyr frag. 2	128	G	C
tyr frag. 2	263	G	A
Ameerega			
28S frag. 1	225	G	A
28S frag. 1	350	C	T
28S frag. 1	387	C	T
COI frag. 1	34	C	A
COI frag. 1	37	A	C
COI frag. 1	47	A	C
COI frag. 1	74	A	C
COI frag. 1	84	T	C
COI frag. 1	129	A	T
COI frag. 1	243	C	T
COI frag. 1	291	T	C
COI frag. 2	80	T	C
COI frag. 2	83	T	C
COI frag. 2	98	A	T
COI frag. 2	179	T	A
COI frag. 2	188	T	C
COI frag. 2	328	A	C
COI frag. 2	331	T	C
COI frag. 2	348	C	G
cytb frag. 1	24	T	C
cytb frag. 1	68	G	A
cytb frag. 2	147	C	T
cytb frag. 2	171	T	C
cytb frag. 2	216	T	C
cytb frag. 2	217	T	A
cytb frag. 2	255	A	T
H3	105	T	G
H3	111	A	G
H3	220	C	T
H1 frag. 1	24	G	C
H1 frag. 2	44	A	C
H1 frag. 2	322	A	T
H1 frag. 2	447	G	A
H1 frag. 2	496	C	T
H1 frag. 2	526	C	T
H1 frag. 2	551	C	T
H1 frag. 2	576	G	A
H1 frag. 2	577	A	G
H1 frag. 2	613	T	C
H1 frag. 2	614	C	T
H1 frag. 2	665	A	—
H1 frag. 2	698	—	C
H1 frag. 3	281	T	A
H1 frag. 4	43	T	C
H1 frag. 4	128	A	G
H1 frag. 4	173	—	C
H1 frag. 4	191	T	C
H1 frag. 4	242	T	C
H1 frag. 6	24	A	C
H1 frag. 6	157	T	C
H1 frag. 6	244	C	—
H1 frag. 6	251	A	T
H1 frag. 6	261	C	T
H1 frag. 6	270	A	T
H1 frag. 6	338	T	C
H1 frag. 6	352	T	C
H1 frag. 6	371	C	T
H1 frag. 6	462	A	T
H1 frag. 6	476	T	C
H1 frag. 7	37	T	C
H1 frag. 8	36	C	T
H1 frag. 8	49	G	A
H1 frag. 8	90	A	C
H1 frag. 8	102	G	A
H1 frag. 8	147	A	T
H1 frag. 8	148	T	C
H1 frag. 8	167	G	A
H1 frag. 8	189	C	T
H1 frag. 8	229	T	C
H1 frag. 8	235	T	C
H1 frag. 8	270	T	C
H1 frag. 8	369	T	C
H1 frag. 8	400	A	T
H1 frag. 8	415	A	C
H1 frag. 8	451	T	C
H1 frag. 8	454	A	C
H1 frag. 8	463	T	C
H1 frag. 8	538	C	T
H1 frag. 8	545	C	A
H1 frag. 8	592	T	C
H1 frag. 9	18	C	T
H1 frag. 9	26	A	T
H1 frag. 9	38	A	G
H1 frag. 9	54	T	C
H1 frag. 9	128	A	—
H1 frag. 9	172	A	—
H1 frag. 9	193	C	T
H1 frag. 9	286	T	A

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Taxon/Locus	Pos	Anc	Des
H1 frag. 9	346	A	C
H1 frag. 9	387	C	A
H1 frag. 9	395	C	T
H1 frag. 9	405	A	C
H1 frag. 9	407	C	A
H1 frag. 10	3	C	T
H1 frag. 10	17	A	C
H1 frag. 10	25	A	C
H1 frag. 10	26	T	C
H1 frag. 10	83	T	—
H1 frag. 10	145	T	C
H1 frag. 10	183	T	C
H1 frag. 10	194	T	C
H1 frag. 10	238	A	T
H1 frag. 12	46	A	G
H1 frag. 12	51	A	G
H1 frag. 12	87	T	C
H1 frag. 12	112	T	C
H1 frag. 12	221	A	—
H1 frag. 12	255	—	C
H1 frag. 12	295	T	—
H1 frag. 12	363	—	C
H1 frag. 12	425	T	C
H1 frag. 13	20	T	C
H1 frag. 13	22	T	A
H1 frag. 13	36	T	A
H1 frag. 13	39	A	—
H1 frag. 13	67	A	T
H1 frag. 13	88	C	A
H1 frag. 13	112	T	A
H1 frag. 13	142	C	T
H1 frag. 13	152	T	A
H1 frag. 13	158	T	C
H1 frag. 13	165	G	A
H1 frag. 13	173	C	T
H1 frag. 13	201	T	C
RAG1 frag. 2	37	A	C
SIA frag. 1	78	A	C
SIA frag. 2	165	T	G
SIA frag. 2	186	C	T
Colostethus			
28S frag. 1	233	C	—
28S frag. 1	345	C	—
COI frag. 1	15	A	T
COI frag. 1	111	C	T
COI frag. 1	150	C	T
COI frag. 1	216	T	C
COI frag. 1	219	A	T
COI frag. 2	102	C	T
COI frag. 2	113	T	C
COI frag. 2	227	T	A
COI frag. 2	293	C	T
COI frag. 2	345	C	T
cytb frag. 1	71	A	C
cytb frag. 1	80	C	T
cytb frag. 2	87	G	A
cytb frag. 2	113	C	T
cytb frag. 2	199	A	G
cytb frag. 3	20	T	C
H1 frag. 1	41	T	C
H1 frag. 2	196	C	T
H1 frag. 4	130	C	T
H1 frag. 4	152	T	C
H1 frag. 5	94	T	C
H1 frag. 6	195	T	A
H1 frag. 6	317	—	A
H1 frag. 6	361	T	—
H1 frag. 7	14	T	A
H1 frag. 8	259	C	A
H1 frag. 8	359	—	C
H1 frag. 9	240	T	C
H1 frag. 9	418	T	C
H1 frag. 10	51	C	A
H1 frag. 10	104	T	C
rhodopsin	185	C	G
rhodopsin	215	T	C
Epipedobates			
cytb frag. 2	10	C	T
cytb frag. 2	44	A	T
cytb frag. 2	87	G	C
cytb frag. 2	98	C	T
cytb frag. 2	150	C	A
H1 frag. 1	24	G	A
H1 frag. 2	41	A	T
H1 frag. 2	48	T	C
H1 frag. 2	107	C	A
H1 frag. 2	148	C	A
H1 frag. 2	316	C	T
H1 frag. 2	397	A	—
H1 frag. 2	666	—	T
H1 frag. 2	667	—	T
H1 frag. 2	668	—	T
H1 frag. 2	682	C	T
H1 frag. 2	690	C	T
H1 frag. 3	187	T	—
H1 frag. 3	193	A	—
H1 frag. 3	201	T	A
H1 frag. 3	287	A	G
H1 frag. 3	324	A	G
H1 frag. 4	128	A	T
H1 frag. 5	50	—	A
H1 frag. 5	73	C	A
H1 frag. 6	24	A	T
H1 frag. 6	134	C	T
H1 frag. 6	203	A	T
H1 frag. 6	218	A	C
H1 frag. 6	240	T	C
H1 frag. 6	315	C	T
H1 frag. 6	352	T	A
H1 frag. 6	431	—	T
H1 frag. 6	525	A	T
H1 frag. 6	538	T	C
H1 frag. 6	570	T	A
H1 frag. 7	15	T	A
H1 frag. 7	30	C	T
H1 frag. 8	41	T	C
H1 frag. 8	52	A	G
H1 frag. 8	270	T	A
H1 frag. 8	355	A	C
H1 frag. 8	538	C	T
H1 frag. 8	543	A	T
H1 frag. 8	577	A	G
H1 frag. 8	612	A	G
H1 frag. 9	40	A	T
H1 frag. 9	65	T	C
H1 frag. 9	92	—	C
H1 frag. 9	109	A	C
H1 frag. 9	174	T	—
H1 frag. 9	202	A	C
H1 frag. 9	214	—	C
H1 frag. 9	245	C	T
H1 frag. 9	248	C	T
H1 frag. 9	298	A	G
H1 frag. 9	305	T	A
H1 frag. 9	351	—	C
H1 frag. 10	32	G	A
H1 frag. 10	51	C	T
H1 frag. 10	72	C	T
H1 frag. 10	85	T	C
H1 frag. 10	99	C	T
H1 frag. 12	66	T	C
H1 frag. 12	112	T	A
H1 frag. 12	160	T	A
H1 frag. 12	253	T	C
H1 frag. 12	295	T	A
H1 frag. 12	368	C	G
H1 frag. 12	439	—	A
H1 frag. 13	97	T	—
H1 frag. 13	112	T	C
H1 frag. 13	275	T	C
H1 frag. 13	278	A	G
H1 frag. 14	2	A	G
Silverstoneia			
28S frag. 1	575	—	C
28S frag. 1	585	—	T
COI frag. 1	59	C	T
COI frag. 1	78	T	C
COI frag. 1	180	T	C
COI frag. 1	217	C	T
COI frag. 2	180	T	C
COI frag. 2	215	T	A
COI frag. 2	290	C	T
cytb frag. 1	69	C	T
cytb frag. 1	92	T	A
cytb frag. 2	56	T	C
H1 frag. 2	541	T	C
H1 frag. 2	542	T	A
H1 frag. 2	545	A	C
H1 frag. 4	30	T	C
H1 frag. 5	42	G	A
H1 frag. 6	34	C	T
H1 frag. 6	338	T	A
H1 frag. 6	535	T	C
H1 frag. 8	349	—	A
H1 frag. 8	378	T	C
H1 frag. 8	391	A	G
H1 frag. 8	463	T	—
H1 frag. 8	541	T	A
H1 frag. 9	131	T	A
H1 frag. 9	176	C	T
H1 frag. 9	238	T	C
H1 frag. 9	408	C	T
H1 frag. 10	1	T	—
H1 frag. 10	95	A	T
H1 frag. 10	108	T	A
H1 frag. 10	266	T	A
H1 frag. 12	349	C	T
H1 frag. 12	378	T	C
H1 frag. 13	39	A	T
H1 frag. 13	138	T	A
RAG1 frag. 1	179	A	G
RAG1 frag. 2	181	A	C
Hyloxalinae/*Hyloxalus*			
28S frag. 1	246	C	—
COI frag. 1	18	A	C
COI frag. 1	68	T	C
COI frag. 1	138	C	T
COI frag. 1	159	T	C
COI frag. 1	191	G	C
COI frag. 1	320	T	A
COI frag. 1	330	A	G
COI frag. 2	101	T	C
COI frag. 2	198	T	C
COI frag. 2	245	T	C
COI frag. 2	247	A	T
cytb frag. 1	15	A	T
cytb frag. 2	187	T	C
H3	78	C	A
H1 frag. 2	16	C	A
H1 frag. 2	31	C	T
H1 frag. 2	54	G	A
H1 frag. 2	345	A	T
H1 frag. 2	397	C	T
H1 frag. 2	448	T	C
H1 frag. 2	492	C	A
H1 frag. 2	697	T	C
H1 frag. 2	718	A	T
H1 frag. 3	15	T	C
H1 frag. 4	41	T	C
H1 frag. 6	204	—	T
H1 frag. 6	233	—	T
H1 frag. 6	261	A	T
H1 frag. 7	14	T	C
H1 frag. 7	49	C	T
H1 frag. 8	55	C	T
H1 frag. 8	79	G	A
H1 frag. 8	197	T	A
H1 frag. 8	297	A	C

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Taxon/Locus	Pos	Anc	Des
H1 frag. 8	337	—	A
H1 frag. 9	165	A	T
H1 frag. 9	248	C	T
H1 frag. 9	286	T	C
H1 frag. 10	228	T	C
H1 frag. 10	271	A	G
H1 frag. 12	89	C	T
H1 frag. 12	102	G	A
H1 frag. 12	279	A	C
H1 frag. 12	387	T	A
H1 frag. 13	172	T	G
H1 frag. 13	178	T	A
H1 frag. 13	274	C	T
H1 frag. 14	3	G	A
RAG1 frag. 2	130	A	C
SIA frag. 2	30	T	C
SIA frag. 2	51	T	C
Dendrobatinae			
28S frag. 1	334	G	C
COI frag. 1	317	C	G
cytb frag. 1	11	C	T
cytb frag. 1	12	C	A
cytb frag. 2	156	A	C
H1 frag. 1	74	T	A
H1 frag. 2	82	A	C
H1 frag. 2	107	C	—
H1 frag. 2	147	C	T
H1 frag. 2	172	A	T
H1 frag. 2	322	A	T
H1 frag. 2	438	T	C
H1 frag. 2	447	G	A
H1 frag. 2	451	A	C
H1 frag. 2	511	A	T
H1 frag. 2	526	C	T
H1 frag. 3	123	C	T
H1 frag. 4	135	A	C
H1 frag. 4	210	C	T
H1 frag. 5	92	A	C
H1 frag. 5	94	T	C
H1 frag. 6	148	—	T
H1 frag. 6	530	—	T
H1 frag. 7	47	C	A
H1 frag. 8	41	T	C
H1 frag. 8	52	A	G
H1 frag. 8	148	T	—
H1 frag. 8	289	—	T
H1 frag. 8	538	C	A
H1 frag. 8	587	T	—
H1 frag. 9	224	A	C
H1 frag. 9	235	—	A
H1 frag. 9	247	A	C
H1 frag. 9	378	T	C
H1 frag. 10	135	A	C
H1 frag. 10	139	A	G
H1 frag. 10	198	C	T
H1 frag. 10	266	T	A
H1 frag. 12	15	A	T
H1 frag. 12	48	G	A
H1 frag. 12	104	A	G
H1 frag. 12	235	T	A
H1 frag. 12	336	C	T
H1 frag. 12	378	T	C
H1 frag. 12	451	—	A
H1 frag. 13	33	T	C
H1 frag. 13	97	T	—
RAG1 frag. 1	47	C	T
rhodopsin	0	A	T
rhodopsin	66	T	C
SIA frag. 1	15	T	C
SIA frag. 1	78	A	G
SIA frag. 2	165	T	C
tyr frag. 1	155	C	T
tyr frag. 1	189	G	A
tyr frag. 2	11	C	T
tyr frag. 2	41	G	A
tyr frag. 2	275	C	T
Adelphobates			
28S frag. 1	239	—	C
COI frag. 1	34	C	T
COI frag. 1	44	C	G
COI frag. 1	78	T	C
COI frag. 1	117	A	G
COI frag. 1	150	C	T
COI frag. 1	317	G	T
COI frag. 2	22	T	C
COI frag. 2	44	T	C
COI frag. 2	56	A	G
COI frag. 2	68	C	T
COI frag. 2	98	T	A
COI frag. 2	128	A	C
COI frag. 2	130	C	T
COI frag. 2	138	C	T
COI frag. 2	179	C	A
COI frag. 2	213	C	T
COI frag. 2	265	A	G
COI frag. 2	296	C	A
COI frag. 2	318	T	C
COI frag. 2	345	C	T
cytb frag. 1	12	A	C
cytb frag. 1	28	A	C
cytb frag. 2	72	A	T
cytb frag. 2	73	T	C
cytb frag. 2	141	C	T
cytb frag. 2	150	C	A
cytb frag. 2	177	C	T
cytb frag. 2	211	C	A
H1 frag. 1	18	G	A
H1 frag. 2	54	G	A
H1 frag. 2	209	C	T
H1 frag. 2	212	C	A
H1 frag. 2	214	G	A
H1 frag. 2	292	T	C
H1 frag. 2	297	T	G
H1 frag. 2	321	C	T
H1 frag. 2	414	A	T
H1 frag. 2	423	T	A
H1 frag. 2	454	C	T
H1 frag. 2	469	G	A
H1 frag. 2	471	C	T
H1 frag. 2	488	A	T
H1 frag. 2	492	C	T
H1 frag. 2	515	A	G
H1 frag. 2	695	C	T
H1 frag. 3	76	A	T
H1 frag. 3	242	A	G
H1 frag. 3	281	T	A
H1 frag. 3	329	G	A
H1 frag. 4	4	C	T
H1 frag. 4	28	C	T
H1 frag. 4	178	C	A
H1 frag. 4	199	—	T
H1 frag. 4	210	T	—
H1 frag. 5	94	C	T
H1 frag. 6	48	T	C
H1 frag. 6	157	G	C
H1 frag. 6	203	A	C
H1 frag. 6	215	T	C
H1 frag. 7	24	A	T
H1 frag. 7	30	C	T
H1 frag. 7	34	T	C
H1 frag. 8	43	—	T
H1 frag. 8	46	—	A
H1 frag. 8	90	A	T
H1 frag. 8	93	A	G
H1 frag. 8	141	G	A
H1 frag. 8	144	T	C
H1 frag. 8	211	—	A
H1 frag. 8	253	T	—
H1 frag. 8	378	T	C
H1 frag. 8	391	A	G
H1 frag. 8	607	T	C
H1 frag. 8	614	C	A
H1 frag. 9	1	A	G
H1 frag. 9	26	A	T
H1 frag. 9	59	—	T
H1 frag. 9	146	—	A
H1 frag. 9	176	C	A
H1 frag. 9	213	T	A
H1 frag. 9	237	T	C
H1 frag. 9	247	C	A
H1 frag. 9	260	A	G
H1 frag. 9	262	C	T
H1 frag. 9	298	A	G
H1 frag. 9	336	C	A
H1 frag. 9	369	—	C
H1 frag. 10	281	G	A
H1 frag. 12	40	C	A
H1 frag. 12	113	C	T
H1 frag. 12	184	T	C
H1 frag. 12	227	—	C
H1 frag. 12	257	—	C
H1 frag. 12	272	—	A
H1 frag. 12	336	T	C
H1 frag. 12	411	A	T
H1 frag. 13	14	A	C
H1 frag. 13	52	—	T
H1 frag. 13	53	—	T
H1 frag. 13	278	G	A
H1 frag. 14	8	T	C
SIA frag. 1	129	T	C
SIA frag. 2	105	A	G
SIA frag. 2	171	A	G
Dendrobates			
28S frag. 1	193	T	A
28S frag. 1	329	—	C
COI frag. 1	11	C	T
COI frag. 1	37	G	A
COI frag. 1	159	T	C
COI frag. 1	252	A	T
COI frag. 2	50	T	A
COI frag. 2	53	A	T
COI frag. 2	125	C	T
COI frag. 2	212	C	A
COI frag. 2	244	G	T
COI frag. 2	278	C	T
COI frag. 2	285	C	T
COI frag. 2	302	T	C
cytb frag. 1	71	C	T
cytb frag. 2	26	A	C
cytb frag. 2	41	T	C
cytb frag. 2	104	A	T
cytb frag. 2	134	T	C
cytb frag. 2	239	C	T
cytb frag. 2	265	A	T
cytb frag. 3	11	A	T
H1 frag. 2	60	C	T
H1 frag. 2	70	T	C
H1 frag. 2	196	T	C
H1 frag. 2	449	C	T
H1 frag. 2	506	G	A
H1 frag. 3	17	A	T
H1 frag. 3	123	T	A
H1 frag. 3	201	T	C
H1 frag. 3	288	C	A
H1 frag. 4	157	T	C
H1 frag. 5	73	T	C
H1 frag. 6	47	A	C
H1 frag. 6	50	T	C
H1 frag. 6	128	T	—
H1 frag. 6	148	C	A
H1 frag. 6	352	T	A
H1 frag. 6	365	—	C
H1 frag. 6	390	—	C
H1 frag. 6	391	—	C
H1 frag. 6	417	—	A
H1 frag. 6	446	C	—
H1 frag. 6	530	T	C
H1 frag. 7	14	T	C

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Taxon/Locus	Pos	Anc	Des
H1 frag. 7	30	C	A
H1 frag. 8	11	T	C
H1 frag. 8	41	C	T
H1 frag. 8	66	T	A
H1 frag. 8	86	T	C
H1 frag. 8	124	A	G
H1 frag. 8	422	C	A
H1 frag. 8	601	A	G
H1 frag. 9	151	C	T
H1 frag. 9	174	T	C
H1 frag. 9	176	C	T
H1 frag. 9	238	T	—
H1 frag. 9	240	T	C
H1 frag. 9	299	T	C
H1 frag. 10	2	C	T
H1 frag. 10	15	A	T
H1 frag. 10	48	A	T
H1 frag. 10	130	A	T
H1 frag. 10	138	A	C
H1 frag. 11	11	—	A
H1 frag. 11	12	—	T
H1 frag. 12	34	T	C
H1 frag. 12	200	—	A
H1 frag. 13	16	A	C
H1 frag. 13	48	A	C
H1 frag. 13	71	A	G
H1 frag. 13	138	T	C
H1 frag. 13	225	A	T
H1 frag. 13	283	C	T
RAG1 frag. 1	153	C	T
RAG1 frag. 2	94	A	G
RAG1 frag. 2	193	A	G
RAG1 frag. 2	214	A	T
rhodopsin	85	A	C
rhodopsin	106	G	A
rhodopsin	291	A	G
SIA frag. 1	12	T	A
SIA frag. 1	36	T	C
SIA frag. 1	69	A	G
SIA frag. 1	123	A	G
SIA frag. 1	171	T	C
SIA frag. 2	93	T	C
SIA frag. 2	108	T	C
SIA frag. 2	132	A	C
SIA frag. 2	135	A	C
SIA frag. 2	204	T	G
Minyobates/M. steyermarki			
H1 frag. 12	51	A	G
H1 frag. 12	109	A	T
H1 frag. 12	110	A	G
H1 frag. 12	184	T	C
H1 frag. 12	197	—	T
H1 frag. 12	249	C	T
H1 frag. 12	307	—	T
H1 frag. 12	311	C	T
H1 frag. 12	373	A	G
H1 frag. 12	405	—	C
H1 frag. 12	406	—	C
H1 frag. 12	408	T	C
H1 frag. 12	425	T	—
H1 frag. 12	447	T	G
H1 frag. 12	448	T	C
H1 frag. 13	22	T	C
H1 frag. 13	36	T	C
H1 frag. 13	46	—	C
H1 frag. 13	71	A	G
H1 frag. 13	111	—	A
H1 frag. 13	149	—	T
H1 frag. 13	166	C	T
H1 frag. 13	172	T	—
H1 frag. 13	181	G	T
H1 frag. 13	201	T	C
H1 frag. 15	6	T	C
H1 frag. 15	16	C	T
H1 frag. 15	29	A	G
Oophaga			
28S frag. 1	181	C	T
28S frag. 1	403	T	A
COI frag. 1	53	C	T
COI frag. 1	68	T	C
COI frag. 1	103	C	T
COI frag. 1	191	G	A
COI frag. 1	194	A	C
COI frag. 1	216	T	C
COI frag. 1	234	A	T
COI frag. 1	336	A	G
COI frag. 2	33	T	C
COI frag. 2	86	C	T
COI frag. 2	89	A	C
COI frag. 2	116	T	C
COI frag. 2	148	A	G
COI frag. 2	154	C	T
COI frag. 2	197	T	C
COI frag. 2	262	T	C
COI frag. 2	269	C	A
COI frag. 2	270	C	T
COI frag. 2	284	C	T
COI frag. 2	287	A	T
COI frag. 2	290	C	T
COI frag. 2	318	T	A
cytb frag. 1	55	T	G
cytb frag. 1	68	G	T
cytb frag. 2	1	A	T
cytb frag. 2	10	C	T
cytb frag. 2	25	T	C
cytb frag. 2	31	A	T
cytb frag. 2	42	C	T
cytb frag. 2	65	C	T
cytb frag. 2	87	G	A
cytb frag. 2	113	C	T
cytb frag. 2	252	C	T
cytb frag. 2	258	T	C
cytb frag. 3	8	T	C
cytb frag. 3	23	T	G
H1 frag. 1	36	C	A
H1 frag. 1	47	A	T
H1 frag. 2	95	A	T
H1 frag. 2	102	A	C
H1 frag. 2	120	—	C
H1 frag. 2	152	G	A
H1 frag. 2	174	T	C
H1 frag. 2	217	T	A
H1 frag. 2	361	—	T
H1 frag. 2	366	—	T
H1 frag. 2	397	C	T
H1 frag. 2	398	T	A
H1 frag. 2	402	T	A
H1 frag. 2	409	T	A
H1 frag. 2	500	A	T
H1 frag. 2	508	C	T
H1 frag. 2	511	T	A
H1 frag. 2	541	T	C
H1 frag. 2	551	C	A
H1 frag. 2	580	A	G
H1 frag. 2	606	C	T
H1 frag. 2	659	—	T
H1 frag. 2	690	C	A
H1 frag. 2	707	C	—
H1 frag. 3	81	T	C
H1 frag. 3	162	T	C
H1 frag. 3	166	A	G
H1 frag. 3	200	T	C
H1 frag. 3	209	T	A
H1 frag. 3	249	A	T
H1 frag. 4	130	C	A
H1 frag. 4	154	T	A
H1 frag. 4	202	T	C
H1 frag. 6	27	C	T
H1 frag. 6	315	C	T
H1 frag. 6	336	C	T
H1 frag. 6	445	T	G
H1 frag. 6	455	G	A
H1 frag. 6	474	A	G
H1 frag. 6	496	G	A
H1 frag. 6	565	G	A
H1 frag. 6	570	T	C
H1 frag. 6	596	G	A
H1 frag. 7	37	T	A
H1 frag. 8	22	C	T
H1 frag. 8	52	G	A
H1 frag. 8	102	G	A
H1 frag. 8	229	C	T
H1 frag. 8	241	G	A
H1 frag. 8	270	T	A
H1 frag. 8	289	T	A
H1 frag. 8	303	A	T
H1 frag. 8	319	C	T
H1 frag. 8	463	T	C
H1 frag. 9	30	A	C
H1 frag. 9	120	T	A
H1 frag. 9	183	T	C
H1 frag. 9	224	C	A
H1 frag. 9	258	A	T
H1 frag. 9	302	T	A
H1 frag. 9	336	C	T
H1 frag. 9	407	C	T
H1 frag. 10	29	T	A
H1 frag. 10	76	A	T
H1 frag. 10	262	A	C
H1 frag. 12	109	A	C
H1 frag. 12	173	T	C
H1 frag. 12	311	C	T
H1 frag. 12	427	T	C
H1 frag. 13	124	T	C
H1 frag. 13	128	—	A
H1 frag. 13	159	A	T
H1 frag. 13	227	T	C
RAG1 frag. 1	144	G	A
RAG1 frag. 2	172	C	T
rhodopsin	12	A	T
rhodopsin	215	T	C
rhodopsin	263	C	T
SIA frag. 1	57	C	G
SIA frag. 1	85	A	C
SIA frag. 1	180	A	G
SIA frag. 2	60	A	C
SIA frag. 2	69	C	G
SIA frag. 2	111	T	C
SIA frag. 2	183	T	C
Phyllobates			
28S frag. 1	197	—	C
28S frag. 1	198	—	C
28S frag. 1	203	—	G
28S frag. 1	204	—	T
28S frag. 1	260	—	T
28S frag. 1	351	—	G
28S frag. 1	352	—	G
28S frag. 1	353	—	G
COI frag. 1	21	T	C
COI frag. 1	25	G	C
COI frag. 1	56	C	T
COI frag. 1	94	G	C
COI frag. 1	114	C	T
COI frag. 1	144	T	C
COI frag. 1	184	A	T
COI frag. 1	197	T	C
COI frag. 1	267	C	T
COI frag. 1	288	A	T
COI frag. 2	1	C	T
COI frag. 2	10	A	T
COI frag. 2	27	G	A
COI frag. 2	47	C	A
COI frag. 2	68	C	T
COI frag. 2	83	A	G
COI frag. 2	86	C	T
COI frag. 2	157	T	A
COI frag. 2	180	T	C
COI frag. 2	188	T	G

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Taxon/Locus	Pos	Anc	Des
COI frag. 2	210	G	A
COI frag. 2	223	T	C
COI frag. 2	232	T	C
COI frag. 2	269	C	A
COI frag. 2	285	C	T
COI frag. 2	293	C	A
COI frag. 2	346	C	T
cytb frag. 2	44	A	C
cytb frag. 2	69	T	A
cytb frag. 2	119	C	A
cytb frag. 2	137	T	A
cytb frag. 2	150	C	A
cytb frag. 2	196	A	C
cytb frag. 3	26	A	T
H3	60	G	A
H1 frag. 1	63	C	A
H1 frag. 2	3	C	T
H1 frag. 2	13	A	—
H1 frag. 2	119	—	A
H1 frag. 2	161	A	T
H1 frag. 2	233	—	T
H1 frag. 2	368	—	T
H1 frag. 2	374	C	T
H1 frag. 2	423	T	A
H1 frag. 2	432	C	A
H1 frag. 2	481	T	—
H1 frag. 2	492	C	T
H1 frag. 2	496	C	T
H1 frag. 2	507	C	A
H1 frag. 2	547	A	T
H1 frag. 2	563	T	C
H1 frag. 2	572	A	T
H1 frag. 2	682	C	T
H1 frag. 2	707	C	T
H1 frag. 3	201	T	A
H1 frag. 3	279	A	T
H1 frag. 3	305	T	—
H1 frag. 3	306	A	—
H1 frag. 4	130	C	A
H1 frag. 4	181	A	C
H1 frag. 4	191	T	A
H1 frag. 4	202	T	A
H1 frag. 5	20	G	A
H1 frag. 5	97	C	T
H1 frag. 6	7	G	A
H1 frag. 6	11	A	G
H1 frag. 6	27	C	A
H1 frag. 6	141	C	T
H1 frag. 6	225	C	A
H1 frag. 6	328	T	C
H1 frag. 6	359	C	T
H1 frag. 6	361	T	A
H1 frag. 6	408	A	G
H1 frag. 6	416	T	C
H1 frag. 6	457	A	C
H1 frag. 6	462	A	C
H1 frag. 6	469	A	G
H1 frag. 6	558	A	C
H1 frag. 6	568	C	T
H1 frag. 7	30	C	T
H1 frag. 8	42	A	T
H1 frag. 8	58	G	A
H1 frag. 8	73	G	T
H1 frag. 8	81	A	C
H1 frag. 8	93	A	G
H1 frag. 8	142	—	C
H1 frag. 8	146	C	T
H1 frag. 8	253	T	A
H1 frag. 8	344	A	—
H1 frag. 8	414	A	C
H1 frag. 8	524	—	A
H1 frag. 8	555	T	A
H1 frag. 9	9	A	G
H1 frag. 9	38	A	G
H1 frag. 9	54	T	C
H1 frag. 9	62	C	A
H1 frag. 9	75	C	T
H1 frag. 9	134	A	T
H1 frag. 9	149	C	T
H1 frag. 9	177	—	A
H1 frag. 9	183	T	A
H1 frag. 9	250	T	A
H1 frag. 9	260	A	—
H1 frag. 9	265	C	A
H1 frag. 9	283	C	A
H1 frag. 9	367	—	C
H1 frag. 9	371	T	C
H1 frag. 9	386	A	T
H1 frag. 9	421	T	C
H1 frag. 10	3	C	A
H1 frag. 10	95	A	T
H1 frag. 10	108	T	C
H1 frag. 10	124	T	C
H1 frag. 10	249	T	C
H1 frag. 10	262	A	C
H1 frag. 12	110	A	C
H1 frag. 12	181	C	T
H1 frag. 12	327	T	C
H1 frag. 12	443	—	T
H1 frag. 13	20	A	C
H1 frag. 13	65	—	T
H1 frag. 13	112	T	—
H1 frag. 13	195	T	C
H1 frag. 13	204	T	A
H1 frag. 13	223	A	T
H1 frag. 13	284	T	C
RAG1 frag. 1	43	G	A
RAG1 frag. 1	174	G	A
RAG1 frag. 2	85	C	T
RAG1 frag. 2	184	G	A
rhodopsin	9	C	T
rhodopsin	60	T	C
rhodopsin	93	C	T
rhodopsin	173	G	A
rhodopsin	203	T	C
SIA frag. 2	105	A	C
Ranitomeya			
COI frag. 1	28	A	C
COI frag. 1	59	C	T
COI frag. 1	105	A	T
COI frag. 1	129	A	C
COI frag. 1	181	C	T
COI frag. 1	200	A	T
COI frag. 2	163	A	C
cytb frag. 1	15	A	T
cytb frag. 2	56	T	C
cytb frag. 2	104	A	T
cytb frag. 2	133	A	G
cytb frag. 2	225	A	T
cytb frag. 2	226	A	C
H1 frag. 2	16	C	—
H1 frag. 2	232	C	A
H1 frag. 2	254	C	T
H1 frag. 2	290	C	T
H1 frag. 2	374	C	A
H1 frag. 2	590	G	A
H1 frag. 2	604	C	T
H1 frag. 2	697	T	C
H1 frag. 3	15	T	C
H1 frag. 3	201	T	C
H1 frag. 3	308	T	C
H1 frag. 4	181	A	T
H1 frag. 4	207	A	T
H1 frag. 5	4	T	C
H1 frag. 6	16	A	C
H1 frag. 6	45	A	C
H1 frag. 6	147	C	A
H1 frag. 6	370	A	C
H1 frag. 6	371	C	T
H1 frag. 6	474	A	T
H1 frag. 6	521	T	A
H1 frag. 6	544	T	A
H1 frag. 6	554	A	C
H1 frag. 8	9	C	T
H1 frag. 8	22	C	T
H1 frag. 8	36	C	T
H1 frag. 8	49	G	A
H1 frag. 8	86	T	C
H1 frag. 8	101	A	C
H1 frag. 8	180	A	C
H1 frag. 8	229	C	—
H1 frag. 8	328	T	A
H1 frag. 8	344	A	C
H1 frag. 8	588	—	C
H1 frag. 9	96	T	A
H1 frag. 9	115	T	C
H1 frag. 9	152	—	T
H1 frag. 9	165	A	C
H1 frag. 9	183	T	C
H1 frag. 9	191	T	C
H1 frag. 9	193	C	A
H1 frag. 10	1	T	C
H1 frag. 10	17	A	T
H1 frag. 10	25	A	T
H1 frag. 10	31	A	T
H1 frag. 10	76	A	C
H1 frag. 10	91	A	C
H1 frag. 10	99	C	—
H1 frag. 10	117	—	G
H1 frag. 10	200	T	C
H1 frag. 10	260	—	C
H1 frag. 12	38	T	C
H1 frag. 12	39	T	C
H1 frag. 12	46	A	G
H1 frag. 12	82	A	G
H1 frag. 12	235	A	T
H1 frag. 12	311	C	—
H1 frag. 12	415	T	A
H1 frag. 13	74	—	G
H1 frag. 13	114	—	C
H1 frag. 13	115	—	C
H1 frag. 13	116	—	A
H1 frag. 13	152	T	A
H1 frag. 13	277	C	T
RAG1 frag. 1	198	T	G
SIA frag. 1	3	T	C
SIA frag. 1	12	T	G
SIA frag. 1	147	C	T
SIA frag. 2	30	T	C

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