The Phylogeny of Poison Dart Frogs (Amphibia: Anura: Dendrobatidae)

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Nomenclatural Disclaimer

The taxonomic changes presented herein, including new taxa, combinations, and synonymy, are disclaimed as nomenclatural acts and are not available, in accordance with Article 8.3 of the International Code of Zoological Nomenclature.

ABSTRACT

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This study was designed to test current knowledge of dendrobatid diversification by performing a total evidence analysis. Evidence included DNA sequences from five mitochondrial and six nuclear loci and 175 phenotypic character transformations of morphology, behavior, and alkaloid profiles. The data set consisted of 412 terminals: 365 terminals of 152 ingroup species and 47 outgroup terminals. Direct optimization parsimony analysis resulted in a single optimal solution. Dendrobatids were recovered as monophyletic, and their sister group consists of *Crossodactylus*, *Hylodes*, and *Megaelosia*. Monophyly was corroborated for *Mannophryne* and *Phyllobates*. *Aromobates nocturnus* and *Colostethus saltuensis* were found to be nested within *Nephelobates* and *Minyobates* to be paraphyletic and nested within *Dendrobates*. *Colostethus* was shown to be rampantly nonmonophyletic. A morphologically and behaviorally diverse clade of median lingual process-possessing species was discovered. This study confirmed reports of multiple origins of alkaloid sequestration, and optimization of alkaloid characters allowed detailed explanations and predictions to be advanced. Multiple origins of phytotelm-breeding, larval oophagy, and endotrophy were discovered. Available evidence indicated that dorsal tadpole transport—a dendrobatid synapomorphy—is primitively carried out by male nurse frogs, with three origins of female transport and five origins of biparental transport. A novel approach to heuristic total evidence analysis of DNA partitions was

developed. All examined partitions contributed to the individuation of clades across vastly different hierarchic levels, each partition differed in the frequency of transformations at different levels, and the relative amount of evidence contributed by each partition varied across hierarchic levels.

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Acknowledgements

Although my first introduction to dendrobatid frogs was in 1986 as a volunteer at the Vancouver Public Aquarium (Canada), my fascination with their evolutionary relationships did not begin until years later, in 1994. Having recently arrived at Fernando Castro's Laboratorio de Herpetología at the Universidad del Valle (Colombia) and eager to start a project, I began field work at a locality in the Cordillera Occidental called Finca San Pedro. Among the frogs I collected on my first outing was a diurnal, extensively webbed, riparian species with bright orange flash marks. As I struggled to identify the San Pedro material, I was informed that an eminent herpetologist had already identified some material collected there previously, and that the species I was suffering over was *Colostethus agilis*. I was further instructed to study the original description and compare it with my specimens, as that would start teaching me to see characters and discriminate species. However, upon doing so, I was confronted with discrepancies between my specimens and the published account. This had to be due to my incompetence, especially considering that the eminent herpetologist was one of the authors who named *Colostethus agilis*! As I delved further into the literature and made comparisons with other species of *Colostethus*, I became convinced that the species from San Pedro was actually *Colostethus abditaurantius*. The eminent herpetologist was wrong!

Not one to take the word of an arrogant, inexperienced Canadian undergraduate with a funny accent over that of an established scientist who had named both *Colostethus agilis* and over 4% of the known global diversity of frogs (but also with a funny accent), Professor Castro understandably insisted that I present him with

the evidence. I did so, and, somewhat reluctantly, he agreed that there was something to what I was saying. We decided that I should present my evidence to the eminent herpetologist on his next visit. With the appropriate nervousness, I did so (learning in the process how to sex frogs), and, after hearing my case and seeing the specimens, Dr. Lynch capitulated immediately and enthusiastically! He even went on to confess that he really didn't know much about these boring little brown frogs, and no one else did either! His plate was more than full with *Eleutherodactylus*, and there was an enormous amount of work to be done on *Colostethus* systematics. He encouraged me to focus on the group and publish my results, and I did.

And so, my first acknowledgement goes to John Lynch, superficially for not knowing much about *Colostethus* and encouraging me to investigate dendrobatid systematics, but much more importantly for teaching me, first, that authority holds no weight in science, and second, that there is no shame in being wrong (and over the years he and many others have given me ample opportunities to be shameless!). The job of the scientist is to formulate and severely test hypotheses. If they are ultimately shown to be wrong, scientific knowledge has increased. I believe these are the central axioms of science, and they govern my research program in general and this study in particular. The safety and certainty of the status quo are illusory, because tomorrow some inexperienced undergraduate may present evidence that decisively overturns it.

For their unrelenting encouragement and patience and countless sacrifices I am grateful to Amanda Grant and Heather Grant, without whom my studies would not have been possible. Similarly, for their early influence at key moments, and without

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I am grateful to my friends and colleagues who facilitated all aspects of my research in Colombia, both as an undergraduate at the Universidad del Valle and during my graduate studies at Columbia University. Fernando Castro took me under his wing when I arrived at the Universidad del Valle, and the bulk of my field work in western Colombia was (and continues to be) done with Wilmar Bolívar. Philip Silverstone-Sopkin shared his knowledge from before he “saw the light” and gave me data, photographs, and literature that have been invaluable resources in my studies of dendrobatid systematics. I am also grateful to Andrés Acosta, Michael Alberico, Santiago Ayerbe, Humberto Álvarez, María Cristina Ardila, Darío Correa, Juán Manuel Daza, Paul Gutierrez, Gustavo Kattan, Pablo Lehmann, Jhon Lynch, Luís Germán Naranjo, Vivian Páez, Juán Manuel Rengifo, Margarita Rios, and Vladimir Rojas for all their help. Colombian institutional support was provided by the Corporación Autónama Regional del Valle del Cauca, EcoAndina, Instituto de

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Chapter 1: Introduction

The past four decades have witnessed a dramatic increase in scientific knowledge of dendrobatid frogs, known commonly as poison dart frogs. Extensive field and collection studies have more than tripled the number of valid species from 66 in 1960 to 238 at present, making Dendrobatidae the third largest family of frogs in South America (Duellman, 1999). 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 Antilles. All species but one are diurnal. So far as is known, all dendrobatids lay terrestrial eggs, either on the ground or in phytotelmata, and many are characterized by elaborate reproductive behaviors, including dorsal tadpole transport and maternal feeding of developing tadpoles.

Approximately one-third of the known species of dendrobatids secrete powerful skin toxins. 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 family its common name. The pioneering work begun 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 may lead to the development of clinically relevant analgesics, and histrionicotoxins are important for studying the neuromuscular subtype of nicotinic receptors (Daly et al., 1997; Daly, 1998; Daly et al., 2000). It is now 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, and melyrid beetles have been identified as likely dietary sources for certain alkaloids (Dumbacher et al., 2004; Saporito et al., 2003; Saporito et al., 2004), 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 toxin research continues to be a highly active area of investigation.

In addition to studies of dendrobatid toxicology, 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; Narins et al., 2003, 2005; Summers and McKeon, 2004), diet specialization (Silverstone, 1975, 1976; Toft, 1980,1995; Donnelly, 1991;

Caldwell, 1996, 1998; Parmelee, 1999; Darst et al., 2005), predation (Test et al., 1966), resource use and partitioning (Crump, 1971; Donnelly, 1989a; Caldwell, 1993; Wild, 1996), learning (Lüddecke, 2003), population dynamics (e.g., Toft et al., 1982; Aichinger, 1987; Donnelly, 1989b; Duellman, 1995), phonotaxis (Gerhardt, 1980), energetics (Navas, 1996b, 1996a), 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. This is unfortunate, because 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., 2003; Graham et al., 2004; Darst et al., 2005), but they have looked at only a small portion of the diversity of dendrobatids and have not incorporated all available evidence. As such, many questions remain unaddressed or unsatisfactorily answered, due mainly to holes in current 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., 2003) 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, 2003; Santos et al., 2003) have provided numerous 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; the principle phylogenetic hypotheses are summarized in Appendix 1. Generally, dendrobatid systematics may be characterized as based on few characters, few rigorous tests, and no comprehensive analysis of available evidence. This is unfortunate, because an evolutionary interpretation of the many discoveries of the past 40 years is not possible without an adequate understanding of the phylogeny of the group.

Difficulties in understanding the phylogeny of dendrobatid frogs are compounded by the taxonomic problems that surround many nominal species and under appreciation of species diversity (Grant and Rodríguez, 2001). Sixty-seven valid species were named over the past decade—more species than were known in 1960—53 of which were 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 (1975, 1976), and Myers and

colleagues (e.g., Myers and Daly, 1976; Myers et al., 1978; Myers, 1982; Myers and Ford, 1986, 1987; Myers et al., 1991), with additional taxonomic contributions by Zimmerman and Zimmerman (1988), and La Marca (1992, 1994) and Kaplan (1997). In that system, approximately two thirds of the species of dendrobatids are assigned to a "basal" grade of usually dully colored, non-toxic frogs (including *Aromobates*, *Colostethus*, *Mannophryne*, and *Nephelobates*), while 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* versus *Epipedobates boulengeri*). Furthermore, recent molecular studies (e.g., Clough and Summers, 2000; Vences et al., 2000, 2003; Santos et al., 2003) have found several aposematic taxa to be more closely related to species of *Colostethus* than to other toxic species.

Compelling evidence for the monophyly of most genera is also lacking. This is especially the case for the "basal" taxa. The non-monophyly of *Colostethus* has been recognized for decades (Lynch, 1982), and the naming of *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 134 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., 2002), and molecular studies are rapidly accumulating data (e.g. Vences et al., 2003; Santos et al., 2003), but little progress has been made to date. Molecular evidence for the monophyly of *Mannophryne* and *Nephelobates* was presented by La Marca et al. (2002) and Vences et al. (2003), but the relationships of those genera to other dendrobatids are 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, 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 them. Additionally, *Phobobates* was found to be monophyletic by Vences et al. (2000), but paraphyletic by Clough and Summers (2000). Similarly, *Minyobates* may or may not be nested within *Dendrobates* (Silverstone, 1975; Myers, 1982, 1987; Jungfer et al., 1996; Jungfer et al., 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. (2003). *Cryptophyllobates* is the most recently named genus, but it is monotypic, and its relationship to other dendrobatids is unclear.

Although the recent studies have demonstrated unambiguously the inadequacies of the status quo in 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., 2003). However, much of the current confusion is due to unreconciled conflict among data sets analyzed in isolation (e.g., regarding the monophyly of *Minyobates*), limited taxon sampling, and failure to include prior evidence in the new analyses (e.g., morphology). 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 knowledge of dendrobatid diversification as severely as possible by combining new and prior genotypic and phenotypic evidence in a total evidence analysis. I included as many species of dendrobatids as possible through my own fieldwork, colleagues' ongoing fieldwork, and existing natural history collections. In light of the many outstanding problems in alpha taxonomy, I included numerous undescribed species and samples of problematic species from multiple localities. I then used the optimal phylogenetic hypothesis to construct a monophyletic taxonomy and address questions about the evolution of particular character systems. Specifically, I examined the evolution of toxicity, breeding biology, morphological diversification, and habitat choice. I also examined the evolution of different data partitions by implementing a novel approach to total evidence analysis of partitions.

I begin in Chapter 2 with a thorough review of the history of dendrobatid systematics prior to the present study, which is necessary to provide general background for the present study and to outline the phylogenetic hypotheses to be tested.

Chapter 3 addresses the choice of outgroup taxa for the present study, including a brief discussion of the theoretical problem of outgroup sampling. One of the messages that emerges from the historical review in Chapter 2 is that knowledge of the relationships between dendrobatids and other anurans remains murky. To adequately resolve that problem would require, minimally, a phylogenetic analysis of neobatrachian anurans, which was beyond the scope of the present study. However, a concurrent study led by Darrel R. Frost, me, and Julián Faivovich investigated the

phylogeny of living amphibians (Frost et al., 2005), and Chapter 3 summarizes the findings of that study as they relate to the placement of Dendrobatidae and the choice of outgroup taxa.

Chapter 4 reports in detail the materials and methods used in this study. My goal in that chapter, and throughout the text, is to be as explicit as possible about both what I did and why I did it. In doing so, I address empirical, theoretical, and analytical problems and the rationale behind my approach to solving them. From afar, phylogenetic analysis may appear to be a simple exercise in point-and-click desktop computing, but in the trenches it is a complex, theory-laden, computationally challenging undertaking. This is especially true of the current study, which aims to resolve species- and higher-level problems in a simultaneous, large-scale phylogenetic analysis. As often as not, disagreements in systematics stem as much from the use of different discovery operations and assumptions as from empirical conflict. By stating my reasoning as explicitly as possible I intend to facilitate criticism of my results, which is necessary to achieve progress.

Although the individuation of phenotypic characters and character-states is, in some sense, a result of phylogenetic study, phenotypic transformation series are reported separately in Chapter 5, and the remaining results are combined in Chapter 6.

Finally, Chapter 7 proposes a monophyletic taxonomy to reflect the results of this study, and Chapter 8 analyzes the implications of these results for the evolution of several characters and character systems. Chapter 9 presents a brief summary of progress to date and highlights promising areas of future research.

Chapter 2: 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., submitted). Over the next two centuries the number of available species-group names that have been associated with the family has grown to 301, of which 238 are currently recognized and included in Dendrobatidae (see Fig. 2.1; for data see Appendix 4). New species continue to be described at a rapid rate, especially in the taxonomically challenging genus *Colostethus*. Of the 67 species named in the decade 1995–2004, 53 are currently referred to *Colostethus*.

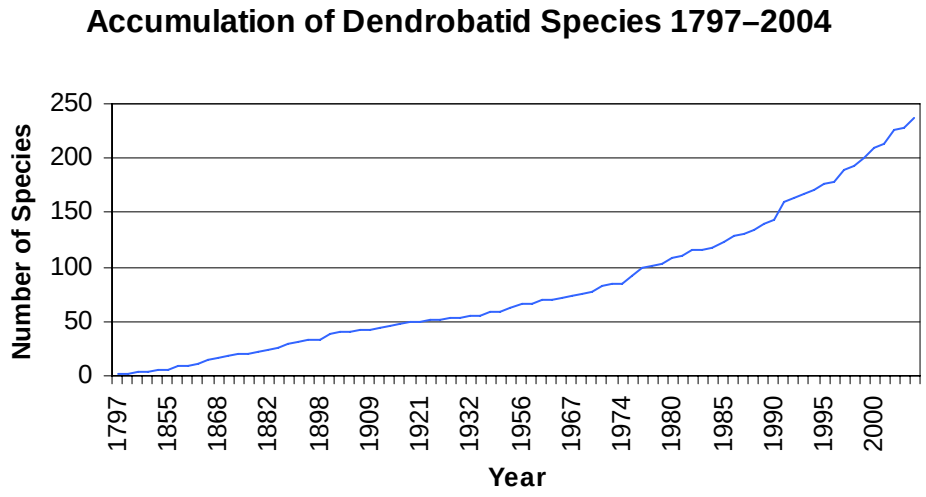

Figure 2.1. Accumulation of dendrobatid species 1797–2004. Only currently valid species are counted. For data see Appendix 3.

My intention in this chapter is to review the development of knowledge of the systematics of dendrobatids as background for the present study. Rather than present a strict chronology, I divide this review 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 I also cover some details here.

This review does not treat every paper published on these frogs. First, I included only systematics papers (and only the most relevant of these; i.e., species descriptions and synonymies are not detailed), and second, I included only papers published for a scientific audience. Due to the elaborate behaviors, brilliant coloration, diurnal activity, and occurrence of toxins in some species, large ecological, ethological, biochemical, and hobbyist literatures have been generated, and reviewing them all lies beyond the scope and purpose of the present work. Also, I included only authorship and date of publication of scientific names where relevant; authorship and date of family-, genus-, and species-group names are included in Appendices 2–4, respectively. I did not address nomenclatural problems. Grant et al. (In press; see also Grant, 2004) and Savage et al. (In press) have pending petitions to the Commission on Zoological Nomencalture regarding the use of the species-group name *panamensis* and the family-group name Dendrobatidae, respectively, and I direct the reader to those papers (especially the latter) for nomenclatural discussion. Throughout,

"dendrobatid frogs" or "dendrobatids" refers to species contained in the modern Dendrobatidae, and formal taxonomic names are used as by the author in question. Finally, insofar as this review aims only to summarize the history of the systematics of Dendrobatidae, I tried to resist the temptation to evaluate critically the evidence and analytical competency of studies on which previous hypotheses were based.

Part I: 1799–1926, Early History

Although scientific study of dendrobatids began roughly 40 years earlier (Cuvier, 1797), little progress was achieved until Duméril and Bibron's (1841) work. 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). Dendrobatids were all 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 considered a junior synonym of the microhylid *Kaloula*; p. 645). Although the dendrobatid genera were placed in different families, Duméril and Bibron (1841:638; 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 Ranidae), while *Hylaplesia* (= *Hysaplesia* = *Dendrobates*) was in its own family, Hylaplesidae.

Cope (1865) named the family Dendrobatidae and placed it in Bufoniformia, but he placed in it only *Dendrobates*. 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 soley 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, while

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* (as *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 *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” (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 on the basis of 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 number of dendrobatid species as procoelous and transferring them to Procoela [pp. 14–15]), and gathered together *Brachycephalus*, *Atelopus*, *Rhinoderma*, *Sminthillus* (now a synonym of the leptodactylid *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, fn. 18), the scheme of the webbed, more aquatic species being basal to the unwebbed, more terrestrial species, and these being basal to the terrestrial, toothless species has yet to be seriously questioned—or tested.

Part II: 1926–Present, Relationships within Dendrobatidae

Having grouped dendrobatids together wholly on the basis of anatomical features, 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*.

That 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 denticles, 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 "The 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, Hyloxalus bocagei*, *Hylixalus chocoensis*, *Hylixalus collaris*, *Hylixalus granuliventris* [now a synonym of *Phyllobates palmatus*], and *Hyloxalus panamansis* [name subsequently emended to *Hyloxalus panamensis* by Dunn, 1940]. Dunn (1933) excluded *Hyloxalus huigrae* [now a junior synonym of the leptodactylid *Eleutherodactylus diastema*] and *Hyloxalus beebei*—the latter exclusion being the only practical consequence of Dunn's

(1933) redefinition of *Hyloxalus*. Dunn did not apply his new diagnosis consistently over subsequent years, however; on occasion he returned to Noble's (1923) diagnosis, i.e., 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 *Hyloxalus panamensis* possessed a swollen third finger, which he had previously observed in *P. 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*, species from "the western part of Colombia . . . [in which] the light color is red or yellow" [i.e., *D. histrionicus*], *D. pumilio*, and *D. speciosus*. He also recognized a second group of "typical *Dendrobates*" with "dorso-lateral 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 eight *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 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* may prove to be conspecific, but he did not propose phylogenetic relationships for the other species.

Dunn's arrangement was adhered to 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 “The 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 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 denticles, 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. 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 1960's, 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 (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 (for example, *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 sets of pale lateral stripes found in most species of *Colostethus*.

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, beautifully prepared 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 a palatine, omosternum, vertebral fusion; he also used fusion and sculpturing of the cranium to diagnose

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 completely rid of the a priori weighting applied to the occurrence of 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 regards 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 similarities of the larvae, 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 1200 m on a tepui). 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 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, and grouped *P. parvulus* with them because some specimens had a calf spot. He 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). He 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 career in botany.

Also in 1976, Charles W. Myers and John W. Daly began publishing on the systematics implications of their work begun 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 yet for dendrobatids. And numerous workers had published observations on dendrobatid parental care and other behaviors (Wyman, 1857, 1859 [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 batrachotoxin was a synapomorphy for a group containing *P. aurotaenia*, *P. bicolor*, *P. lugubris*, *P. terribilis*, *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 denticles in larvae, although Rivero did mention 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 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 charcaterized the *trivittatus* group based on vocalizations, and they added *D. silverstonei* to it. 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 denticle 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.

Also 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 in order 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, monophyletic *histrionicus* group delimited by the synapomorphic occurrence of a "chirp call." This group contained *D. arboreus*, *D. granuliferus*, *D. 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. In contrast, 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; Myers et al., 1984; Myers and Burrowes, 1987) augmented with observations of a few species in captivity. Bauer's contributions were overlooked by all workers except Wells (1994), and as a result the literature is now quite confusing; for that reason I break from chronological order to summarize Bauer's contributions here together. 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 an 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 this 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), viz. *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 (Grant, 2004).

Bauer (1986; 1988; 1994) was the only worker to recognize subfamilies within Dendrobatidae. In the most recent proposal (Bauer, 1994), he recognized Dendrobatinae for *Dendrobates*, *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, and 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.

Myers (1987) proposed a major taxonomic rearrangement aimed to better reflect hypotheses of monophyly, whereby “Dendrobatids 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 of *Phyllobates* sensu Silverstone (1976) minus the species Myers et al., (1978) had placed in their restricted *Phyllobates*. Note that 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). With only a few exceptions noted below, Myers's taxonomy remains the standard, as shown in Appendix 4.

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 characters (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*
- *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 on the basis of 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 an apparently (no audiospectrographic analysis was performed) similar fundamental frequency of the call. 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 La Marca, 1998 "1996"; Rivero, 1991a; Rivero, 1991b; Rivero and Almendáriz, 1991; Rivero and Granados-Díaz, 1990 "1989"; Rivero and Serna, 1991; Rivero and Serna, 2000 "1995"), 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, 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. 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 regards 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 (for discussion see Coloma, 1995).

Caldwell and Myers (1990) further elucidated the systematics of the *Dendrobates quiquevittatus* 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 group 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 external 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 (1990 "1989") *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, with the topology (*Aromobates*(*Hyloxalus Colostethus* sensu stricto (aposematic dendrobatids))).

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 (one undescribed) as definitely possessing the collar, and two more as possibly having it. 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, 1989 "1988") by including species of the *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. The tree he presented showed the following relationships: (*olmonae neblina*(*trinitatis riveroi*(*herminae*(*collaris* sp. *oblitterata yustizi*)))). 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 was employed). In addition to the above species, *Mannophryne* 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, in a second nomenclatural change, La Marca (1994) named *Nephelobates* for the *alboguttatus* group. The group was delimited by the occurrence of elongate teeth (also present in *Aromobates*; see Myers et al., 1991; La Marca, 1993) and a dermal covering of the cloaca (also reported in the *edwardsi* group; Lynch, 1982), and 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 speculated 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, the taxonomic changes he made had numerous phylogenetic implications. For example, some of the species he synonymized 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, while 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), he tentatively supported the following relationships:

- 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)
- 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. Explicitly, he proposed a cladogram of

the topology (*Aromobates*(*Mannorphyne Nephelobates Hyloxalus*1(*Hyloxalus*2 *Colostethus* sensu stricto(*Epipedobates* aposematic dendrobatids)))). 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. praderoi, 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, C. saltuarius* (Grant and Ardila-Robayo, 2002). (I have subsequently observed this character-state in *C. anthracinus* and an undescribed species from the slopes of the Magdalena valley, Colombia.)

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 I 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 (pp. 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]
- 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, I will point 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 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 within Dendrobatidae 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 data sets have appeared (Summers et al., 1999; Clough and Summers, 2000; Vences et al., 2000; Widmer et al., 2000; Symula et al., 2001; La Marca et al., 2002; Santos et al., 2003; Symula et al., 2003; Vences et al., 2003). The cladograms that resulted from those studies are presented in chronological order in Appendix 4. Interpretation of these studies is complicated by their use of different methods, non-overlapping 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, 2003; Santos et al., 2003).

- *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. (2003).
- *Allobates*: This small genus fell out in a clade with species of *Colostethus* in Vences et al. (2000, 2003) 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*))) (outgroups were *Epipedobates azureiventris* and *Dendrobates sylvaticus*, and the tree was rooted on *E. azureiventris*). In their more inclusive study, Vences et al. (2003) 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 of *Minyobates* itself. Vences et al. (2003) included *M. steyermarki* (type species), *M. minutus*, and *M. fulguritus* and found it 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. (2003).

Lötters et al. (2000) erected the new genus *Cryptophyllobates* for *Phyllobates azureiventris* (which was placed in *Epipedobates* by Myers, 1987). The justification for this monotypic genus is somewhat convoluted. On pp. 235–236, the authors state 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 assert that “It 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) “negate that both species are representatives of the same genus for *C. bocagei* is dully coloured, lacking dorsal stripes at all, and possesses webbed feet.” Insofar as this change did not solve the problem of the nonmonophyly of *Epipedobates*, the creation of this monotypic genus does little to improve matters.

Morales (2002) combined Rivero's Groups II (*brunneus*) and III (*alagoanus*) into a newly defined *trilineatus* group (but excluding *C. kingsburyi* and *C. peruvianus*) on the basis of an analysis of 12 characters. However, in a 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 all states of the derived states of all 12 characters are found elsewhere in Dendrobatidae.

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, fn. 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.

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

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

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 the leptodactylid *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), he 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.” 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 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 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 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' claims regarding dendrobatid thigh musculature were also false. Against Lynch (1971), the thigh musculature in hylodines conforms with Noble's (1922) hyloid (bufonoid) 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 contain 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 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), 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 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. Ford (1993) favored the ranoid hypothesis (based on Ford's unpublished dissertation). 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. 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 non-ranoid frog. Burton (1998) 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 anuran tadpoles included *Phyllobates bicolor*, which was found to possess the neobatrachian (plus Pelobatidae) 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

data set 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. Vences et al. (2003) also included two species of hylodines in their analysis of 12S and 16S mtDNa sequences, but they found dendrobatids to be sister to *Telmatobius simmonsi*. Darst and Cannatella (2004) analyzed 12S, $tRNA^{val}$, and 16S mtDNA sequences and found dendrobatids to be nested within Hylidae (parsimony) or sister to a group consisting of ceratophryines, hemiphractines, and telmatobiines (maximum likelihood).

Summary

The picture that emerges from the review of the history of dendrobatid systematics is one of considerable conflict and confusion. The single point of near universal agreement is the overwhelmingly supported monophyly of the family, which has not been seriously challenged since it was first proposed by Noble nearly 90 years ago. 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 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 each hypothesis. 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 analysis have included a limited sample of the diversity of dendrobatids.

Chapter 3: Phylogenetic Placement of Dendrobatidae and Outgroup Sampling

Theoretical Background

Although the present study was not designed primarily to test the relationships between Dendrobatidae 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 non-dendrobatids constitute “the outgroup” and outgroup taxa are sampled for the purpose of testing hypothesized patristic and cladistic relationships. Ideally, one would code all non-dendrobatids 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.

It should be noted that although this approach to outgroup testing 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 therefore is not formally quantifiable does not deny its relevance. The goal is to test phylogenetic hypotheses as rigorously as possible, and prior knowledge is key to that undertaking.

Empirical Background

As summarized in Chapter 2, 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 (for references and discussion see Chapter 2). Minimally, evaluation of these hypotheses would require a phylogenetic analysis of Neobatrachia, which was beyond the scope of the present study.

Nevertheless, in a concurrent study led by Darrel Frost, me, and Julián Faivovich, we sampled 532 terminals for the mitochondrial H-strand transcription unit 1 (H1), which includes 12S ribosomal, $tRNA^{val}$, and 16S ribosomal sequence, 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 (Frost et al., 2005). That study included approximately 10% of each of the major amphibian clades (caecilians, salamanders, and frogs), including eight species (and genera) of dendrobatids and all putative sister groups of

Dendrobatidae. Insofar as that study is the most complete analysis of amphibian phylogeny undertaken to date, I used those results to inform outgroup sampling for the current study.

The Frost et al. (2005)study resulted in 4 trees of 126929 steps, the relevant portion of which is shown in Fig. 3.1. Relevant to the present study, Frost et al. 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 a the sister clade of the remaining species). 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) were tested explicitly by inputting constraint topologies for diagnosis and swapping, but they all required additional transformations (breaking up the *Thoropa* + Dendrobatidae clade requires at least 39 extra steps).

Although detailed knowledge of the placement of *Thoropa* did not exist prior to our analysis, its placement as the sister of Dendrobatidae is heterodox, to say the least. That is, 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. (2005) hypothesis provides the most epistemologically sound and empirically rich basis for

outgroup sampling. Also the immediately relevant nodes are all well supported (Bremer support for Dendrobatidae + *Thoropa* = 39, Dendrobatidae + *Thoropa* + Bufonidae = 30); considering that *Thoropa* was only scored for the mtDNA and Histone 3a loci (i.e., over 1500 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. (2005), *Brachycephalus* and *Eleutherodactylus* are part of the distantly related Brachycephalidae (not shown in Fig. 3.1), but *Atelopus*, and *Rhinoderma*, are placed in the same general neighborhood as Dendrobatidae. As such, Frost et al. (2005) provide both an objectively sound and subjectively “reasonable” basis for outgroup sampling, and I therefore sampled outgroup taxa from among these closely related groups.

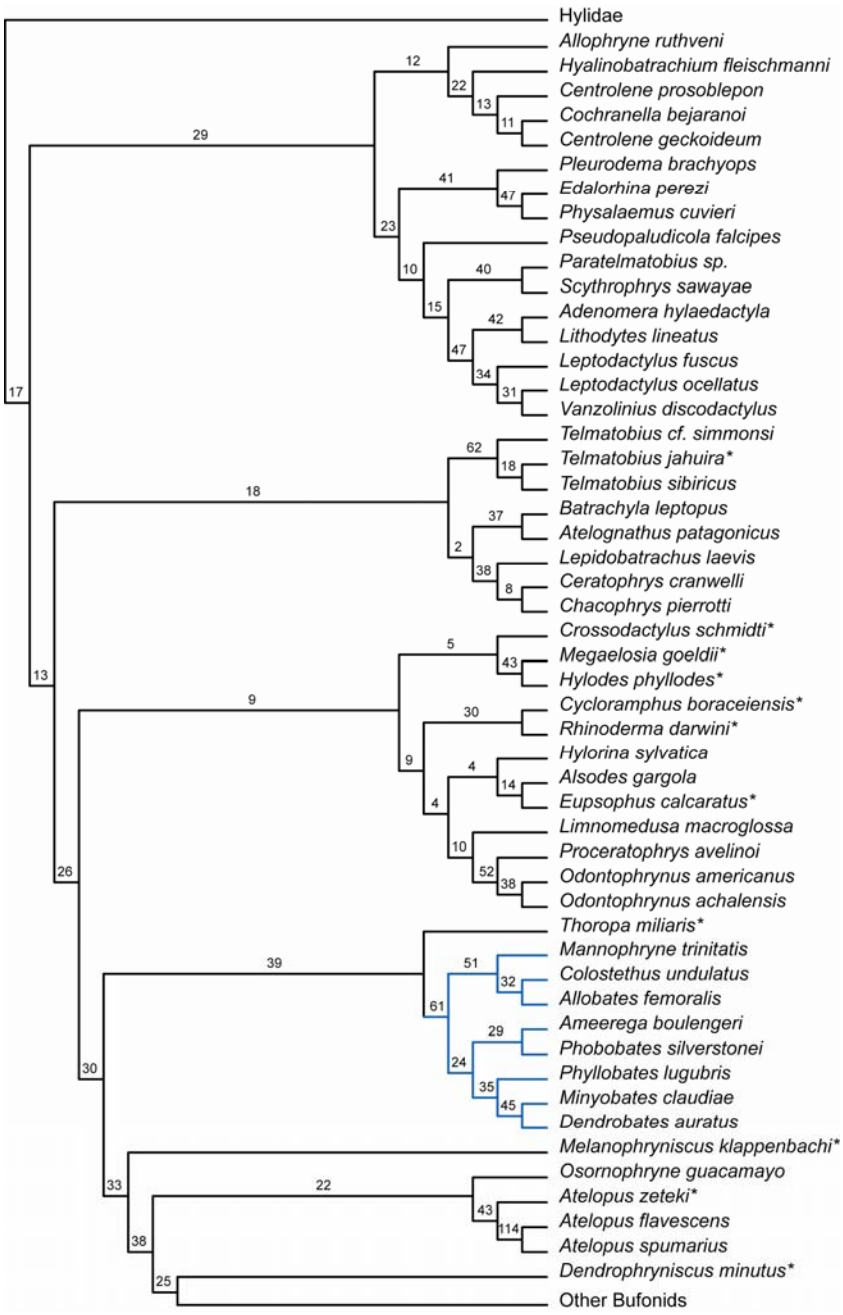


Figure 3.1. Phylogenetic placement of Dendrobatidae according to Frost et al. (2005). The Frost et al. study sampled 532 terminals, 51 of which are included here to show the placement of Dendrobatidae (marked in blue) with respect to its closest relatives. All of the terminals shown were included in 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 a star (see text for details). Numbers are Bremer values.

Outgroup Sampling

In light of Frost et al.'s (2005) 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 for the monophyly of Cycloramphidae (BS = 9) and several of the cycloramphid nodes (BS as low as 4). With that in mind, I targeted the following 46 outgroup taxa: *Adenomera hylaedactyla, Allophryne ruthveni, Alsodes gargola, Atelognathus patagonicus, Atelopus spurrelli, Atelopus zeteki, Batrachyla leptopus, Bufo guttatus, Bufo haematiticus, Centrolene geckoideum, Centrolene prosoblepon, Ceratophrys cranwelli, Chacophrys pierottii, Cochranella bejaranoi, Crossodactylus schmidti, Cycloramphus boraceiencis, Dendrophryniscus minutus, Edalorhina perezi, Eupsophus calcaratus, Hyalinobatrachium fleischmanni, Hyla boans, Hyla cinerea, Osteocephalus taurinus, Hylodes phyllodes, Hylorina sylvatica, Lepidobatrachus laevis, Leptodactylus fuscus, Leptodactylus ocellatus, Limnomedusa macroglossa, Lithodytes lineatus, Megaelosia goeldii, Melanophryniscus klappebachi, Odontophrynus achalensis, Odontophrynus americanus, Paratelmatobius sp, Physalaemus cuvieri, Pleurodema brachyops, Proceratophrys avelinoi, Pseudopaludicola sp., Rhinoderma darwinii, Scythrophrys sawayae, Telmatobius jahuira, Telmatobius sibiricus, Telmatobius cf simmonsi,*

Thoropa miliaris, Vanzolinius discodactylus. Hyla boans was designated as the root for analyses.

All but one of these terminals (and tissues) were the same species used by Frost et al. (2005), the exception being *Atelopus spurrelli*, which I included because (1) sequences proved difficult to generate for our *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 are available at AMNH to allow morphological study.

I included all molecular data from the Frost et al. analysis for these terminals. Additionally, I included phenotyic characters and sequences for cytochrome oxidase *c* I, cytochrome *b*, recombination activating gene 1, and several fragments that were missing from Frost et al. (2005) for 12 of those terminals (marked with a star in Fig. 3.1): *Atelopus spurrelli, Atelopus zeteki, Crossodactylus schmidti, Cycloramphus boraceiencis, Dendrophryniscus minutus, Eupsophus calcaratus, Hylodes phyllodes, Megaelosia goeldii, Melanophryniscus klappebachi, Rhinoderma darwinii, Telmatobius jahuira, Thoropa miliaris.* These terminals were targeted for increased sampling because of their phylogenetic proximity to Dendrobatidae and the availability of whole specimens and other data (e.g., behavior, alkaloid profiles) to score phenotypic characters.

As discussed in greater detail in Chapters 4 and 5, character-states were coded for each ingroup species and were not extrapolated from other species (e.g., I did not assume that all *Colostethus* lack lipophilic alkaloids and instead only coded species that have been examined for alkaloids); however, I relaxed that requirement to

incorporate additional outgroup information. Specifically, for *Crossodactylus* alkaloid data were derived from *Crossodatylus* sp. from Teresopolis (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 *Cyloramphus 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 klappebachi*, 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 data have been gathered, I coded *Megalosia goeldii* as polymorphic for this character. The osteological data reported for *Thoropa miliaris* were taken from *Thoropa lutzi*. I 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.

Chapter 4: 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), the recent application of Bauer's overlooked generic names (e.g., *Ameerega*), recognition (as well as continued rejection) of Zimmerman and Zimmerman 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 a state of flux with no universally accepted standard around which to structure discussion of dendrobatid diversity. As such, to avoid confusion due to disagreements between the current taxonomies and my proposal for a monophyletic taxonomy (Chapter 7), I use binominals only in the introductory chapters and after proposing the new taxonomy. Elsewhere (e.g., in the character matrix and in Chapter 5) I refer to species using only their trivial names (e.g., *fraterdanieli*). Currently there are 238 technically valid species of dendrobatids, very few of which have the same trivial names. Where giving the trivial name only would engender confusion I refer to species using their *original* binomen. For example, I use *Phyllobates sylvaticus* to avoid confusion with *Dendrobates sylvaticus*, even though the current taxonomy treats *Phyllobates sylvaticus* as *Colostethus sylvaticus*,. All species-group names and their original, current, and proposed placements are listed in Appendix 4.

Commands used in computer programs are italicized. Tissues are referenced with the permanent collection number for the voucher specimen or, if that is unavailable, the tissue collection number, as follows:

AM-CC (Ambrose Monell Cryo Collection, American Museum of Natural History, New York, USA), **AMNH** (American Museum of Natural History, New York, USA), **ARA** (Andrés Acosta; specimens at MUJ), **BPN** (Brice P. Noonan, specimens to be deposited at UTA), **CFBH** (Célio F. B. Haddad collection, Brazil), **CH** (Colección Herpetológica, Panamá), **CPI** (D. Bruce Means, to be deposited at USNM), **KU** (University of Kansas Natural History Museum), **LSUMZ** (Louisian State University Museum of Natural Science, Baton Rouge, USA), **MACN** (Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Buenos Aires, Argentina), **MAR** (Marco Antonio Rada; specimens at MUJ), **MLPA** (Museo de la Plata, Buenos Aires, Argentina), **MUJ** (Museo de Historia Natural, Universidad Javeriana, Bogotá, Colombia), **MVZ** (Museum of Vertebrate Zoology, University of California at Berkeley, USA), **PK** (Philippe Kok; specimens at l'Institut royal des Sciences naturelles de Belgique, **RDS** (Rafael de Sá tissue collection), **ROM** (Royal Ontario Museum, Canada), **SIUC** (Southern Illinois University at Carbondale, USA), **UMMZ** (University of Michigan Museum of Zoology, Ann Arbor, Michigan, USA), **USNM** (National Museum of Natural History, USA), **UTA** (University of Texas at Arlington, USA).

Unless otherwise noted, all images and illustrations are mine.

General Analytical Approach: Theoretical Considerations

Choice of Phylogenetic Method

The general goal of phylogenetic systematics is to explain observed biodiversity 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 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; valid 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, i.e., 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-state transformations. Unweighted (equally weighted) parsimony analysis minimizes hypothesized transformations globally, whereas assumptions (expressed as differential probabilities or costs) about the evolution or importance 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 (2005) reviewed the justifications for parsimonious phylogenetic inferences previously considered sufficient, viz., conviction (Hennig, 1966), descriptive efficiency (Farris, 1979), minimization of ad hoc hypotheses of homoplasy (Farris, 1983), and statistical, model-based (maximum likelihood, Sober, 1988). Finding significant inconsistencies in all of those justifications, Kluge and Grant (2005) proposed a novel justification for parsimony. Drawing on recent advances in the understanding of phylogenetics as a strictly ideographic 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 observed diversity, equally weighted parsimony analysis maximizes explanatory power. As such, in the present study I 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 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 non-heritable 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 there is no structural or developmental complexity to distinguish nucleotides that share a common evolutionary history (i.e., those that are homologous, being physico-chemically identical by descent from a common ancestor) from those that evolved independently (i.e., those that are homoplastic, being physico-chemically identical by convergent evolution). For example, in terms of object properties, all adenines are physico-chemically identical, regardless of whether or not they were inherited from the same ancestor and share the same history. 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. In order to visualize homologous nucleotides, multiple

sequence alignments codify insertions and deletions (indels) as gaps, i.e., place-holders 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 data set aligned according to different criteria or under different indel treatments may result in strong support for contradictory solutions. 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 are 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 and tree evaluation are logically independent and must be performed separately (e.g., Simmons and Ochoterena, 2000; Simmons, 2004).

The position I take here is that indels are evidentially equivalent to any other kind 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., 1999; Frost

et al., 2001). In recognition of these considerations, I 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; Wheeler, 2003a; Wheeler, 2003b; Wheeler, 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 optimal scheme of nucleotide homologies for a given topology is that which requires the fewest transformation events when optimized onto that topology, i.e., that which minimizes patristic distance, thus providing the most parsimonious explanation of the observed diversity. Determining the optimal alignment for a given topology is NP-complete (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 data set, 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 et al., 1977; Garey and Johnson, 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 trees and

alignments 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., In prep.). However, current hard- and software limitations make those indicators unreachable in reasonable amounts of time for the present data set analyzed under Direct Optimization, and the adequacy of my analysis may only be judged intuitively in light of the computational effort and strategic use of multiple algorithms designed for large data sets (see below for details).

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 (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 permits and weakens this divide-and-conquer approach. Assuming that a group is in fact monophyletic, 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, the relationships within a clade are independent of the relationships between that clade and more distant relatives. Nevertheless, although this is a valid and presently necessary strategy, it relies on assumptions that may ultimately be found to be problematic, 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 terminals that are not immediately relevant to the problem at hand 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.

There are many obstacles, computational and otherwise, that prevent this ideal from being achieved in the foreseeable future. Nevertheless, the current study represents a step in that direction. It was designed to address both the species limits of problematic taxa as well higher level relationships among dendrobatid clades. And, to a lesser degree, by incorporating data from Frost et al. (2005) and combining them with new data collected from key outgroup taxa, this study also addresses relationships between dendrobatids and other anurans. That this study aimed to simultaneously address problems of such different levels had important consequences in taxon sampling, character sampling, and the analytical strategy that was undertaken.

Taxon Sampling

Outgroup taxa and the rationale for their selection are provided in Chapter 3. 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, I 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*). I did not include the type species *alboguttatus* (*Nephelobates*), *fuliginosus* (*Hyloxalus*), or *latinasus* (*Colostethus*) or *yustizi* (*Mannophryne*), because adequate data were not available to allow their inclusion in the present study. Nevertheless, I included numerous representatives of these genera and made taxonomic changes accordingly.

Phenotypic Character Sampling

I anticipate that a criticism of the present study will be that I was 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 pre-cladistic 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 indicators. 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 entirely unreliable and should be excluded in their entirety. I disagree.

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

and results in the ad hoc dismissal or overlooking of evidence should be eliminated from systematics procedures.

In addition to the novel characters and character-states discovered in the course of this study, my 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 I do not always cite the original sources for these traditional characters. However, I do cite more recent papers that have addressed them in the context of dendrobatid systematics, and I cite original sources for all more recent characters. All phenotypic character-states for *caeuleodactylus*, *humilis*, and *nicidola* were coded from the literature (Caldwell and Lima, 2003; Caldwell et al., 2002; La Marca et al., 2002; Lima and Caldwell, 2001). Other sources for phenotypic data are cited in the relevant sections of Chapter 5. 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 in Chapter 5. In anticipation of the expansion of the present dataset, I 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. I have illustrated either

photographically or in line drawings those character-states I 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, I 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 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. I considered tissue with alizarin red-positive crystals to be calcified and uniformly alizarin red-positive tissue to be ossified.

I 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, whereas those that are fleshy appear to insert or originate directly on the adjacent structure. I refer to the distinct fibrous connective tissue that binds muscles to other structures (e.g., skin, other muscles, bone) as tendon, and the connective tissue binding other organs (e.g., two bones) as ligament (i.e., tendons are a kind of ligament). I refer to the outer sheet of thick fibrous connective tissue that enwraps particular muscles and the particular slips of a given muscle as epimysium. A muscle is a bundle of fasciculi that shares a common origin and/or insertion. A slip is a

distinct bundle of fasciculi isolated from adjacent fasciculi of the same muscle by epimysium.

I 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 microns, 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, I examined histological sections of *baeobatrachus*, *tepuyensis*, *panamensis*, and *auratus* (the latter two lacking the MLP). For comparison I examined the histology of *Arthroleptis variabilis*, *Mantidactylus femoralis*, *Phrynobatachus natalensis*, *P. petropedetoides*, *Platymantis dorsalis*, *Staurois natator*, although none of these species were coded for the present study. I also performed detailed dissections of the tongues of *atopoglossus*, as well as *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 a promising source of characters, 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. (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*. Spermatozoa structure of the sampled outgroup species is unknown.

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 detailed studies of larval anatomy. The evidential value of such data is manifest, but adequate samples were unavailable for most species included in this study, and time constraints prevented me from scoring these characters for those that were available. Haas found that the four included dendrobatids were monophyletic, and that the sister group was *Hylodes* + *Crossodactylus* (*Megaelosia* was not included).

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). Although I scored some visceral characters (e.g., pigmentation of the testes, pigmentation of the large intestine), in light of time constraints and the observation that specific characters used by Bhaduri have not been used since and have therefore not played an important role in dendrobatid systematics, I did not study this system in detail.

Likewise, I did not examine hand musculature in this study due to time constraints. Burton (1998) 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

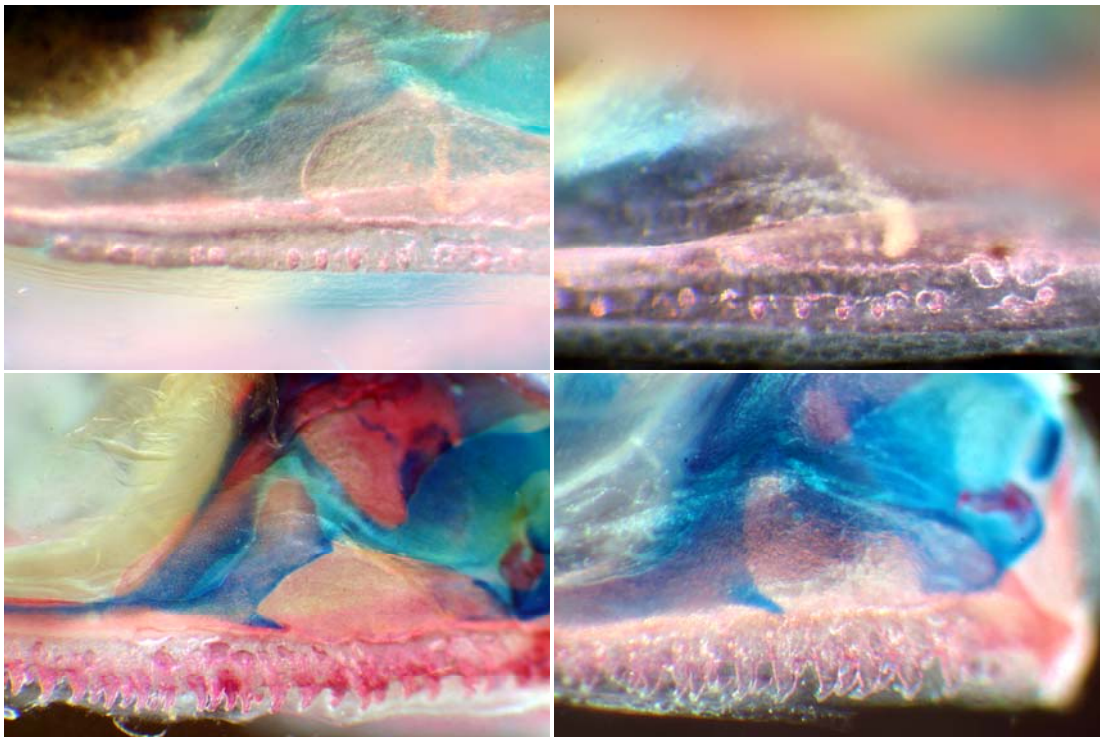
hylodine monophyly and a sister-taxon relationship with Dendrobatidae, as implied by Burton, the occurrence of this character-state would optimize as either independently evolved in Dendrobatidae and *Hylodes* + *Megaelosia* or as a synapomorphy of the inclusive clade with subsequent loss in *Crossodactylus*.

Trewavas (1933) included *Dendrobaties tinctorius*[1] in her study of the anuran hyoid and larynx. I examined the osteology of this system, but time constraints prevented me from examining its musculature. My experience with other groups suggests that hyoid musculature may be a rich source of characters, and its exclusion is unfortunate and will hopefully be corrected in the future.

There are also several morphological variants that have been claimed as characters in the literature that I reject in the present study. First, La Marca (1994; 2004) claimed the occurrence of enlarged, fanglike 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 I 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, I was unable to individuate transformations series for several reasons: (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

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

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” teeth of species referred to *Nephelobates* and *Aromobates* is no greater than those referred to *Colostethus*. In light of these considerations, I coded the presence and absence of maxillary teeth, as well as their structure (see Chapter 5), but not variation in size and shape.



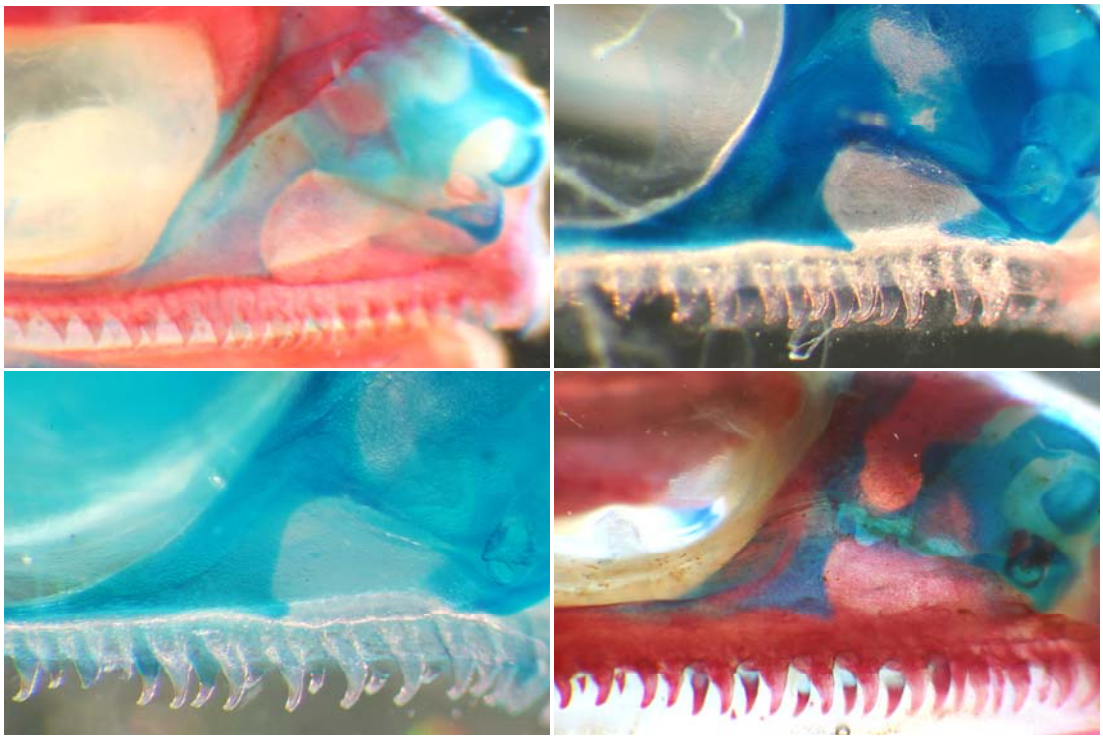


Figure 4.1. Examples of variation in dendrobatid maxillary teeth. **First row** (from top): lateral (**left**) and lingual (**right**) views of *pictus* (UMMZ 184099). Note that the teeth do not protrude beyond the edge of the maxilla. **Second row, left**: lateral view of *riveroi* (AMNH 134144). **Second row, right**: lateral view of *subpunctatus* (UMMZ 221159). **Third row, left**: lateral view of *undulatus* (AMNH 159142). **Third row, right**: lateral view of *molinarii* (UMMZ 176207). **Fourth row, left**: lateral view of *dunni* (UMMZ 167131). **Fourth row, right**: lateral view of *nocturnus* (AMNH 129940).

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 this 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., 2003), 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 my doubt is that, as shown in Fig. 4.2 (top left), only the two species originally placed in the *edwardsi* group (exemplified here by *edwardsi*) possess a conspicuously modified vent. Variation 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 roll 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. I did not include the cloacal sheath, thus delimited, in the character matrix because I did not include *edwardsi* or *ruizi* due to inadequate material.

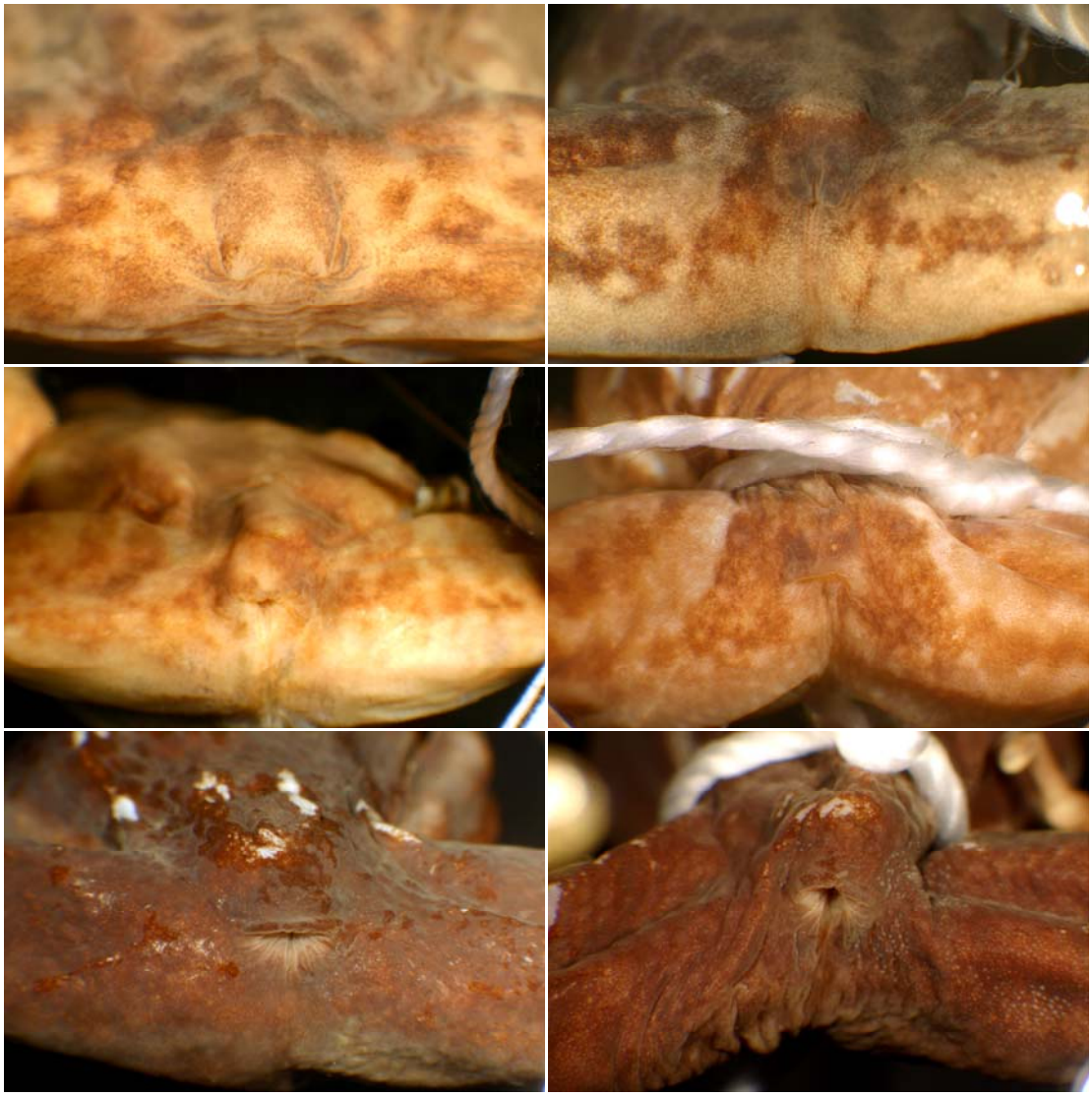


Figure 4.2. Posterior view of several species of dendrobatids, showing cloacal variation. **Top left**: *edwardsi* (ICN 21936). Contrary to the other species depicted, the vent of *edwardsi* is conspicuously enlarged and elongated relative to other anurans. **Top right**: *molinarii* (UMMZ 176222, paratype), a species referred to *Nephelobates* by La Marca (1994). The vertical folds vary as an artifact of preservation. **Middle left**: *alboguttatus* (AMNH 10503), the type species of *Nephelobates*. **Middle right**: *trinitatis* (AMNH 125796), a species referred to *Mannophryne* by La Marca (1992). **Bottom left**: *petersi* (AMNH 42546). **Bottom right**: *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 cloaca as an artifact of preservation.

Third, in reference to the *m. sartorius* of the superficial thigh musculature, Dunlap (1960:8) reported that "the major differences from the ranid condition are found in *Crossodactylus* and *Phyllobates* in which the origin is fleshy rather than tendinous," a statement that could be taken as suggestive of this as a synapomorphy of these taxa. Nevertheless, although Dunlap's observation of variation among anurans is correct, the *m. sartorius* is fleshy in all terminals included in this study and I therefore did not include this character here.

Finally, Savage (1968) was followed by Silverstone (1975) in identifying dark pigmentation of the flesh as a synapomorphy of *Dendrobates* and *Phyllobates*. I 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 (catalogued and uncatalogued) at AMNH. The variation I 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. I was 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), I sought to sample genes of differing degrees of variability. I targeted the mitochondrial H-strand transcription unit 1 (H1), which

includes 12S ribosomal, $tRNA^{val}$, and 16S ribosomal sequence, yielding approximately 2,400 base pairs (bp) generated in 5–7 overlapping fragments. I also targeted a 385 bp fragment of cytochrome *b* and a 658 bp fragment of cytochrome *c* oxidase I (COI). In addition to those five mitochondrial genes, I targeted the nuclear protein coding genes histone H3 (328 bp), rhodopsin (316 bp), tyrosinase (532 bp), recombination activating gene 1 (RAG1, 435bp), 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 4.1. Included in this study is a novel primer pair (RAG1 TG1F and TG1R) I designed to amplify the RAG1 product using the web-based program Primer3 (Rozen and Skaletsky, 2000), available at http://frodo.wi.mit.edu/cgi-bin/primer3/primer3_www.cgi.

As noted above, I targeted loci that varied to differing degrees in order to test hypotheses of relationships at all levels, and I included multiple samples from the same and different localities of the same species in an effort to address problems in alpha taxonomy. I attempted to sequence all loci for at least one sample from every locality, but I did not sequence nuclear loci for all samples. I 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. Sequencing all loci for all specimens from every locality would therefore have been a misuse of resources.

Table 4.1. PCR primers used in this study. The solid line separates mitochondrial (above) and nuclear (below) loci. See text for PCR and cycle sequencing protocols.

Gene Locality	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
16S rDNA	L2A	Forward	CCAAACGAGCCTAGTGATAGCTGGTT	Hedges, 1994
	H10	Reverse	TGATTACGCTACCTTTGCACGGT	Hedges, 1994
12S rDNA	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
$tRNA^{val}$	tRNAval-H	Reverse	GGTGTAAGCGARAGGCTTTKGTTAAG	Goebel et al., 1999
12S rDNA	L13	Forward	TTAGAAGAGGCAAGTCGTAACATGGTA	Feller and Hedges, 1998
	Titus I	Reverse	GGTGGCTGCTTTTAGGCC	Titus and Larson, 1996
cytochrome oxidase *c* subunit I	LCO1490	Forward	GGTCAACAAATCATAAAGATATTGG	Folmer et al., 1994
	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[2]	SIA1 (T3)	Forward	TCGAGTGCCCCGTGTGYTTYGAYTA	Bonacum et al., 2001
	SIA2 (T7)	Reverse	GAAGTGGAAGCCGAAGCAGSWYTGCATCAT	Bonacum et al., 2001

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

I augmented my own data with sequences from GenBank, listed in Appendix 6, in order to include otherwise unsampled ingroup species and additional localities for taxonomically problematic species, i.e., the data set analyzed includes all species on GenBank as well as samples of some species from multiple localities. Nevertheless, I did not include all GenBank data. First, I only included loci for which I also generated data. For example, I did not include Widmer et al.'s (2000) cytochrome *b* data because their fragment did not overlap with mine. Second, although I included multiple samples to address taxonomic problems, I 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 data set.

Laboratory Protocols

Whole cellular DNA was extracted from frozen and ethanol preserved tissues (liver or muscle) using the Qiagen DNeasy kit following 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 minutes at 94°C, 35-40 cycles of 1 minute at 94°C, 1 minute at 45-62°C, and 1-1.25 minutes at 72°C, followed by a final extension step of 6 minutes 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) were run in 8 µl reactions, and products were cleaned and desalted by standard isopropanol-ethanol precipitation or using cleanSEQ

(Agencourt Biosciences Corporation). and sequencing on either an ABI 3700 or ABI 3730XL automated DNA sequencer. Contigs were assembled and edited using Sequencher (Gene Codes).

Molecular Sequence Formatting

To allow 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, I broke complete sequences into contiguous fragments. (This also improves the performance of POY's implementation of the parsimony ratchet; see Heuristic Tree Searching, below.) I did so sparingly, however, as these breaks constrain homology assessment by prohibiting nucleotide comparisons across fragments, i.e., 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.

I therefore inserted as few breaks as were necessary to maximize the amount of sequence data included, minimize the introduction of Ns (see Character Sampling Strategy, above), and attain maximum length fragments of around 500 bases (see Table 4.2). Breaks were placed exclusively in highly conserved regions (many of which correspond to commonly used PCR primers), as recovery of such highly invariable regions tends to be alignment-method independent (unpublished data) and therefore do 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

Table 4.2. Summary of DNA sequence data. Approximate number of base pairs refer to complete sequences.

Sequence	No. Basepairs (bp)	No. Fragments	No. Terminals
mitochondrial H-strand transcription unit 1	2400	16	417
cytochrome *b*	385	3	322
cytochrome *c* oxidase I	658	2	235
recombination activating gene 1	435	2	130
28S	700	2	138
histone H3	328	1	171
rhodopsin	316	1	155
seventh in absentia	397	2	137
tyrosinase	532	2	54

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.

Analytical Approach

Total Evidence Analysis

I did not discriminate between classes of evidence in the phylogenetic analyses. In order to allow the molecular data to have bearing on alpha taxonomic problems, I treated every specimen sequenced as a separate terminal, i.e., I 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 shortcoming 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 may result in males, females, and juveniles being grouped in separate clades. (b) Similarly, tissue samples usually are not available for specimens representing all relevant semaphoronts. As such, many semaphoront-specific characters would be excluded from analysis, or would 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 overlooking 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, i.e., terminals judged conspecific on phenotypic grounds could not be held together on those grounds alone in phylogenetic analysis. Although I see some validity in this argument, given the relative sizes of the phenotypic and genotypic partitions (ca. 170 characters versus ca. 5,500 unaligned basepairs), I am not concerned about the ability of molecular data to overwhelm the phenotypic evidence. Moreover, the identical entries that would potentially hold those specimens together in the face of molecular evidence are in fact synapomorphies 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 with another, but to allow all evidence to interact simultaneously to discover the hypothesis that best explains all the evidence.

As such, I opted to duplicate the morphological entries coded for the species, i.e., 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. Any non-monophyly of species is therefore due to the genotypic data actually overturning the phenotypic evidence that treated them as single species. An important caveat is that I did not associate GenBank sequences with phenotypic data unless I lacked my own genotypic data for the taxon (e.g., *sauli*), and then only for one sample if >1 was on GenBank (e.g., I associated the phenotypic entries for *kingsburyi* with AY364549 only).

Simultaneous phylogenetic analysis was performed using the program POY (Wheeler et al., 1996–2003) version 3.0.11a (released May 20, 2003) and the MPI version 3.0.12a-1109195780.71 (released November 19 2004). 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 I verified POY results and analyzed implied alignments using NONA (Goloboff, 1999) spawned from Winclada.

Heuristic Homology Assessment

Numerous algorithms of varying exhaustiveness have been proposed to optimize unaligned DNA sequences on a given topology. My 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), I 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. My 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, I 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.)

I did not employ the *exact* command during most searches, although I 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, I 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 I 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 (e.g., reverse complements; see Sequence Pre-Analysis, above).

Heuristic Tree Searching

Efficient search strategies for large data sets are to a certain degree dataset-dependent (Goloboff, 1999), and, as discussed above, common indicators of sufficiency are unrealistic given current technological limitations. Therefore, rather than apply a simple, predefined search strategy (e.g., 100 random addition Wagner builds + TBR branch swapping), I employed a variety of tree searching algorithms, spending more time on those that proved most fruitful. 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 4.3.

Table 4.3. Summary of tree searching methods combined in overall search strategy. Different runs combined multiple procedures, and all runs included SPR and/or TBR refinement. See text for details and references.

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 data set.
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 311, 131, and 113, 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.

Random addition sequence Wagner builds (RAS) were performed holding one or three trees. I conducted searches without *slop* or *checkslop*, both of which increase the pool or 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 data set.

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 4.2), so *ratchetpercent 15* randomly reweighted five fragments, regardless of their length or relative position. I reweighted 15-35% of the fragments and applied weights of 2-8×.

As a complementary approach, I also performed quick searches (few random addition sequence Wagner builds + SPR) under indel, transversion, and transition costs of 311, 131, and 113 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 data set, 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.

I also performed constrained searches by calculating the strict consensus of trees within an arbitrary number of steps of the present optimal, 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 I 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 speed-ups 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 Icollapsed 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, I 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, I analyzed subsets of taxa separately by defining reduced data sets with *terminals* files that listed only the targeted terminals. Rigorous searches (at least 100 RAS + TBR for each of the reduced data sets) of these reduced data sets were then performed, and the results were then used to specify starting topologies for additional searching of the complete data set.

Static matrices may be thoroughly analyzed in a fraction of the time required to perform an equivalent analysis under dynamic homology. I therefore output implied alignments of current optima from POY and ran 200 rounds of the parsimony ratchet using Winclada and NONA. Improvements were not always attained through this procedure, but when they were I then input the optimal cladorgram(s) from the static search as a starting point for further analysis in POY.

As a final attempt to discover more parsimonious solutions, I 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, I 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 I ensured that the more heterodox aspects of my results were not due to simply failing to evaluate the orthodox alternatives during the automated searches.

Heuristic data exploration

Methods of data exploration were limited to those that could be justified in terms of their scientific heurism (Grant and Kluge, 2003). To estimate support (sensu Grant and Kluge, 2003), I calculated Bremer (decay) values for all nodes present in

the strict consensus of equally parsimonious solutions (Bremer, 1994). To accomplish this I 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 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 represent the upper bound. Additional a posteriori character analysis is discussed in Chapter 8.

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 I examine the bearing of evidence from DNA sequences and phylogenetic analysis on alpha taxonomic problems.

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 monophyletic group (Skinner, 2004; see also Frost and Kluge, 1994). Incongruence between the true history of different parts (as opposed to incongruence due to false hypotheses of homology, i.e., independent origins of "similar" objects) 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, i.e., there is no way to discriminate intra- from interspecific hierarchic structure without additional information. For example, dividing a pectinate cladogram 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 individuals (Kluge, 1990; Grant, 2002), meaning that species boundaries occur at the point where properties of contemporary individuals dissolve. 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 evidence is warranted (Grant, 2002). Ultimately, species individuation requires diagnostic characters, and phylogenetic analysis facilitates their discovery.

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

My primary reason for including pairwise distances in this analysis is that they provide a rapid and efficient heuristic for species identification without conducting a complete phylogenetic analysis, in the same way that dichotomous keys are efficient identification tools (Grant, 2002). I wish to clarify that I do not mean to 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 species 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 real 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

[3] 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.

(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, i.e., 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.

Chapter 5: Phenotypic Characters

0. Dorsal skin texture (Fig. 5.1): smooth = 0; posteriorly granular = 1; strongly granular = 2; spiculate =3. [nonadditive].

Dorsal skin texture has generally been used descriptively in alpha 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.

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 was evident in life. Conversely, granularity may be exaggerated in desiccated specimens. As noted by Myers and Daly (1979:5, fn 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.

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 prevalent posteriorly, especially in the sacral region and on the thigh and/or shank, and absent or weaker and sparser anteriorly

Figure 5.1. Character 0, dorsal skin texture. **Top left**: State 0, smooth (*galactonotus*, AMNH live exhibit). **Top right**: State 1, posteriorly tubercular (*fraterdanieli*, TG 1491). **Bottom left**: State 2, granular (*macero*, AMNH 129473). **Bottom right**: State 3, spiculate (*Dendrophryniscus minutus*, AMNH 93856).

(e.g., *boulengeri*, *fraterdanieli*). They 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 are qualitatively different and there is no developmental evidence to suggest that transformations between states 0 and 2 pass through state 1. Heyer (1983:322) provides electronmicrographs showing the skin texture for *Cycloramphus boraceiensis.* I coded *pulcherrmus* 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, 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 what reported as *Phyllobates latinasus* (actual species unknown but probably not *latinasus*; see Grant, 2004 for discussion of *latinasus* alpha 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 all 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 was been presented in support of his thesis and their functional significance remains unknown.

2. Supernumerary tubercles on hand: absent = 0; present = 1.

Most dendrobatids possess a large, subcircular palmar tubercle and an elliptical thenar tubercle. Many non-dendrobatids 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 this I do not consider this to be homologous with the supernumerary tubercles of other taxa.

3. Distal tubercle on finger 4 (Fig. 5.2): 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 is further reinforced by examination of outgroup taxa, as *Thoropa miliaris* possesses a long finger IV and lacks the distal subarticular tubercle.

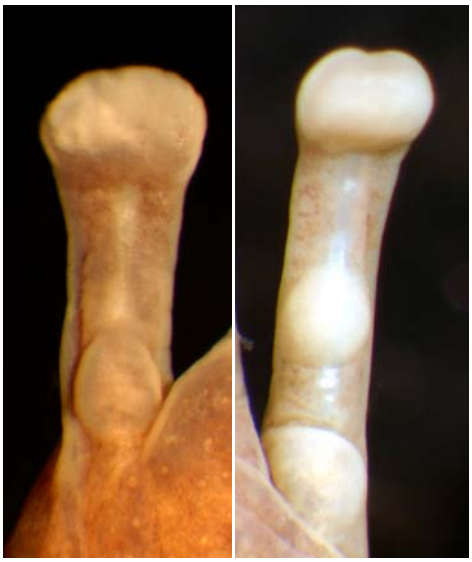


Figure 5.2. Character 3, distal subarticular tubercle of finger IV. **Left**: State 1, absent (*degranvillei*, AMNH 90876). **Right**: State 1, present (*pictus*, AMNH 79209).

4. Finger IV length (Fig. 5.3): 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 I have conflated transformations involving the length 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, i.e., 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 length of finger II. And it is further supported by the loss of the distal subarticular tubercle in species with 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).

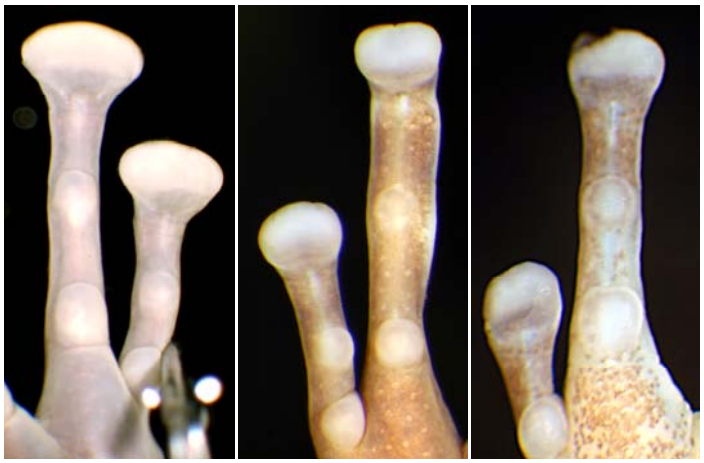


Figure 5.3. Character 4, length of finger IV. **Left**: State 0, surpassing distal subarticular tubrcle of finger III (*histrionicus*, AMNH 88259). **Center**: State 1, reaching distal half of distal subarticular tubrcle of finger III (*tricolor*, USNM 286082). Note also the strong preaxial swelling of finger III. **Right**: 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.

5. Relative lengths of fingers I and II: I<<II (1.2 or more times longer) = 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, i.e., bringing finger I further towards 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 is less prone to error, and I employed this method here. Any means of measuring finger length requires that the fingers be straight; when well preserved hands were unavailable digits were straightened for measurement. This method also assumes that there are no carpal changes that affect the distance from the palm to finger tips differentially (no such variation was observed). 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 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, i.e., 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, i.e., one involving variation in the length of finger I, the other variation in the length of finger II. It should also be noted that I 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 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 be differ in only minor structural details (e.g., number of epidermal cell layers). Also, I am 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). I have therefore treated the evolution of digital discs as a single transformation series. All dendrobatids possesses digital discs, but they are absent in several of the sampled outgroup taxa.

7–10. Expansion of Finger Discs (Fig. 5.4)

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 disc 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 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.

I detected four discrete states in finger (and three in toe) disc expansion, shown schematically in Fig 5.4. 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 is 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 (1976:203) tested the claim quantitatively in *histrionicus* they found it to be unsupported. Although I detected (and coded) polymorphism in disc expansion in some species (including *histrionicus*), I concur with Myers and Daly (1976) 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.

I 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).

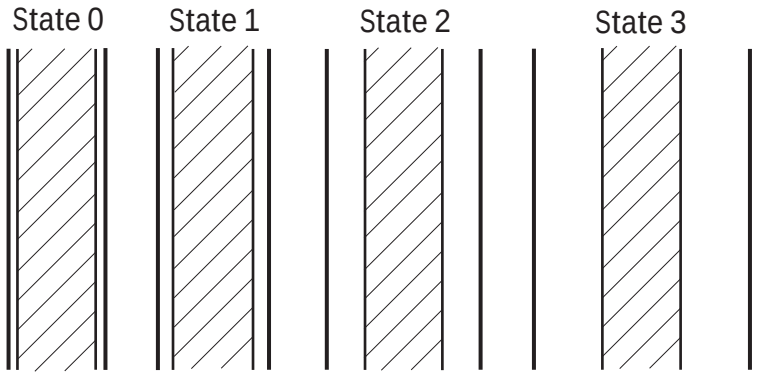


Figure 5.4. Characters 7–10 and 31–35, schematic illustration of the four states observed in the expansion of digital discs. The digital shaft is indicated by the inner crosshatched area and the outer edges of the disc are indicated by the heavier outer line.

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].

11–18. Finger Fringes (Fig. 5.5)

The occurrence and extent of lateral keels and/or fringes have 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 I coded them as separate characters.

Although lateral dermal expansions of the digits are widely described in the dendrobatid literature, explicit delimitations of character-states are generally lacking, which has lead 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." While 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 "When 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). For the purpose of phylogenetic analysis, I 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. 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 I agree that these descriptors encompass the observed variation, and despite numerous dissections, I was 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 post mortem 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.

In state 1, the skin that extends from the dorsal surface extends ventrad and appears to fold over the side of the digit, which I refer to as a fringe (see fig. 5.5). In ventral (palmar) view the folding-over can be seen to create a deep longitudinal crease or groove. I have not 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 I was unable to delimit distinct states.

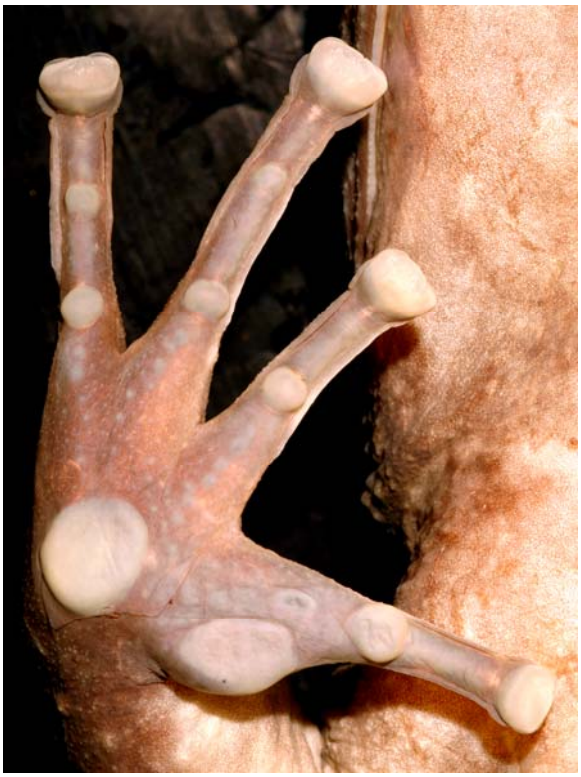


Figure 5.5. Characters 11–18, finger fringes. In *Megaelosia goeldii* (AMNH 103949) fringes are present on pre- and postaxial edges of all fingers.

Webbing between the fingers does not occur in any dendrobatid I 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 I examined. Similarly, Coloma (1995) described and illustrated webbing between the fingers in an undescribed species (as *Colostethus chocoensis*; see Grant et al., 1997:24, fn. 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* reveals 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 leptodactylids.

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. 5.6): 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 flatten palm meets the rounded side of the hand, but I 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 I was unable to delimit discrete states. As with other dermal characters, the metacarpal ridge may be exaggerated or lost as an artifact of preservation.

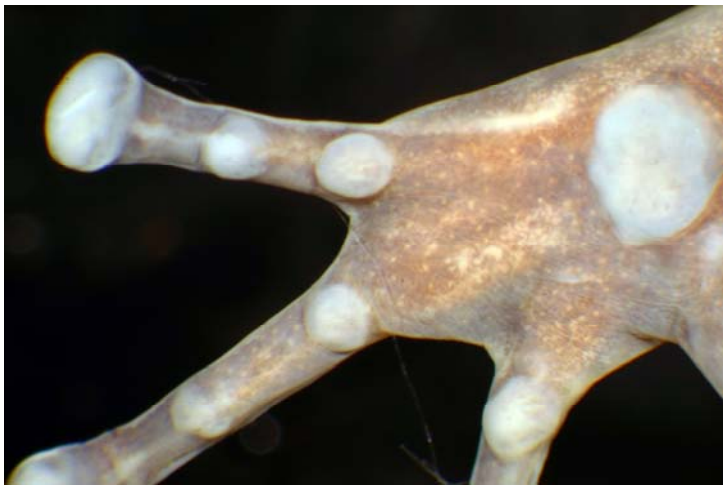


Figure 5.6. Character 19, metacarpal ridge. State 1, present (*abditaurantius*, ICN 9853).

20–21. Finger III swelling

Reproductively active males of numerous dendrobatids present swollen third fingers, a condition that is unknown in non-dendrobatids. 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), I 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 apparatus (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 thrid 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 is mentioned by Dunn, 1931; Dunn, 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; Silverstone, 1976; but it is not mentioned 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, fn. 14) dissertation (Edwards, 1974).

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 (1974) 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 are 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 (1974) 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 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), Myers (1991), Myers and Donnelly (1997), Myers et al. (1998, see especially fig. 4), 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 I examined.

21. Morphology of swollen third finger in males (Fig. 5.7): pre- and postaxial swelling = 0; weak preaxial swelling = 1; strong preaxial swelling = 2; swelling extending from wrist, mainly preaxial on digit = 3. [nonadditive].

Figure 5.7. Character 21, morphology of swollen third finger in males. **Top left**: State 0, pre- and postaxial swelling (*mertensi*, ICN 43698). **Top center**: State 1, weak preaxial swelling (*insperatus*, KU 149676). **Top right**: For comparison, a female of *insperatus* (KU 149684). **Bottom left**: State 2, strong preaxial swelling (*nubicola*, AMNH 114574). **Bottom center and left**: State 3, swelling extending from wrist, mainly preaxial on digit (*baeobatrachus*, AMNH 140650).

22. Carpal pad (Fig. 5.8): 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. I did not find this character to be present in any other species, but I include it here in anticipation of future discoveries.

Figure 5.8. Character 22, male nuptial pad (*undulatus*, AMNH 159134).

23. Male nuptial 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).

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

24. Morphology of male nuptial excrescences on thumb: large, cornified spines = 0; small, uncornified spines = 1; nonspinous asperities = 2. [additive].

Lavilla and Ergueta (1995:49) described the nuptial excrescences of *Telmatobius jahuira* as “escasas espinas corneas que dejan amplios espacios no queratinizados entre si.”

25. Female nuptial excrescences on thumb: absent = 0; present (large, cornified spines) = 1.

See Noble (1931:122, 126) for illustrations and comments on the large, cornified spines on the thumb of females of species of *Crossodactylus*.

26. Thenar tubercle (Fig. 5.9): absent or small, inconspicuous swelling = 0; large, conspicuous, well defined tubercle = 1.

Most dendrobatids have a conspicuous, protuberant, elliptical thenar (outer 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 that there is some variation in the expression of the thenar tubercle in *quinquevittatus*; in some specimens it is altogether undetectable, while in others “possible vestiges of it” were detected as “possibly

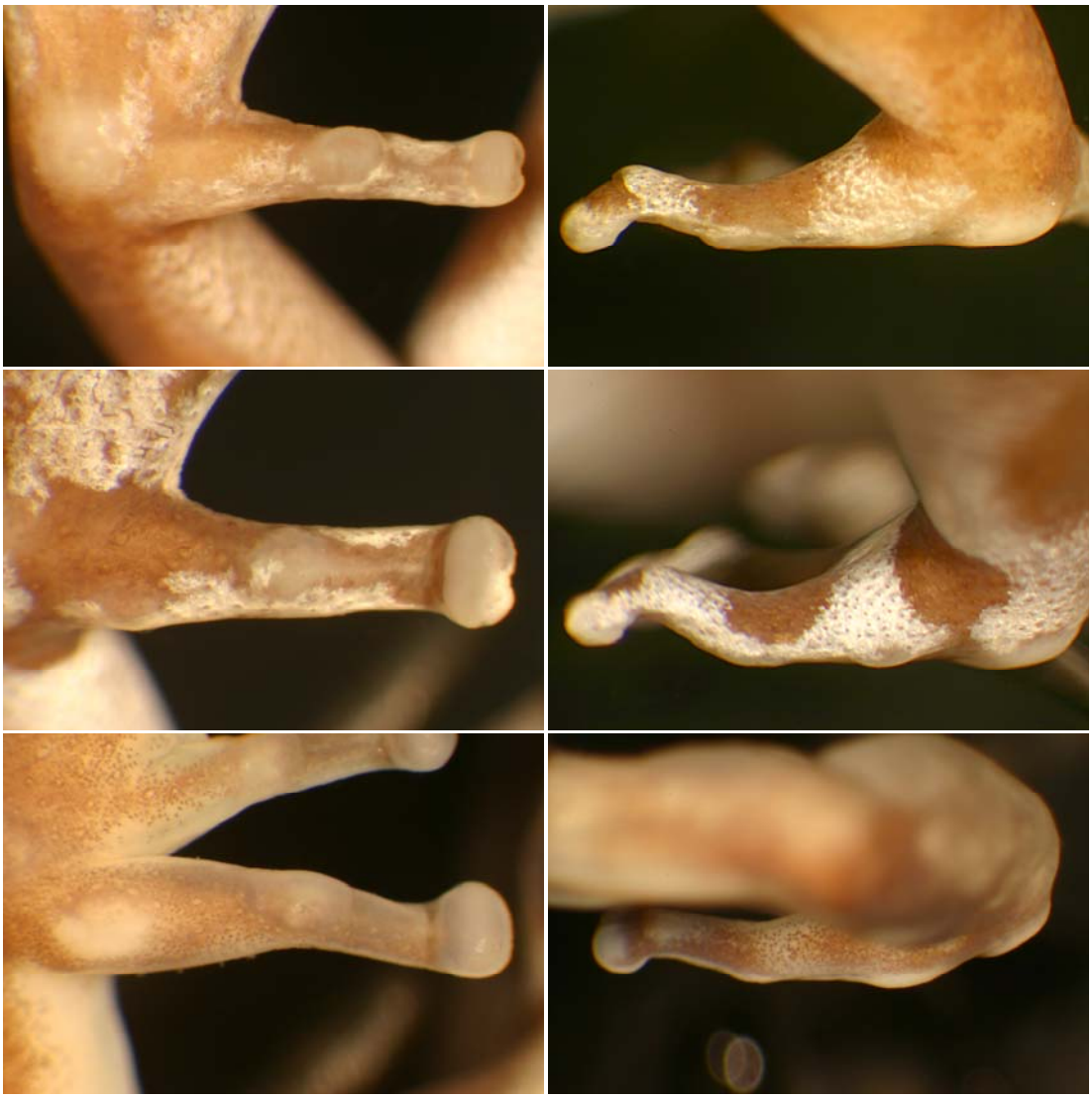


Figure 5.9. Character 26, thenar tubercle. **Top**: State 0, absent or small, inconspicuous swelling (*pumilio*, AMNH 102262). In this specimen, the thenar tubercle appears absent in both palmar aspect and profile. **Middle**: Another specimen of the same species (*pumilio*, AMNH 102263). In this specimen, the thenar tubercle is inconspicuous but clearly seen in profile. **Bottom**: State 1, large, conspicuous, protuberant tubercle (*nubicola*, AMNH 114574).

represented by slight epidermal thickening." My 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, inadequate fixation, among other causes), I 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 *nubicola* and *stepheni* (roughly the same size 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 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 increased expression 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 Ibague species.

28. Tarsal keel: absent = 0; present = 1.

The tarsal keel is a dermal structure that extends obliquely along the plantar (ventral) surface of the tarsus. Regardless of its point of origin (see character 27), it always terminates medially, not on the margin of the tarsus (see character 28).

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 *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 non-aposematic 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 tarsal and does not conform to the rounded structures usually referred to as tubercles.

29. Morphology of tarsal keel (Fig. 10): straight or very weakly curved, extending proximolaterad from preaxial edge of inner metatarsal tubercle = 0; tuberclelike (i.e., enlarged) and strongly curved at proximal end, extending from metatarsal tubercle = 1; short, tuberclelike, curved or directed transversely across tarsus, not extending from metatarsal tubercle = 2; weak, short dermal thickening, not extending from metatarsal tubercle = 3. [additive].

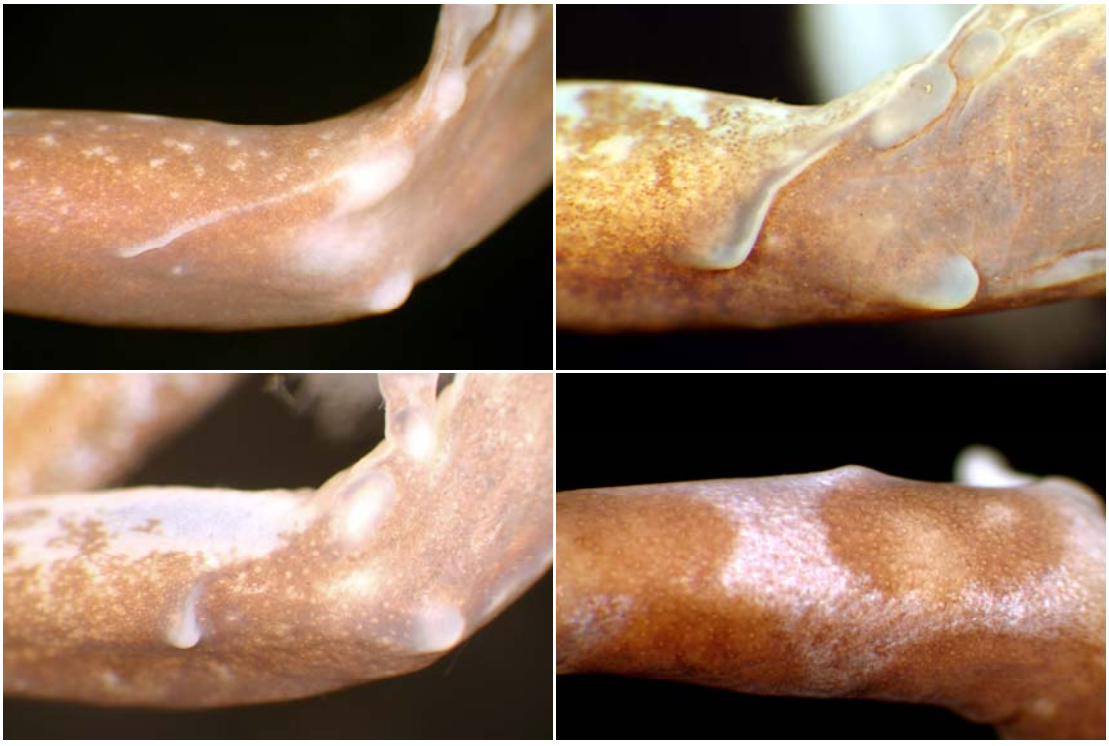


Figure 5.10. Character 29, morphology of tarsal keel. **Top left**: State 0, straight or very weakly curved, extending proximolaterad from preaxial edge of inner metatarsal tubercle (*imbricolus*, AMNH 102082). **Top right**: State 1, tuberclelike and strongly curved at proximal end, extending from metatarsal tubercle (*degranvillei*, AMNH 90876). **Bottom left**: State 2, short, tuberclelike, curved or directed transversely across tarsus, not extending from metatarsal tubercle (Neblina species, AMNH 118657). **Bottom right**: 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.

30. Tarsal fringe (Fig. 5.11): 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 1. The tarsal fringe differs from the tarsal keel (characters 26–27) in that the latter extends proximolaterad across the tarsus to terminate at roughly the middle of the

tarsus on the plantar (ventral) surface, whereas the former never crosses the tarsus and extends along it's entire length.

Figure 5.11. 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 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. 5.4, 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). I consider toe fringes (defined as for fingers, above) to be homologous with webs. I do not consider lateral fringes that meet between the toes to constitute a web unless it is expanded relative to lateral fringes, i.e., if the continuous lateral fringes are broader at the base than along the sides of the digits, I 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 species of *Atelopus*, and I have therefore treated webbing as a single transformation series and allow character congruence to be the ultimate arbiter.

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 I 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 there is no trace of webbing in the specimens I 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 of state 4) for *talamancae* than I 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**), but there is no trace of webbing in the specimens I 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 *Phyllobates sylvaticus* from Duellman (2004), who reported it as absent in them all.

46. Metatarsal fold (Fig. 5.12): 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 and edge is formed where the relatively flatten sole meets the rounded side of the foot, but I 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.

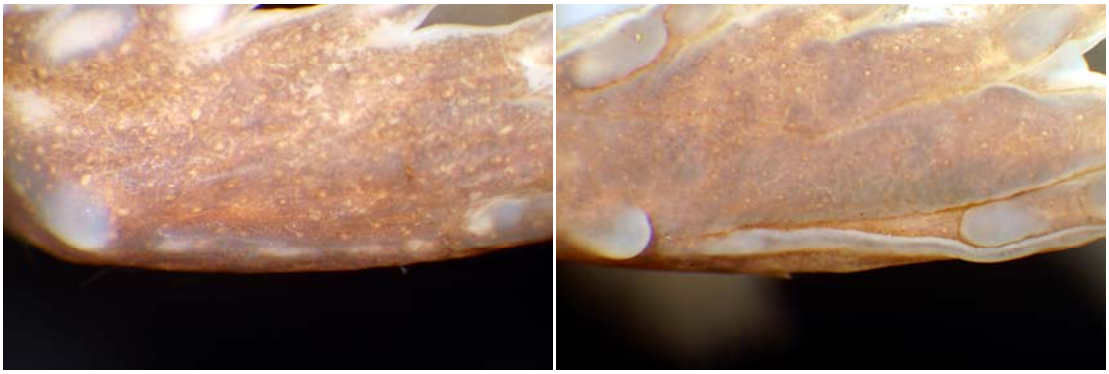


Figure 5.12. Character 46, metatarsal fold. **Left**: State 1, weak (Neblina species, AMNH 118657). **Right**: State 2, strong (*degranvillei*, AMNH 90876).

47. Cloacal tubercles: absent = 0; present = 1.

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 post mortem artifacts.

48–66. External coloration

Much of the diversity of dendrobatids involves variation in 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 under-sampled in this study—sources of variation. Several aposematic dendrobatids (especially *pumilio* and *histrionicus*) are renowned for the 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 (1976) account of

histrionicus. Practically speaking, the two main difficulties are (1) detection of objective boundaries between different characters and character-states, (2) requirement of many states per character, and (3) distinguishing between color and color pattern. I 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) I focused more on color pattern than color, but by doing so I undoubtedly conflated characters and character-states. For example, I 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 including 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 non-independent of the thigh coloration characters.

49. Pale paracloacal mark (Fig. 5.13): 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 48).

Figure 5.13. Character 49, pale paracloacal mark. State 1, present (*degranvillei*, AMNH 90880).

50. Thigh dorsal color pattern (Fig. 5.14): 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 bands/blotches = 4; dark with pale longitudinal stripe = 5. [nonadditive].

Figure 5.14. Character 50, dorsal thigh color pattern. **Top left**: State 0, pale with dark spots (*quinquivittatus*, AMNH 124069). **Top right**: 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. **Middle left**: State 2, dark with pale spots/bands (*aurotaenia*, AMNH live exhibit). **Middle right**: State 3, solid pale (*terribilis*, AMNH live exhibit). **Bottom left**: State 4, brown with dark brown bands/blotches (*inguinalis*, LACM 42409). **Bottom right**: State 5, dark with pale longitudinal stripe (*flavopictus*, AMNH 88642).

51. Discrete pale proximoventral calf spot (Fig. 5.15): 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 I therefore follow Silverstone in treating this character as absent for those species.

Figure 5.15. Character 51, discrete pale proximoventral calf spot. State 1, present (*imbricolus*, AMNH 102082).

52–57. Pale Lateral Stripes

Edwards (1974) 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. 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, more recently, 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., *ideomelus* 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 (1974) 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 I have designated A (character 52) and B (character 53), the latter also having been confused with the oblique lateral stripe previously.

52. Dorsolateral stripe A (does not drop to thigh; Fig. 5.16): 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) observed that in *bicolor* and *terribilis* the dorsolateral stripe is present in juveniles and is lost ontogenetically (state 1). This "loss" is peculiar, however. In this case, the loss of the stripe is due to the hypertrophy of the bright dorsolateral stripes, which expand ontogenetically to cover the entire dorsum, thus creating a uniformly colored, stripeless color pattern. In state 2, the dorsolateral stripe is short, narrow, and inconspicuous (often more conspicuous in juveniles than adults), running from the posterior edge of the eye to a point just past the insertion of the arm. The dorsolateral stripe of most species is complete, reaching or surpassing the level of the sacrum, and persists throughout ontogeny (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" 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. I therefore did not specify a particular additivity for this transformation series.

Figure 5.16. Character 52, dorsolateral stripe A. **Top**: State 1, present in juveniles (left), absent in adults (right) (*terribilis*, left: captive-raised specimen; right: AMNH live exhibit). **Bottom left**: State 2, anterior, narrow, faint (*atopoglossus*, holotype UVC 12068). **Bottom right**: State 3, complete (*aurotaenia*, AMNH live exhibit).

53. Dorsolateral stripe B (drops to top of thigh, not groin; Fig. 5.17): 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 to the level of the thigh, but unlike dorsolateral stripe A it drops toward the thigh posteriorly.

Figure 5.17. Character 53, dorsolateral stripe B. State 1, present (*femoralis*, AMNH 140646).

54. Ventrolateral stripe (Fig.5.18): absent = 0; wavy series of elongate spots = 1; straight = 2. [nonadditive].

The ventrolateral stripe 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 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 did not observe this in the specimens examined. Caldwell and Lima (2003) reported the ventrolateral stripe as absent and described the holotype as having “irregular white blotches, not forming a stripe.” However, a wavy VLS is evident in the photograph shown in their Fig. 3B (gravid female). It should be noted that 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 right).

Figure 5.18. Character 54, ventrolateral stripe. **Left**: 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. **Right**: State 2, straight (*talamancae*, AMNH 69829, photo by R. Zweifel). Note also that the pale dorsolateral stripe does not drop toward the thigh posteriorly.

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 (OLS; Fig. 5.19): partial = 0; complete = 1.

Edwards (1974) 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. It should be noted that there is no evidence that the stripe develops from one end to the other, which is why I did not combine length with presence/absence as an additive multistate character (i.e., absent ↔ partial ↔ complete).

Edwards (1974:10) 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 I have also observed it to be complete. I therefore scored this character as polymorphic.

Figure 5.19. Character 56, oblique lateral stripe length. **Left**: State 0, partial (*panamensis*, AMNH 69836, photo by R. Zweifel). **Right**: State 1, complete (*fraterdanieli*, TG 1491).

57. Oblique lateral stripe structure (OLS; Fig. 5.20): solid = 0; series of spots = 1; diffuse = 2. [nonadditive].

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).

Figure 5.20. Character 57, oblique lateral stripe structure. **Top**: State 0, solid (*pulchripectus*, AMNH 137290). **Middle**: State 1, series of spots (*mertensi*, ICN 43698). **Bottom**: State 2, diffuse (*trilineatus*, AMNH 171974).

58. Gular-chest markings (Fig. 5.21): 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. I 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.

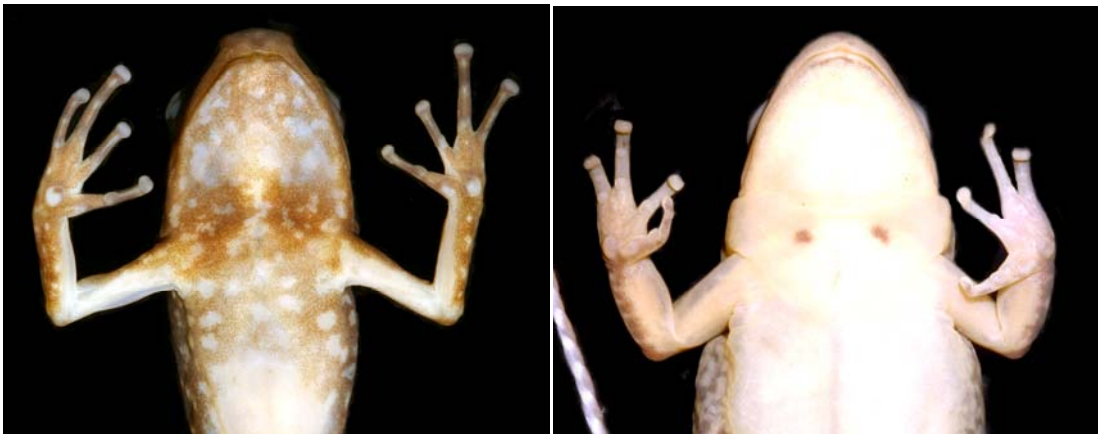


Figure 5.21. Character 58, markings on gular-chest region, state 1 (present). **Left**: Diffuse, white-spotted blotches (*awa*, AMNH 111542). **Right**: Discrete, small dark spots (*vertebralis*, USNM 28232). Despite their differing shapes and patterns, I treated the occurrence of these markings as a single character-state.

Coloma (1995:10) reported several variants in the shape and pattern of the gular-chest markings. Much of this variation is intraspecific, and Coloma reported ontogenetic changes. Consequently, until this variation is better understood, in I 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 I did not treat them as part of this transformation series.

Coloma (1995) reported the presence of diffuse band-like markings in *bocagei*, but it was absent from all the specimens I examined.

59. Dermal collar (Fig. 5.22): absent = 0; present = 1.

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

Figure 5.22. Character 59, dermal collar, state 1 (present) in *trinitatis*. **Left**: Male (UMMZ 167474). **Right**: 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.

Rivero (1978 "1976":330; translated from the Spanish) noted that “In 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 collar-like pigmentation on the throat of many specimens of *nocturnus*. Closer examination and dissection revealed that the dark collar is not caused by melanophores in the skin, as it is 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 show through the semi-translucent skin (Fig. 5.23). 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. 5.23), 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 in Chapter 4, I suspect there are valid transformation series here, but I was unable to delimit them objectively for the present study.

Figure 5.23. Extensive subdermal melanosis of the collar region. **Top row**: *nocturnus* (AMNH 130008). **Bottom row**: *galactonotus* (AMNH 128233).

60. Dark lower labial stripe (Fig. 24): 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.

Figure 5.24. Character 60, dark lower lip line. State 1, present (*fraterdanieli*, TG 1491).

61–64. Male and female throat and abdominal coloration and color pattern

The coloration 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 common, especially in throat coloration and color pattern, but most states occur in both sexes. A few points apply to all the following characters. First, as discussed above, I emphasized color pattern over coloration. Second, spotting, marbling, and reticulation grade form a continuous gradient that, though unambiguous in the extremes, I was unable to delimit objectively. I therefore treat these as a single character-state, although I 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 other were either ambiguous or

exhibited both states and were therefore coded as polymorphic. Fourth, I also treated irregular stippling (i.e., clumped stippling) and the occurrence of diffuse dark spotting as a single state because I was unable to discriminate two states objectively. Finally, it should be noted that the collar and gular-chest markings (characters 58–59) are independent of the region referred to as the throat. For my purposes, throat refers to the region of the central-gular region, i.e., the region area of the vocal sac.

61. Male throat color (Fig. 5.25): 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].

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.

Figure 5.25. Character 61, male throat color. From top to bottom. **Row 1, left**: State 0, pale, free or almost free of melanophores (Neblina species, AMNH 118689). **Row 1, right**: State 1, dark due to absence of iridophores (*abditaurantius*,ICN 9853). **Row 2, left and right**: State 2, evenly stippled gray (left: *espinosai*, USNM 541916; right: *infraguttatus*, AMNH 104846). Note that in *espinosai* the pale sagittal stripe remains anteriorly but is absent from the area of the vocal sac. Note also that the gular-chest markings (character 58) of *infraguttatus* do not interfere with the even stippling of the throat. **Row 3, left**: State 3, pale with dark spots (*punctiventris*, TG 1363, deposited at Universidad del Cauca). **Row 3, right**: State 4, solid dark (*inguinalis*, LACM 42329). **Row 4, left**: State 5, dark with discrete pale spotting/reticulation/marbling (*tricolor*, USNM 286082). **Row 4, right**: State 6, irregular (clumped) stippling or faint, diffuse spotting (*nocturnus*, AMNH 130008).

62. Female throat color (Fig. 5.26): 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].

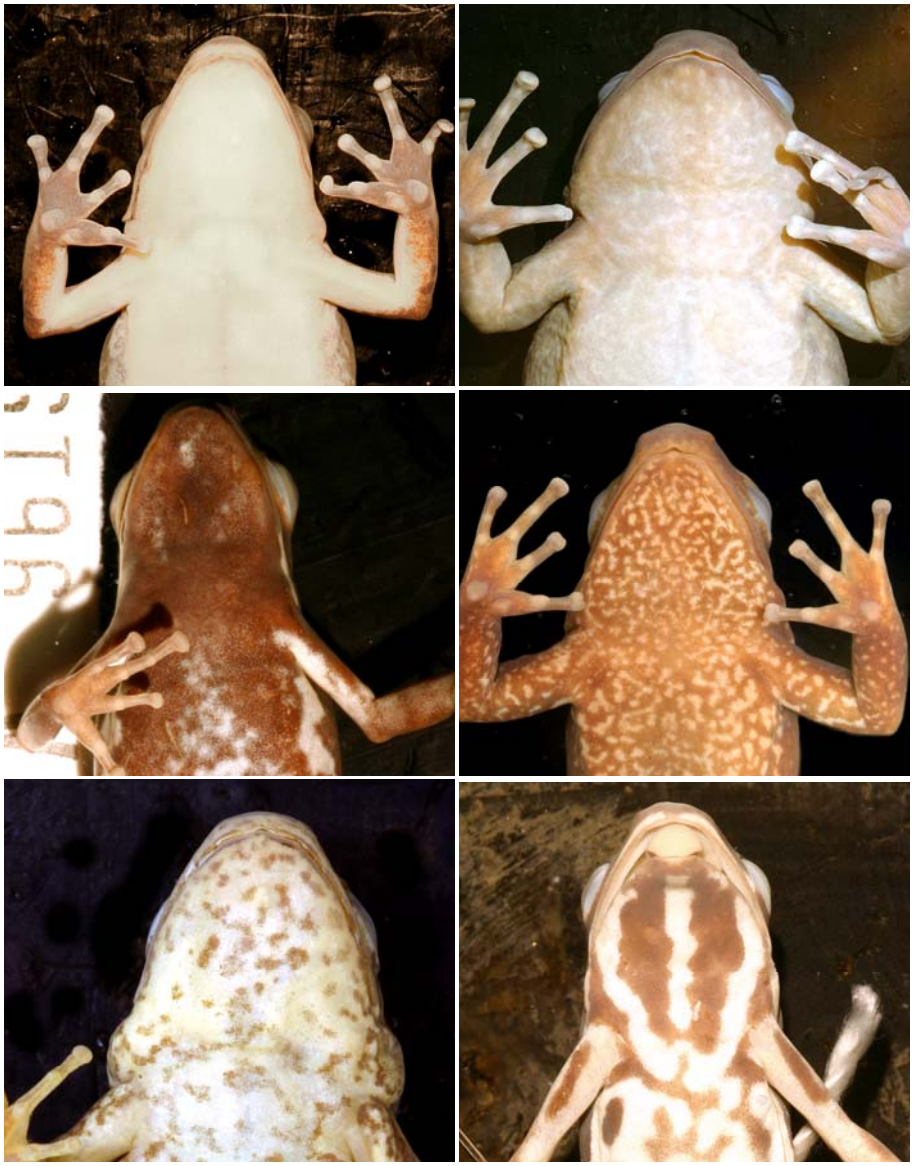


Figure 5.26. Character 62, female throat color. **Top left**: State 0, pale, free or almost free of melanophores (*undulatus*, AMNH 159128). **Top right**: State 1, irregular (clumped) stippling or faint, diffuse spotting (*nocturnus*, AMNH 130018). **Middle left**: State 2, solid dark (*hahneli*, AMNH 96190). **Middle right**: State 3, dark with discrete pale spotting/reticulation/marbling (*imbricolus*, AMNH 102083). **Bottom left**: State 4, pale with discrete dark spotting/reticulation/marbling (*fraterdanieli*, AMNH 148021). **Bottom right**: State 5, dark with pale medial longitudinal stripe (*boulengeri*, USNM 145281).

63. Male abdomen color (Fig. 5.27): pale, free or almost free of melanophores = 0; pale with discrete dark spotting/reticulation/marbling = 1; evenly stippled = 2; dark with discrete pale spotting/reticulation/marbling = 3; irregular (clumped) stippling or faint, diffuse spotting = 4; solid dark = 5. [nonadditive].

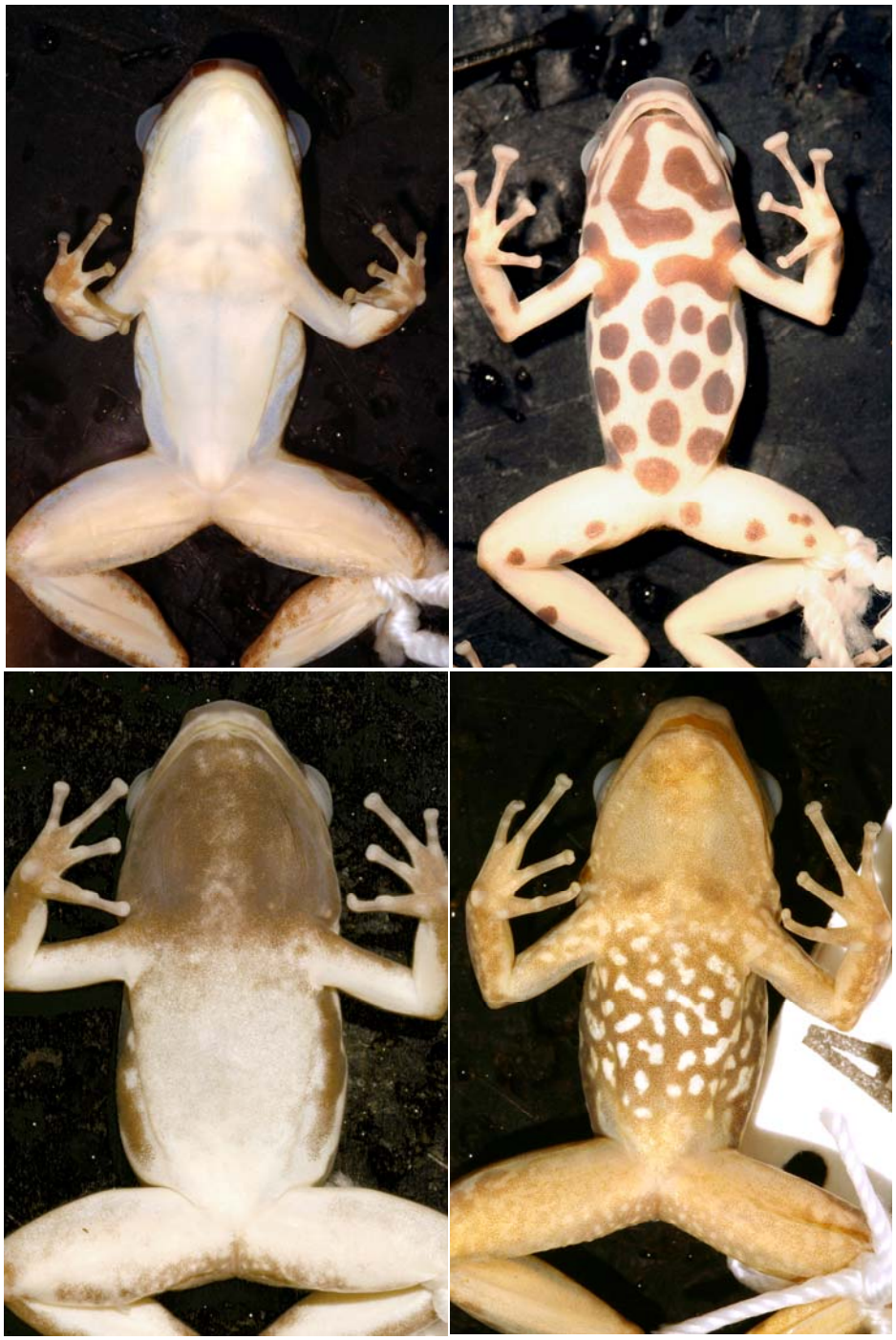


Figure 5.27. Character 63, male abdomen color. Top to bottom. **Row 1, left**: State 0, pale, free or almost free of melanophores (Neblina species, AMNH 118689). **Row 1, right**: State 1, pale with discrete dark spotting/reticulation/marbling (*quinquevittatus*, AMNH 124069). **Row 2, left**: State 2, evenly stippled (*talamancae*, AMNH 113893). **Row 2, right**: State 3, dark with discrete pale spotting/reticulation/marbling (*infraguttatus*, AMNH 104846). **Row 3, left**: State 4, irregular (clumped) stippling or faint, diffuse spotting (*nocturnus*, AMNH 130012). **Row 3, right**: State 5, solid dark (*inguinalis*, LACM 42329).

64. Female abdomen color (Fig. 5.28): 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 *Colostethus 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 possess any stippling on the abdomen, while all males do. Although I coded *riveroi* as having the abdominal region evenly stippled, in life it is posteriorly orange (Donoso-Barros, 1965 "1964").

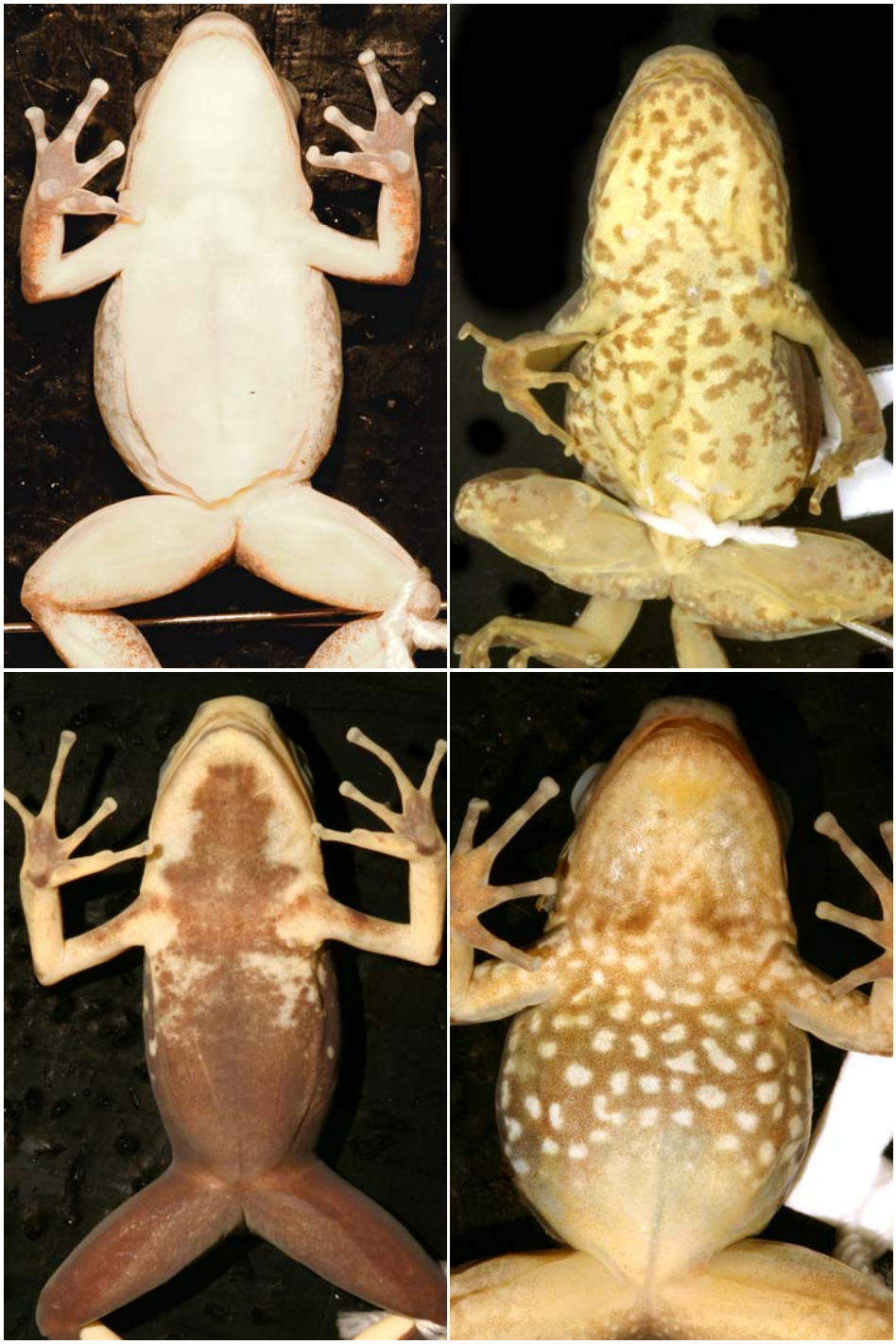


Figure 5.28. Character 64, female abdomen color. Top to bottom. **Row 1, left**: State 0, pale, free or almost free of melanophores (*undulatus*, AMNH 159128). **Row 1, right**: State 1, pale with dark spotting/reticulation/marbling (*fraterdanieli*, AMNH 39360). **Row 2, left**: State 2, solid dark (*silverstonei*, AMNH 91845). **Row 2, right**: State 3, dark with discrete pale spotting/reticulation/marbling (*infraguttatus*, AMNH 104849). **Row 3, left**: State 4, irregular (clumped) stippling or faint, diffuse spotting (*nocturnus*, AMNH 130018). **Row 3, right**: State 5, evenly stippled (*riveroi*, AMNH 134141).

65. Iris coloration (Fig. 5.29): lacking metallic pigmentation and pupil ring = 0; with metallic pigmentation and pupil ring = 1.

Silverstone (1975: 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." I diagnose this character somewhat more precisely, but I 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. I dissected the eyes of preserved specimens of several species but failed to detect differences between pigmented and unpigmented irises. I 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 Massary, 1999; Lescure and Marty, 2000); *Dendrobates lehmanni* (Myers and Daly, 1976); *Dendrobates sylvaticus* (Myers and Daly, 1976 [as *histrionicus*]; Lötters et al., 1999); *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); *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); *Phyllobates sylvaticus* (Duellman, 2004); *pulchellus* (Coloma, 1995); *pulchripectus* (Silverstone, 1975); *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); *talamancae* (Coloma, 1995); *terribilis* (Myers et al., 1978); *toachi* (Coloma, 1995); *trinitatis* (Wells, 1980; La Marca, 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., 1996); *vittatus* (Silverstone, 1976; Savage, 2002); *zaparo* (Silverstone, 1976).

Figure 5.29. Character 65, iris coloration. **Left**: State 0, lacking metallic pigmentation and pupil ring (*castaneoticus*, AMNH live exhibit). **Right**: State 1, with metallic pigmentation and pupil ring (*subpunctatus*, ICN specimen).

66. Large intestine color (Fig. 30): 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 ¼ 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 to state to state 2, which I interpret as evidence for the additivity of this transformation series.

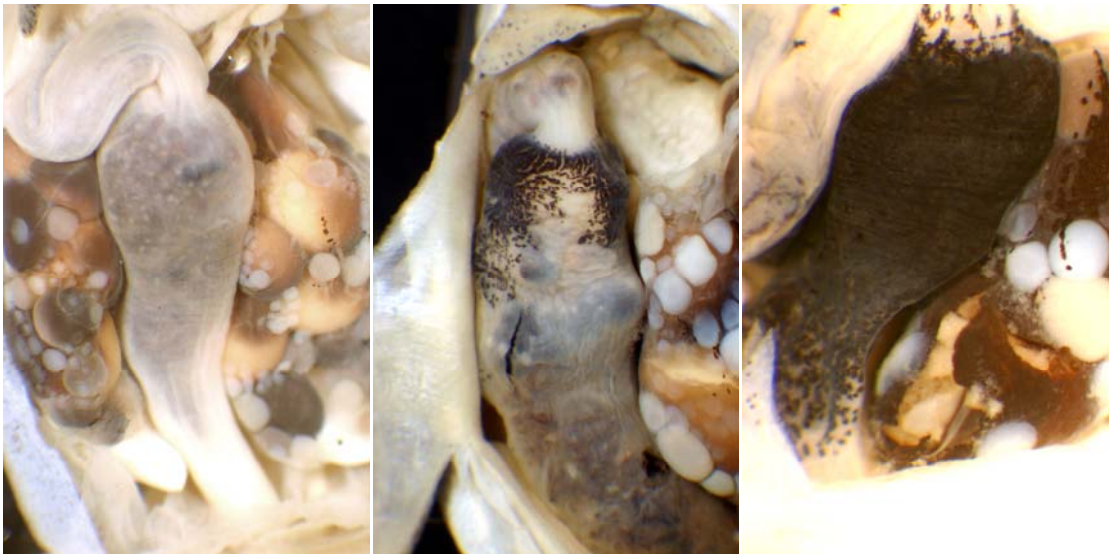


Figure 5.30. Character 66, large intestine color. **Left**: State 0, unpigmented (Neblina species, AMNH 118679). Note that the distended tissue is translucent. **Center**: State 1, anteriorly pigmented (*pratti*, SIUC 07654). **Right**: State 2, extensively pigmented (*beebei*, ROM 39631).

67. Adult testis (mesorchium) color (Fig. 31): unpigmented = 0; pigmented medially only = 1; entirely pigmented = 2. [additive].

Testis color is scored from adult males only. In all dendrobatids I 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 to state 2, which I 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 while the right testes

were pigmented brown. Grant (2004) also documented unusual variation in the testis pigmentation of *inguinalis*. Testes of all adults 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 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.

Figure 5.31. Character 67, adult testis (mesorchium) color. State 2, entirely pigmented testes (*claudiae*, AMNH 124257) in ventral view.

68. Color of mature oocytes (Fig. 5.32): unpigmented (white or creamy yellow) = 0; pigmented (animal pole brown) = 1.

The entire oocyte may be white or creamy yellow (state 0) or melanin may be deposited in the vitelline membrane of the animal hemisphere, making that part of the egg brown (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 *Rhinderma darwinii* possesses unipgmented ova, but specimens examined had pigmented ova.

Figure 5.32. Character 68, mature ova color. **Left**: State 0, white or yellowish (*Atelopus spurrelli*, AMNH 50983). **Right**: State 1, pigmented (brown) (Neblina species, AMNH 118679).

69. *M. semitendinosus* insertion (Figs.5.33–5.34): "bufonid type" (ventrad) = 0; "ranid type" (dorsad) = 1.

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 dorsad to the *mm. gracilis*, the apparent intermediacy being due 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. I am unaware of developmental evidence of migration of the *m. semitendinosus* tendon of insertion.

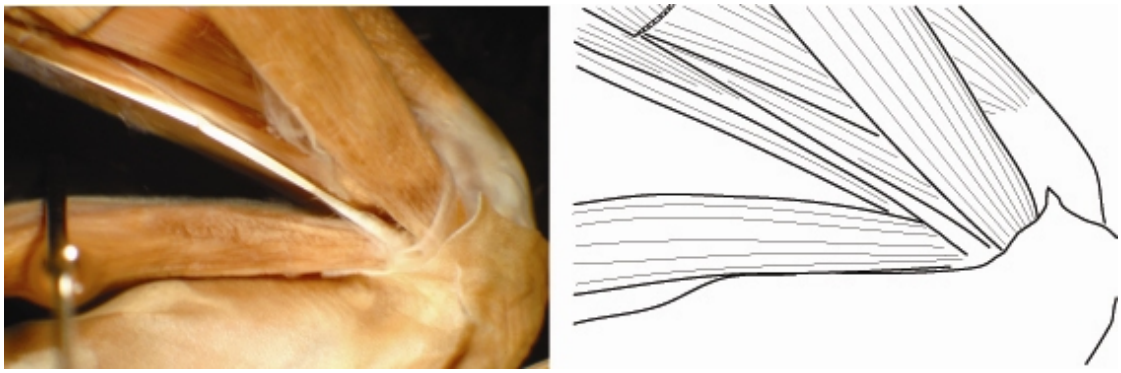


Figure 5.33. Character 69, *m. semitendinosus* insertion. Photograph (left) and outline drawing (right) of ventral view of distal thigh of *Thoropa miliaria* (AMNH 17044), showing state 0, ventrad "bufonid" path of insertion.

70. *M. semitendinosus* binding tendon (Fig. 5.34): absent = 0; present = 1.

As first described and illustrated by Noble (1922:41 and plate XV, fig. 6[1]), the dendrobatid thigh has a well-defined binding tendon[2] that straps the *m. semitendinosus*

[1] I 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

distal tendon to the dorsal edge of the inner surface of the *mm. gracilis* complex (state 1). 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.

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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; I 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.

[2] I 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*.

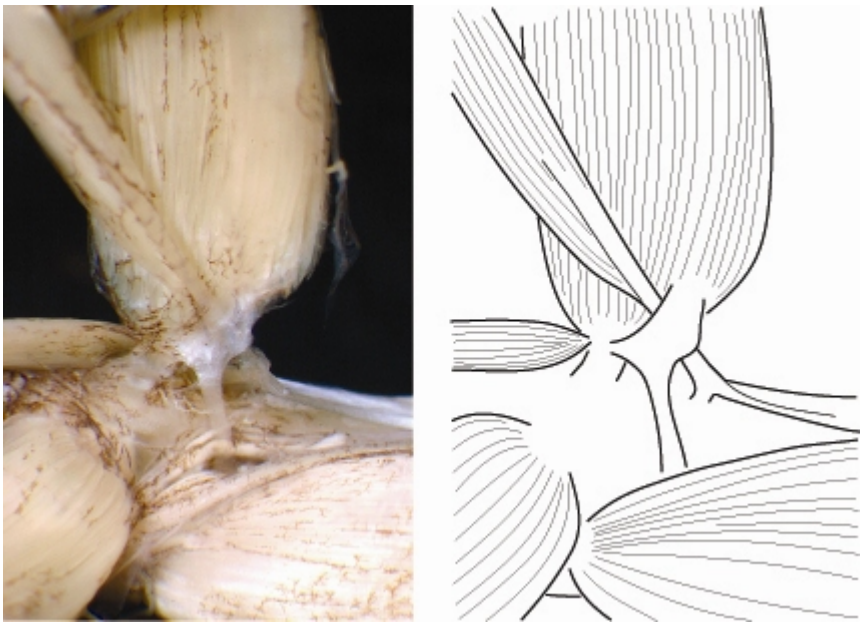

Figure 5.34. Character 70, *m. semitendinosus* binding tendon. State 1, present (*aurotaenia*, AMNH 161109), photograph (left) and outline drawing (right) showing view of the concealed surface of the knee. The *mm. gracilis* complex is deflected ventrally to reveal the dorsad "ranid" path of the *m. semitendinosus* and the secondary binding tendon that straps it to the outer edge of the *mm. gracilis* complex.

71. *M. adductor mandibulae externus superficialis*: absent = 0; present = 1.

In her dissertation, Starrett (1968[3]) found that the adductor musculature of dendrobatids includes a single muscle originating from the zygomatic ramus of the squamosal that lies medial (deep) to the mandibular ramus of the trigeminal nerve, 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 (1975) found this in all 41 species he

[3] Although generally I did not take characters from unpublished sources, the influence of this dissertation has been so great that it would be inappropriate not to attribute these characters to any other source.

examined, and Myers and co-workers (Myers et al., 1978; Myers and Daly, 1979; Myers and Ford, 1986; Myers et al., 1991; Grant et al., 1997; Grant, 1998) have found this in *almost* all dendrobatids. My observations conform generally to the accounts of previous workers, with the exception that fibers generally originate on the anterior edge of the *anulus tympanicus* as well.

The sole published exception to the “s” morphology in dendrobatids is *nocturnus*, in which Myers et al. (1991) found some specimens (or one side) to have a second muscle originating on the zygomatic ramus of the squamosal and lying superficial to both the trigeminal nerve and the *m. adductor posterior mandibulae subexternus*, i.e., the *m. adductor mandibulae externus superficialis* is present, or condition “s+e” in Starrett's terminology (state 1). The only other apparent exception to standard “s” condition was a specimen of *vanzolinii* (AMNH 108332) in which the trigeminal nerve on both sides pierces the *m. adductor posterior mandibulae subexternus*, creating the impression of the occurrence of deep and superficial muscles. However, I did not code the superficial and medial fibers as different muscles (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). That said, only a single specimen was available to me for dissection, and the symmetry of this morphology suggests this could be more than just individual variation.

Additional intraspecific variation was observed in *Hylodes phyllodes.* Of the 11 frogs in the series AMNH 103885–95, two (AMNH 103888, 103890) the trigeminal nerve runs medial to a distinct *m. adductor mandibulae externus*

superficialis (“s+e”) on both sides of the head, whereas the remaining nine specimens all lack that muscle (“s”). As in *nocturnus*, and in contrast to *vanzolinii*, the superficial fibers form a distinct muscle. Indeed, in *H. phyllodes* all of the superficial fibers appear to originate on the rim of the *anulus tympanicus*, whereas the deeper muscle originates from the squamosal. Although this latter consideration is suggestive of non-homology of the *m. adductor mandibulae externus superficialis* in these taxa, I 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 anulus. The combined morphology was codified as $DFSQ_dAT$. Lynch (1993:37) further 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 (1975) confirmed that all 41 species of dendrobatids he examined have this morphology, and this was further confirmed in additional species by Myers and co-workers (e.g., Myers et al., 1978; Myers and Daly, 1979; Myers and Ford, 1986; Myers et al., 1991).

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. My dissections confirm Lynch's observations in dendrobatids and the sampled outgroup taxa as well, leading me 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 valid transformation series. In all frogs, some fibers originate from the otic ramus of the squamosal. In all dendrobatids examined, the vast majority of fibers originate 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 I follow his terminology here (character 73). I 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 *anulus 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*. My 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. I examined 20 uncatalogued AMNH skinned carcasses of *auratus* from IslaTobago, 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 bilateral asymmetry in some specimens. Given the continuous variation, I was unable to delimit states objectively. Moreover, the extensive individual variation suggests that the differences are likely nongenetic, although I cannot offer any direct evidence to that effect. (3) Manzano et al. reported fibers originating from the *anulus tympacus* in *Rhinoderma darwinii*. However, although I observed fibers to extend toward the *anulus*, in the specimens I 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 *anulus tympanicus*: no fibers originating from *anulus tympanicus* = 0; some fibers originating from *anulus tympanicus* = 1.

Among dendrobatids, the fibers that attach to the anulus 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 sensu Liu, 1935): absent = 0; median, subgular = 1; paired lateral = 2. [additive].

I coded the vocal sac as for the species *Megaelosia goeldii*, in which males lack vocal sacs and slits and presumably do not call (Giaretta et al., 1993). However, it should be noted that 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. 35)

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 (1998) also reviewed the occurrence and variation in supplementary elements of Neotropical leptodactylids.

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 non-homologous (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, 1998; Mendelson III 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. I have therefore submitted the hypothesis of supplementary slip homology to the

simultaneous test of character congruence by coding its occurrence as a 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, I observed two patterns. In the first (state 0), the fibers radiate anteriolaterally from a sagittal raphe. In the second, the fibers extend anteromedially from the mandible. Burton (1998) reported both of these morphologies for a variety of Neotropical "leptodactylids." However, my coding deviates from Burton's (1998) in that he treated species with anterolateral supplmentary 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 I 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).

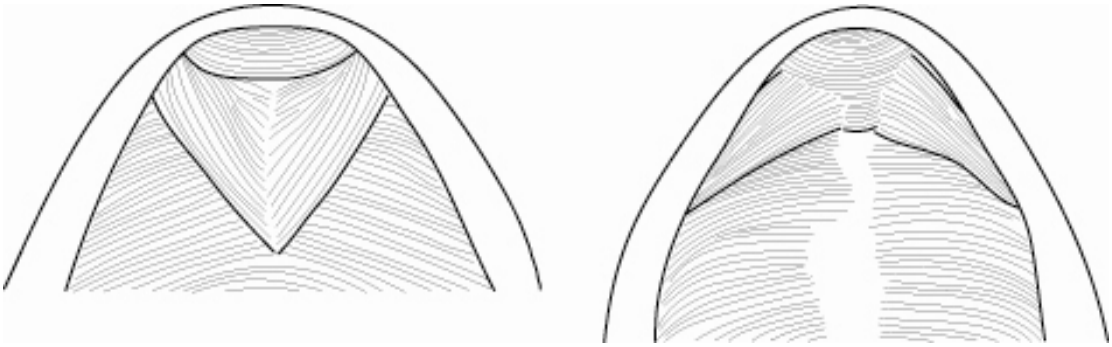

Figure 5.35. Character 79, *M. intermandibularis* supplementary element morphology. **Left**: State 0, anterolateral (*Rhinoderma darwinii*, AMNH 37849). **Right**: State 1, anteromedial (*trinitatis*, uncatalogued AMNH specimen, part of series collected with AMNH 87392–93).

79–86. Median lingual process (MLP; Figs. 5.36–5.37)

Grant et al. (1997) discovered the median lingual process (MLP) in dendrobatids and documented its occurrence and variation throughout Anura (for additional dendrobatid records see Myers and Donnelly, 1997; Grant and Rodríguez, 2001). Of great 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 I 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 forms to four “types.” For phylogenetic analysis it was necessary to decompose those types into their component transformation series.

Furthermore, given the relevance of this anatomical structure to the placement of Dendrobatidae, I 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 I 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 I therefore score all of these characters here.

To discover differences between the type C processes of Old World and New World taxa, I examined the histology of two species of the dendrobatids *tepuyensis* and *baeobatrachus*, and I compared them to *Phrynobatrachus natalensis* *Phrynobatrachus petropedetoides*. These two species of *Phrynobatrachus* have retractile type C processes, which I 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, while the other one had it retracted below the surface of the tongue. I 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 in order to delimit transformation series more rigorously and were not coded for phylogenetic analysis). Due to lack of specimens, I did not examine any type B or D processes.

The MLP of all examined taxa (i.e., types A and C, retractile and non-retractile) is formed through the same modification of 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. 5.36) 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 I 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.

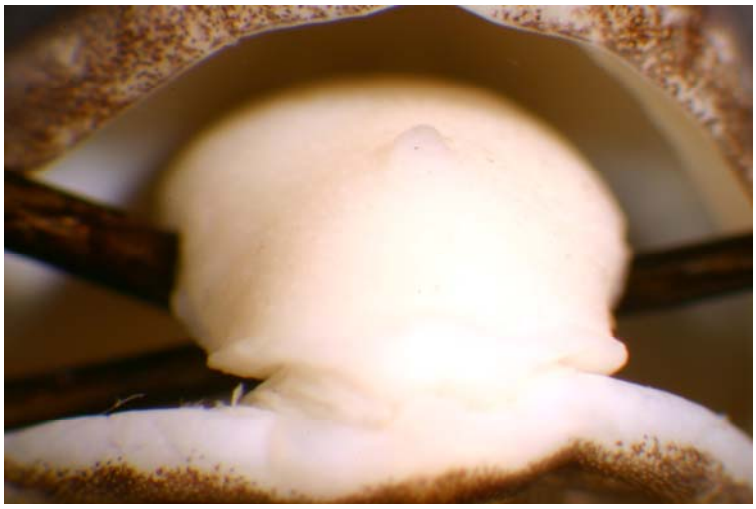

Figure 5.36. Anterior view of the open mouth of the dendrobatid *praderioi* (CPI 10203) showing the short, tapered median lingual process (MLP).

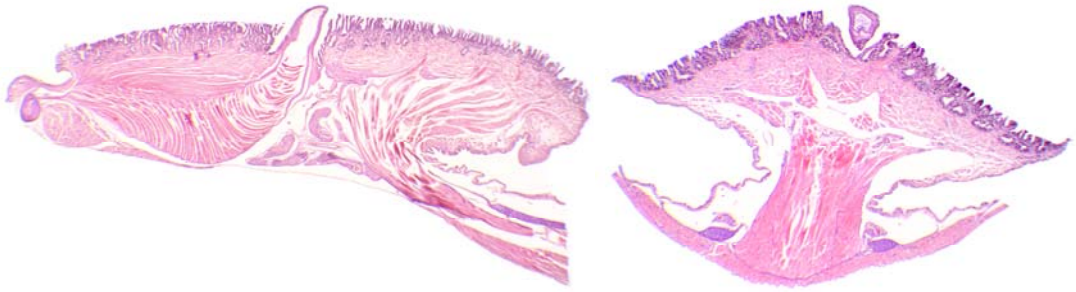

Figure 5.37. Histological sections of the median lingual process (MLP) of the dendrobatid *baeobatrachus*. **Left**: Longitudinal section of AMNH 140672 showing that the MLP is an extension of the *m. genioglossus*. Note that the muscle fibers do not extend to the tip of the MLP. **Right**: Transverse section of AMNH 140665 showing the distal, free portion of the MLP. Note the conspicuous pit that surrounds the MLP.

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

In order to count the origin of the MLP as a single event (and not as multiple origins of each of the nested characters), I score 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.

I 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.

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. 5.38): nonretractile = 0; retractile = 1.

Following the reasoning of Grant et al. (1997), retractility was inferred from the position of the MLP in preserved specimens. I was unable to detect any histological differences between retractile and non-retractile processes. However, the fact that even very small series of some species show the MLP in various stages of retraction while 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 Fig. 5.38 (left) 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 5.38, right), 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.

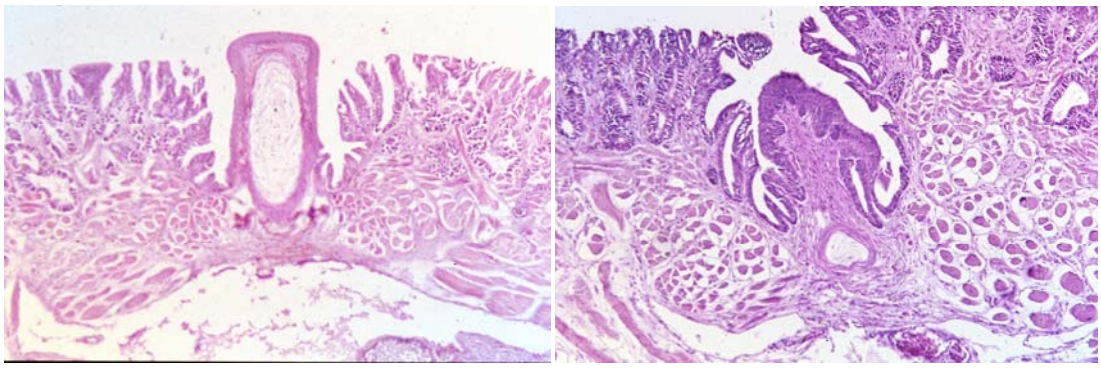

Figure 5.38. Character 84, median lingual process (MLP) retractility, state 1 (retractile). **Left**: Transverse section of a protruded MLP in *Phrynobatrachus natalensis* (AMNH 129714). **Right**: Transverse section of a retracted MLP in *Phrynobatrachus petropedetoides* (AMNH 129626).

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. It should be noted that 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. 5.39): glandular = 0; nonglandular = 1.

Data are available for a very limited number of species, In state 0 the surface of the MLP is pitted with invaginations of the epithelium which 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.

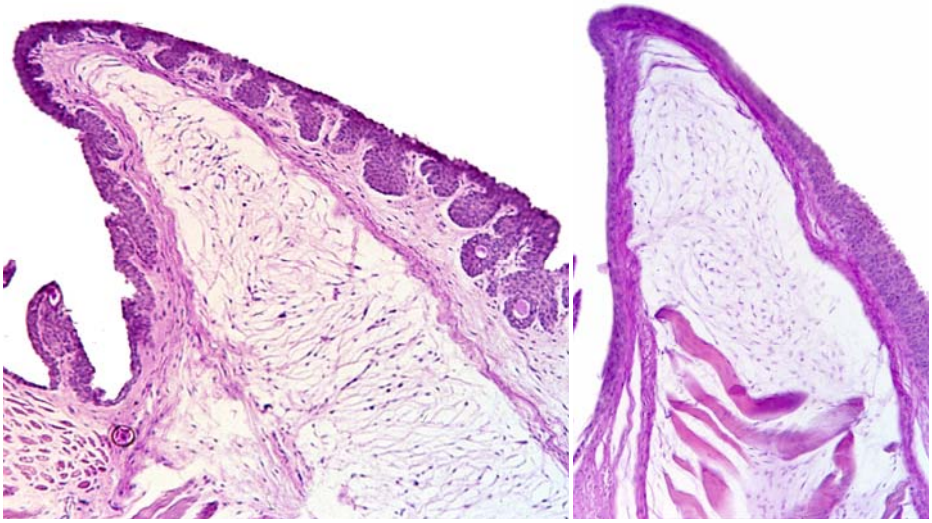

Figure 5.39. Character 86, median lingual process (MLP) epithelium. **Left**: State 0, glandular (*Phrynobatrachus petropedetoides*, AMNH 129593 The surface of the MLP is pitted with invaginations of the epithelium which form alveolar glands. **Right**: State 1, nonglandular (*Phrynobatrachus natalensis*, AMNH 129732). The alveolar glands are absent, and the surface of the MLP consists of unmodified stratified epithelium.

87–98. Larvae

With a few remarkable exceptions, dendrobatid larvae are largely invariable. 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, 1974),

Lynch (1971), McDiarmid (1971), Silverstone (1975a; 1976), Lescure (1976), Duellman (1978), 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 (1997a), Lötters et al. (1997), Grant and Castro-Herrera (1998), Faivovich (Faivovich, 1998), Lindquist and Hetherington (1998), Lötters et al. (2000), Caldwell et al. (2002), Caldwell and Lima (2003), Nuin (2003), Castillo-Trenn (2004), and Duellman (2004).

87. Larval caudal coloration: vertically striped = 0; scattered melanophores clumped to form irregular blotches = 1; evenly pigmented = 2. [nonadditive].

Caldwell et al. (2002) 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 inconspicuous 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: “normal” = 0; umbelliform = 1; absent = 2; suctorial = 3. [nonadditive].

As described by Haas (2003:54), “The 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 an thick, fleshy upper lip that is attached medially and lacks marginal papillae and a lower lip that is free but relatively narrow and bears marginal papillae. The umbelliform (funnel-shaped) oral disc (state 1; Fig. 5.40) is greatly enlarged relative to state 0. The upper lip is free and the marginal papilae 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 and consists of

Figure 5.40. Character 88, larval oral disc. **Top**: State 0, "normal" (Neblina species, AMNH 118673). State 1, umbelliform disc (*nubicola*, AMNH 94849). **Top**: Ventral view. Note also the median papillae (character 91). **Bottom**: Lateral view.

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).[1] The marginal papillae of some

[1] 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

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. (2002).

91. Submarginal papillae of larval oral disc (Fig. 5.40): absent = 0; present = 1.

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

92. Median gap in marginal papillae of lower labium: absent = 0; present = 1.

Among the species included in the present study, the median gap in the marginal papillae of the lower labium occurs only in the outgroup. 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.

93. Anterior larval tooth rows: 0 = 0; 1 = 1; 2 = 2. [additive].

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papillae remains constant, i.e., as the tadpole grows the number of marginal papillae increases while the size of each papilla remains approximately the same.

Haddad and Martins (1994) reported the absence of anterior tooth rows in *hahneli*, and I confirmed their observations in tadpoles of early stages. However, tadpoles of later stages possess a single anterior tooth row. The unusual shape of the mouth, illustrated by Haddad and Martins, is retained until metamorphosis.

94. Posterior larval tooth rows: 0 = 0; 1 = 1; 2 = 2; 3 = 3. [additive].

Haddad and Martins (1994) reported the absence of posterior tooth rows in *hahneli*, and I confirmed their observations in small (e.g., stages 25 or 26) tadpoles. However, tadpoles of later stages possess two posterior tooth rows.

95. Larval jaw sheath: absent = 0; lower jaw only, not keratinized = 1; entire, keratinized. [additive].

96. Larval anus position: dextral = 0; median = 1.

Myers (1987) claimed the position of the larval anus 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). Donnelly et al. (1990) later reported that the anus of *aurotaenia*, *lugubris*, *terribilis*, and *vittatus* is medial at Gosner stages 24 and 25 but migrates to become dextral by stage 37 (or earlier). Because ontogenetic series were unavailable for most dendrobatids, and I coded the position of the larval anus as observed in the most developed larva examined. As such, for example, I coded the anus of *aurotaenia*, *lugubris*, *terribilis*, and *vittatus* as dextral.

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

98. Lateral line stitches: absent = 0; present = 1.

The lateral line system is composed of receptor organs (mechanoreceptive neuromasts ad 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 actually due to the absence of the stitches. The occurrence of stitches varies among dendrobatids, and I 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; Myers and Donnelly, 2001; Castillo-Trenn, 2004), but they are frequently overlooked, and their absence is usually not reported. Although stitches are large and conspicuous in some species, they are barely detectable in others, due 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, I scored the lateral line stitches as absent when the authors were either explicit or provided adequate

illustrations for the them to have been seen or extremely thorough descriptions that (I assume) would have noted stitches had they been visible.

In addition to the presence and absence of stitches, I observed variation in the system of rami they form. However, as also observed by Castillo-Trenn (2004) in *kingsburyi* and R. W. McDiarmid (pers. comm.) in other anurans, I 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; Zimmermann and Zimmermann, 1988; Weygoldt, 1987; Summers et al., 1999). 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 stereotypic 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 stereotypical 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, I proposed hypotheses of homology of behaviors judiciously.

An example of over-interpretation of behavioral observations is Zimmermann and Zimmermann (1988), who performed a phenetic analysis of 62 variables (including vocalizations and larval morphology) for 32 species. I 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 non-independent (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 [personal observation; A. Suárez-Mayorga, personal communication], whereas *fraterdanieli* carries up to at least 12 (personal observation), and *palmatus* nurse frogs transport up to 31 tadpoles [Lüddecke, 2000 "1999"]), the number of dorsal tadpoles observed is highly variable (e.g., Myers et al. [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 transported and 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 much more information is needed before characters can be delimited meaningfully.

There is extensive missing data for behavioral characters, which necessarily limits the impact of these characters on the present analysis. However, one of my 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, I hope to draw attention to them for use in future behavioral studies. Especially problematic are absences; for the present purposes, I coded conspicuous behaviors not reported in detailed studies as absent, but it is possible that they were simply not noted. A similar problem is that even detailed notes may fail to mention expected observations, such as diurnal activity in dendrobatids. I did not make assumptions regarding these characters and only scored them from personal observation or explicit statements.

In addition to personal observations and unpublished field notes, behavioral data (not 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), 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), Lüddecke (1976, 2000 "1999"), Wells (1978; 1980a; 1980b; 1980c), Myers et al.

(1978), Myers and Daly (1976a; 1979; 1980; 1983), Cei (1980), Limerick (1980), Weygoldt (1980; 1987), Vigle and Miyata (1980), E. Zimmerman (1981), Zimmermann and Zimmermann (1981, 1984, 1985, 1988), Kneller (1982), Hardy (1983), Heyer (1983), Myers et al. (1984), Dixon and Rivero-Blanco (1985), Jungfer (1985, 1989), Frost (1986), Duellman and Lynch (1988), Formas (1989), Summers (1989; 1990; 1992; 1999; 2000), Caldwell and Myers (1990), Aichinger (1991), Myers et al. (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. (1996), La Marca (1996 "1994", 1998 "1996"), Caldwell (1997), Fandiño et al. (1997), Grant et al. (1997), Caldwell and Araújo (1998; 2004), Juncá (1998), Grant and Castro-Herrera (1998), Morales and Velazco (1998), Boistel and de Massary (1999), Caldwell and de Oliveira (1999), Summers et al. (1999), Haddad and Giaretta (1999), Hoff et al. (1999), Kok (2000), Köhler (2000), Lescure and Marty (2000), Lötters (2000), Bourne et al. (2001), Downie et al. (2001), Lima et al. (2001, 2002), Myers and Donnelly (2001), Summers and Symula, (2001), Caldwell and Lima (2003), Giaretta and Facure (2003), Lima and Keller (2003), Grant (2004), Lehtinen et al. (2004), Toledo et al. (2004), and Summers and McKeon (2004).

99. Advertisement calls: peep = 0; buzz = 1; croak = 2; trill = 3; chirp = 4; retarded trill = 5; harsh peep train = 6; whistled trill = 7. [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., 2003), but their use in systematics has been predicated on their classification as 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), retarded chirp (Myers and Burrowes, 1987:16) or harsh peep train (Rodríguez and Myers, 1993), and the diversity of dendrobatid calls extends far beyond these few types. Additional characterizations such as peeps, cricket-like chirps, croaks, whistled trills (e.g., Grant and Castro-Herrera, 1998; Bourne et al., 2001) have been employed, although none of these is defined precisely.

It is clear that all of these call types are composites of independent temporal and spectral transformation series that must decomposed into independent transformation series for phylogenetic analysis. Unfortunately, time constraints prevented me from accomplishing this in the present study. However, in order to incorporate limited information from vocalizations and test prior hypotheses (e.g., the buzz call as a synapomorphy of the *histrionicus* group) I scored advertisement calls according to the present scheme. 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.

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 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 other species by several authors (Weygoldt, 1987, Jungfer, 1985; Jungfer et al., 1996; Jungfer et al., 2000; Lötters et al., 2000). Jungfer et al. (1996) 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 straight-forward as Jungfer et al. implied.

105. Copulatory amplexus (Fig. 5.41): absent = 0; axillary = 1; cephalic = 2. [nonadditive].

Myers and Daly (1978:324–325) first described and illustrated cephalic amplexus in *tricolor*; it is unknown in non-dendrobatid frogs. Although copulatory amplexus is absent in numerous dendrobatids (a variety of pseudo-amplectant positions—including cephalic grasping—may be employed in aggressive and/or courtsip behavior), cephalic amplexus was cited by numerous authors (e.g., Myers and Ford, 1986; Myers et al., 1991; Duellman and Trueb, 1986) as a dendrobatid synapomorphy, with the absence in numerous dendrobatids explained as a derived loss. The sampled outgroup species exhibit axillary amplexus.

Figure 5.41. Character 105, copulatory amplexus. State 2, cephalic amplexus (*anthonyi*, AMNH live exhibit).

106. Cloaca-cloaca touching: 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 bring their cloacae into contact.

107. Egg deposition site: aquatic = 0; terrestrial: leaf litter, soil, under stones = 1; terrestrial: above ground in 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].

109. Dorsal tadpole transport (Fig. 5.42): absent = 0; present = 1.

Noble (1927:103) noted that his grouping together 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).

Males of *Rhinoderma darwini* 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 known to have terrestrial (non-transported) 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 (1993) reported male egg attendance, which leaves open the possibility of tadpole transport.

Dorsal tadpole transport is here coded as a single transformation series, but even the extremely limited evidence that is available suggests this is much more complex and probably involves multiple characters. Stebbins and Hendrickson

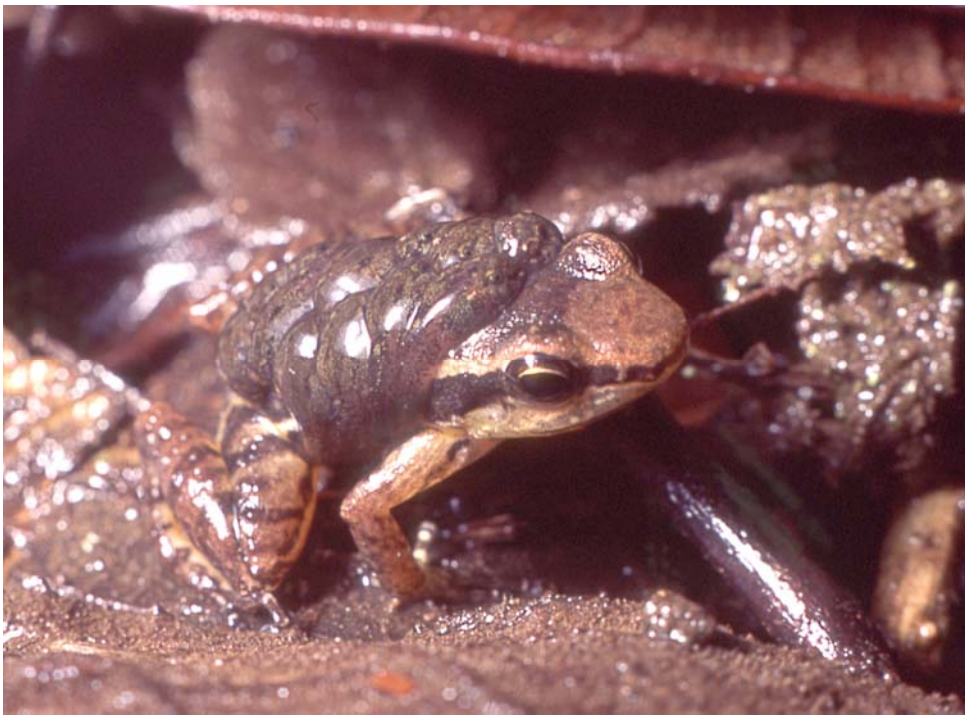


Figure 5.42. Character 109, dorsal larval transport. State 1, present (*fraterdanieli*, specimens at UVC). This male nurse frog was transporting 12 tadpoles.

(1959:509) reported in *subpunctatus* that "The tadpoles are anchored to the back of the frog by a sticky mucus. Myers and Daly (1980:19) further noted that

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

To this I 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 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, but would only mount and settle on a live frog, with no sexual discrimination. In a less controlled experiment with hatching *anthonyi* I found that that barely touching the jelly capsule with a finger was sufficient to stimulate hatching, immediate mounting, settling, and attachment (i.e., the tadpoles remained attached to my 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].

I follow Ruthven and Gaige (1915:3) in referring to the individual that performs larval transport as the *nurse frog*. Among species that transport larvae, the role of the nurse frog is typically assumed by one sex (Wells, 1978; Wells, 1980a; Wells, 1980b; Wells, 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, i.e., 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. J. P. Caldwell (*in litt.*, 08/24/00) also observed that females will occasionally be found transporting tadpoles in several species in which the male usually performs 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. H. 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 primitve.

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 transformation event. For the time being, I coded each species based on available information. I 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.

I 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, i.e., it involves more than just the co-occurrence of states 1 and 2. Also, I did not specify any particular additivity for this transformation series, as there is no evidence that the shift between sexes requires a coorperative (or competitive) intermediate biparental stage (although this could be revealed through 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; nurse frogs of both sexes have been reported for *femoralis* (Silverstone, 1976; Lescure, 1976), *hahneli* (as *pictus*; Aichinger, 1991) and *trilineatus* (Aichinger, 1991), and exclusively female nurse frogs have been reported for *talamancae* (Grant, 2004 and references cited therein). Insofar as Savage and Summers and McKeon did not dispute those reports or provide specimen documentation, I dismiss their scoring as erroneous.

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 Johnson, 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 ground level pool, stream or other body of water, and nurse frogs

may transport larvae to either level pool or slow-flowing stream or other body of water or phytotelmata.

Although "phytotelm" often refers to chambers above ground (e.g., bromeliads), technically the term applies to any plant-held waters. 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 I therefore did not discriminate between ground-level and higher phytotelmata. For example, I followed Caldwell and de Araújo (1998; 2004), scored *castaneoticus* as a phytotelm breeder because it uses Brazil nut husks.

112. Larval diet: detritivorous = 0; predaceous = 1; oophagous = 2; endotrophic. [nonadditive].

The vast majority of anurans have detritivorous tadpoles (state 0). I 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 Araújo, 1998; state 1). Several species consume sibling oocytes (oophagous, state 1), either exclusively (*histrionicus* group; Limerick, 1980) or as part of a predaceous diet (e.g., *vanzolinii*; Caldwell and Araújo, 1998). I coded the latter taxa as polymorphic; see also character 113 (Provisioning of oocytes for larval oophagy).

Four species with endotrophic larvae have been described (state 2): *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.

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 (demonstrated experimentally for *pumilio* by Brust, 1993), while the others are predaceous (Caldwell and Araújo, 1998).

Zimmerman and Zimmerman (1988) reported biparental provision of oocytes in *ventrimaculatus* (as *quinquevittatus*) in captivity, but Summers et al. (1999) 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 at 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, i.e., 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; Wells, 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." Territorial and courtship behaviors occur well away from ground water. Although their density may be greater nearer to streams, even in extremely wet environments such as the Colombian Chocó (personal observation) 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 water.

A potential fourth character-state would be arboreality. For example, Myers et al. (1984) named *arboreus* in recognition of that species' arboreal habitat preference, while 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 meters above ground to deposit larvae in bromeliads (personal observation; A. Suárez-Mayorga, pers. comm.). 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 I 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 I have failed to recognize the additional transformation(s) from state 2a (terrestrial) to state 2b (arboreal).

115. Diel activity: nocturnal = 0; diurnal = 1.

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, I coded these species as polymorphic.

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

Several species have been observed 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 to 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 does not seem to correlate with any particular stimulus. Toe trembling may (or may not) occur while foraging and during inter- and intraspecific interactions with individuals of the same or opposite sex. As far as I know, toe trembling is known only in dendrobatids.

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; I 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 the 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 of absence of epicoracoid horns (for historical usages see Kaplan, 2004), with the epicoracoids of dendrobatids characterized as entirely fused and non-overlapping and lacking epicoracoid horns, as in "firmisternal" taxa.[2] However, this is clearly an oversimplification (e.g., Noble, 1926; Kaplan, 1994; Kaplan, 1995; Kaplan, 1997a;

[2] I place "firmisternal" and "arciferal" in quotes and use the terms to refer to the taxonomic groups 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), and their conflation has led to much unnecessary confusion in anuran systematics. Although it may potentially 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 I concur with Kaplan that the terms should be abandoned.

Kaplan, 1997b; Kaplan, 2000; Kaplan, 2001; Kaplan, 2004). Recently, Kaplan (2004) proposed dividing girdle architecture variats into separate transformation series relating to degree of fusion (freedom) and overlap (nonoverlap), and he proposed explicit character-states, which I 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 (1971), 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).

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 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).

Precise assessment of these characters requires detailed histological study that was infeasible for the present study. However, given the importance of epicoracoid morphology in all previous discussions of dendrobatid phylogeny, I believe it would be inappropriate to exclude it altogether. Therefore, although I am cognizant of the potential errors that may be incorporated into the analysis, I coded degree of fusion and overlap in adults (or near adults) as precisely as possible through only 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 I coded this species as lacking overlap. Insofar as I 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.]

State 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 I considered to be evidence of for the hypothesis of 0↔1↔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.]

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 I was unable to find evidence to select one hypothesis of additivity over another; I therefore treated this character nonadditively.

121. Angle of clavicles (Fig. 5.43): 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.

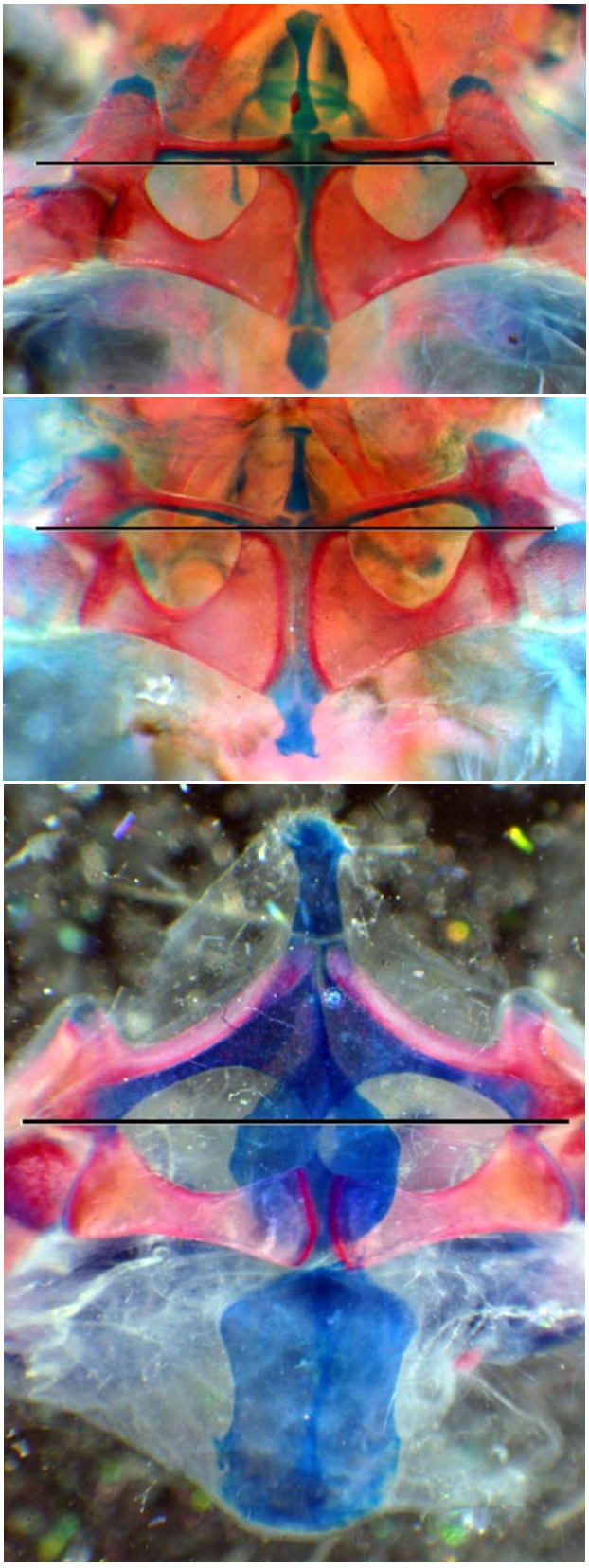


Figure 5.43. Character 121, angle of clavicles. **Left**: State 0, directed laterad (*steyermarki*, AMNH 118572). **Middle**: State 1, directed anteriad, approximately parallel to the posterior margin of the coracoid (*opisthomelas*, AMNH 102582). **Bottom**: State 2, directed anteriad (*Eupsophus roseus*, KU207501). In each image, the horizontal black bar provides the reference for lateral orientation.

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

The acromion processes of some taxa are cartilaginous (state 0) in mature specimens, whereas in others they are extensively calcified or ossified (state 1). I did not distinguish between extensive calcification and ossification.

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× or greater = 2. [additive].

125. Prezonal element (omosternun) 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.

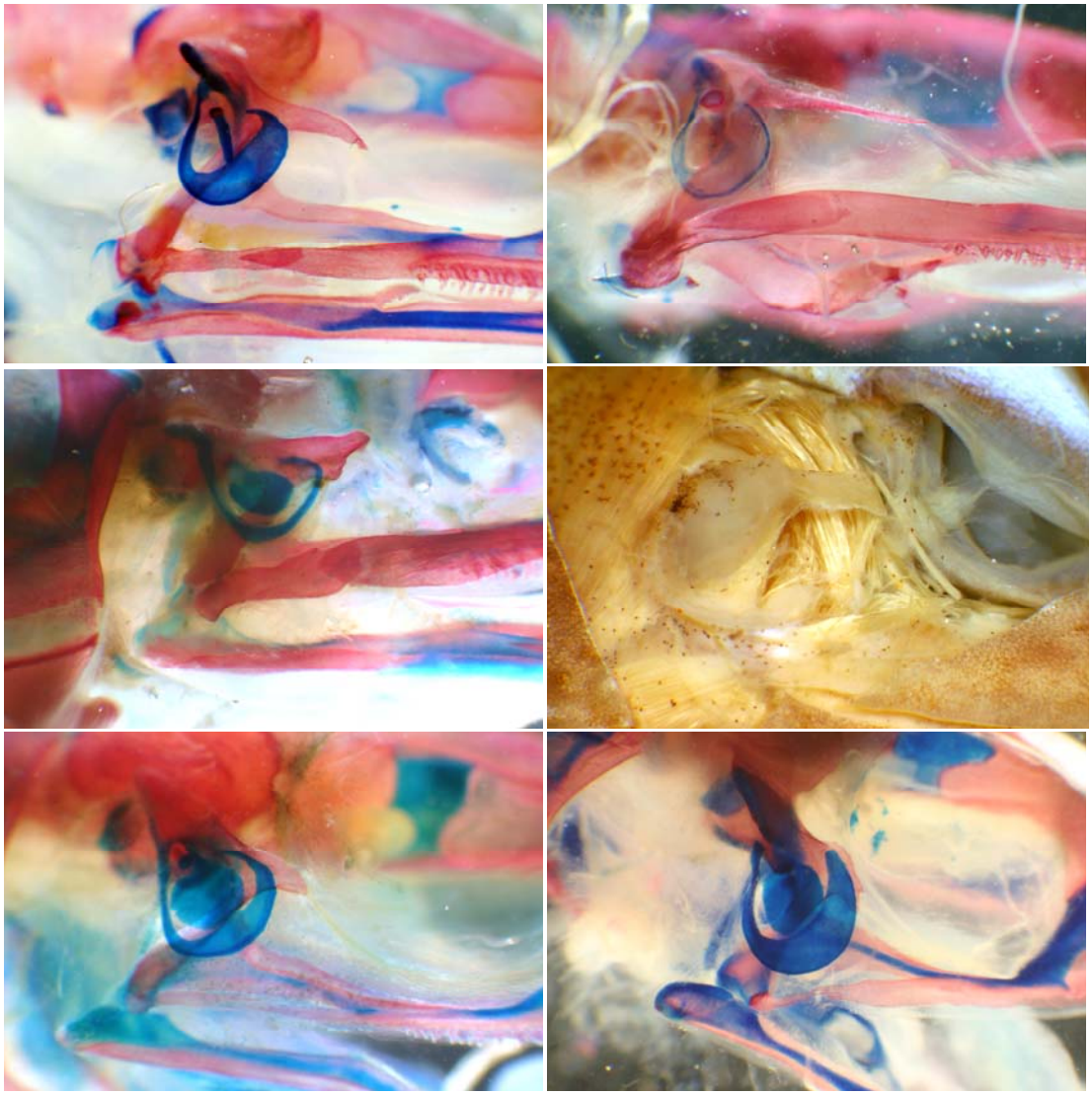
129. Sternum shape: simple (rounded, irregular) = 0; medially divided = 1.

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. I 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, I also observed confounding intermediate and other variation and was unable to individuate states objectively for the current study.

130. Zygomatic ramus of squamosal (Fig. 5.44): 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, hook-like = 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 extending 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, i.e., 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, hook-like process (state 6). McDiarmid (1971) considered the zygomatic ramus to be absent in *Melanophryniscus*; however, I found a miniscule bump (state 7) is observed in *Melanophryniscus stelzneri*, which I considered to be homologous with the zygomatic ramus. (Regardless, I 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 zygomatic ramus is (state 8).



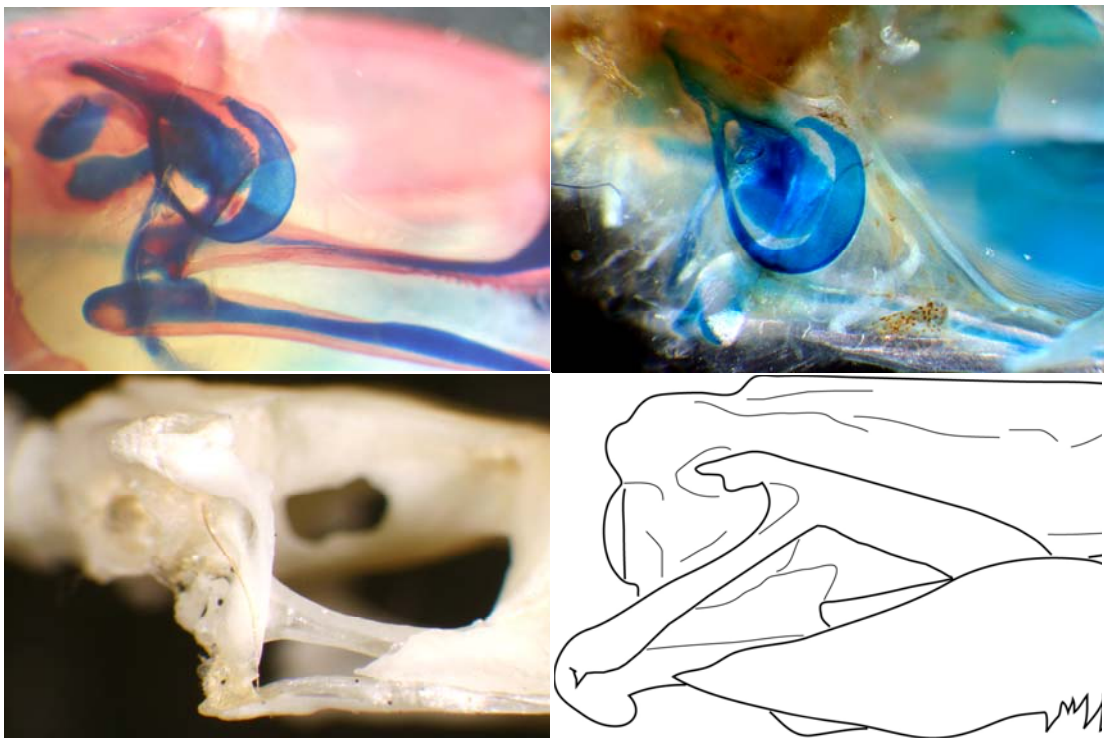


Figure 5.44. Character 130, zygomatic ramus of squamosal. From top to bottom: **Row 1, left**: State 0 (*Eupsophus roseus*, KU 207501). **Row 1, right**: State 1 (*Cycloramphus fuliginosus*, KU 92789). **Row 2, left**: State 2 (*nocturnus*, AMNH 130041). **Row 2, right**: State 2 shown in a dissected whole specimen (*palmatus*, AMNH 20436). **Row 3, left**: State 3 (*trinitatis*, AMNH 118389). **Row 3, right**: State 4 (*trivittatus*, AMNH 118428). **Row 4, left**: State 5 (*espinosai*, AMNH 118417). **Row 4, right**: State 6 (*bocagei*, UMMZ 182465). **Row 5, left**: State 7 (*Melanophryniscus stelzneri*, AMNH 77710). **Row 5, right**: State 8 (*Megaelosia goeldii*, redrawn from Lynch, 1971:169, fig. 110).

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). I treated this transformation series additively (0↔1↔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, 1975; 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, i.e., it is a conclusion of phylogenetic analysis, not a premise. I 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. 5.45): separated = 0; in contact = 1.

The nasal and maxilla may be separate (state 0) or contact each other. I 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.

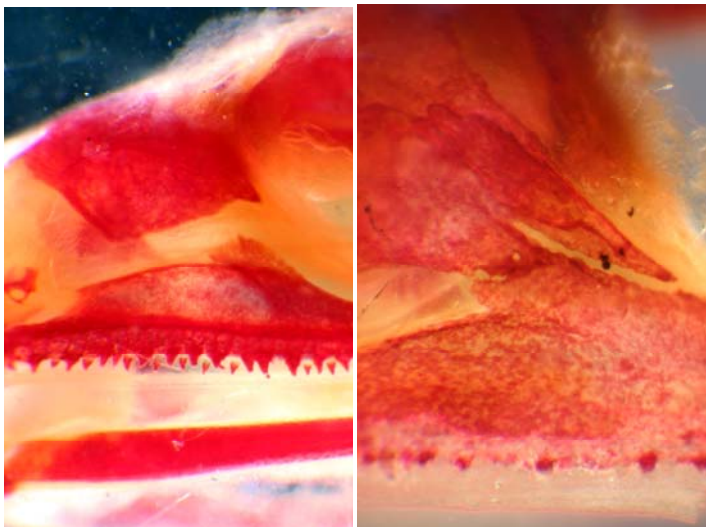


Figure 5.45. Character 134, nasal–maxilla relation. **Left**: State 0, nasal and maxilla broadly separated (*silverstonei*, AMNH 91847). **Right**: State 1, greater magnification showing nasal and maxilla overlapping or fused (*bassleri*, AMNH 43402).

135. Nasal–sphenethmoid relation (Fig. 5.46): 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. I did not distinguish between overlapping and fusion as the necessary histological analysis was infeasible for the present study.

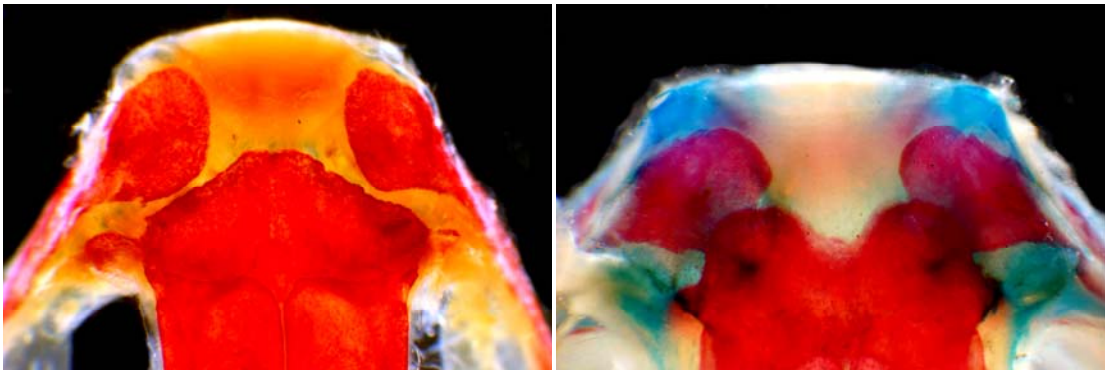


Figure 5.46. Characer 135, nasal–sphenethmoid relation. **Left**: State 0, separate (*bassleri*, AMNH 43402). **Right**: State 1, overlapping or fused (*nocturnus*, AMNH 130014). In this case the nasals clearly overlap but are not fused with the sphenethmoid, but in other species the distinction between the bones is not as clear.

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. I 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 I 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 lacking maxillary teeth (*Dendrobates*) and those having maxillary teeth (*Phyllobates* and *Colostethus*)." Silverstone (1975) showed that the situation is somewhat more complicated due to character conflict and polymorphism. (See also Chapter 4 for 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." I

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. 5.47): absent = 0; present = 1.

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 Fig. 5.47, there is considerable interspecific variation in the length of the retroarticular process. However, I was unable to delimit states, in part because there is no clear choice for a standard reference.

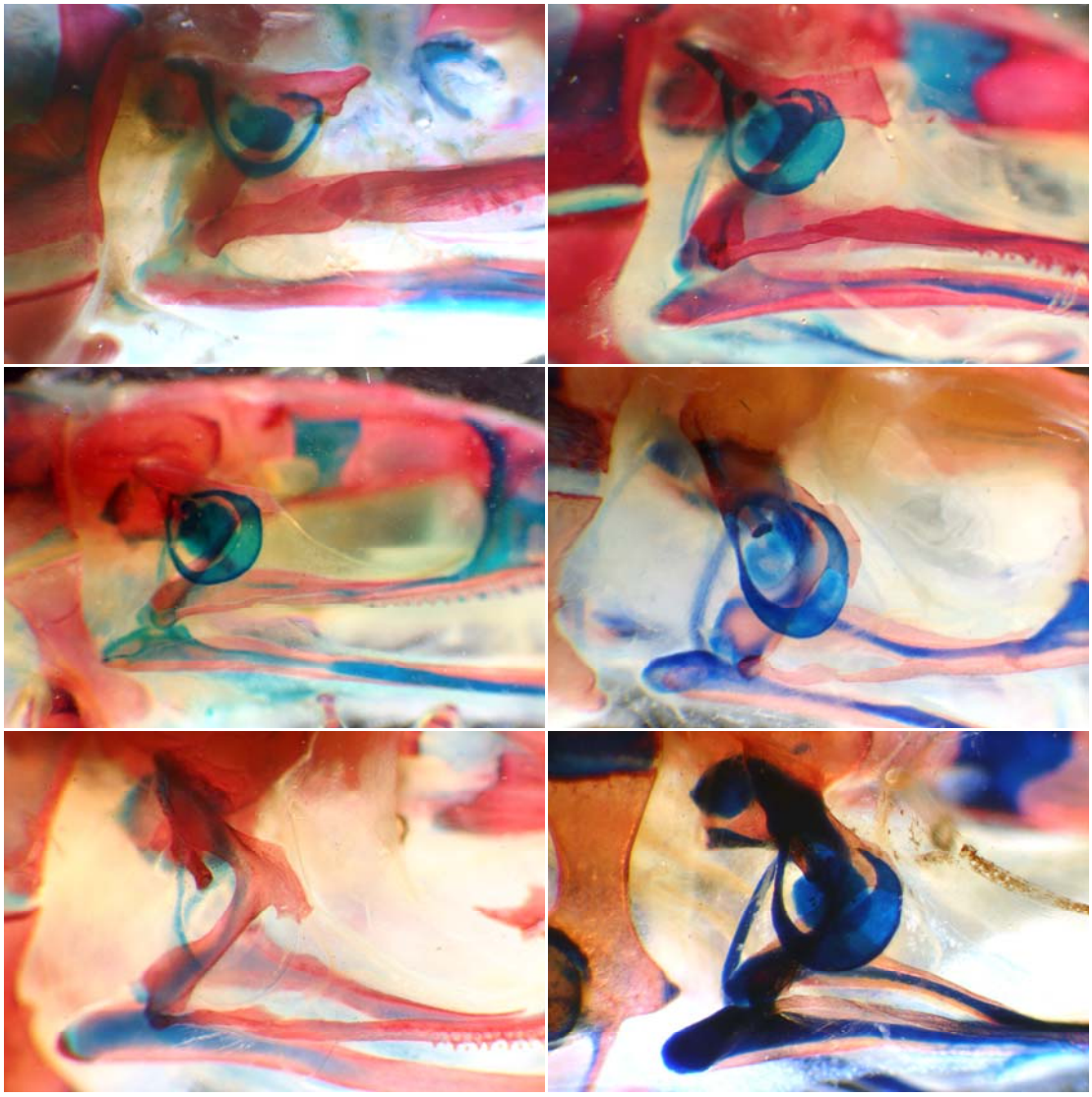


Figure 5.47. Length variation in character 142, retroarticular process of the mandible. **Top left**: *nocturnus*, AMNH 130041. **Top right**: *riveroi*, AMNH 134142. **Middle left**: *vittatus*, AMNH 118386. **Middle right**: *lehmanni* AMNH118442. Bottom left: *pratti*, AMNH118364. **Bottom right**: Neblina species, AMNH 118667.

143. Expansion of sacral diapophyses (Fig. 5.48): 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 roll 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 I refer instead to the degree expansion of the sacral diapophyses. Emerson (1982) quantified expansion by measuring the angle formed by the expansion. Here I code this character as the ratio of the width of the tip of the diapophysis to the width of the base of the diapophysis. Unexpanded diapophyses are subequal at the base and tip. Moderately expanded diapophyses are 1.5–2.5× wider at the tip than at the base; greatly expanded diapohyses are at least 2.7× greater at the tip. Sacral diapophyses often bear irregular flanges that I did not include in the measurement of width.

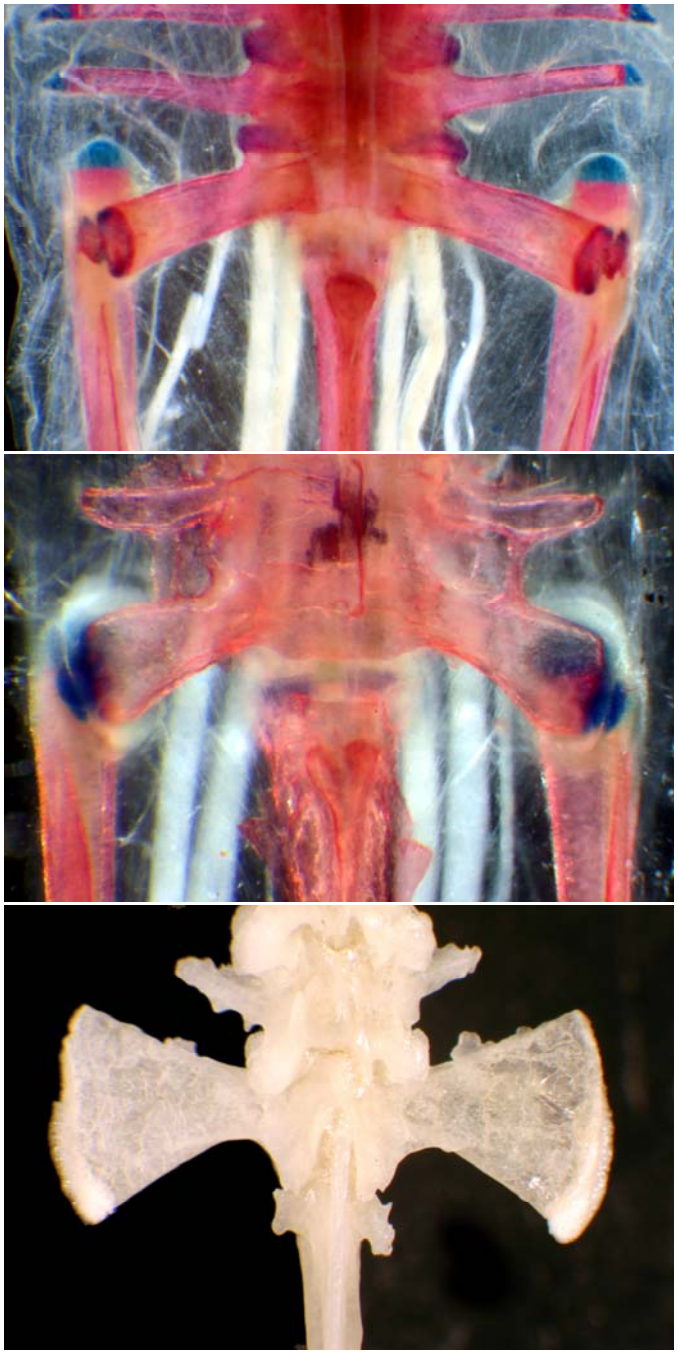


Figure 5.48. Character 143, expansion of sacral diapophyses. **Top**: State 0, unexpanded (*riveroi*, AMNH 134143l). **Middle**: State 1, moderately expanded (*pumilio*, AMNH 118514). **Bottom**: State 2, greatly expanded (*Melanophrybiscus stelzneri*, AMNH 77710).

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 *Dendrobates sylvaticus* [discussed under the tentative name *Dendrobates tinctorius*]). Silverstone (1975:5) 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. I 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.

146. Vertebrae 2 and 3: free = 0; fused = 1.

147–175. 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, 1976: 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., 1994a; Daly et al., 1994c; Daly et al., 1992).

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., 2003; Daly et al., 1994c; Garraffo et al., 2001), i.e., 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 by certain dendrobatid species and not others (see character 174). 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, I coded alkaloid profiles as "any instance" (Campbell and Frost, 1993). That is, I 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; Grant and Kluge, 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 I 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 *D. lehmanni* (Myers and Daly, 1976), Garraffo et al. (2001:421) report that "Feeding experiments indicated that *D. lehmanni* readily accumulated histrionicotoxin into skin when fed alkaloid-dusted fruit flies."

It should be noted that 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, i.e., most of the alkaloids are unknown elsewhere in nature. Potential sources were reviewed by Daly et al (1993:226), as follows: Pyrrolizidines are known to occur in the ants *Solenopsis xenovenenum*, *Monomorium* spp. from New Zealand, and *Megalomyrex* from Venezuela. Pyrrolidines (including 2,5-pyrrolidines, known among amphibians only in dendrobatids) and pyrrolidines occur in *Solenopsis*, *Monomorium*, and *Megalomyrex*. 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), and two pumiliotoxins found in *pumilio* is are obtained from formicine ants (Saporito et al., 2004). Batrachotoxins are probably obtained from melyrid beetles (Dumbacher et al., 2004).

That the actual dietary source is unknown is an important consideration given the recent finding of Daly et al. (2003) that some species convert dietary pumiliotoxin to allopumiliotoxin via a specific hydroxylation event (see character 175, below). Whereas prior to this discovery it was assumed that all of the over 450 alkaloids known in these frogs were incorporated "as-is" 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 seems unlikely that such conversion will

be found to be widespread, 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, I was 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, I scored the occurrence of the major and minor classes of alkaloids, following Daly et al. (1993; 1987) and incorporating more recent developments (e.g., Daly et al., 1994c; Daly, 1998; Garraffo et al., 1997; Garraffo et al., 2001; Garraffo et al., 1993; Daly et al., 1999; Daly et al., 2003; Mortari et al., 2004; J. W. Daly, *in litt.*, 01/25/05). I 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, I 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.

I did not distinguish between major, minor, and trace occurrences of alkaloids (i.e., I treated all as "present"), but, following Daly's recommendation (J. W. Daly, *in litt*., 02/02/00), I did not consider "trace, trace" occurrences as evidence of presence of an alkaloid, as merely having recently eaten an alkaloid-containing prey item could give this result.[1] I also did not discriminate based on uptake efficiency. For example, although uptake of piperidines is poor in most species (e.g., *auratus*, in which it they are trace alkaloids), and uptake of piperidine **241D** appears highly efficient in *speciosus* (in which this is a major or minor alkaloid), I 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 for *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 174), there is no evidence that they share a common biosynthetic origin, and even if they do, that would pertain to the arthropods,

[1] 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 me 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."

not the frogs. Historical independence is demonstrated by the fact that no classes of alkaloids share identical taxonomic distributions. I therefore treated alkaloid profiles as multiple binary characters.

I coded unambiguously only those species whose alkaloid profiles have been examined; taxa whose profiles have not been examined were coded as unknown ("?"). The most widely accepted taxonomy (Myers, 1987; Myers et al., 1991; La Marca, 1992; La Marca, 1994) was based in part on extrapolation from known profiles in light of the distribution of other characters—primarily (but not exclusively) bright coloration, (implicitly) because it is assumed to be correlated with toxicity. This resulted in all relatively dull species being assigned to *Aromobates*, *Colostethus*, *Mannophryne*, and *Nephelobates*, while the brighter, more colorful dendrobatids were assigned to a "toxic" or "aposematic" clade composed of *Dendrobates*, *Epipedobates*, *Minyobates*, and *Phyllobates*. By coding the unexamined species as unknown ("?"), I employed the same strategy, with the exception that I did not prohibit *a priori* the inclusion of these untested species in clades with demonstrably toxic species. The discovery that an untested species is embedded within a toxic clade provides 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, I coded it as absent (e.g., epibatidine). If there was any doubt as to the tests samples were subjected to, I coded the character as unknown ("?").

I did not constrain the evolution of toxin sequestration to be irreversible, as was implicitly done by some previous workers. Apart from the epistemological advantages of this approach, this allows loss and reacquisition of toxins to be discovered empirically as a result of a cladistic analysis.

Data were taken from reviews (Daly et al., 1993; Daly et al., 1999; Daly et al., 1987), the primary literature (Tokuyama et al., 1992; Garraffo et al., 1993; Badio and Daly, 1994; Myers et al., 1995; Daly et al., 1997; Garraffo et al., 2001; Daly et al., 2003; Fitch et al., 2003; Saporito et al., 2003; Mortari et al., 2004), 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 for each class I list the individual non-steroidal alkaloids following the convention of Daly et al. (1987). I did not include unclassified alkaloids, although they may provide relevant information once their structures are elucidated. I did not list unpublished alkaloids in the character descriptions (although I did code their presence in the matrix), and I only listed alkaloids that occur in the species sampled in the present study.

147. Ability to sequester alkaloids. absent = 0; present = 1.

I 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. I scored species that are incapable of sequestering any alkaloid as state 0 for this character and missing ("–") for all other lipophilic alkaloid characters; I 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 has not been subjected to critical test (i.e., no attempt has been made to isolate the genetic basis of sequestration).

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). The ability of these frogs (and the inability of all other dendrobatids) to sequester these highly toxic compounds is likely to be related to their modified sodium channel (as demonstrated for *aurotaenia* and *terribilis*) that is insensitive to BTX. In the absence of this insensitivity to the effects of BTX, BTX-containing prey items would presumably be rejected.

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

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

Alkaloid **283A'** (found in *Dendrobates sylvaticus*) is closely related to and was treated as an HTX by Daly et al. (1987), but was not included by Daly et al. (1993), or Daly et al. (Daly, 1999).

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, 223I, 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.

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.

193A, **193C, 201B, 205B, 205E, 207J, 207P, 207R, 209G, 219I, 221G, 221M, 235M, 235P,**

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

251F

168. Spiropyrrolizidines: absent = 0; present = 1.

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

222, 236, 252A, 254

169. Indolic alkaloids (chimonanthine/calycanthine): absent = 0; present = 1.

346B, 346C

170. Epibatidines: absent = 0; present = 1.

208/210, 308/310

171. Pyridine alkaloids: absent = 0; present = 1.

172. Noranabasamine (=pyridyl-piperidines): absent = 0; present = 1.

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

239J.

173. Pumiliotoxin 7-hydroxylase: absent = 0; present = 1.

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 problematic 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 though 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*, I 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**. I 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), I coded this character as unknown ("?") (e.g., *truncatus*). If available evidence indicates that a species is incapable of sequestering pumiliotoxins, I coded this character as missing ("–") (e.g., *trivittatus*).

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

174. 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. (2004: 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.

175. 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; Bogart, 1973; Bogart, 1991), *trinitatis* (Rada de Martínez, 1976), *auratus*, *granuliferus*, *histrionicus*, *lugubris*, *pumilio*, and *Dendrobates sylvaticus* (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., 2002) 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. (Silva et al., 2001) for *Cycloramphus boraceiensis*, Rosa et al. (2003) for *Megaelosia*, Ramos et al. (Ramos et al., 2002) for *Atelopus zeteki*, and Aguiar et al. (Aguiar et al., 2004) for *Crossodactylus* and *Hylodes phyllodes*.

Coding chromosome variation as transformation series is complicated by imprecision in determining chromosome identity. For the most part, chromosomes are simply arranged according to size and named (numbered) consecutively. As such, chromosome 1 of one species may be homologous with chromosome 2 of another, yet variation in chromosome morphology would be assessed by comparing it with chromosome 1. 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 is due 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 I coded only chromosome number because (1) it is reported in all karyological studies, (2) it is less dependent on individual chromosome identity (but see below), 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 look back on as an oversimplification.

Chapter 6: Results

General Results

Direct optimization phylogenetic parsimony analysis resulted in a single optimal solution of 46,598 steps. Owing to the size of the cladogram, it is divided among Figures 6.1–6.7. I begin with higher-level relationships, shown in Figure 6.1, and proceed to the relationships among dendrobatids in the subsequent figures. Rather than describe the cladogram and associated support values exhaustively, I 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. Detailed analysis of character evolution is found in Chapter 8. The complete list of transformations for each clade is given in Appendix 9.

Dendrobatid Monophyly and Outgroup Relationships

Dendrobatid monophyly was corroborated strongly in the present analysis. Unambiguous phenotypic transformations include the gain of the tarsal keel (Character 28, 0→1), the "ranid" type insertion of the distal tendon of insertion 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 139, 0→1), the occurrence of the retroarticular process of the mandible (Character 141, 0→1), and the reduction in chromosome number from 26 to 24 (Character 174, 4→3). Behavioral

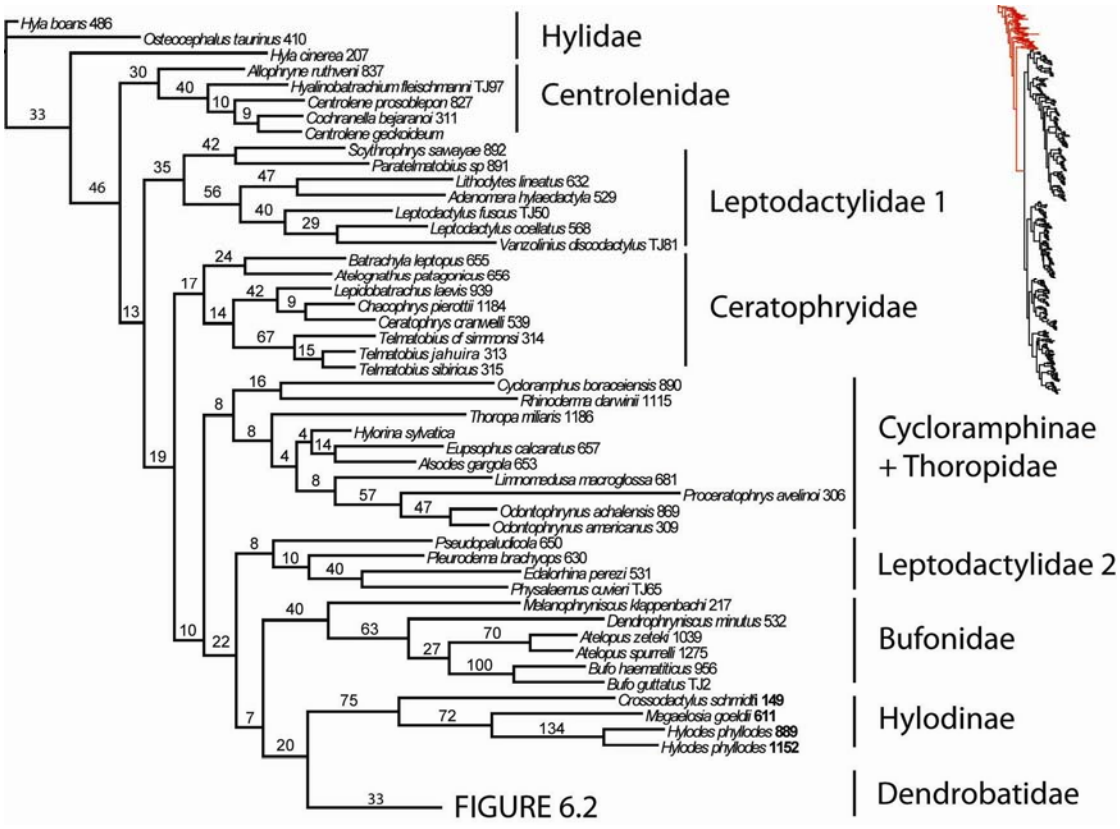


Figure 6.1. Outgroup relationships and placement of Dendrobatidae. Branch lengths are proportional to number of unambiguous transformations. Numbers above branches are Bremer support values. Family group names applied as in Frost et al. (2005). Cycloramphinae and Hylodinae were nested within Cycloramphidae in Frost et al.'s study. Upper right inset shows entire cladogram with present view in red. Numbers following terminal names are unique sample numbers. Terminals without numbers were not sequenced for the present study or Frost et al. (2005) and were taken from Genbank.

synapomorphies include cephalic copulatory amplexus (Character 104, 1→0), dorsal tadpole transport (108, 0→1), and the occurrence of toe trembling Character 115, 0→1).

The present results generally resemble those of Frost et al. (2005) 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 (2005) placement of *Thoropa* and Dendrobatidae 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 117, 1→0) and the occurrence of an oblique lateral stripe (Character 55, 0→1). This arrangement is congruent with the traditional hypothesis (see Chapters 2 and 3). Except for the removal of hylodines and insertion of *Thoropa*, the relationships among cycloramphines are identical to those of Frost et al. (2005). 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 (2005) results and the present hypothesis involves the placement of leptodactylids. The clades here labeled Leptodactylidae 1 and Leptodactylidae 2 were a monophyletic group in Frost et al., and that clade was sister to Centrolenidae. 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, i.e., it is 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 (Fig. 6.2). Six unambiguous phenotypic transformations occur at this node, including the origins of fringes on the preaxial edges of fingers II and III (Characters 13 and 15, 0→1).

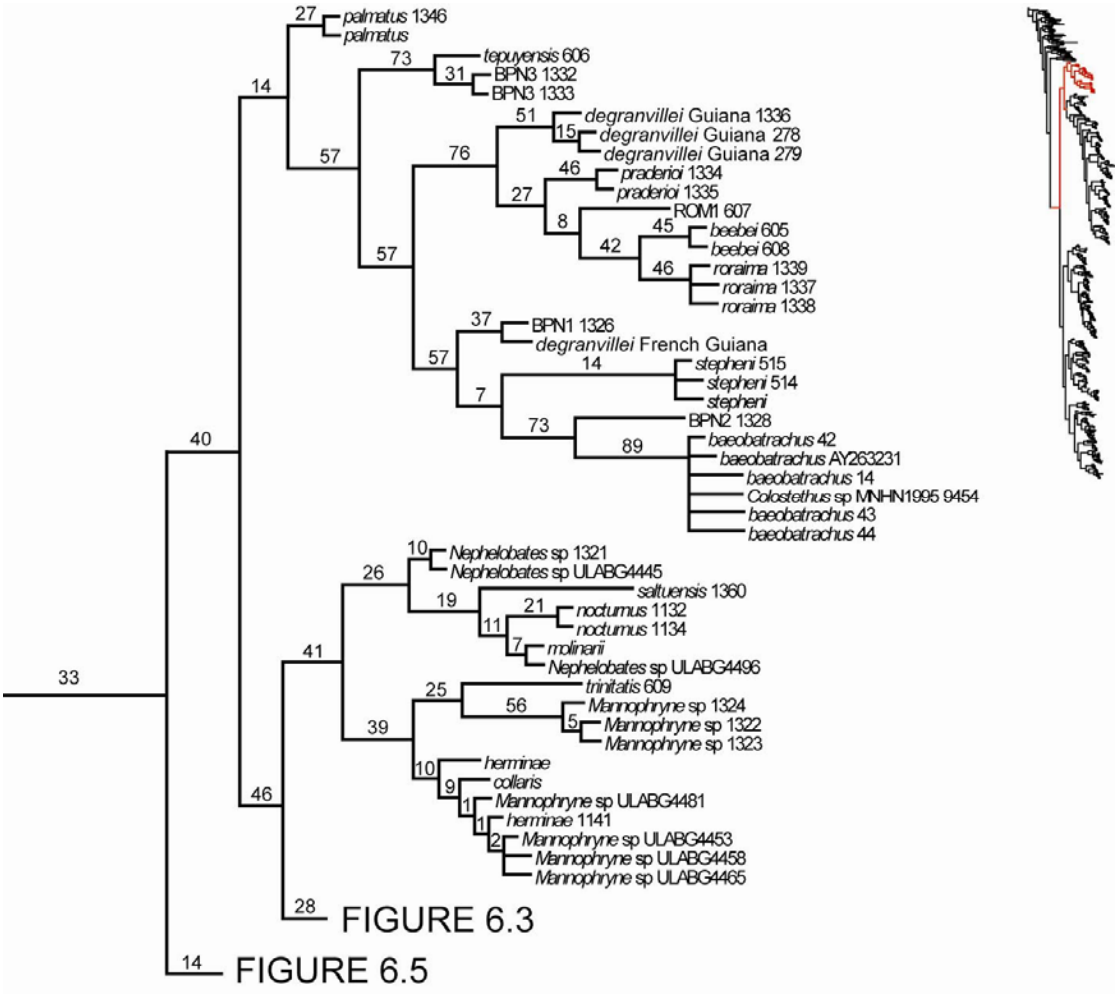


Figure 6.2. Relationships among dendrobatids. Branch lengths are proportional to number of unambiguous transformations. Numbers above branches are Bremer support values. Upper right inset shows entire cladogram with present view in red. Numbers following terminal names are unique sample numbers. Terminals without sample numbers were taken from Genbank. Unidentified species taken from Genbank are labeled as originally published.

Within the median lingual process clade, *tepuyensis* and the undescribed species BPN3 are relatively robust frogs with extensive webbing. Their monophyly is strongly supported (Bremer support = 73), although only a single phenotypic synapomorphy optimizes unambiguously to this node (expansion of toe disc I, Character 31, 1→2). Percent pairwise distances are shown in Table 6.1.

Table 6.1. Percent uncorrected pairwise distances between cytochrome *b* sequences of *tepuyensis* and BPN3. Dotted lines separate species.

	Sample ID	1	2	3
1	*tepuyensis* 606	–		
2	BPN3 1332	4.4	–	
3	BPN3 1333	4.4	0.0	–

It should be noted that the identification of sample 606 as *tepuyensis* will likely require revision. That species was described by La Marca (1998 "1996") from Auyantepui, whereas sample 606 was taken over 200 km away on Mt. Ayanganna (ca. 50 km WNW Kaieteur, Guyana). Given the high degree of endemism of many tepui species, it is doubtful that these samples are conspecific. Nevertheless, I 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. My prediction is that additional specimens and/or molecular data will reveal that these are different species, but for the

time-being I apply the name *tepuyensis* to specimens from both localities. BPN3 is an undescribed species from Guyana, Mazaruni-Potoro, Mt. Thomasing.

Among the species that possess the median lingual process are several species that resemble, superficially at least, *degranvillei*. Species delimitation is hindered by the extensive morphological variation observed 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 I did not detect morphological differences, they appear not to be conspecific with true *degranvillei*. 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 relatively close to the type locality and, therefore, likely to represent *degranvillei* sensu stricto. The cladogram indicates that the Guyanan material I refer to *degranvillei* is not conspecific with the GenBank sample. Cytochrome *b* sequences for the Vence et al. specimen were not available, but the pairwise distance between BPN1 and the Guyanan *degranvillei* is >17.5%.

The two samples of *praderioi* were both collected at 1310 m on Roraima, Guyana. Sample 1336 of the Guyanan *degranvillei* was also collected on Roraima but was taken at 1075 m. The two remaining Guyanan *degranvillei* samples were taken in the Mereme mountains, and ROM1 was collected on Mt. Ayanganna, ca. 50 km WNW Kaieteur, Guyana.

Despite the morphological similarity and geographic proximity of *praderioi* and the *degranvillei*-like species on Roraima, and only <300 m difference in elevation between the localities, the pairwise distance is 2.6% (see Table 6.2). Although this is

Table 6.2. Percent uncorrected pairwise distances between cytochrome *b* sequences of *degranvillei* from Guyana, *praderioi*, and the undescribed species ROM1. Dotted lines separate localities and species.

	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	ROM1 607 Ayanganna	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	–

not overwhelming, it is illustrative to consider that the same distance is observed between *auratus* and *truncatus* (see below) which are clearly diagnosable morphologically, and, furthermore, that the pairwise distance between the three Guyanan samples of *degranvillei* is only 1.6–1.8%, despite the much greater geographic distance.

According to the cladogram, it is possible that ROM1 and *praderioi* may be conspecific. Nevertheless, they differ morphologically (e.g., webbing) and at 8.3% of their cytochrome *b* sites.

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 6.3. There is no confusion surrounding the identity of *beebei*, with the exception that the French Guianan species

Table 6.3. Percent uncorrected pairwise distances between cytochrome *b* sequences of *beebei* and *roraima*.

	Sample ID	1	2	3	4	5
1	*beebei* 605	—				
2	*beebei* 608	0.5	—			
3	*roraima* 1337	6.0	5.5	—		
4	*roraima* 1338	5.7	5.2	0.3	—	
5	*roraima* 1339	6.0	5.5	0.5	0.3	—

discussed under that name (e.g., Kok, 2000; Lescure and Marty, 2000) is not conspecific with true *beebei* 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 and1338 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.

The clade composed of *baeobatrachus, stepheni,* BPN1, and BPN2 has a Bremer value of 57. All of the phenotypic synapomorphies that optimize to this node are fast-optimization dependent.

The nomenclatural history of *baeobatrachus* and *stepheni* is convoluted. The name "baeobatrachus" originally appeared in Edwards's widely distributed but never published PhD dissertation. The type locality Edwards intended to designate was Ducke Reserve in Amazonas State, just outside Manaus (Brazil). The two samples (514, 515) are from that locality. On the 25th anniversary 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 at 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* (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 the 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 being in 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 ~17% pairwise distance between the Reserva Ducke and Montagne Belvédère samples strongly suggests they are not conspecific (see Table 6.4). Moreover, tadpoles of *stepheni* are nidicolous with reduced mouth parts and a median anus (Juncá et al., 1994; Juncá, 1998), whereas a male nurse frog was

Table 6.4. Percent uncorrected pairwise distances between cytochrome *b* sequences of *stepheni baeobatrachus*, and undescribed species BPN1 and BPN2. Dotted lines separate localities and species.

	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	BPN1 1326	19.0	19.2	16.9	17.1	16.9	16.9	–	
8	BPN2 1328	17.1	16.9	11.9	12.2	11.9	11.9	15.6	–

collected at Serra do Navio, Amapá, Brazil transporting three tadpoles with fully developed mouth parts and dextral anus.[1] Assuming that the Montagne Belvédère and Serra do Navio samples are conspecific, there is strong evidence that these

[1] 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 in his 1974 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.

baeobatrachus and *stepheni* are not conspecific, despite the apparent lack of diagnostic characters for adults. That *baeobatrachus* and *stepheni* are valid species is further supported by the phylogenetic analysis, which places the undescribed species BPN2 (1328), from Guyana, as sister to *baeobatrachus* to the exclusion of *stepheni*.

The remaining species, BPN1 (1326) is another undescribed species from Guyana, which 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 *degranvillei* sample, but the number of unambiguous transformations that occur on the terminal branches (14 for BPN1, 19 for *degranvillei*) suggests they are not conspecific.

The other clade shown in Figure 6.2 is composed mainly of species currently referred to *Aromobates*, *Mannophryne,* and *Neophelobates.* The monophyly of this clade is strongly supported (Bremer support = 41), 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 was included in the *alboguttatus* group of Rivero (1990 "1988"), but was excluded without comment when La Marca (1992) named that 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 relative of *Aromobates*.

Although *Nephelobates* is paraphyletic with respect to *Aromobates*, the monophyly of the controversial *Mannophryne* is solidly corroborated in this analysis. This clade has a Bremer value of 39, and it may be diagnosed morphologically by the synapomorphic dermal collar, which optimizes unambiguously to this node. The conclusions, based on morphological criteria, that the collar-like 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 in Chapter 5) are supported by the distant relationships of these taxa in the optimal cladogram.

Among the nominal species included in the cladogram, the *herminae* samples were not taken from the same species. The cytochrome *b* sequences for the two samples of *nocturnus* are identical.

The clade shown in Figures 6.3 is a large, primarily cis-Andean (east of the Andes) group. Unambiguous phenotypic transformations include the diffuse oblique lateral stripe (Character 57, 0/1→2) and the loss of palatines (Character 131, 1→0).

The sister of the remainder of this clade is *olfersioides*, from the Atlantic forest of Brazil, followed by the undescribed Neblina species and *undulatus*. The

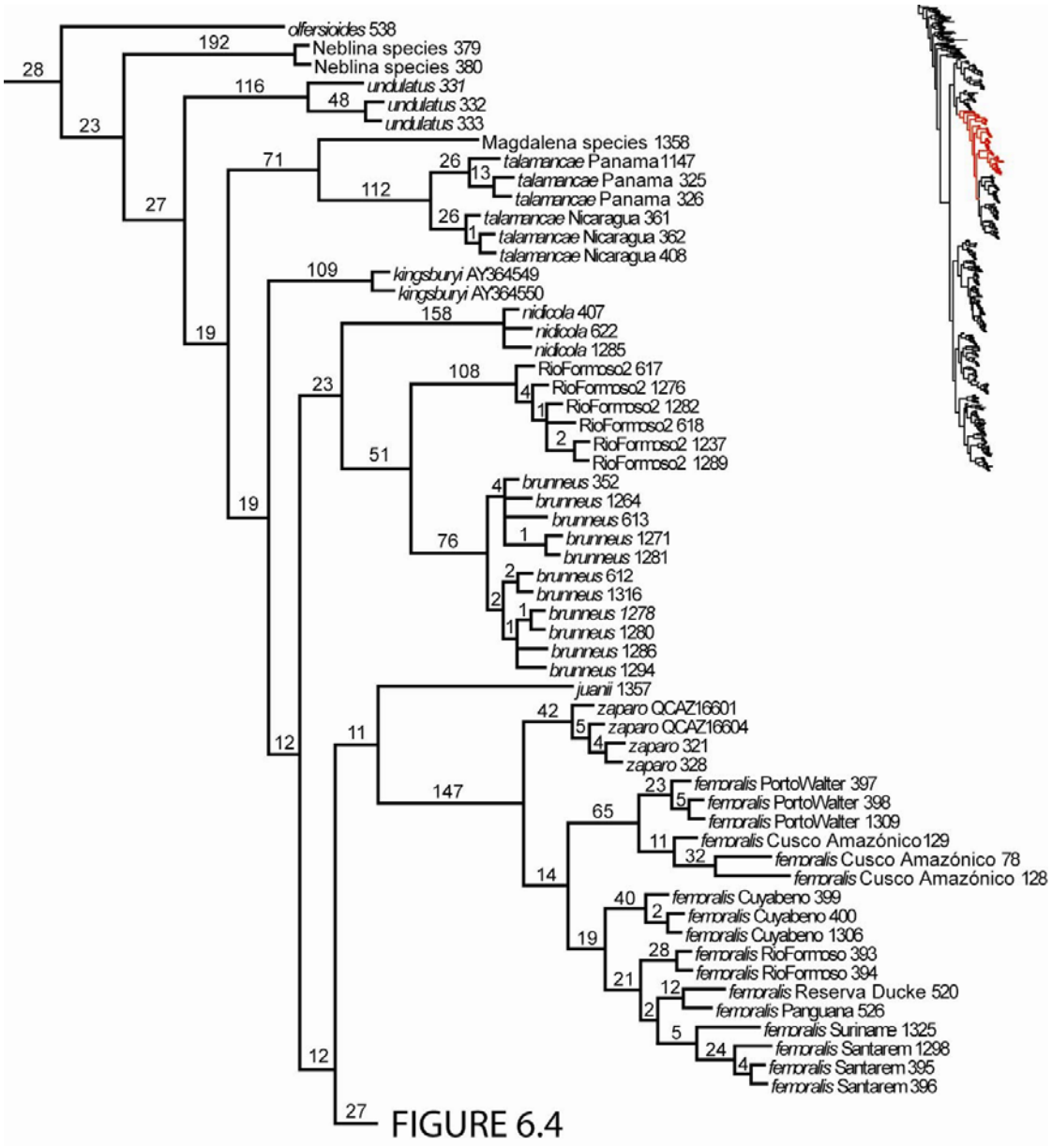


Figure 6.3. Relationships among dendrobatids. Branch lengths are proportional to number of unambiguous transformations. Numbers above branches are Bremer support values. Upper right inset shows entire cladogram with present view in red. Numbers following terminal names are unique sample numbers. Terminals without sample numbers were taken from Genbank.

undescribed Neblina species was collected at the base of the tepuy Neblina, in Venezuela. The cytochrome *b* sequences of the two specimens are identical. Myers

and Donnelly (2001) described *undulatus* from the Yutajé massif in Venezela. The three samples were all collected in the same vicinity (see Table 6.5 for pairwise distances).

Table 6.5. 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	—

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 undescribed Magdalena species. 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.

The undescribed Magdalena species and *talamancae* share the unambiguous transformation from an evenly stippled to solid dark throat in males (Character 61, 2→4). These two species are allopatric, with Magdalena species known only from

sites on the floor of the middle Magdalena river valley and *talamancae* widespread from the Pacific lowlands of South America (Ecuador and Colombia) north to Nicaragua. Pairwise distances for cytochrome *b* sequences of these species are shown in Table 6.6. The *talamancae* samples are from two localities in Panama (Bocas del Toro: 325, 326; Coclé: 1147) and one in Nicaragua (361, 362, 408). The second species is a morphologically similar, but unquestionably heterospecific, undescribed taxon from the middle Magdalena river valley in Colombia.

Although the most parsimonious cladogram recovers monophyletic Panamanian and Nicaraguan samples of *talamancae*, the 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.

Table 6.6. Percent uncorrected pairwise distances between cytochrome *b* sequences of *talamanae* and Magdalena species. Dotted lines separate localities and species.

	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 species 1358	16.1	16.6	16.1	15.6	15.6	15.6	—

Much of the diversity of small, brown, relatively nondescript cis-Andean dendrobatids has been associated with the names *brunneus*, *marchesianus*, and *trilineatus*. Progress in documenting the 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. (2002) 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 (I have subsequently examined material referable to 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. (2002), as well as the Colombian material I have examined, and the account is therefore rejected. I 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 I was unable to include sequences for *marchesianus* sensu stricto.

Having resolved the identities of *marchesianus* and *trilineatus* (but see below), the remaining taxonomic problem is *brunneus*. Grant and Rodríguez (2001) provided data for the topotypic and other material, but they did not attempt to decisively address the problem of *brunneus* identity. La Marca et al. (2004) improved matters considerably by clarifying that the "*brunneus*" from northern Venezuela were in fact a

new species (named as *Colostethus pettieri*) most closely related to *humilis*. In what appears superficially to be the most thorough study of the systematics of these frogs, Morales (2002 "2000") provided an account for *brunneus*. Like the remainder of his 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 I therefore apply the name in his sense. I included in this study 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 I 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 Santarem to *brunneus* (see Figure 6.4). The minimum pairwise distance between that sample and either of the others he referred to *brunneus* is 16.6%. I therefore exclude that sample from the pairwise comparisons in Table 6.7 and instead include it with the other samples from Santarem (see below). The pairwise distances between *brunneus* and its sister species from Rio Formoso (RioFormoso2) are 14.3–15.3%.

Table 6.7. 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	—

Terminals identified as RioFormoso2 represent one of three undescribed species of dendrobatids collected on the Rio Formoso, Rondônia, Brazil (see Table 6.8). The pairwise distances between the samples of this species and *brunneus* are 14.3–15.3%.

Table 6.8. Uncorrected pairwise distances between cytochrome *b* sequences of RioFormoso2.

	Sample ID	1	2	3	4	5	6
1	RioFormoso2 617	—					
2	RioFormoso2 618	1.3	—				
3	RioFormoso2 1237	1.6	0.3	—			
4	RioFormoso2 1276	1.3	0.5	0.8	—		
5	RioFormoso2 1282	1.6	0.3	0.5	0.8	—	
6	RioFormoso2 1289	1.6	0.3	0.0	0.8	0.5	—

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 conflicts strongly with the traditional view, which allied them with 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., 2003) could not be refuted by the inclusion of phenotypic and additional DNA evidence. Furthermore, *femoralis* is incapable of accumulating alkaloids, which suggests that the remarkable resemblance of *femoralis* and those species may be due to Batesian mimicry.

The type locality of *femoralis* isYurimaguas, Peru, but it 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-mark; see Silverstone, 1976). I generated cytochrome *b* sequences for 17 samples of *femoralis* collected at the following eight localities, covering much of the nominal species' range: Porto Walter, Brazil (397, 398, 1309); Cusco Amazónico, Peru (78, 128, 129); Cuyabeno, Ecuador (399, 400, 1306); Rio Formoso, Brazil (393, 394); Reserva Ducke, Brazil (520); Panguana, Peru [nearest the type locality] (526); Sipaliwini, Suriname (1325); Santarem, Brazil (395, 396, 1298).

The taxonomy of *zaparo* is less problematic, but I include it here as a point of reference for *femoralis*. Vences et al. (2003) united these two species formally in *Allobates*. It should be noted that the species Duellman and Mendelson (1995) referred to as *zaparo* is a distantly related, probably toxic species (details discussed below).

As shown in Table 6.9, 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*, 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 greatly increase the known diversity of this clade.

Table 6.9. Percent uncorrected pairwise distances between cytochrome *b* sequences of *femoralis* and *zaparo*. Dotted lines separate localities and species.

Abbreviations are: PW (Port Walter), CA (Cusco Amazónico), CU (Cuyabeno), RF (Rio Formoso), RD (Reserva Ducke), SIP (Sipaliwini), SAN (Santarem).

	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 RF	14.6	14.6	14.6	14.0	14.0	14.0	9.9	10.7	10.4	—									
11	*femoralis* 394 RF	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 SAN	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 SAN	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 SAN	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	—

Thirty-four unambiguous transformations establish the monophyly of the clade shown in Fig. 6.4, with a Bremer value of 27. The *caeruleodactylus*–RioFormoso3 clade is united by 36 unambiguous transformations. Lima and Caldwell (2001) named *caeuleodactylus*, and Caldwell et al. (2002) described its distinctive tadpole. Based on tadpole morphology. Pairwise distances between specimens of *caeruleodsactylus* are shown in Table 6.10. The samples were collected at the type locality.

Table 6.10. 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	—

Sample 1277 from Rio Ituxi was referred to *gasconi* by Morales (2002), 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 al lado izquierdo del Río Juruá, Amazonas, Brazil” (Morales, 2002:30). Although Porto Walter is located on the Rio Juruá, Rio Ituxi is slightly

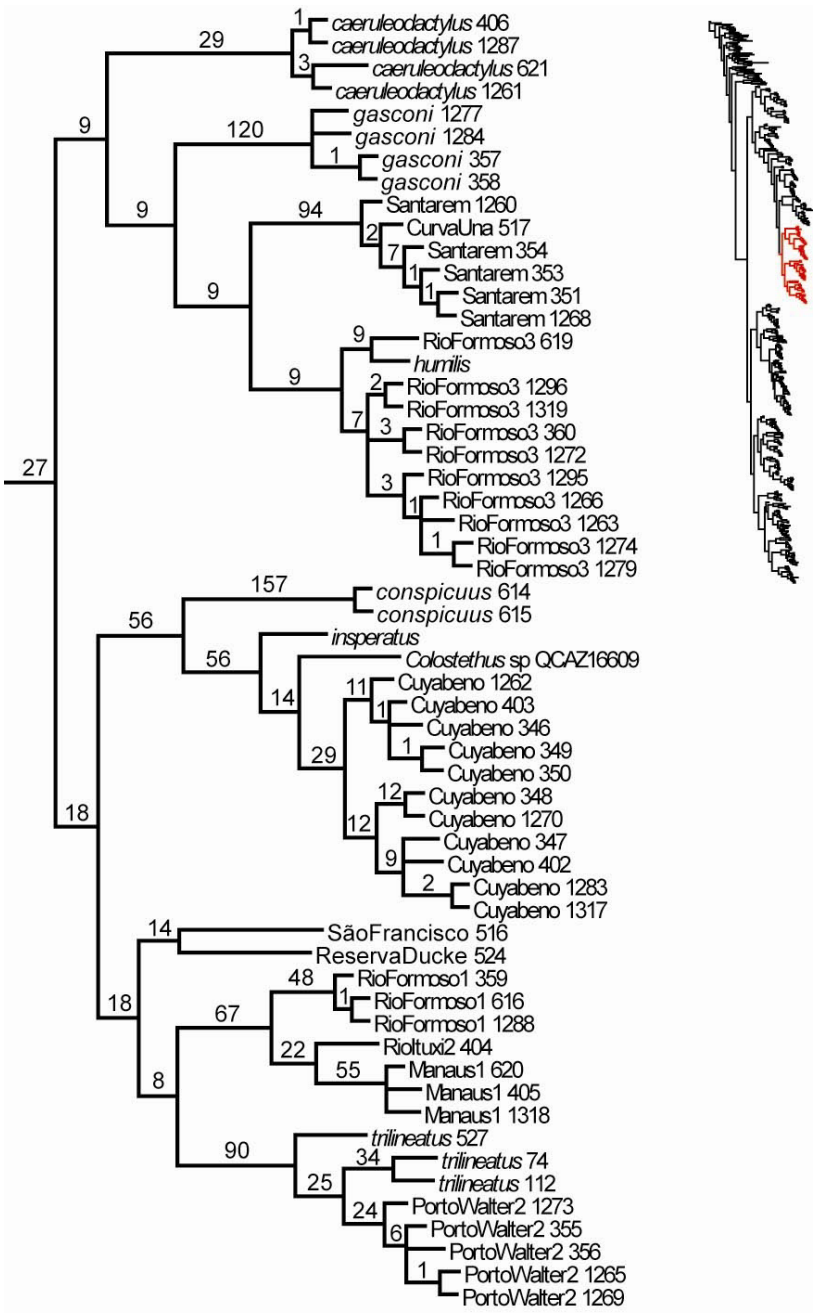


Figure 6.4. Relationships among dendrobatids. Branch lengths are proportional to number of unambiguous transformations. Numbers above branches are Bremer support values. Upper right inset shows entire cladogram with present view in red. Numbers following terminal names are unique sample numbers. Terminals without sample numbers were taken from Genbank. Note that Morales (2002) identified PortoWalter2 356 as *gasconi*, and Santerem 354 as *brunneus* (see Fig. 6.3).

closer, and on that basis I refer these terminals to *gasconi*. Comparison with topotypes will be required to confirm the identity of these samples. The pairwise distance between this species and *caeruleodactylus* is 14.0–14.5%; between this species and the undescribed species from Santarem/CurvaUna (see below) 13.5–14.2%; and between this species and Rioformoso3 15.8–16.4%. Pairwise cytochrome *b* distances for *gasconi* are given in Table 6.11.

Table 6.11. Percent uncorrected pairwise distances between cytochrome *b* sequences of RioItuxi. Sample 1277 was referred to *gasconi* by Morales (2002 “2000”).

	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	—

Samples from CurvaUna and Rio Formoso represent an undescribed species (see Table6.12). The pairwise distances between the samples of this species and RioFormoso3 (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%.

Table 6.12. Percent uncorrected pairwise distances between cytochrome *b* sequences of an undescribed brunneus-like species from Santarem and Curva Una localities in Brazil. Morales (2002 "2000") referred sample 354 to the distantly related *brunneus*. Dotted lines separate localities.

	Sample ID	1	2	3	4	5	6
1	Santarem 351	—					
2	Santarem 353	0.3	—				
3	Santarem (*brunneus*) 354	0.3	0.0	—			
4	Santarem 1260	0.8	0.5	0.5	—		
5	Santarem 1268	0.0	0.3	0.3	0.8	—	
6	CurvaUna 517	0.8	0.5	0.5	0.0	0.8	—

RioFormoso3 is one of three undescribed species of dendrobatids collected at Rio Formoso (see Table 6.13). The pairwise distance between the samples of this species and the one from Santarem/CurvaUna is 9.9–10.9%. In the current analysis, *humilis* is nested within the samples of RioFormoso3. However, it is highly unlikely that the populations are conspecific: the sample of *humilis* was collected at 2,100 m in the Venezuelan Andes (La Marca et al., 2002), whereas RioFormoso3 is from the Amazonian lowlands of western Brazil. Sequence data for *humilis* is limited to ~500 bp of 16S.

Table 6.13. Percent uncorrected pairwise distances between cytochrome *b* sequences of RioFormoso3.

	Sample ID	1	2	3	4	5	6	7	8	9
1	RioFormoso3 360	—								
2	RioFormoso3 619	0.0	—							
3	RioFormoso3 1263	0.3	0.3	—						
4	RioFormoso3 1272	0.0	0.0	0.3	—					
5	RioFormoso3 1274	0.3	0.3	0.0	0.3	—				
6	RioFormoso3 1279	0.3	0.3	0.0	0.3	0.0	—			
7	RioFormoso3 1295	0.3	0.3	0.0	0.3	0.0	0.0	—		
8	RioFormoso3 1296	0.0	0.0	0.3	0.0	0.3	0.3	0.3	—	
9	RioFormoso3 1319	0.0	0.0	0.3	0.0	0.3	0.3	0.3	0.0	—

The clade composed of *conspicuus*, *insperatus*, and the unidentified Ecuadorian species reported by Santos et al. (2003; no locality was given), and an undescribed species from Cuyabeno, Ecuador, is strongly supported (Bremer support = 56) and united by 70 unambiguous transformations. The samples referred to *conspicuus* were collected at Porto Walter, and sample 614 was referred to *conspicuus* by Morales (2002). Bremer support for this node is 157, and 157 synapomorphies optimize to it unambiguously. The remaining three species in this clade are all from Ecuador. Cytochrome *b* data are not available for the *insperatus* and the unnamed "*Colostethus* sp.", but pairwise distances are shown in Table 6.14 for *conspicuus* and the samples from Cuyabeno.

Table 6.14. Percent uncorrected pairwise distances between cytochrome *b* sequences of *conspicuus* and a undescribed species form Cuyabeno, Ecuador. Dotted lines separate species.

	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	—

The remaining species in Figure 6.4 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 from 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*, but 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., 2002b; Caldwell et al., 2002a; pers. 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 Sao Francisco (516), Reserva Ducke (524), and Rio Ituxi (404), and several samples each from Rio Formoso (359, 616, 1288), Manaus (620, 405, 1318), Cusco Amazónico (74, 112), and Porto Walter (355, 356, 1265, 1269, 1273).

The monophyly of this clade has a Bremer support value of 18, with 25 unambiguous transformations at this node. As shown in Fig. 6.4 and Table 6.15, the pattern of diversification is suggestive of eight species—one at each locality. The least pairwise distance between localities is 5.7% between the *trilineatus* from Cusco Amazónico and the samples from Porto Walter.

Table 6.15. Percent uncorrected pairwise distances between cytochrome *b* sequences of *trilineatus* and related undescribed species. Abbreviations are as follows: MAN1 (Manaus1), PW2 (PortoWalter2), RD (ReservaDucke), RI2 (RioItuxi2), RF1 (RioFormoso1), SF (São Francisco), triCA (*trilineatus* Cusco Amazónico), triPAN (*trilineatus*, Panguana). Dotted lines separate localities.

	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	RF1 359	16.1	16.4	–														
4	RF1 616	16.1	16.4	0.0	–													
5	RF1 1288	16.1	16.4	0.0	0.0	–												
6	RI2 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	–

The clade shown in Fig. 6.5 is united by 84 unambiguous transformations, including reduction in the length of finger IV (Character 4, 0→1) and lengthening of finger I (Character 5, 1/2→3). The next clade, shown at the top of Fig. 6.5, includes the *nubicola* group and Silverstone's (1976) *tricolor* group + *machalilla*. This inclusive clade is delimited by 81 unambiguous transformations in DNA sequences.

The *nubicola* group, represented by *flotator, nubicola*, and the undescribed species to be named *punctiventris* by Grant and Myers (in prep.) 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 (Characters 88, 89, 91, and 94). This clade includes sequences download from Genbank that were attributed to *pratti* from western Colombia by Vences et al. (2003). However, one of the authors of that study informed me that they did not examine a voucher specimen (S. Lötters, *in litt*. 2/23/2005), and *nubicola* and *pratti* are often confused by collectors. These three species are part of a morphologically compact clade. The Central American species *flotator* was 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 6.16).

The remainder of this 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 seven

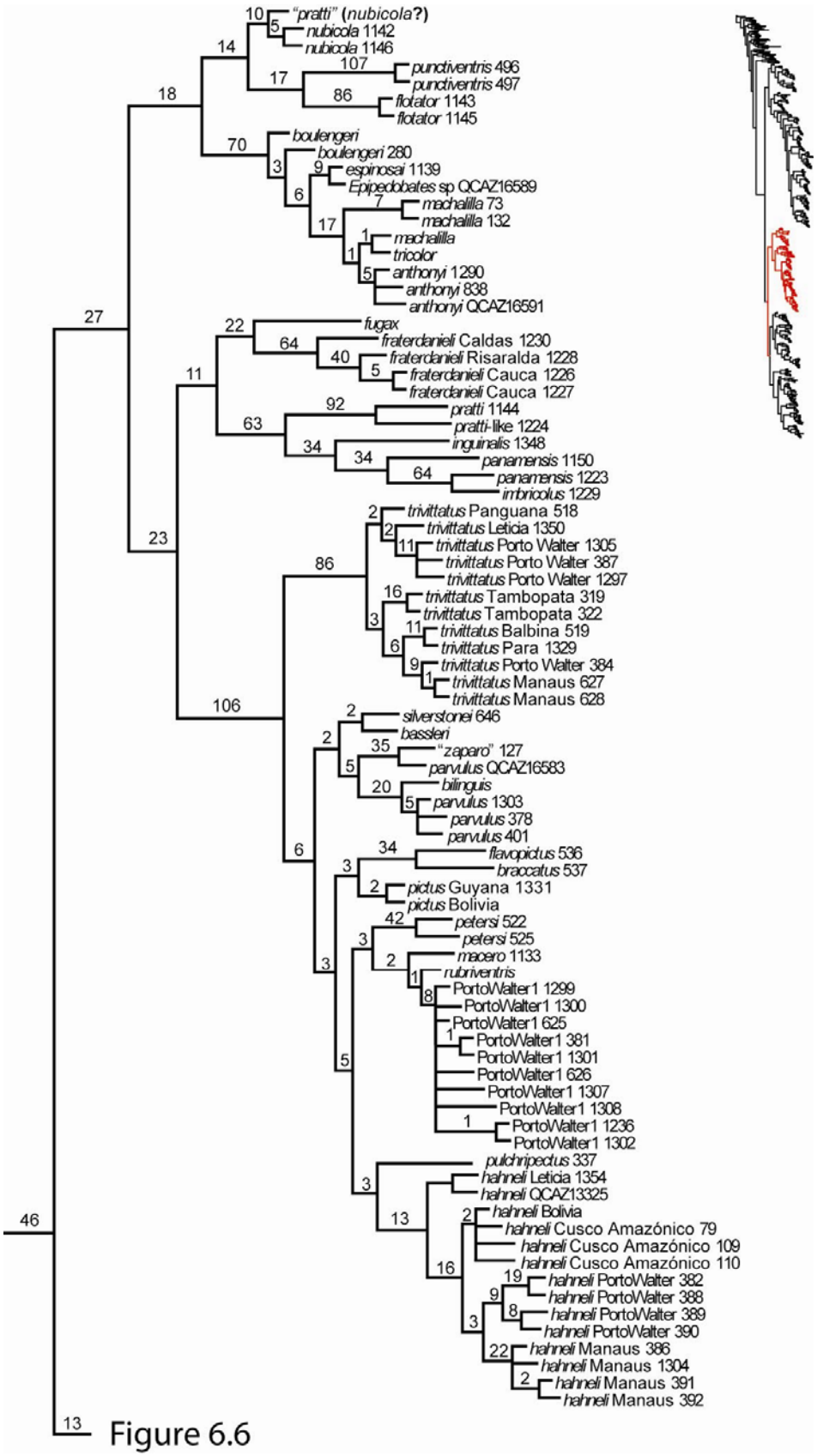

"pratti" (nubicola?)
nubicola 1142
nubicola 1146
punctiventris 496
punctiventris 497
flotator 1143
flotator 1145
boulengeri
boulengeri 280
espinosai 1139
Epipedobates sp QCAZ16589
machalilla 73
machalilla 132
machalilla
tricolor
anthonyi 1290
anthonyi 838
anthonyi QCAZ16591
fugax
fraterdanieli Caldas 1230
fraterdanieli Risaralda 1228
fraterdanieli Cauca 1226
fraterdanieli Cauca 1227
pratti 1144
pratti-like 1224
inguinalis 1348
panamensis 1150
panamensis 1223
imbricolus 1229
trivittatus Panguana 518
trivittatus Leticia 1350
trivittatus Porto Walter 1305
trivittatus Porto Walter 387
trivittatus Porto Walter 1297
trivittatus Tambopata 319
trivittatus Tambopata 322
trivittatus Balbina 519
trivittatus Para 1329
trivittatus Porto Walter 384
trivittatus Manaus 627
trivittatus Manaus 628
silverstonei 646
bassleri
"zaparo" 127
parvulus QCAZ16583
bilinguis
parvulus 1303
parvulus 378
parvulus 401
flavopictus 536
braccatus 537
pictus Guyana 1331
pictus Bolivia
petersi 522
petersi 525
macero 1133
rubriventris
PortoWalter1 1299
PortoWalter1 1300
PortoWalter1 625
PortoWalter1 381
PortoWalter1 1301
PortoWalter1 626
PortoWalter1 1307
PortoWalter1 1308
PortoWalter1 1236
PortoWalter1 1302
pulchripectus 337
hahneli Leticia 1354
hahneli QCAZ13325
hahneli Bolivia
hahneli Cusco Amazónico 79
hahneli Cusco Amazónico 109
hahneli Cusco Amazónico 110
hahneli PortoWalter 382
hahneli PortoWalter 388
hahneli PortoWalter 389
hahneli PortoWalter 390
hahneli Manaus 386
hahneli Manaus 1304
hahneli Manaus 391
hahneli Manaus 392

Figure 6.6

Figure 6.5. Relationships among dendrobatids. Branch lengths are proportional to number of unambiguous transformations. Numbers above branches are Bremer support values. Upper right inset shows entire cladogram with present view in red. Numbers following terminal names are unique sample numbers. Terminals without sample numbers were taken from Genbank.

unambiguous transformations group *boulengeri* 280 with the other species of this clade. Cytochrome *b* sequences are also unavailable for Genbank specimen

Table 6.16. Percent uncorrected pairwise distances between cytochrome *b* sequences of *flotator*, *nubicola*, and *punctiventris*. Dotted lines separate species.

	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	*punctiventris* 496	15.3	15.3	22.1	22.1	—	
6	*punctiventris* 497	15.3	15.3	22.1	22.1	0.0	—

Epipedobates sp. QCAZ 16589, but the occurrence of only four unambiguous transformations—all autapomorphies—to distinguish it from *espinosai* 1139 suggests that it is probably conspecific with *espinosai*. Like Santos et al. (2003), I found that *machalilla* is nested within this clade of otherwise toxic species. However, the specimens I 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 has a Bremer value of 0, indicating that the clade was absent from at least one of the equally parsimonious solutions). In my analysis, only a single unambiguous synapomorphy unites these samples of *tricolor* and *machalilla*, and the critical node has a Bremer value of only 1. There is little unambiguous evidence to group these samples to the exclusion of *machalilla* samples 73 and 132 (only five transformations), but it is worth noting that those two samples are united by 24 unambiguous transformations and differ in only nine.

Grant and Castro (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, in the Cordillera Occidental (1226, 1227), Reserva Otún Quimbaya, Risaralda, in the Cordillera Central (1228).These localities are widely separated in both latitude and elevation, the former occurring near 1800 m, the latter near 2400 m. An additional sample was collected at 2800 m in the Departamento de Caldas in the Cordillera Central (1230). All localities face the Cauca valley. As seen in Table 6.17, despite the geographic distance between the Cauca and Risaralda samples, their cytochrome *b* sequences are identical. The pairwise distance between those samples and the Caldas specimen is 6.5%. Likewise, these three specimens are united by 41 unambiguous transformations, and the Caldas sample further differs by a additional 64 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 1900 m (Silverstone, 1971).

Table 6.17. Percent uncorrected pairwise distances between cytochrome *b* sequences of *fraterdanieli*. Dotted lines separate species.

	Sample ID	1	2	3	4
1	*fraterdanieli* Cauca 1226	–			
2	*fraterdanieli* Cauca 1227	0.0	–		
3	*fraterdanieli* Risaralda 1228	0.0	0.0	–	
4	*fraterdanieli* Caldas 1230	6.5	6.5	6.5	–

The terminal 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 with Colombia. Roberto Ibáñez noted differences in their vocalizations (*in litt.*, 12/20/2003). Moreover, only female nurse frogs are known to occur in *pratti* (Grant, 2004), whereas a male nurse frog was collected at Jungurudó. These diagnostic behavioral differences are further reinforced by the observation that, although these two samples are united by 105 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 straight-forward, is nomenclaturally complicated. The type locality of *pratti* is in western Colombia, the relationship of topotypic *pratti* to either of these samples has not yet been assessed. The proximity of

the Darién species suggests it may be true *pratti*, but direct evidence is required. As noted above, the specimen reported as *pratti* from western Colombia by Vences et al. (2003) is most likely 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 of flash marks, degree of webbing, sexual dimorphism, occurrence of tetrodotoxin). Although the identities of *inguinalis* and *imbricolus* are clear, *panamensis* is widespread and highly variable. Dunn (1933) and Savage (1968) drew attention to differences between western and eastern samples. However, Grant (2004) found that variation between localities was no greater than that observed in samples from each locality and therefore concluded that the samples of *panamensis* constituted a single species. The two *panamensis* samples 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 distances (Table 6.18) 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 western sample appears to be more closely related to *imbricolus*, from which its cytochrome *b* sequence differed by only 3.9%. Denser sampling of intervening

localities, as well as additional data (e.g., vocalizations, behavior) are required to address this problem decisively.

Table 6.18. Percent uncorrected pairwise distances between cytochrome *b* sequences of *imbricolus*, *inguinalis*, and two distant localities of *panamensis*. Dotted lines separate localities.

	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	—

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 Silverstone's (1976) *pictus* and *trivitattus* groups, with the addition of species described subsequently. The clade is delimited by 127 unambiguous transformations, including the almost-unique gain of 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 in color and color patter variation (Silverstone, 1976), the pattern and extent of diversity are not suggestive of more than a single species (see Table 6.19). I 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 (384, 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).

Table 6.19. Percent uncorrected pairwise distances between cytochrome *b* sequences of *trivittatus*. Dotted lines separate localities and species. Abbreviations are: TAM (Tambopata Reserve), PW (Port Walter), PAN (Panguana), LET (Leticia), BAL (Balbina), MAN (Manaus), and PAR (Para).

	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* 384 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	–

The monophyly of *trivitattus* is given by 95 unambiguous transformations, and the pairwise 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

trivitattus 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 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. This relative homogeneity is suggestive of either more continuous distribution or greater dispersal distances in *trivitattus* than in other species.

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. Sufficient data (e.g., locality) are unavailable to determine if this sample and Santos et al.'s (2003) *parvulus* QCAZ16583 are conspecific. The *parvulus* QCAZ16583 sample is not conspecific with the samples referred to *parvulus* from Cuyabeno (378, 401, and 1303).

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 apparently undescribed species from Porto Walter. The sister of this species is *rubriventris*. Although only three unambiguous transformations diagnose PortoWalter1 from *rubriventris*, only 566 bp of 16S data

were available for *rubriventris* (see Appendix 6). Cytochrome *b* sequences are identical in these specimens, 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. I included 12 samples 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 6.20, and these sequences differ from those of *pulchripectus* 337 in 10.4–11.7% of their sites. The *hahneli* samples are united by 51 unambiguous transformations. 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. The cytochrome *b* distances between the remaining *hahneli* localities are 2.1–3.1%.

Table 6.20. Percent uncorrected pairwise distances between cytochrome *b* sequences of *hahneli*. Dotted lines separate localities. Abbreviations are: CA (Cusco Amazónico), PW (Porto Walter), LET (Leticia), BAL (Balbina), and MAN (Manaus).

	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	–

In Fig. 6.6, the Colombia species *subpunctatus* is sister to a clade diagnosed by a 80 unambiguous transformations, including several changes in hand and foot morphology (Characters 13, 15, 36–44), the appearance of posteriorly angled clavicles (Character 120, 0→1), gain of palatine bones (Character 131, 0→1), and the shift to riparian habitat (Character 113, 2→1).

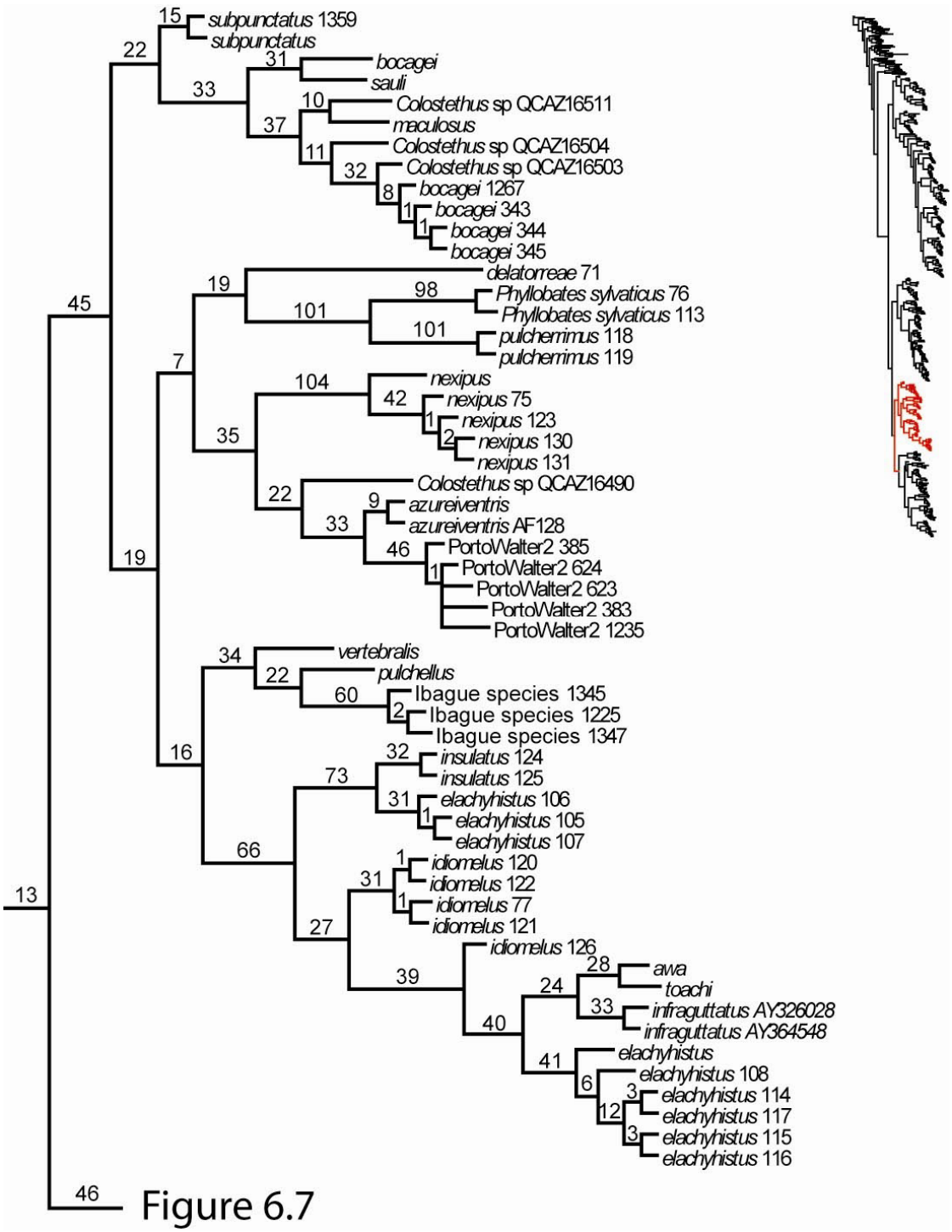


Figure 6.6. Relationships among dendrobatids. Branch lengths are proportional to number of unambiguous transformations. Numbers above branches are Bremer support values. Upper right inset shows entire cladogram with present view in red. Numbers following terminal names are unique sample numbers. Terminals without sample numbers were taken from Genbank.

Santos et al. (2003) resurrected *maculosus* from the synonymy of *bocagei*, where it had been placed by Coloma (1995). Key to that interpretation is the identity of the specimen they identified as true *bocagei*, as that species falls out with *sauli* both here and in Santos et al.'s 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. QCAZ 16511, *Colostethus* sp. QCAZ 16504, and *Colostethus* sp. QCAZ 16503, which complicates understanding of 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, my preliminary interpretation is that *Colostethus* sp. QCAZ 16511 and *Colostethus* sp. QCAZ 16504 are different, possibly undescribed species, and that *Colostethus* sp. QCAZ 16503 is conspecific with the terminals from Cuyabeno. Although the topology is consistent with *Colostethus* sp. QCAZ 16511 being conspecific with *maculosus* sensu Santos et al., 50 and 47 unambiguous transformations in mtDNA subunit H1 occur at these terminal nodes, respectively, which suggests they represent different species .

The clade composed of *delatorreae, pulcherrimus,* and *sylvaticus* is delimited by 41 unambiguous transformations. These species are all from mid- to high elevations in the Andes of northern Ecuador (*delatorreae*) and northern Peru

(*pulcherrimus* and *sylvaticus*). Duellman (2004) recently named *pulcherrimus* and compared it to the similar *Phyllobates sylvaticus* (as *Colostethus*). The two samples of *pulcherrimus* (118 and 119) are topoparatypes (Cajamarca, Peru), and both samples of *Phyllobates sylvaticus* were collected at 2820 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 6.21) and each is diagnosed by approximately 100 unambiguous transformations.

Table 6.21. Percent uncorrected pairwise distances between cytochrome *b* sequences of *pulcherrimus* and *sylvaticus*. Dotted lines separate species.

	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	—

The sister group to that clade includes *nexipus, azureiventris*, an undescribed species from Porto Walter (PortoWalter2) 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 52 unambiguous transformations. Lötters et al. (2000) proposed the genus *Cryptophyllobates* for the putatively aposematic *azureiventris*. However, Daly (1998:171) reported that in feeding experiment this species did not accumulate dietary

alkaloids. The undescribed species PortoWalter2 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 PortoWalter2 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 Tarapoto, 730 m: 75, 130, 131; and San Martin, 6 km ESE Shapaja, 300 m: 123). As shown in Table 6.22, the specimen from the lower locality is identical to two of the three specimens from the higher locality; those specimens differ from one of the 730 m specimens in 2 nucleotides. Santos et al. (2003) also omitted locality data for the sample they identified as *nexipus* and for which data were included from Genbank. Forty-five unambiguously optimized transformations optmize to the terminal node (all from myDNA subunit H1), suggesting that it may not be conspecific with the remaining *nexipus*.

The terminals referred to as Ibague species are an undescribed species from the slopes of the Magdalena valley in Colombia. The species possesses the black arm band in adult males and is thus the sole exemplar of the *ramosi* group (Grant and Castro, 1998; Grant and Ardila-Robayo, 2002). Other species that possess this structure (and included in the *ramosi* group) are *anthracinus*, *cevallosi*, *fascianiger*, *exasperatus*, *lehmanni*, *ramosi*, and *saltuarius*. Ibague species is nested in a clade with *vertebralis* and *pulchellus*, all of which are small, identically striped, and similarly

colored Andean frogs. Forty-one synapomorphies optimize unambiguously to this node, and 34 unambiguous transformations unite Ibague species with *pulchellus*, including change in male abdomen color (Character 63, 1→0) and loss of the metatarsal fold (Character 46, 1→0). Pairwise cytochrome *b* distances for samples of Ibague species are given Table 6.22

Table 6.22. Percent uncorrected pairwise distances between cytochrome *b* sequences of Ibagué species. Dotted lines separate localities.

	Sample ID	1	2	3
1	Ibagué species 1225	—		
2	Ibagué species 1347	0.3	—	
3	Ibagué species 1345 La Mesa	0.5	0.3	—

Originally described from Loja, Ecuador, *elachyhistus* is a widespread, highly variable Andean species. Duellman (2004) recently redescribed *elachyhistus* from several localities 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). Locality data were not given by Santos et al. (2003) for the Genbank *elachyhistus* included, but it is probably from Ecuador, like the bulk of the species in Santos et al.'s study, which suggests that the northern species is *elachyhistus* and the southern species is undescribed.

Rivero (1991) described *ideomelus* based on a single specimen, 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* in that paper. Three specimens (120–122) are from 2180 m at Abra Pardo de Miguel, San Martín and the other two (77 and 126) are from 2150 m at Pomachochas, Amazonas. Four of the specimens form a clade (with Abra Pardo paraphyletic with respect to the Pomachochas). Sample 126 is shown as sister to the Piura *elachyhistus*. However, this appears to be due to an erroneous cytochrome oxidase *c* I (COI) sequence. All other sequences are identical to those of the syntopic sample 77 (including cytochrome *b*; see Table 6.23), but the distance between the COI sequences of these specimens is 27%, and sample 126 only differs in 0.7% from *elachyhistus* samples 116 and 117. As such, the COI sequence for this specimen must be confirmed.

Table 6.23. Percent uncorrected pairwise distances between cytochrome *b* sequences of *idiomelus*. Dotted lines separate localities.

	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	—

Although toxic species also occur elsewhere in the cladogram (e.g., *anthonyi*, *petersi*), the remaining clade, shown in Fig. 6.7, consists of exclusively brightly colored and (insofar as is known) toxic species. Evidence for the monophyly of this

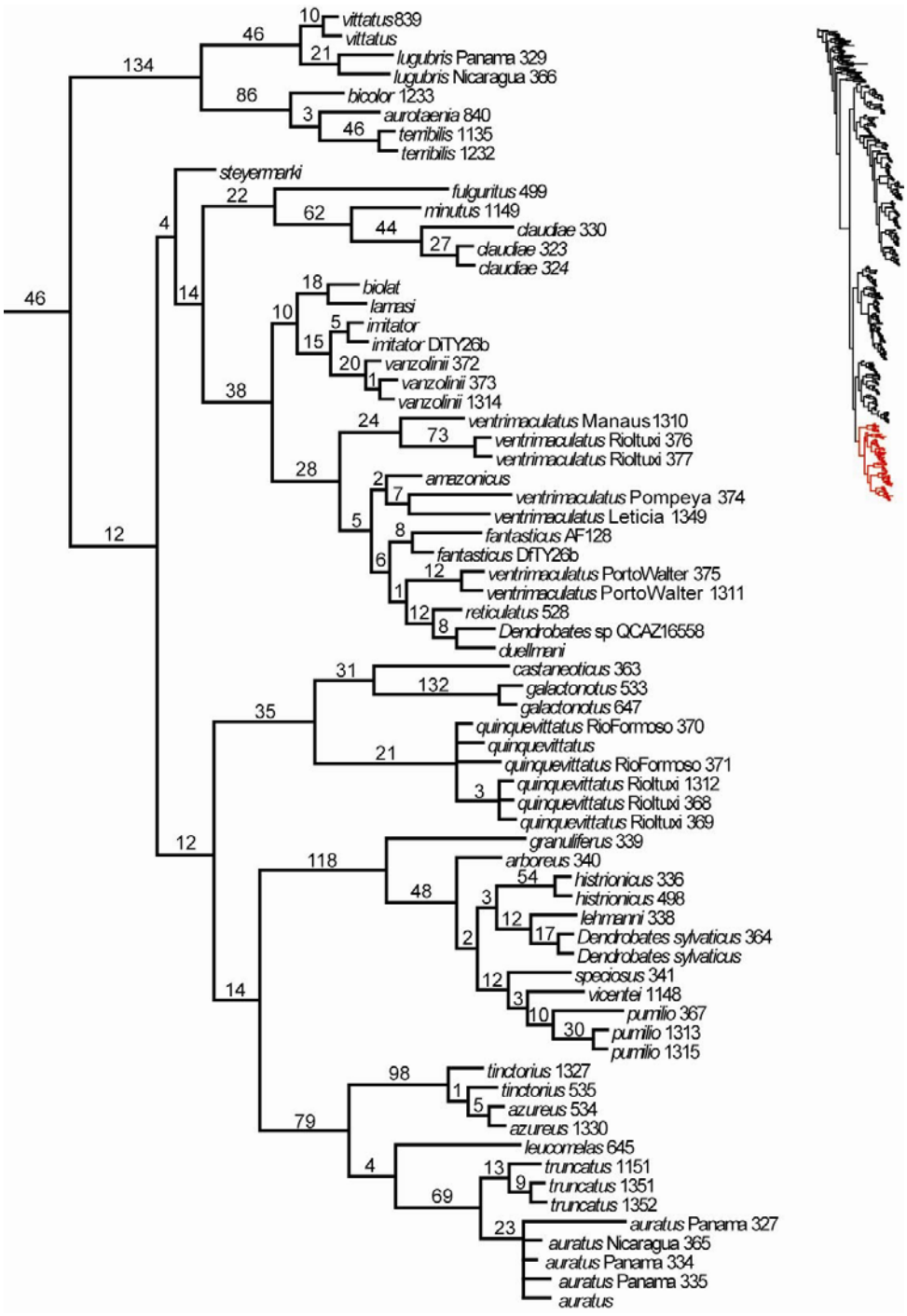


Figure 6.7. Relationships among dendrobatids. Branch lengths are proportional to number of unambiguous transformations. Upper right inset shows entire cladogram with present view in red. Numbers following terminal names are unique sample numbers. Terminals without sample numbers were taken from Genbank.

clade is given by 62 unambiguous changes, including origin of smooth dorsal skin (Character 0, 1→0), loss of the obligue lateral stripe (Character 55, 1→0), the loss of metallic pigmentation of the iris (Character 65, 1→0), larval use of phytotelmata (Character 110, 0→1), and the origin of the ability to sequester lipophilic alkaloids (Character 146, 0→1).

The clade composed of *aurotaenia, bicolor, lugubris, terribilis*, and *vittatus* constitutes *Phyllobates* sensu Myers et al. (1978), and its monophyly is established by 141 unambiguous transformations, including the lengthening of finger I (Character 5, 1/2→3), the appearance of the dorsolateral stripe in juveniles (Character 52, 0→1), and the ability to accumulate batrachotoxin (Character 147, 0→1). Species identities are clear, the sole potential exception being the possibility that *terribilis* represents the southern extreme of clinal variation of *bicolor* (Myers et al., 1978). 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 6.24). The distance between *terribilis* and *bicolor* is 7.1%, whereas the distance between *terribilis* and *aurotaenia* is only 5.7%. The two *lugubris* samples are from Panama (329) and Nicaragua (366), representing the opposite extremes in the species' distribution. These specimens form a monophyletic group and there is no indication in morphology or otherwise that *lugubris* may refer to more than a single species. Nevertheless, the distance between 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.

Table 6.24. Percent uncorrected pairwise distances between cytochrome *b* sequences of *aurotaenia*, *bicolor*, *lugubris*, *terribilis*, and *vittatus*. CR = captive reared. GB = GenBank. Dotted lines separate species.

	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	—

Maxson and Myers (1985) proposed that the South American *bicolor* and *terribilis* were sister species, and that they were 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 of dorsolateral stripes. Widmer et al. (2000) tested that hypothesis with 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. Analysis of a greatly enlarged dataset corroborated Widmer et

al.'s hypothesis of Central and South American monophyly, but I found that *bicolor* is the sister of *aurotaenis* + *bicolor*. Maxson and Myers (1985; see also Myers et al., 1978) hypothesized that the dorsolateral stripe was "a primitive pattern that is retained by the adults of *aurotaenia*, *lugubris*, and *vittatus,*" the available evidence supports the opposite conclusion: the occurrence of dorsolateral stripes in juveniles evolved first, and its retention in adults evolved independently in *aurotaenia* and the ancestor of *lugubris* and *vittatus*, respectively (Character 147, 1→2; see also discussion in Chapter 5, above).

Myers (1987) designated *steyermarki* as the type species of *Minyobates*, which he proposed for several species previously included in Silvestone's (1975) *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. The present study corroborated both the monophyly of Silverstone's *minutus* group, and its placement inside in a clade with other species of *Dendrobates* sensu Silverstone to the exclusion *Phyllobates,* thus refuting Myers's hypothesis (but see discussion of *castaneoticus* and *quinquevittatus*, below). Nevertheless, the monophyly of this clade is evidenced by only six unambiguously optimized synapomorphies, owing largely to the lack of evidence for *steyermarki*, for which only phenotypic characters and 547 bp of 16S (the latter sequenced by Vences et al., 2003) could be included.

Silverstone (1976) named the distinctive *fulguritus* from the Chocó region of western Colombia, and the sample is from near Bahía Solano. The sister-species *claudiae* and *minutus* are extremely similar morphologically. Nevertheless, their

cytochrome *b* sequences are 8.31% dissimilar (see Table 6.25). The monophyly of this group of three species is established by 70 unambiguous transformation, including the occurrence of dorsolateral and oblique lateral stripes (Characters 52 and 55) and the fusion of vertebrae 2 + 3 (Character 145, 0→1).

Table 6.25. Percent uncorrected pairwise distances between cytochrome *b* sequences of *claudiae*, *fulguritus*, and *minutus*. Dotted lines separate species.

	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	—

This 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 the Amazon region from Peru to French Guiana, probably consists of a complex of similar species. Symula et al. (2003) have prevented molecular evidence that at least two distantly related species are included in Peruvian "*ventrimaculatus.*" The current results indicate three species of "*ventrimaculatus*," one at Rio Ituxi, Brazil, a second at Manaus, Brazil, a third at Leticia, Colombia (1349)

and Pompeya, Ecuador (374), and a fourth at Porto Walter, Brazil. Although the cladogram does not falsify the hypothesis that the samples from Rio Ituxi and Manaus are a single species, 73 unambiguous synapomorphies unite the two Rio Ituxi specimens, 59 autapomorphies optimize unambiguously to the Manaus terminal node, and cytochrome *b* sequences differ in 8.1% of their sites (Table 6.26). The Leticia–Pompeya localities are closest to the type locality of Sarayacu, Ecuador, suggesting that this is probably *ventrimaculatus* sensu stricto and that the other species are undescribed.

Table 6.26. Percent uncorrected pairwise distances between cytochrome *b* sequences of nominal *ventrimaculatus*. Dotted lines separate localities.

	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	–

The sister clade to the *minutus* group consists of the remaining species referred traditionally to *Dendrobates*. Fifty-two unambiguous transformations occur at this node, including the expansion of finger disc III (Character 9, 2→3), origin of even caudal pigmentation in larvae (Character 87, 1→2), and the ability to sequester 3,5-pyrrolizidines.

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 placement of *galactonotus*, but its placement in the *tinctorius* group by Silverstone (1975) was noncontroversial. The monophyly of *galactonotus, castaneoticus,* and *quinquevittatus* was first proposed by Vences et al. (2003), although these three taxa were unresolved in their topology. In the present study, 105 unambiguous synapomorphies optimize to this node, 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 6.27.

Table 6.27. Percent uncorrected pairwise distances between cytochrome *b* sequences of *castaneoticus*, *galactonotus*, and *quinquevittatus*. CR = captive reared. Dotted lines separate localities and species.

	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	—

The next clade is individuated by 39 unambiguous transformations. The first clade included in this group consists of the *pumilio* group of Myers et al. (1984). The evidence for the monophyly of this group is overwhelming, consisting of 136 unambigously optimized synapomorphies, including several larval modifications (Characters 90, 93, and 94), tadpole transport by female nurse frogs (Character 109, 0→1), larval oophagy (Character 111, 1→2), fusion of the sacrum and vertera 8 (Character 143, 0→1), and fusion of vertabrae 2 and 3 (Character 145, 0→1).

Myers and Daly (1976) 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, Myers and Daly named *lehmanni*, based primarily on differences in vocalizations, coloration and color pattern, and, especially, the absence of histrionicotoxins from skin alkaloid profiles. Nevertheless, Garraffo et al. (2001) showed experimentally that *lehmanni* efficiently sequesters histrionicotoxins administered in the diet. Based on differences in vocalizations and coloration and color pattern, Lötters et al. (1999) resurrected *Dendrobates sylvaticus* 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 et al., 1976; see their Plate 1C for color morph), while 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* sample is from the region of the type locality.

The sample of *Dendrobates sylvaticus* is from Ecuador. Cytochrome *b* sequences were not available for the GenBank specimens shown in the cladogram.

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* and *Dendrobates sylvaticus* (see Table 6.28).

Table 6.28. Percent uncorrected pairwise distances between cytochrome *b* sequences of *histrionicus*, *Dendrobates lehmanni*, and *Dendrobates sylvaticus*. Dotted lines separate localities.

	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	—

Similarly, *Dendrobates sylvaticus*, which had been in the synonymy of *histrionicus* until recently, is more closely related to *lehmanni*. 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 sister-species pairs *bicolor* and *terribilis* (7.0%) and *minutus* and *claudiae* (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, *Dendrobates lehmanni* and *Dendrobates*

sylvaticus are still diagnosable on the basis of phenotypic evidence (Myers and Daly, 1976; Lötters et al., 1999) and are therefore 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 6.29) distance supports the historical reality of these species.

Table 6.29. Percent uncorrected pairwise distances between cytochrome *b* sequences of *arboreus*, *pumilio*, *speciosus*, and *vicentei*. Dotted lines separate species.

	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	—

The sister of the *histrionicus* group is equivalent to Silverstone's (1975) *tinctorius* group, with the exclusion of *galactonotus* (see above). This clade is individuated by 91 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 (1975) considered it to be closely related to and potentially derived

from that species. The extensive variation in *tinctorius* that has been discovered subsequently has only strengthened the suspicion that these two nominal taxa are conspecific. This is highly relevant to conservation initiatives. Because of its restricted distribution and ongoing habitat destruction, a captive *azureus* breeding program has been implemented, led by the Aquarium of the Americas in Baltimore. However, if *azureus* is simply yet another variant of the widespread *tinctorius*, limited conservation resources would be better allocated to conservation projects of higher priority.

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 6.30), 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 Brazilian and Suriname *tinctorius* is greater than that between it and *azureus*. All of this is consistent with the hypothesis that these samples are conspecific, which places the conservation of the *azureus* population at a lower priority.

Table 6.30. Percent uncorrected pairwise distances between cytochrome *b* sequences of *azureus* and *tinctorius*. Dotted lines separate species.

	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	–

Despite the considerable variation in coloration and color pattern in *auratus*, there are no known problems surrounding the identities of *auratus* and *truncatus* (see Table 6.31). Silverstone (1975) hypothesized that these two species are closely related,

Table 6.31. Percent uncorrected pairwise distances between cytochrome *b* sequences of *auratus* and *truncatus*. CR = captive reared. Dotted lines separate species and localities.

	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	—

and the available evidence corroborates that claim with a total of 86 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

The present study resolved the phylogeny of most of the included terminals of dendrobatid frogs. The results are generally consistent with prior hypotheses, especially species the groups proposed by Silverstone (1975, 1976). At the level of genera, *Allobates*, *Ameerega*, *Dendrobates* (including or excluding *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 egregiously nonmonophyletic. Nevertheless, the density of taxon sampling allowed coherent clades to be delimited, which will permit a monophyletic taxonomy to be developed in Chapter 7.

In addition to resolving the relationships among species, this study clarifies the identities of numerous problematic species. 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*, but consideration of cladistic and patristic distances identifies 152 species for the 365 dendrobatid terminals included in this analysis. Several nominal species appear to be composed of multiple species. The widespread Amazonian taxon *femoralis* includes eight species, *hahneli* includes two species. Highlighting the effectiveness of bringing DNA sequence evidence to bear on problem

in alpha taxonomy, both *elachyhistus* and *trilineatus* are composed of more than one species, corroborating the suspicions by Duellman (2004) and Grant and Rodríguez (2001) that they may have conflated multiple species in their treatments of these species. Similarly, although the diversity of small, dully colored Amazonian frogs is greater than the current taxonomy identifies, and the names proposed by Morales (2002) 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 parts of different species. Although I have referred populations to Morales's names, this is provisional, and topotypic material must be examined to clarify the taxonomy.

As a quick heuristic to identify species, pairwise comparisons of cytochrome *b* sequences are useful, but not a panacea. Focusing on well-delimited, uncontroversial species, intraspecific cytochrome *b* sequence distances ranged from 0.0–6.0%. 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, I expected the evidence to indicate that the widespread 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, this highlights the pitfalls of generalizing across taxa.

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 how morphologically different these species are, this is unsurprising. However, it is only slightly greater than that observed between the morphologically more similar (but not more closely 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 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.

Chapter 7: A Monophyletic Taxonomy

Preliminary Considerations

Evolutionary relationships provide 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 aspects of dendrobatid frogs. To facilitate understanding and application of the phylogenetic results, herein I propose a revised taxonomy for dendrobatid frogs that reflects as closely as is presently feasible (see below) current knowledge of phylogeny. The remainder of this study (i.e., Chapters 8 and 9) employs this new taxonomy.

My 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 our 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 that would, should they be adopted, surely impede scientific progress, e.g., 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) that hemiphractines are distant relatives of other hylids makes Ford and Cannatella's (1993) node-based definition of

Hylidae apply to all hyloids except eleutherodactylines (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 explicitly endorsed) 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 towards 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 I continue to apply the existing Code.

Over the past four decades the number of recognized dendrobatid species has exploded from 66 to 238, 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 (2005) new taxonomy recognizes only 41 families for approximately 5,000 species of anurans—prior to the Frost et al. update there were only 30 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 mammal species as there are

anuran species. Indeed, in all of these groups the order rank is approximately equivalent to the family rank 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 15% of since 1985) 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 under appreciation 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 relevant of scientific discussion (if this were not the case, then the optimal solution to non-monophyly would always be accretion, with recognized taxa growing ever larger and obscuring more of phylogenetic structure as knowledge increases), and in this sense anuran taxonomy is much less refined than in other vertebrate groups. I 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 I 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. I 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, I fit names to the cladogram somewhat loosely, i.e., 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 promotes antiscientific practice. 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 ~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 appropriate comparisons and thereby greatly facilitate species-level work.

In addition to a summary of the unambiguous transformations that delimit each named clade (including phenotypic synapomorphies and branch length), I report the Bremer support value for the clade and, for genera, 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.

As noted in Chapter 4, I 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*), and *tinctorius* (*Dendrobates*), *tricolor* (*Epipedobates*), and *trivittatus* (*Ameerega*). I did not include the type species *alboguttatus* (*Nephelobates*), *fuliginosus* (*Hyloxalus*), or *latinasus* (*Colostethus*) or *yustizi* (*Mannophryne*), because adequate data were not available to permit their inclusion in the present study. Nevertheless, I included numerous

putatively closely related species and made taxonomic changes accordingly. That is, I 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.

Included in the revised taxonomy are four new genera. For two of these I employ proper names, provide etymologies, and use them in italics (but see Nomenclatural Disclaimer in the Cover Pages of this document). I refer to the remaining two genera simply as Newgenus1 and Newgenus2 without italics.

The Revised Taxonomy

Dendrobatoidea Cope, 1865

Dendrobatidae Cope, 1865

Colostethinae Cope, 1867

Ameerega Bauer, 1986

Colostethus Cope, 1866

Epipedobates Myers, 1987

Silverstoneia New Genus

Dendrobatinae Cope, 1865

Dendrobates Wagler, 1830

Oophaga Bauer, 1988

Phyllobates Duméril and Bibron, 1841

Ranitomeya Bauer, 1988

Newgenus2 New Genus

Hyloxalinae New Subfamily

Hyloxalus Jiménez de la Espada, 1871 “1870”

Aromobatidae New Family

Aromobatinae New Subfamily

Allobates Zimmermann and Zimmermann, 1988

Aromobates Myers, Daly, and Paolillo, 1991

Mannophryne La Marca, 1992

Anomaloglossinae New Subfamily

Anomaloglossus New Genus

Newgenus1 New Genus

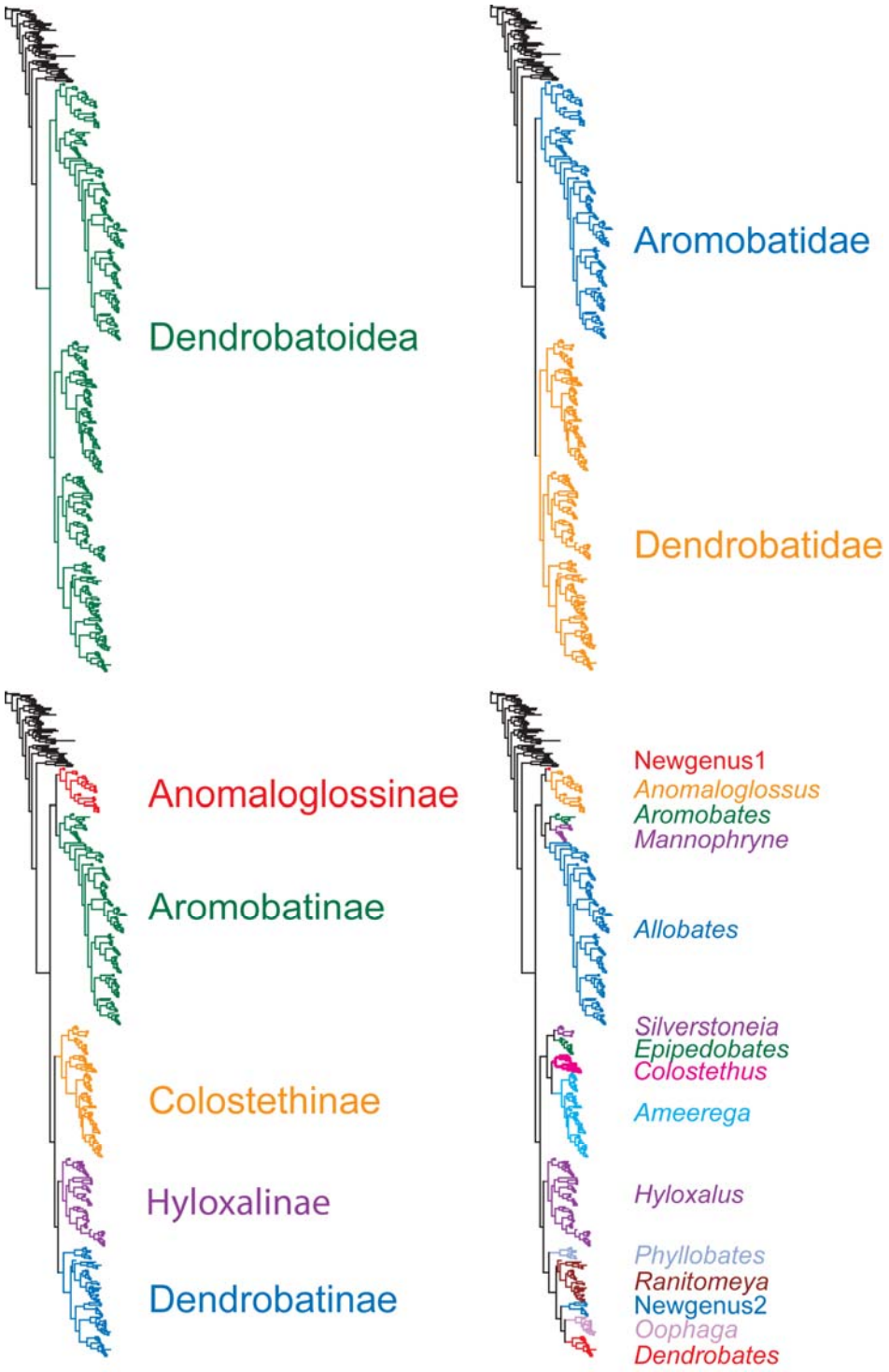


Figure 7.1. Graphic summary of the proposed monophyletic taxonomy for dendrobatid frogs showing clades named at the superfamily, family, subfamily, and genus ranks.

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: Ripanuntio (see Frost et al., 2005).

Sister taxon: Hylodidae (see Comment).

Content (2 families): Dendrobatidae Cope, 1865 and Aromobatidae New Family.

Characterization, diagnosis, and support: Branch length (unambiguous transformations only) = 178. Bremer support = 33.

Unambiguous phenotypic transformations include **(1)** gain of the tarsal keel (Character 28, 0→1), **(2)** the "ranid" type insertion of the distal tendon of insertion of the *m. semitendinosus* (Character 69, 0→1), **(3)** gain of the *m. semitendinosus* binding tendon (Character 70, 0→1), **(4)** occurrence of the dorsal flap of the *m. depressor mandibulae* (Character 72, 0→1), **(5)** relation of the tympanum and *m. depressor mandibulae* (Character 75, 0→1), **(6)** orientation of the *m. intermandibularis* supplementary element (Character 78, 0→1), **(7)** maxillary tooth structure (Character 139, 0→1), **(8)** the occurrence of the retroarticular process of the mandible (Character 141, 0→1), and **(9)** the reduction in chromosome number from 26 to 24 (Character 174, 4→3). Behavioral synapomorphies include **(10)** cephalic copulatory amplexus

(Character 104, 1→0), **(11)** dorsal tadpole transport (108, 0→1), and **(12)** the occurrence of toe trembling Character 115, 0→1).

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. Gross examination reveals fused, non-overlapping epirocaroid cartilages (i.e., firmisterny in the traditional sense), although histological study has shown this to differ in one species (Noble, 1926; Kaplan, 1995; see also Kaplan, 2004).

Distribution: Dendrobatoid frogs occur throughout large parts of Nicaragua, Costa Rica, Panama, Colombia, Ecuador Peru, Bolivia, Venezuela, Guyana, French Guiana, Suriname, and Brazil.

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. (2005) applied Dendrobatoidea to the clade of dendrobatids + *Thoropa* (i.e., Dendrobatidae + Thoropidae). In the present analysis *Thoropa* is nested among cyclorhamphids, and the sister group of dendrobatids is the cyclorhamphid subfamily Hylodinae (*Crossodactylus*, *Hylodes,* and *Megaelosia*). In recognition of the placement of the hylodine genera outside of Cyclorhamphidae, I recognize them as a family, Hylodidae.

FAMILY: Dendrobatidae Cope, 1865.

Immediately more inclusive taxon: Dendrobatoidea Cope, 1865.

Sister taxon: Aromobatidae New Family.

Content (3 Subfamilies): Colostethinae Cope, 1867, Dendrobatinae Cope, 1865, and Hyloxalinae New Subfamily.

Characterization, diagnosis, and support: Branch length (unambiguous transformations only) = 50. Bremer support = 46.

Unambiguously optimized phenotypic synapomorphies for this clade are **(1)** webbing on the postaxial side of toe I absent (Character 37, 2→0), **(2)** webbing on the preaxial side of toe II absent (Character 38, 1/2→0), **(3)** webbing on the postaxial side of toe II absent (Character 39, 1/2→0), **(4)** webbing on the preaxial side of toe III absent (Character 40, 2/3/4→0), and **(5)** palatines absent (Character 131, 1→0).

Distribution: As for Dendrobatoidea.

Comment: For synonymy see Dendrobatoidea, above. Dendrobatidae occurs as far north as Nicaragua and on both sides of the Andes, but most few species are cis-Andean.

SUBFAMILY: Colostethinae Cope, 1867.

- Colostethidae Cope, 1867. Type genus: *Colostethus* Cope, 1866 by monotypy.

Immediately more inclusive taxon: Dendrobatidae Cope, 1865.

Sister taxon: Unnamed clade composed of Dendrobatinae Cope, 1865 and Hyloxalinae New Subfamily.

Content (Four Genera): *Ameerega* Bauer, 1986; *Colostethus* Cope, 1866; *Epipedobates* Myers, 1987; and *Silverstoneia* New Genus.

Characterization, diagnosis, and support: Branch length (unambiguous transformations only) = 84. Bremer support = 27.

Unambiguously optimized phenotypic synapomorphies for this clade include **(1)** finger IV reaching the distal ½ of the subarticular tubercle of finger III (Character 4, 0→1), **(2)** finger I longer than finger II (Character 5, 1/2→3), **(3)** finger III swollen in adult males (Character 20, 0→1), and **(4)** female crouching in courtship (Character 101, 0→1).

Distribution: As for Dendrobatidae. *Silverstoneia* and *Epipedoabates* 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* as *Calostethus* 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.
- *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 taxon: *Colostethus* Cope, 1866.

Content (27 species): *Epipedobates andinus* Myers and Burrowes, 1987; *Dendrobates bassleri* Melin, 1941; *Epipedobates bilinguis* Jungfer, 1989[1]; *Prostherapis bolivianus* Boulenger, 1902; *Dendrobates braccatus* Steindachner, 1864; *Epipedobates cainarachi* Schulte, 1989; *Dendrobates erythromos* Vigle and Miyata, 1980; *Hysaplesia* [misspelled *Hylaplesia*] *flavopicta* Lutz, 1925; *Dendrobates hahneli* Boulenger, 1883; *Dendrobates ingeri* Cochran and Goin, 1970; *Dendrobates labialis* Cope, 1874; *Epipedobates macero* Rodríguez and Myers, 1993; *Dendrobates parvulus* Boulenger, 1882; *Phyllobates petersi* Silverstone, 1976; *Hysaplesia* [misspelled *Hylaplesia*] *picta* Tschudi, 1838; *Epipedobates planipaleae* Morales and Velazco, 1998; *Epipedobates pongoensis* Schulte, 1999; *Phyllobates pulchripectus* Silverstone, 1976; *Epipedobates rubriventris* Lötters, Debold, Henle, Glaw, and Kneller, 1997; *Dendrobates silverstonei* Myers and Daly, 1979; *Epipedobates simulans* Myers, Rodriguez, and Icochea, 2000; *Phyllobates smaragdinus* Silverstone, 1976; *Hyla trivittata* Spix, 1824.

Characterization, diagnosis, and support: Branch length (unambiguous transformations only) = 127. Bremer support = 106.

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

[1] In a recent book on frog 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, I continue to recognize both taxa as valid species.

(usually blue) spotting/reticulation/marbling (Character 64, 0→3), and **(3)** the ability to sequester lipophilic alkaloids (Character 146, 0→1).

Other characteristics include: (1) Dorsal coloration variable (dull 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 anus 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: East of the Andes from Colombia to Bolivia and in the Atlantic forest of Brazil. Most species occur at low elevations, but some reach middle elevations (ca. 1400 m). This clade is almost entirely cis-Andean, the sole exceptions being the presumed sister species *Ameerega andina* and *A. erythromos*, which occur a low to moderate elevations of the Pacific Andean slopes.

Comment: *Ameerega* is most easily distinguished 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 Chapter 5, character 0). Species of other genera that possess strongly granular dorsal skin are *Allobates femoralis*, *A. zaparo*, and *D. granuliferus*.

In content, *Ameerega* is equivalent to the combination of Silverstone's (1976) *pictus* and *trivitattus* groups. Most species previously referred to *Epipedobates* (sensu Myers, 1987) pertain to this group, i.e, it is equivalent to *Phyllobates* sensu Silverstone (1975) following the removal of the *bicolor* and *femoralis* groups.

Vigle and Miyata (1980) described *A. 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 referral of these species to *Ameerega* if it were not for their biogeographically anomalous placement west of the Andes, while the remainder of the clade is entirely *cis*-Andean. 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 occur in bromeliads, and it is likely that tadpoles are also deposited in phytotelmata, which suggests these species could be part of Dendrobatinae (see below).

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 taxon: *Ameerega* Bauer, 1986.

Content (18 species): *Colostethus agilis* Lynch and Ruiz-Carranza, 1985; *Colostethus alacris* Rivero and Granados-Diaz, 1990 "1989"; *Colostethus brachistriatus* Rivero and Serna, 1986; *Colostethus dysprosium* Rivero and Serna, 2000 "1995"; *Colostethus fraterdanieli* Silverstone, 1971; *Colostethus fugax* Morales and Schulte, 1993; *Colostethus furviventris* Rivero and Serna, 1991; *Colostethus imbricolus* Silverstone, 1975; *Prostherapis inguinalis* Cope, 1868; *Colostethus jacobuspetersi* Rivero, 1991; *Phyllobates mertensi* Cochran and Goin, 1964; *Phyllobates latinasus* Cope, 1863; *Colostethus lynchi* Grant, 1998; *Hyloxalus panamensis* Dunn, 1933; *Phyllobates pratti* Boulenger, 1899; *Colostethus ruthveni* Kaplan, 1997; *Phyllobates thorntoni* Cochran and Goin, 1970; *Colostethus yaguara* Rivero and Serna, 1991.

Characterization, diagnosis, and support: Branch length (unambiguous transformations only) = 37. Bremer support = 11.

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 discs moderately expanded; (9) median lingual process absent; (10) larval anus dextral; (11) larval oral disc shape normal (not umbelliform); (12) larval oral disc emarginate; (13) lipophilic alkaloids absent; (14) chromosome number 2n=24 (known in *Colostethus fraterdanieli* and *C. panamensis*); (15) testes entirely pigmented in most species, partially or unpigmented in others; (16) dark throat collar absent.

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 trans-Andean species is *C. fugax*, which is know from the eastern slope of the Cordillera Oriental of 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 including 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, *A. 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.

The moderately to extensively webbed species *Colostethus agilis*, *C. mertensi*, and *C. thorntoni* are referred to this genus because (1) they have a short zygomatic ramus of the squamosal (thus differing from Newgenus1), (2) swollen third finger in adult males (thus differing from *Hyloxalus*), and (3) lack dorsolateral stripes (thus differing from *Allobates*); other general lack moderate to extensive webbing.

DNA sequence data for *Colostethus fugax* was 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 should be noted that it resembles other species of *Colostethus* in possessing a swollen third finger in adult males (unlike *Hyloxalus*), lacking a dorsolateral stripe (ulke almost all species of *Allobates*), and other apparently compact clades also occur on both sides of the Andes (e.g., the *Hyloxalus ramosi* group; Grant and Ardila-Robayo, 2002).

GENUS: *Epipedobates* Myers, 1987.

- *Epipedobates* Myers, 1987. Type species: *Prostherapis tricolor* Boulenger, 1899 by original designation.

Immediately more inclusive taxon: Colostethinae Cope, 1867.

Sister taxon: *Silverstoneia* New Genus.

Content (5 species): *Phyllobates anthonyi* Noble, 1921; *Prostherapis boulengeri* Barbour, 1909; *Phyllobates espinosai* Funkhouser, 1956; *Colostethus machalilla* Coloma, 1995; *Prostherapis tricolor* Boulenger, 1899.

Characterization, diagnosis, and support: Branch length (unambiguous transformations only) = 73. Bremer support = 70.

Due to the lack of phenotypic data for the Genbank sample of *E. boulengeri*, all phenotypic transformations that occur at this node are optimization-dependent. However, assuming fast optimization, phenotypic transformations for *Epipedobates* are **(1)** loss of metatarsal fold (Character 46, 0→1), **(2)** female throat and chest color dark with pale median longitudinal stripe (Character 62, 0→5), **(3)** female abdomen color dark with discrete pale spotting/reticulation/marbling (Character 64, 0→3), and **(4)** ability to sequester lipophilic alkaloids (Character 146, 0→1).

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 are 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 expaned; (10) median lingual process absent; (11) larval anus 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 boulengeri E. espinosai,* and *E. machalilla* occur in the Pacific lowlands of northern South American, with the northernmost species . *Epipedobates anthonyi*, , and *E. tricolor* are all montane species, occurring up to 1800 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 below).

Silverstone (1976:29) expressed doubt regarding the identity of some Ecuadorian specimens he referred to *E. boulengeri*, and Lötters et al. (2003) 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 non-monophyletic. However, insofar as Santos et al. (2003) provided no locality data for the sample they referred to this species (sequence obtained for this study from 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. I follow their usage here, although it should be noted that 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 taxon: *Epipedobates* Myers, 1987.

Content (2 species): *Phyllobates flotator* Dunn, 1931; *Phyllobates nubicola* Dunn, 1924; *Colostethus erasmios* Rivero and Serna "1995" 2000.

Characterization, diagnosis, and support: Branch length (unambiguous transformations only) = 46. Bremer support = 14.

Unambiguously optimized phenotypic synapomorphies include **(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 tooth rows in larvae.

Other characteristics include: (1) Dorsal coloration cryptic, brown; (2) pale oblique lateral 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–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 anus 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: Middle America (as far north as Nicaragua) and the Chocó region of western Colombia. Nominal and undescribed species (see below) all occur below 1200 m.

Etymology: *Silverstoneia* is named in honor of Phillip A. Silverstone for his outstanding contribution to knowledge of dendrobatid frogs. Silverstone abandoned herpetology in 1980 after "seeing the light" of botany. Nevertheless, during the course of his short career in herpetology, Silverstone named 11 species (all of which are still considered valid) and produced two superb monographs (Silverstone, 1975 , 1976). After 30 years, and despite the many advances that have occurred, Silverstone's monographs remain an essential starting point for all studies of dendrobatoid frogs. Furthermore, Silverstone carried out extensive field work in South America in the late 1960s and early 1970s, particularly in the Pacific lowlands of Colombia. Those collections have been key to understanding dendrobatoid diversity (e.g., Grant, 2004) and are especially central to discovering the diversity of this clade (see Comments).

Comment: At present, *Silverstoneia* contains only three species, one of which (*S. erasmios*) is a probable synonym of *S. nubicola*. However, I name this genus in anticipation of the description of five additional species (including *punctiventris* from

the present analysis) currently in manuscript form (Grant and Myers, in progress). These species form a morphologically compact clade, and all known larvae have an umbelliform oral disc with submarginal papillae and reduced tooth rows.

SUBFAMILY: Hyloxalinae New Subfamily.

Immediately more inclusive taxon: Dendrobatidae Cope, 1865.

Sister taxon: Dendrobatinae Wagler, 1865.

Content: *Hyloxalus* Jiménez de la Espada, 1871 "1870"

Characterization, diagnosis, and support: Branch length (unambiguous transformations only) = 51. Bremer support = 45. No phenotypic character-states optimize unambiguously to this node.

Distribution: Andean South America.

Comment: Although this name is currently redundant with *Hyloxalus*, I anticipate that the available names the *Cryptophyllobates* and *Phyllodromus* will be resurrected in the near future, making Hyloxalinae an informative name (for recognized 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 taxon: Dendrobatinae Wagler, 1865.

Content (54 species): *Colostethus abditaurantius* Silverstone, 1975; *Colostethus aeruginosus* Duellman, 2004; *Colostethus anthracinus* Edwards, 1971; *Colostethus argyrogaster* Morales an dSchulte, 1993; *Colostethus awa* Coloma, 1995; *Phyllobates azureiventris* Kneller and Henle, 1985; *Colostethus betancuri* Rivero and Serna 1991; *Hyloxalus bocagei* Jiménez de la Espada, 1871; *Colostethus borjai* Rivero and Serna, 2000 “1995”; *Colostethus breviquartus* Rivero and Serna, 1986; *Colostethus cevallosi* Rivero, 1991; *Colostethus delatorrea* Coloma, 1995; *Colostethus edwardsi* Lynch, 1982; *Colostethus elachyhistus* Edwards, 1971; *Colostethus eleutherodactylus* Duellman, 2004; *Colostethus exasperatus* Duellman and Lynch, 1988; *Colostethus excisus* Rivero and Serna 2000 “1995”; *Colostethus faciopuntulatus* Rivero, 1991; *Colostethus fallax* Rivero, 1991; *Colostethus fascianiger* Grant and Castro-H., 1998; *Hyloxalus fuliginosus* Jiménez de la Espada, 1871; *Colostethus idiomelus* Rivero, 1991; *Phyllobates infraguttatus* Boulenger, 1898; *Colostethus insulatus* Duellman, 2004; *Colostethus lehmanni*, Silverstone, 1971; *Colostethus leucophaeus* Duellman, 2004; *Colostethus littoralis* Péfaur, 1984; *Colostethus maculosus* Rivero, 1991; *Colostethus maquipucuna* Coloma, 1995; *Colostethus marmoreoventris* Rivero, 1991; *Colostethus mittermeieri* Rivero, 1991; *Colostethus mystax* Duellman and Simmons,

1988; *Colostethus nexipus* Frost, 1985; *Colostethus patitae* Lötters, Morales, and Proy, 2003; *Colostthus pecularis* Rivero, 1991; *Phyllobates peruvianus* Melin, 1941; *Colostethus pinguis* Rivero and Granados-Diaz, 1990 "1989"; *Phyllodromus pulchellum* Jiménez de la Espada, 1871; *Colostethus pulcherrimus* Duellman, 2004; *Colostethus pumilus* Rivero, 1991; *Colostethus ramosi* Silverstone, 1971; *Colostethus ruizi* Lynch, 1982; *Colostethus sauli* Edwards, 1974; *Colostethus shuar* Duellman and Simmons, 1988; *Colostethus sordidatus* Duellman, 2004; *Colostethus spilotogaster* Duellman, 2004; *Prostherapis subpunctatus* Cope, 1899; *Phyllobates sylvaticus* Barbour and Noble, 1920; *Colostethus toachi* Coloma, 1995; *Colostethus utcubambensis* Morales, 1994; *Hyloxalus vergeli* Hellmich, 1940; *Phyllodromus vertebralis* Boulenger, 1899; *Prostherapis whymperi* Boulenger, 1882

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. ; (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 anus 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*. *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*, i.e., *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. At present, at least two clearly delimited clades are evident: (1) The *Hyloxalus ramosi* group is delimited by the unique occurrence of black, apparently glandular tissue on the inner surface of the arm. I have observed this character-state in *H. anthracinus*, *H. cevallosi*, *H. exasperatus*, *H. fascianiger*, *H. lehmanni*, *H. ramosi*, and *H. saltuarius*, as well as the undescribed *H*. Ibagué species, included in the present analysis. No genus-group name exists for this clade. (2) A group I refer to herein as the *H. azureiventris* group lacks unique synapomorphies, but several color pattern characters are synapomorphic locally, the species included in the present study were strongly monophyletic, and the morphological resemblance of the species is undeniable. This group includes *H.*

azureiventris, *H. eleutherodactylus*, *H. nexipus*, and *H. patitae*, as well as the undescribed *H*. PortoWalter2 from the present analysis. A species sequenced by Santos et al. (2003) is also part of this clade, but its identity must 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.

Sister taxon: Hyloxalinae, New Subfamily

Content: *Dendrobates* Wagler, 1830; Jiménez de la Espada, 1871 "1870"; *Oophaga* Bauer, 1988; *Phyllobates* Duméril and Bibron, 1941; *Ranitomeya* Bauer, 1988; and NewGenus2.

Characterization, diagnosis, and support: Branch length (unambiguous transformations only) = 62. Bremer support = 46.

Unambiguously optimized phenotypic synapomorphies for this clade include **(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, **(4)** larvae deposited in phytotelmata (Character 110, 0→1), and **(5)** the ability to sequester lipophilic alkaloids (Character 146, 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.

Sister taxon: Unnamed clade composed of *Dendrobates* Wagler, 1830; Jiménez de la Espada, 1871 "1870"; *Oophaga* Bauer, 1988; *Ranitomeya* Bauer, 1988; and NewGenus2.

Content (5 species): *Dendrobates aurotaenia* Boulenger, 1913; *Phyllobates bicolor* Duméril and Bibron, 1841; *Dendrobates lugubris* Schmidt, 1857; *Phyllobates terribilis* Myers, Daly, and Malkin, 1978; and *Dendrobates vittatus* Cope, 1893.

Characterization, diagnosis, and support: Branch length (unambiguous transformations only) = 141. Bremer support = 134.

Unambiguously optimized phenotypic synapomorphies of this clade are **(1)** finger I longer than finger II (Character 5, 1/2→3), **(2)** pale dorsolateral stripe present in juveniles (Character 52, 0→1), and **(3)** the uniquely derived ability to sequester batrachotoxin (Character 147, 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 anus dextral; (12) larval oral disc shape “normal” (not umbellifomr); (13) larval oral disc emarginate; (14) lipophilic alkaloids present; (15) chromosome number 2n=24 (known in *Phyllobates lugubris*); (16) testes unpigmented; (17) dark throat collar absent.

Distribution: Exclusively trans-Andean, ranging from Costa Rica through the Chocó region of south western Colombia.

Comment: *Phyllobates* in the present taxonomy unchanged from that proposed by Myers et al. (1978).

GENUS: *Ranitomeya* Bauer, 1988

- *Ranitomeya* Bauer, 1988. Type species: *Dendrobates reticulatus* Boulenger, 1884 “1883” by original designation.
- *Minyobates* Myers, 1987. Type species: *Dendrobates steyermarki* Rivero, 1971 by original designation.

Immediately more inclusive taxon: Dendrobatinae.

Sister taxon: Unnamed clade composed of Newgenus2, *Dendrobates* Wagler, 1830; Jiménez de la Espada, 1871 “1870”; *Oophaga* Bauer, 1988.

Content (25 species): *Dendrobates abditus* Myers and Daly, 1976; *Dendrobates altobueyensis* Silverstone, 1975; *Dendrobates biolat* Morales, 1992; Dend*robates bombetes* Myers and Daly, 1980; *Dendrobates claudiae* Junger, Lötters, and Jorgens, 2000; *Dendrobates duellmani* Schulte, 1999; Dendrobates fantasticus Boulenger, 1884 "1883"; *Dendrobates flavovittatus* Schulte, 1999; *Dendrobates fulguritus* Silverstone, 1975; *Dendrobates igneus* Melin, 1941; *Dendrobates imitator* Schulte, 1986;

Dendrobates intermedius Schulte, 1999; *Dendrobates lamasi* Morales, 1992; *Dendrobates minutus* Shreve, 1935; *Dendrobates mysteriosus* Myers, 1982; *Dendrobates opisthomelas* Boulenger, 1899; *Dendrobates reticulatus* Boulenger, 1884 "1883"; *Dendrobates rubrocephalus* Schulte, 1999; *Dendrobates sirensis* Aichinger, 1991; *Dendrobates steyermarki* Rivero, 1971; *Dendrobates vanzolinii* Myers, 1982; *Dendrobates variabilis* Zimmerman and Zimmerman, 1988; *Dendrobates ventrimaculatus* Shreve, 1935; *Dendrobates viridis* Myers and Daly, 1976; *Minyobates virolinensis* Ruiz-Carranza and Ramírez-Pinilla, 1992

Characterization, diagnosis, and support: Branch length (unambiguous transformations only) = 6. Bremer support = 4.

Unambiguously optimized phenotypic synapomorphies for this clade are **(1)** toe disc II unexpanded (Character 32, 1→0) and **(2)** large intestine entirely pigmented (Character 66, 0→2).

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 in all but *R. steyermarki*; (9) finger discs II-IV greatly expanded in most species; (10) median lingual process absent; (11) larval anus 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 on *R. steyermarki* and *R. imitator*); (17) dark throat collar absent.

Distribution: As for Dendrobatinae, above.

Comment: *Ranitomeya* is equivalent to Silverstone's (1975) *minutus* group with the removal of *Dendrobates quinquevittatus* sensu stricto. The type species of *Minyobates* is *Dendrobates steyermarki*, which is found to be sister to the remaining species of *Ranitomeya*. Nevertheless, with the exception of *D. steyermarki*, *Minyobates* sensu Myers (1987) is a monophyletic radiation found in Central America, the Colombian Chocó, and cloud forest localities of the Colombian Andes. That clade is absent from the Amazon basin and eastern slope of the Cordillera Oriental (*Ranitomeya virolinensis* occurs on the western slope of the Cordillera Oriental). The sister clade to that radiation is an exclusively Amazonian group. For taxonomic purposes, I recommend referring to these clades as the *minutus* and *ventrimaculatus* groups, respectively, pending increased taxon and character sampling required to further refine the taxonomy.

GENUS: Newgenus2

- Newgenus2. Type species: *Dendrobates castaneoticus* Caldwell and Myers, 1990.

Immediately more inclusive taxon: Dendrobatinae.

Sister taxon: Unnamed clade composed of *Dendrobates* Wagler, 1830; Jiménez de la Espada, 1871 "1870"; *Oophaga* Bauer, 1988.

Content (4 species): *Dendrobates captivus* Myers, 1982; *Dendrobates castaneoticus* Caldwell and Myers, 1990; *Dendrobates galactonotus* Steindachner, 1864, *Dendrobates quinquevittatus* Steindachner, 1864.

Characterization, diagnosis, and support: Branch length (unambiguous transformations only) = 105. Bremer support = 35. All phenotypic synapomorphies for this clade are ambiguous.

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 anus 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 Newgenus2 *castaneoticus* and Newgenus2 *galactonotus*, pigmented in Newgenus2 *quinquevittatus*; (17) dark throat collar absent.

Distribution: Eastern Amazonia

Comment: Newgenus2 *galactonotus* was previously considered to be a species of the *Dendrobates tinctorius* group (e.g., Silverstone, 1975), and the remaining species were placed in what is herein called *Ranitomeya*. Caldwell and Myers (1990) considered Newgenus2 castaneoticus and Newgenus2 quinquevittatus to be sister species; however, in addition to the extensive support from DNA sequence evidence for the proposed relationships, Newgenus2 *castaneoticus* and Newgenus2 *galactonotus* share the derived loss of testis pigmentation.

GENUS: *Oophaga* Bauer, 1988

- *Oophaga* Bauer, 1988. Type species: *Dendrobates pumilio* Schmidt, 1857 by original designation.

Immediately more inclusive taxon: Dendrobatinae.

Sister taxon: *Dendrobates* Wagler, 1830.

Content (9 species): *Dendrobates arboreus* Myers, Daly, and Martínez, 1984; *Dendrobates granuliferus* Taylor, 1958; *Dendrobates histrionicus* Berthold, 1845; *Dendrobates lehmanni* Myers and Daly, 1976; *Dendrobates occultator* Myers and Daly, 1976; *Dendrobates pumilio* Schmidt, 1857; *Dendrobates speciosus* Schmidt, 1857; *Dendrobates sylvaticus* Funkhouser, 1956; *Dendrobates vicentei* Jungfer, Weygoldt and Juraske, 1996.

Characterization, diagnosis, and support: Branch length (unambiguous transformations only) = 136. Bremer support = 118.

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 row (Character 93, 2→1), **(3)** single posterior larval tooth row (Character 94, 3→1), **(4)** the uniquely derived "chirp" advertisement call (Character 98, 1→4), **(5)** cloacal touching during courtship/oviposition (Character 105, 0→1), **(6)** female nurse frog (Character 109, 0→1), **(7)** larvae strictly oophagous (Character 111, 1→2), **(8)** egg provisioning undertaken without male participation (Character 112, 0→1), **(9)** omosternum entirely cartilaginous (Character 126, 1→0), **(10)** anterior projection of suprascapula heavily calcified (Character 127, 0→1), **(11)** sacrum and vertebra 8 fused (Character 143, 0→1), **(12)** vertebrae 2 and 3 fused (Character 145, 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. granuliferus*, 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 anus 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 granuliferus*, *O. pumilio*, and *O. sylvaticus*); (16) testes pigmented (entirely in most; medially only in *O. sylvaticus*); (17) dark throat collar absent.

Distribution: Nicaragua through the Colombian Chocó to northern Ecuador at elevations below 1200 m.

Comment: *Oophaga* is identical to the *histrionicus* group of Myers et al. (1984), with the addition of newly discovered taxa.

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.

Sister taxon: *Oophaga* Bauer, 1988.

Content (6 species): *Dendrobates auratus* Girard, 1855; *Dendrobates azureus* Hoogmoed, 1969; *Dendrobates leucomelas* Steindachner, 1864; *Dendrobates nubeculosus* Jungfer & Böhme, 2004; *Rana tinctoria* Cuvier, 1797; *Phyllobates truncatus* Cope, 1861.

Characterization, diagnosis, and support: Branch length (unambiguous transformations only) = 91. Bremer support = 79. There are no unambiguously optimized phenotypic synapomorphies for this clade.

Other characteristics include: (1) Dorsal coloration conspicuous, bright; (2) pale oblique lateral stripe absent; (3) pale dorsolateral stripe absent in most (present in *D. truncatus*); (4) pale ventrolateral stripe absent; (5) dorsal skin texture smooth; (6) toe webbing absent; (7) third finger of adult males absent; (8) finger I shorter than finger II; (9) finger discs moderately to greatly expanded; (10) median lingual process absent; (11) larval anus 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 *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 (1975) *Dendrobates tinctorius* group (minus *galactonotus*) and *Dendrobates auratus* group.

FAMILY: Aromobatidae New Family

- Aromobatidae New Family. Type genus: Aromobates Myers, Daly, and Paolillo, 1991.

Immediately more inclusive taxon: Dendrobatoidea.

Sister taxon: Dendrobatidae.

Content: Anomaloglossinae and Aromobatinae

Characterization, diagnosis, and support: Branch length (unambiguous transformations only) = 71. Bremer support = 40.

Unambiguously optimized synapomorphies of this clade are **(1)** medially pigmented adult testis (Character 31, 0→1), **(2)** toe disc III moderately expanded (Character 33, 1→2), **(3)** toe disc IV moderately expanded (Character 34, 1→2), and **(4)** testes unpigmented (Character 67, 2→0).

Distribution: Almost entirely cis-Andean, occurring on the eastern slopes of the Andes, throughout the Amazon region, and in the Atlantic forest of Brazil. A few trans-Andean species occur in *Anomaloglossus* and *Allobates* (for discussion see generic accounts).

Comment: All species of Aromobatidae lack the ability to sequester alkaloids.

SUBFAMILY: Anomaloglossinae New Subfamily

- Anomaloglossinae. Type genus: *Anomaloglossus* New Genus (see below).

Immediately more inclusive taxon: Aromobatidae.

Sister taxon:

Content: *Anomaloglossus* and Newgenus1.

Characterization, diagnosis, and support: Branch length (unambiguous transformations only) = 42. Bremer support = 14.

Unambiguously optimized phenotypic synapomorphies of this clade are **(1)** fringe present on preaxial surface of finger II (Character 13, 0→1), **(2)** fringe present on preaxial surface of finger III (Character 14, 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), **(6)** distal 2 phalanges of postaxial side of toe I free of webbing but with fringe (Character 39, 1→2), **(7)** fringe present on postaxial side of toe V (Character 45, 0→1), **(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 tepuy regions. Three species also occur on the Pacific slopes of Colombia and Ecuador.

GENUS: *Anomaloglossus* New Genus

- *Anomaloglossus* New Genus. Type species: *Colostethus stepheni* Martins, 1989.

Immediately more inclusive taxon: Anomaloglossinae New Subfamily.

Sister taxon: NewGenus1

Content (16 species): *Colostethus atopoglossus* Grant, Humphrey, & Myers, 1997; *Colostethus ayarzaguenai* La Marca, 1997 "1996"; *Colostethus baeobatrachus* Boistel and Massary, 1999; Hyloxalus beebei Noble, 1923; *Colostethus* "*chocoensis*" auctorum [not of Boulenger, 1912]; *Colostethus degranviellei* Lescure, 1975; *Colostethus guanayensis* La Marca, 1997 "1996"; *Colostethus lacrimosus* Myers, 1991; *Colostethus parimae* La Marca, 1997 "1996"; *Colostethus parkerae* Meinhardt and Parmelee, 1996; *Colostethus praderioi* La Marca, 1997 "1996"; *Colostethus roraima* La Marca, 1997 "1996"; *Prostherapis shrevei* Rivero, 1961; *Colostethus stepheni* Martins, 1989; *Colostethus tamacuarensis* Myers and Donnelly, 1997; *Colostethus tepuyensis* La Marca, 1997 "1996".

Characterization, diagnosis, and support: Branch length (unambiguous transformations only) = 70. Bremer support = 57.

Unambiguously optimized phenotypic synapomorphies of this clade are **(1)** male throat (vocal sac) with irregular (clumped) stippling or faint, diffuse spotting (Character 61, 4→6) and **(2)** 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 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 anus 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.

Distribution: Most species are cis-Andean, but no species is known to occur west or south of the region of Manaus, and there is a large number of tepuy 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. (This name should not be mistaken for *Anomaloglossa* Percival, 1978, which is a genus of brachiopod.)

Comment: *Anomaloglossus* is most simply diagnosed on the basis of 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. (2005) showed decisively that dendrobatoids are not closely related to Old World ranoids, and their MLP is independently derived.

La Marca (1997 "1996") did not note the occurrence of the MLP in *A. ayarzaguenai*, *A. guanayensis*, *A. murisipanensis*, or *A. parimae*, and I have not examined these species; as such, their reference to this clade is a prediction, based

geography and their resemblance to MLP-possessing species, and must be confirmed. The presence of the MLP is confirmed for all other species referred to this clade.

Within *Anomaloglossus* there are basically two "flavors" of frogs: small, slender frogs with minimal toe webbing (e.g., *A. stepheni*), and usually larger, robust frogs with moderate to extensive webbing (e.g., *A. tepuyensis*). The former group is strictly cis-Andean, whereas the latter group 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 more thoroughly test this hypothesis. Similarly, the trans-Andean MLP-possessing species must be included explicitly in phylogenetic analysis to corroborate their placement in *Anomaloglossus*. Nevertheless, the finding that the two morphological variants of MLP-possessing aromobatids form a clade is suggestive the inclusive group is also monophyletic.

GENUS: NewGenus1

- NewGenus1. Type species: *Phyllobates palmatus* Werner, 1899.

Immediately more inclusive taxon: Dendrobatinae.

Sister taxon: *Anomaloglossus* New Genus.

Content (2 species): *Hyloxalus palmatus* Werner, 1899; *Colostethus pseudopalmatus* Rivero and Serna 2000 "1995"

Characterization, diagnosis, and support: Branch length (unambiguous transformations only) = 27. Bremer support = 27.[2] Insofar as this genus is represented by a single species in this analysis, I cannot distinguish between autapomorphies and synapomorphies and therefore do not report 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 anus 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 Newgenus1 *palmatus*); (16) testes unpigmented; (17) dark throat collar absent.

Distribution: Eastern slopes of the Cordillera Oriental, western 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 2000 m.

Comment: Phylogenetic analysis showed Newgenus1 *palmatus* is the sister taxon of *Anomaloglossus.* I refer Newgenus1 *pseudopalmatus* to this genus provisionally based on Rivero and Serna's (2000 "1995") assertion that they are sister species. Nevertheless, I caution that the diagnostic characters provided by Rivero and Serna are inadequate to validate their claim and exclude Newgenus1 *pseudopalmatus* from

[2] The relevance of these values is minimal, given that this clade consists only of two specimens of the same species, but I report them for consistency.

Hyloxalus or *Aromobates*. Nevertheless, the diagnostic differences given by Rivero and Serna all occur within the variation of Newgenus1 *palmatus* at localities in the Cordillera Oriental, and given the type locality of Amalfi within the known distribution of Newgenus1 *palmatus* on the eastern slope of the Cordillera Central, it is also possible that these two taxa are conspecific.

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.

SUBFAMILY: Aromobatinae New Subfamily

- Aromobatinae New Subfamily. Type genus: *Aromobates* Myers, Daly, Paolillo, 1991.

Immediately more inclusive taxon:.

Sister taxon:Anomaloglossinae New Subfamily.

Content: *Aromobates* and *Mannophryne*.

Characterization, diagnosis, and support: Branch length (unambiguous transformations only) = 36. Bremer support = 46.

Unambiguously optimized phenotypic synapomorphies of this clade are **(1)** finger I shorter than finger II (Character 5, 1→2), **(2)** distal 2.5 phalanges of preaxial side of toe II free of webbing (Character 38, 2→1), **(3)** distal 3.5 phalanges of preaxial side of toe III free of webbing (Character 40, 4→2), **(4)** male throat (vocal sac) evenly stippled (Character 61, 4→2), and **(5)** zygomatic ramus of squamosal shorter but still robust and well defined (Character 129, 2→3).

Distribution: East of the Andes to the Atlantic forest and Bolivia.

Comment: The inclusion of *Allobates* in Aromobatinae is nomenclaturally expedient but taxonomically unsatisfactory. The three genera are a clade, but *Aromobates* and *Mannophryne* form a morphologically and geographically compact group, and it would be appropriate to restrict Aromobatinae to that clade. However, that would require the designation of a subfamily for, and redundant, with *Allobates*. *Allobates* is a large, broadly distributed and heterogeneous clade whose internal phylogenetic structure is worthy of formal taxonomic recognition. Current knowledge is inadequate to name additional genera and assign species not included explicitly in the present phylogenetic 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, I anticipate that the paucity of knowledge will be remedied quickly, at which time the recognition of a subfamily for the taxa currently referred to *Allobates* would be feasible .

GENUS: *Aromobates* Myers, Daly, and Paolillo, 1991.

- *Aromobates*. Type species *Aromobates nocturnus* Myers, Daly, and Paolillo, 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 taxon: *Mannophryne* La Marca, 1991.

Content (12 species): *Phyllobates alboguttatus* Boulenger, 1903; *Colostethus capurinensis* Péfaur, 1993; *Colostethus duranti* Pefaur, 1985; *Colostethus haydeeae* Rivero, 1978 "1976"; *Colostethus leopardalis* Rivero, 1980 "1978"; *Colostethus mayorgai* River, 1980 "1978"; *Colostethus meridensis* Dole and Durant, 1972; *Colostethus molinarii* La Marca, 1985; *Aromobates nocturnus* Myers, Paolillo, and Daly, 1991; *Colostethus orostoma* Rivero, 1978 "1976"; *Colostethus saltuensis* Rivero 1980 "1978"; *Colostethus serranus* Péfaur, 1985.

Characterization, diagnosis, and support: Branch length (unambiguous transformations only) = 56. Bremer support = 26. No phenotypic synapomorphies optimize unambiguously to this node.

Other characteristics include: (1) Dorsal coloration cryptic, brown or gray; (2) pale 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 or than finger II; (9) finger discs weakly to moderately expanded; (10) median lingual process absent; (11) larval anus 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 in that I 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 2400 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 taxon: *Aromobates* Myers, Paolillo, and Daly, 1991.

Content (12 species): *Mannophryne caquetio* Mijares-Urrutia & Arends R., 1999; *Hyloxalus* [misspelled *Hylixalus*] *collaris* Boulenger, 1912; *Mannophryne cordilleriana* La Marca, "1994" 1995; *Prostherapis herminae* Boettger, 1893; *Mannophryne lamarcai* Mijares-Urrutia and Arends R., 1999; *Colostethus larandina* Yustiz, 1991; *Prostherapis neblina* Test, 1956; *Colostethus oblitterata* Rivero, 1986 "1984"; *Colostethus olmonae* Hardy, 1983; *Prostherapis riveroi* Donoso-Barros, 1965 "1964"; *Phyllobates trinitatis* Garman, 1887; *Colostethus yustizi* La Marca, 1989.

Characterization, diagnosis, and support: Branch length (unambiguous transformations only) = 69. Bremer support = 39.

Phenotypic synapomorphies that optimize unambiguously to this node are **(1)** tarsal keel straight of weakly curved, extending from inner metatarsal tubercle to center of tarsus (Character 29, 1→0), **(2)** presence of a dermal collar (Character 59, 0→1), **(3)** male abdomen color evenly stippled (Character 63, 3→2), **(4)** male jumping

up and down during courtship (Character 100, 0→1),**(5)** frontoparietals fused posteriorly (Character 135, 0→1), and **(6)** frontoparietal and otoccipital fused (Character 136, 0→1).

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 naroow to moderately expanded; (10) median lingual process absent; (11) larval anus 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.

GENUS: *Allobates* Zimmermann and Zimmermann, 1988

- *Allobates* Zimmermann and Zimmermann, 1988. Type species *Prostherapis femoralis* Boulenger, 1884, by original designation.

Immediately more inclusive taxon: Aromobatinae New Subfamily

Sister taxon: Unnamed clade composed of *Aromobates* Myers, Daly, and Paolillo, 1991 and *Mannophryne* La Marca, 1992.

Content (42 species): *Phyllobates alagoanus* Bokermann, 1967; *Colostethus alessandroi* Grant and Rodríguez, 2001; *Phyllobates bromelicola* Test, 1956; *Prostherapis brunneus* Cope, 1887; *Colostethus caeruleodactylus* Lima and Caldwell, 2001; *Phyllobates capixaba* Bokermann, 1967; *Phyllobates carioca* Bokermann, 1967; *Colostethus cepedai* Morales 2002 "2000"; *Colostethus chalcopis* Kaiser, Coloma, and Gray, 1994; *Colostethus conspicuus* Morales 2002 "2000"; *Colostethus craspedoceps* Duellman, 2004; *Colostethus crombei* Morales 2002 "2000"; *Prostherapis femoralis* Boulenger, 1883; *Colostethus fratinescus* Morales 2002 "2000"; *Colostethus fuscellus* Morales 2002 "2000"; *Colostethus gasconi* Morales 2002 "2000"; *Colostethus goianus* Bokermann, 1975; *Colostethus humilus* Rivero, 1980 "1978"; *Colostethus insperatus* Morales 2002 "2000"; *Colostethus juanii* Morales, 1994; *Phyllobates kingsburyi* Boulenger, 1918; *Prostherapis mandelorum* Schmidt, 1932; *Phyllobates marchesianus* Melin, 1941; *Colostethus masniger* Morales 2002 "2000"; *Colostethis mcdiarmidi* Reynolds and Foster, 1992; *Colostethus melanolaemus* Grant and Rodríguez, 2001; *Dendrobates myersi* Pyburn, 1981; *Colostethus nidicola* Caldwell and Lima, 2003; *Eupemphix olfersioides* Lutz, 1925; *Colostethus ornatus* Morales 2002 "2000"; *Colostethus picachos* Ardila_Robayo, Acosta-Galvis, and Coloma, 2000 "1999"; *Colostethus pittieri* La Marca, Manzanilla, and Mijares-Urrutia, 2004; *Dendrobates ranoides* Boulenger, 1918; *Dendrobates rufulus* Gorzula, 1990 "1988"; *Colostethus sanmartini* Rivero, Langone, and Prigioni, 1986; *Colostethus sumptuosus* Morales 2002 "2000"; *Dendrobates talamancae* Cope, 1875; *Phyllobates trilineatus* Boulenger 1884 "1883"; *Colostethus undulatus* Myers and Donnelly, 2001; *Colostethus vanzolinius* Morales 2002 "2000"; *Colostethus*

wayuu Acosta, Cuentas, and Coloma, 2000 "1999"; *Phyllobates zaparo* Silverstone, 1976.

Characterization, diagnosis, and support: Branch length (unambiguous transformations only) = 52. Bremer support = 14.

Unambiguously optimized phenotypic synapomorphies of this clade are **(1)** finger IV reaching distal ½ of distal subarticular tubercle of finger III (character 4, 0→1), **(2)** finger III swollen in adult males (Character 20, 0→1), **(3)** tarsal keel short, tubercle-like, not extending from the metatarsal tubercle (Character 29, 1→2), **(4)** webbing absent on postaxial side of toe I (Character 37, 2→0), **(5)** webbing absent on preaxial side of toe II (Character 38, 1→0), **(6)** webbing absent on postaxial side of toe II (Character 39, 1→0), **(7)** webbing absent on preaxial side of toe III (Character 40, 2→0), **(8)** webbing basal (distal 3 phalanges free) on postaxial side of toe III (Character 41, 2→1), **(9)** webbing basal (distal 4 phalanges free) on preaxial side of toe IV (Character 42, 2→1), **(10)** webbing absent on postaxial side of toe IV (Character 43, 1→0), **(11)** webbing absent on preaxial side of toe V (Character 44, 1→0), **(12)** pale paracloacal mark present (Character 49, 0→1), **(13)** oblique lateral line diffuse (Character 57, 0→2), **(14)** male abdomen pale, free or almost free of melanophores (Character 63, 3→0), **(15)** palatines absent (Character 131, 1→0), **(16)** frontoparietals fused posteriorly (Character 135, 0→1), **(17)** frontoparietal and otoccipital fused (Character 136, 0→1), **(18)** sacral diapophyses unexpanded (Character 142, 1→0).

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 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 anus 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 *Allobates 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: Cis-Andean with only two exceptions: (1) *A. talamancae* occurs in the Pacific lowlands of Colombia and Ecuador and north through Central America to Nicaragua, (2) its undescribed sister species *A.* Magdalena species from this study, which occurs in the Magdalena Valley.

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 diversity morphological, genetic (e.g., chromosome numbers), and behavioral diversity, additional partitioning will be required. Although formal recognition at this time is premature because it would leave the remaining species in a paraphyletic group and 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.

Chapter 8: 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 otherwise unrelated fields of biology, which often leads to unpredicted insights and identifies novel problems for further investigation. It is this potential for cross-discipline unification that makes phylogenetic systematics a fundamental part of an ampliative, progressive research program.

In the present chapter, I 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, my approach in this chapter remains decidedly phylogenetic. That is, rather than search for statistical correlations to explain biological variation in terms of its adaptive or functional significance, I explain it in terms of its evolutionary origins. This leaves aside the question of their possible adaptive value and the selective pressures that may have favored them (e.g., Summers and Earn, 1999; Caldwell and Araújo, 2004), but is a prerequisite to any such study (e.g., Coddington, 1988; Coddington, 1994). I also analyzed character evolution by exploring the evolution of characters partitioned according to putative functional or "process" constraints. Particularly, I tested the claim that more variable genes (such as cytochrome *b*)

provide resolution near the tips, whereas less variable genes (such as 28S) resolve deeper nodes, as well as the evolution of alkaloid sequestration.

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. This consideration is especially germane to the evolution of toxicity, where repeated sampling may be required to ameliorate the effects of temporary (e.g., seasonal) prey unavailability or the persistent rarity of certain prey items. Second, there are extensive missing data for several of the characters I analyze below, and, although the most parsimonious optimization often allows unambiguous prediction of unknown states, it is possible that future discoveries will overturn some predictions 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.

Natural History Evolution

As noted in Chapter 1, many aspects of the natural history of dendrobatoids have been studied. Here I 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 108), and I 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., *Ranitomeya mysteriosus* [as *Dendrobates*]). Also, they followed Myers et al. (1991) in considering *Aromobates nocturnus* to be the sister of all other dendrobatids, which is falsified in the present analysis. Additionally, as mentioned in Chapter 5, some character-states were misattributed by Summers and McKeon, which has implications for the evolutionary scenarios they proposed.

Adult Habitat Selection

The traditional view of dendrobatoid evolution inherited from Noble (1926) is that of a progression 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 more aquatic "*Hyloxalus* sensu stricto" and more terrestrial "*Colostethus* sensu stricto" and aposematic taxa. Adult association with water was coded as Character 113.

The ancestral state for Dendrobatoidea is ambiguous in the present 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 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. Rather than being the ancestral condition for all dendrobatoids, the fully aquatic behavior of *Aromobates nocturnus* is unambiguously derived and not primitive, as was postulated by Myers et al. (1991).

In both clades, it is clear that there is no simple progression from a more aquatic lifestyle to a more terrestrial one. Nevertheless, despite this complexity, adult association with water is relatively conserved phylogenetically, with a retention index (ri) 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*, *Hyloxalus nexipus*, Newgenus1 *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 II and III).

Sex of Nurse Frogs

Previous studies have claimed dorsal tadpole transport as a synapomorphy of Dendrobatoidea (e.g., Weygoldt, 1987, Myers, 1987), which is corroborated unambiguously in the present study. Moreover, the two included dendrobatoids known to lack dorsal transport (*Anomaloglossus nidicola* and *H. stepheni*; both aromobatids) lost it independently, as discussed in greater detail below in the context of larval endotrophy.

Tadpole transport by male nurse frog is also the unambiguously primitive state for dendrobatoids. Transport by female nurse frogs and biparental transport 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* (Magdalena species), 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, I 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 Guyana, and Aichinger (1991) of male nurse frogs from Peru (explicit reports of both sexes are by Weygoldt, 1987; see also Caldwell, *in litt*. 08/24/00). In light of the evidence that *A. femoralis* is a complex of species, it is possible that each species has nurse frogs of a single sex. Nevertheless, observations of biparental transport in *A. trilineatus* occurred at a single locality (Panguana; Aichinger, 1991), and, whether or not this is viewed as a complex of species, there is no evidence that more than one *trilineatus*-like species occurs at there. Larval transport is unknown in the close 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*. In *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.* fraterdanieli-like, *C. toachi*, *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 111). 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 110) 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.[1] *Ameerega hahneli* and *A. petersi* are closely related species, but biparental care optimizes unambiguously as separately evolved.

[1] Weygoldt (1987:55) disputed Mudrack's 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 males and females actually transport tadpoles. I therefore accept Mudrack's report at face value.

Larval Habitat and Diet

Three habitats are exploited by larval dendrobatoids (Character 110). 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, I also found that its sister species *H. roraima* is a phytotelm breeder. Adults and tadpoles of *H. roraima* were collected from tank bromeliads at 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 base pairs (0.3–0.8% uncorrected pairwise distance; see also Chapter 6). Larval habitat is unknown for all close relatives of *H. beebei* and *H. 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 is in *Allobates femoralis*, as reported by Caldwell and de Araújo (2004). Nevertheless, in this species phytotelm breeding is most likely opportunistic, i.e., ground-level phytotelmata are exploited like any other ground-level body of water and are not targeted preferentially. This species is not known to exploit above-ground phytotelmata. (Caldwell and de Araújo also mentioned finding *Colostethus* 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* + *Ranitomeya* + Newgenus2 + *Oophaga* + *Dendrobates*). Within that clade, *Dendrobates leucomelas* re-evolved the larval use of ground-level streams and pools, and *Dendrobates auratus* and *D. truncatus* evolved a generalist strategy, whereby they transport larvae to above-ground phytotelmata or ground-level water bodies.

Larval oophagy (i.e., larval consumption of nutritive eggs provided by the mother; character 111) 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) 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.

However, in both Aromobatidae and Dendrobatidae a form of biparental care has evolved in which courtship culminates in the female depositing oocytes directly in the water for larval consumption, i.e., male involvement in courtship is required to stimulate the female to release oocytes (character 112). 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., 1999, 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, the absence of the male at the moment of oviposition (which precludes fertilization) and the deposition of oocytes directly in the water (and not above on the dry leaf surface) indicate that oocytes 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 develop into frogs (Jungfer and Weygoldt, 1999).

Nidicolous larvae evolved at least twice in Aromobatidae and never in Dendrobatidae. *Anomaloglossus stepheni* (Juncá et al., 1994; Juncá, 1996; Juncá, 1998) and *Allobates nidicola* are not closely related. *Anomaloglossus degranvillei* is also endotrophic, but this species is exoviviparous (Altig and Johnson, 1989), i.e., tadpoles develop while being transported by the male nurse frog (see reviewed 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 Chapter 7 for further discussion of hypothesized relationships).

As coded for the present analysis, endotrophy optimizes unambiguously as the primitive state for the non-webbed clade of *Anomaloglossus*. Nevertheless, this is due to (1) the extensive missing data and (2) the fact that I coded observed specimens of *H. "degranvillei"* according to reproductive observations made on "true" *H.*

degranvillei. As discussed in chapter 6, these are almost undoubtedly different species. In that case, ad assuming that *H. "degranvillei"* is not endotrophic, endotrophy would optimize as homologous in the less inclusive clade that includes *H. 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. Modifications in other species include a novel pattern of gastrulation involving the formation of an embryonic disc in *Gastrotheca riobambae*. Likewise, multinuclear oogenesis in some species provides the embryo with a great reserve of ribosomal DNA (e.g., some 2000 nuclei in early oocytes of *Flectonotus pygmaeus*, each of which amplifies its own ribosomal DNA prior to degeneration of all but one nucleus during vitellogenesis), while other species (e.g., *Gastrotheca riobambae*) are mononuclear throughout all stages of development. The variation observed in other endotrophic anurans suggests that this may be a fruitful area of research to pursue in these species of 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 jaw, oral disc, and spiracle, whereas nidicolous larvae of the closely related *H. stepheni* lack the jaw 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 *A. nidicola* possess an unkeratinized lower jaw and lack the oral disc and spiracle.

The close phylogenetic relationship between *Anomaloglossus degranvillei* and *H. stepheni* to *H. 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. That is, in terms of tadpole ecomorphological guilds, the endo- and exotrophic dichotomy is explanatorily relevant (Altig and Johnson, 1989: 82–83), but it is less so in the broader context of the evolution of anuran life history, where oophagy and endotrophy are different but equivalent adaptive pathways. This observation 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 normal-sized oocytes for larval consumption versus expansion of the nutritive endoderm, but they will be essential to understanding the tradeoffs involved in these transitions.

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 is potentially greater, in nidicolous species (Juncá, 1996) than other dendrobatids, 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 non-nidicolous species, which is also costly and may increase the risk of predation and loss of territory (Cummins and Swan, 1995). 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 clarification that it is not the paternal investment that matters per se, but the cost it entails in terms of lost mating opportunities.

Alkaloid Sequestration

The evolution of dendrobatid toxicity has attracted considerable attention in recent years. Summers and Clough (2001) tested for correlation between a composite measure of "toxicity", defined as (0.1)(diversity)+(quantity)+(lethality), and a measure of overall brightness of coloration in relation to a molecular phylogeny. There are a number of problems with the approach followed in that study. First, the proposed index of toxicity is arbitrary and has no biological foundation. The assumption that the effects of distinct alkaloid classes are necessarily additive is unfounded, especially

given that some are known to have different biological effects (e.g., batrachotoxins stabilize [preferentially open] voltage dependent Na^+ channels, whereas histrionicotoxins are believed to block nicotinic receptor-channel conductance, reduce conductance of voltage dependent Na^+ channels, and reduce conductance of K^+ channels). Similarly, Daly et al. (1993) clarified repeatedly that the term "toxin" is a misnomer for histrionicotoxins and decahydroquinolines, whereas data on biological activity are lacking for quinolizidines and pyrrolizidines (for similar clarifications see also Daly et al., 1987; Rodríguez and Myers, 1993). Second, extremely limited taxon sampling strongly biased the results of that study. Not only does the sample of only 21 species of dendrobatids greatly under-sample the diversity of both coloration and toxicity, including only two closely related, dully colored, non-toxic species and designating one of them as the root forces all topological comparisons to be made among brightly colored and toxic species. Finally, although Summers and Clough focused explicitly on "the evolutionary change in coloration and toxicity" (p. 6230), the arbitrary phenetic measures of both characteristics are incapable of undergoing evolution directly and are merely proxies for the underlying character variation.

Santos et al. (2003) greatly improved taxon sampling, which allowed them to discover multiple origins of toxicity (an impossibility in the Summers and Clough study), and they avoided the problem of assessing degree of toxicity. Nevertheless, in doing so, their study incorporated less information on dendrobatid toxicology, treating species only as toxic or nontoxic. Rather than elucidate the diversification of dendrobatoid toxicity per se, Santos et al. focused primarily on correlations between bright coloration, toxicity, and ecological specialization. Errors in coding also inflated

the actual number of independent origins implied by their topology. Santos et al. coded *Cryptophyllobates* (following the taxonomy of that study) *azureiventris* as toxic, but Daly (1998) had already noted that it did not accumulate dietary alkaloids, despite its bright coloration. Likewise, there is no published report on the toxicity of *Allobates zaparo*.

The approach taken here differs from those of prior studies. Like previous authors, I assumed that alkaloid profiles evolve, which is a potentially problematic assumption (see Chapter 5). However, rather than summarizing information on toxicity as an arbitrary phenetic measure or excluding detailed information on toxicity, I converted alkaloid profiles into hypotheses of homology that are explicitly testable and causally interpretable in an evolutionary, phylogenetic framework. All unambiguous optimizations of alklaoid characters are shown in Figure 8.1. In the following I highlight several results of this analysis.

Among dendrobatoids, the ability to sequester lipophilic alkaloids is confined entirely to Dendrobatidae, where it is optimally explained as having evolved independently three times (Character 146, 0→1), with no evidence of subsequent losses. Although Santos et al. (2003) reported finding lipohilic alkaloid accumulation as originating five times on their optimal hypothesis, our results are actually identical once their erroneous attributions of toxicity to *Hyloxalus azureiventris* (absent) and *Allobates zaparo* (unknown) are corrected. The only non-dendrobatoid capable of sequestering lipophilic alkaloids that was included in this study, *Melanophryniscus stelzneri*, evolved this ability independently.

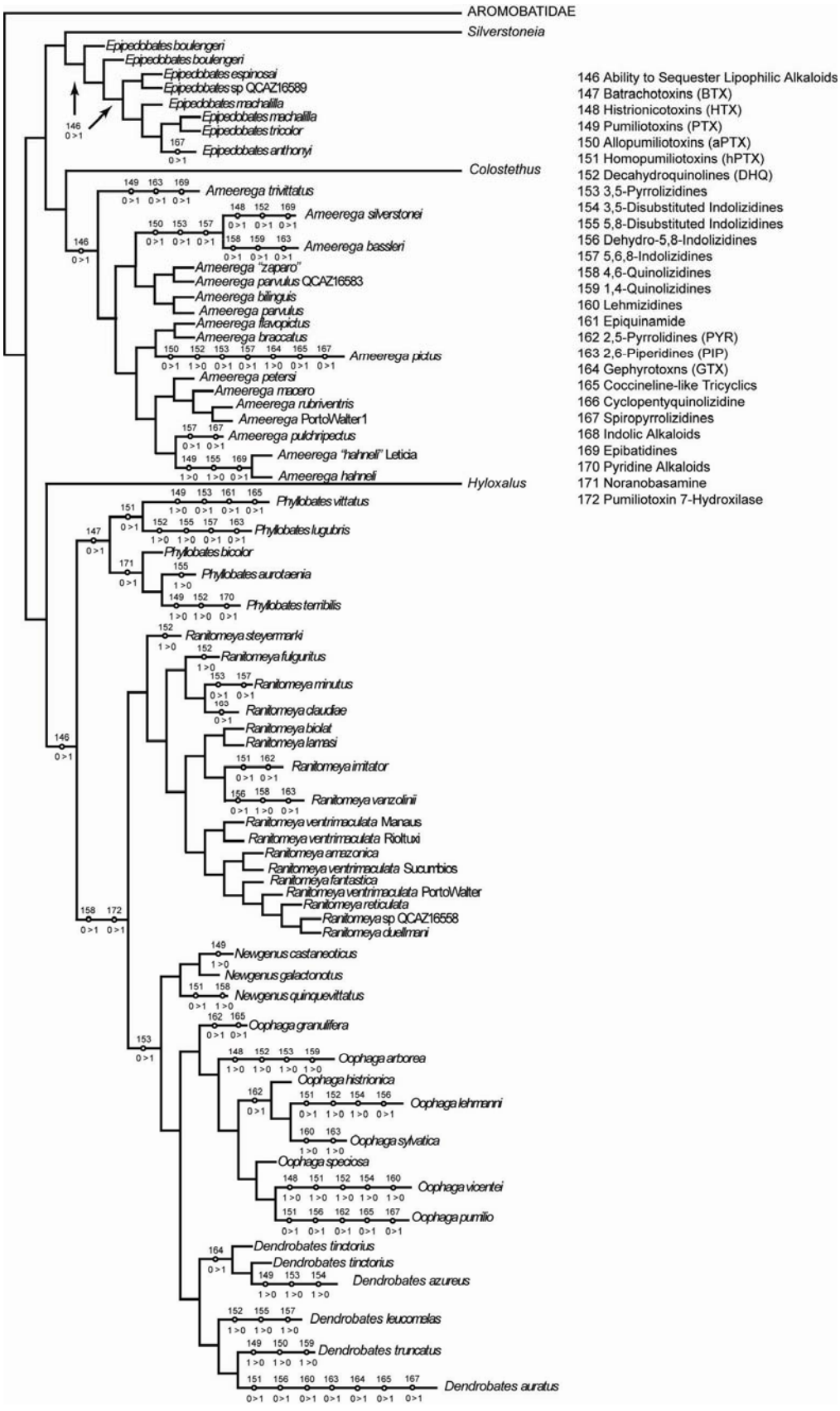

AROMOBATIDAE
Silverstoneia
Epipedobates boulengeri
Epipedobates boulengeri
Epipedobates espinosai
Epipedobates sp QCAZ16589
Epipedobates machalilla
Epipedobates machalilla
Epipedobates tricolor
Epipedobates anthonyi
Colostethus
Ameerega trivittatus
Ameerega silverstonei
Ameerega bassleri
Ameerega "zaparo"
Ameerega parvulus QCAZ16583
Ameerega bilinguis
Ameerega parvulus
Ameerega flavopicta
Ameerega braccatus
Ameerega pictus
Ameerega petersi
Ameerega macero
Ameerega rubriventris
Ameerega PortoWalter1
Ameerega pulchripectus
Ameerega "hahneli" Leticia
Ameerega hahneli
Hyloxalus
Phyllobates vittatus
Phyllobates lugubris
Phyllobates bicolor
Phyllobates aurotaenia
Phyllobates terribilis
Ranitomeya steyermarki
Ranitomeya fulgurita
Ranitomeya minuta
Ranitomeya claudiae
Ranitomeya biolat
Ranitomeya lamasi
Ranitomeya imitator
Ranitomeya vanzolinii
Ranitomeya ventrimaculata Manaus
Ranitomeya ventrimaculata Rioltuxi
Ranitomeya amazonica
Ranitomeya ventrimaculata Sucumbios
Ranitomeya fantastica
Ranitomeya ventrimaculata PortoWalter
Ranitomeya reticulata
Ranitomeya sp QCAZ16558
Ranitomeya duellmani
Newgenus castaneoticus
Newgenus galactonotus
Newgenus quinquevittatus
Oophaga granulifera
Oophaga arborea
Oophaga histrionica
Oophaga lehmanni
Oophaga sylvatica
Oophaga speciosa
Oophaga vicentei
Oophaga pumilio
Dendrobates tinctorius
Dendrobates tinctorius
Dendrobates azureus
Dendrobates leucomelas
Dendrobates truncatus
Dendrobates auratus
146 Ability to Sequester Lipophilic Alkaloids
147 Batrachotoxins (BTX)
148 Histrionicotoxins (HTX)
149 Pumiliotoxins (PTX)
150 Allopumiliotoxins (aPTX)
151 Homopumiliotoxins (hPTX)
152 Decahydroquinolines (DHQ)
153 3,5-Pyrrolizidines
154 3,5-Disubstituted Indolizidines
155 5,8-Disubstituted Indolizidines
156 Dehydro-5,8-Indolizidines
157 5,6,8-Indolizidines
158 4,6-Quinolizidines
159 1,4-Quinolizidines
160 Lehmizidines
161 Epiquinamide
162 2,5-Pyrrolidines (PYR)
163 2,6-Piperidines (PIP)
164 Gephyrotoxns (GTX)
165 Coccineline-like Tricyclics
166 Cyclopentyquinolizidine
167 Spiropyrrolizidines
168 Indolic Alkaloids
169 Epibatidines
170 Pyridine Alkaloids
171 Noranobasamine
172 Pumiliotoxin 7-Hydroxilase

Figure 8.1. Evolution of lipophilic alkaloid sequestration in Dendrobatoidea. Only unambiguously optimized transformations are shown, with the exception of the origin of the ability to sequester lipophilic alkaloids in *Epipedobates*, which evolved in either the most recent common ancestor of a clade that includes or excludes *E. boulengeri* (for which alkaloid sequestration is unknown). Non-toxic clades and species sampled for multiple individuals are collapsed into single lineages.

The ability to sequester lipophilic alkaloids evolved first in *Epipedobates*, although it is unclear if it evolved in the common ancestor of those species or subsequent to the divergence of *E. boulengeri*, both *Silverstoneia flotator* and *S. nubicola* tested negative for alkaloid sequestration, so the transformation unambiguously occurred in the *Epipedobates*lineage. The placement of *E. machalilla* inside the toxic clade is strongly suggestive that this species will be found to be able to sequester lipophilic alkaloids as well.

The second origin of lipophilic alkaloid sequestration occurred in the common ancestor of *Ameerega*. Based on their phylogenetic placement, the untested species *A. bilinguis*, *A. braccatus*, *A. parvulus*, *A. rubriventris*, and the undescribed species from Loreto, Peru ("*zaparo*" of Duellman and Mendelson, 1995) and Porto Walter, Brazil (PortoWalter1) are all predicted unambiguously to accumulate lipophilic alkaloids. Although one species of the sister group of *Ameerega, Colostethus panamensis*, possesses tetrodotoxin, that evolutionary event is phylogenetically and presumably physiologically unrelated to the origin of lipophilic sequestration in the *Ameerega* lineage.

The third origin of lipophilic alkaloid accumulation occurred in the ancestor of *Phyllobates*, *Ranitomeya*, *Oophaga,* Newgenus2, and *Dendrobates*. Untested species

predicted to be capable of sequestering alkaloids are *R. amazonicus, R. biolat*, *R. lamasi*, *R. duellmani*, and the unidentified species of *Ranitomeya* sp. QCAZ16558 (Santos et al., 2003).

Inferences and predictions regarding the evolution of sequestration of several classes of alkaloids may also be advanced. The corroboration of Myers et al.'s (1978) hypothesis of the monophyly *Phyllobates* further corroborates their claim that the ability to sequester batrachotoxin (BTX; Character 147, 0→1) evolved only once among dendrobatoid frogs. As noted in the description for Character 147, the ability of these frogs (and the inability of all other dendrobatids) to sequester these highly toxic compounds is likely to be related to their modified sodium channel (as demonstrated for *aurotaenia* and *terribilis*), which is insensitive to BTX. In the absence of this insensitivity to the effects of BTX, BTX-containing prey items would presumably be rejected.

The ability to sequester histrionicotoxins (HTX) is highly homoplastic (consistency index = 0.11, retention index = 0.52), but, nonetheless, its presence or absence diagnoses several clades. The occurrence of HTX is an unambiguous synapomorphy of *Ameerega,* and though not strictly diagnostic due to optimization ambiguities, the absence of HTX characterizes parts of *Phyllobates* (*P. lugubris, P. terribilis*, and *P. vittatus*; either independently evolved in *P. bicolor* and *P. aurotaenia* or evolved in their common ancestor and lost in *P. terribilis*) and the *minutus* group of *Ranitomeya*, are likely not to be due to sampling error. On the other hand, although I coded *A. silverstonei*, *Oophaga arborea*, and *O. vicentei* as lacking the ability to sequester HTX, which optimizes as independent losses (Character 148, 1→0), their

placement nested deeply within HTX-sequestering clades suggests this absence may be due to dietary deficiency or inadequate sampling[2] and warrants direct investigation through feeding experiments. On the other hand, among species of *Epipedobates*, HTX are known to occur in *E. espinosai* and be lacking in *E. anthonyi* and *E. tricolor*; however, the lack of information for *E. boulengeri* and *E. machalilla* must be corrected for inferences to be made for this clade.

A similar situation occurs in the evaluation of sequestration of 3,5-pyrrolidines (PYR; Character 162). The distribution of this character is optimally explained as having arisen independently in *Ranitomeya imitator*, *Oophaga ganulifera*, the common ancestor of *O. histrionica*, *O. lehmanni*, and *O. sylvatica*, and *O. pumilio*. That 3,5-pyrrolidines have not been detected in any other species of *Ranitomeya* suggests this probably refers to a real evolutionary event in *R. imitator*. However, the rarity of this character elsewhere and its occurrence in five of the eight included species of *Oophaga* explained as owing to two independent events suggests the absence of 3,5-pyrrolidines in *O. arborea*, *O. speciosa*, and *O. vicentei* may be due to dietary deficiency or inadequate sampling and not an evolutionary transformation event.

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[2] Dietary deficiency occurs when the dietary source is absent in the natural environment, but the species has an efficient uptake system. This appears to explain the absence of histrionicotoxins in large samples of wild-caught specimens even though specimens accumulate histrionicotoxins efficiently when they are present in the diet (Garraffo et al., 2001). *Oophaga lehmanni* occurs at higher elevations than close relatives, and it is likely that the histrionicotoxin-containing prey is restricted to lower habitats. Inadequate sampling occurs when the dietary source is present and samples are either too small or temporally restricted to detect the presence of the alkaloid in the population. In terms of hypotheses of homology and phylogenetic inference these two explanations are indistinguishable. However, the dietary deficiency explanation is "real" (not an artifact) and has possible biological consequences, such as preferentially targeting sources of alternative alkaloid classes or losing aposematic coloration, whereas the other explanation is nothing more than error.

Homopumiliotoxins (hPTX; Character 151) are rare, and their occurrence is phylogenetically scattered: *Ameerega flavopicta*, *Dendrobates auratus*, *Oophaga lehmanni*, *O. pumilio*, Newgenus2 *quinquevittatus*, *Ranitomeya imitator*, *Phyllobates lugubris*, and *P. vittatus*. Dietary deficiency and inadequate sampling of other species are potential explanations for this distribution, but the species that possess hPTX differ ecologically as well (i.e., it is unlikely that they would have access to prey items not also available to close relatives), and several closely related species that lack the hPTX were sampled heavily (e.g., *O. histrionica*).

One of the synapomorphies claimed by Myers (1987) for *Phyllobates* + *Dendrobates* (= *Oophaga,* Newgenus2*,* part of *Ranitomeya*, and *Dendrobates* of the new taxonomy) was the occurrence of 3,5-disubstituted indolizidine alkaloids. Although the present topology is largely congruent with Myers's proposal (the relevant difference being my inclusion of his *Minyobates* in this clade), the unambiguous optimization of this character at this node requires taxa that lack the ability to sequester alkaloids also be scored as lacking the ability to sequester 3,5-disubstituted indolizidines, which counts the same transformation event twice (see also Strong and Lipscomb, 1999). Nevertheless, although the general problem of inapplicables impedes understanding of the evolution of this character, and its variation within this clade limits its usefulness somewhat, the fact that it is not known to occur in any dendrobatid that is not part of this clade makes it diagnostically useful (see Chapter 7).

Epibatidine is a pharmacologically important compound, and its analgesic properties have potential to be developed for pharmaceuticals (e.g., Daly et al., 2000).

Sequestration of epibatidine (Character 169) originated three times in distantly related lineages, once (ambiguously) in *Epipedobates*, a second time in *Ameerega silverstonei,* and a third time in *A. hahneli*. I cannot offer a compelling explanation for this distribution. The *Epipedobates anthonyi* and *E. tricolor* occur primarily at montane localities in the western Andes, E. espinosai is restricted to <500 m in the southern portion of the Chocó region, *A. silvestonei* occurs in montane habitats on the Amazonian slopes, and *A. hahneli* is from the Amazonian lowlands, suggesting that the dietary source is widespread, at least at this scale. At a finer scale, all three species are terrestrial (i.e., not aquatic or riparian; Character 113) and breed at ground level (i.e., not in phytotelmata; Character 110). Although there is no evidence that these species exploit particular environmental aspects that are not used by close relatives, none of these species occurs in microsympatry with other alkaloid-sequestering species (which would provide a test). The only predictions that can be made based on available evidence are that *E. machalilla* will be found to sequester epibatidine, and, though not strictly predicted by the phylogeny, consideration of life history, habitat, and phylogeny suggest that *E. boulengeri* also sequesters epibatidine.

Based on the available evidence, pumiliotoxin 7-hydroxylase (Character 172) optimizes unambiguously as a synapomorphy of the dendrobatine genera *Dendrobates*, *Oophaga*, Newgenus2, and *Ranitomeya*. Feeding experiments demonstrated conclusively the conversion of PTX **251D** to aPTX **267A** in *Dendrobates auratus* and the sister species Newgenus2 *castaneoticus* and Newgenus2 *galactonotus* (Daly et al., 2003) but the remainder of the positive instances were coded from wild-caught specimens that could have obtained aPTX **267A** from a dietary

source (see discussion of this character in Chapter 5). The first test of this scenario should be to duplicate the feeding experiments in a species of the as yet untested clade *Ranitomeya*—preferably in *R. steyermarki*, but more feasibly (due to availability in the pet trade) in *R. fulguritus*.

Genotypic Process Partitions

A central question for many evolutionary biologists is whether or not data drawn from different sources have different and conflicting histories, i.e., whether or not different functional or other constraints caused the partitions to undergo different processes of evolution. Regardless of authors' preference for total evidence or taxonomic congruence approaches to phylogenetic inference, almost all published phylogenetic studies over at least the past decade explored data partitions, and there is no indication that the practice is declining.

Under what Grant and Kluge (2003) called the strong interpretation, data partitions found to have incongruent phylogenetic signals are either segregated for separate analysis (i.e., conditional combination; Huelsenbeck et al., 1996) or weighted differentially to mitigate the presumably confounding effects of differing processes of evolution. However, that approach is ad hoc, as no independent evidence for the confounding processes is ever presented, and the majority of contemporary workers explore the effects of separate analyses of data partitions without permitting the results of partitioned analyses to directly alter the phylogenetic analysis. The rationale for the latter weak interpretation is that the only way to gain insight into the different evolutionary processes is to analyze each partition separately, i.e., partitioned analysis

is valued for its heurism. For example, Nixon and Carpenter (1996: 221) concluded unequivocally that simultaneous, total-evidence analysis is superior to the partition methods of taxonomic congruence, but they still allowed that "Separate analyses are useful and of interest to understanding the differences among data sets." Likewise, Huelsenbeck et al. (1996) suggested that discovery of different evolutionary processes and histories can only be achieved through partitioned analyses, and Remsen and DeSalle (1998:233) cautioned that "without knowledge of the signal emanating from the various partitions, it will not be possible to diagnose particularly striking interactions among them." As a consequence of these and related arguments, analysis of data partitions has become one of the most popular kinds of data exploration.

Grant and Kluge (2003) reviewed methods and justifications for exploring the evolution of data partitions (i.e., process partitions), and, although they agreed that the evaluation of data partitions may be highly heuristic, they concluded that all existing methods are inadequate because inferences are necessarily drawn from the separate analysis of partitions and not the evolutionary or evidential implications of the globally optimal phylogenetic explanation. Grant and Kluge went on to highlight the potential for the development of heuristic methods of partition analysis, and I implement one such method here.

Hierarchic Distribution of Transformations among Partitions

It is widely believed that some loci provide resolution (or phylogenetic signal) at relatively low levels of diversification (i.e., near the tips of the cladogram), while others provide resolution at deeper levels (i.e. toward the base), and this is interpreted

heuristically to inform the choice of loci for new studies and design means of further refining and testing prior results. Nevertheless, the evidential contribution of different data partitions is an empirical problem, and no method is currently available to examine it in a total evidence framework. In this section I develop a method to address this problem, and I use it to explore the behavior of various partitions of the present dataset. This data set is ideal for this kind of analysis because it spans levels of diversification from within species to among large and presumably ancient clades and includes multiple loci of differing variability. Although one or more partitions of phenotypic transformation series could also be analyzed, most concern about process partitions focuses on DNA sequences, and I limit my comparisons to those partitions.

It should be noted that the problem investigated here is related to, but differs significantly from, two other common problems in phylogenetic systematics. First, the explanation of differences in resolving power is usually expressed in terms of evolutionary rates, i.e., fast genes provide resolution towards the tips, slower genes resolve mid-level nodes, and slow genes provide resolution toward the root. Although the approach developed here may be adaptable to investigate relative rates and clock-likeness, that is not my purpose here. Instead, I restrict myself to the question of the evidential contribution of each partition at differing hierarchic levels. Nevertheless, finding that the transformations of different loci are distributed at different hierarchic levels is suggestive of different evolutionary processes, which may be investigated in independent studies (cf. Farris, 1983).

Second, the present method quantifies the hierarchic distribution of evidence among partitions, but it does not quantify the hierarchic distribution of *support* among

partitions, or as Farris et al. (2001) summarized succinctly, branch lengths do not equal support. Consistent with Farris et al.'s position, Grant and Kluge (2003:383) defined support explicitly as "the degree to which critical evidence refutes competing hypotheses." The distinction is drawn because it is not uncommon for a great deal of evidence to favor a particular hypothesis (i.e., long branches, many unambiguously optimized synapomorphies), but for that preference to be extremely weak (i.e., low support). The most defensible method of assessing the contribution of data partitions to the support at different levels of the total evidence hypothesis is partitioned Bremer support (1997), which addresses this problem on a clade-by-clade basis by calculating, for each clade in the total evidence solution (or strict consensus), the length (or mean length, if multiple most parsimonious trees obtain) of a given partition on the total evidence solution(s) lacking the node in question minus the length of that partition on the globally optimal total evidence solution(s).

The Method

Assessment of the hierarchic distribution of transformations requires the standardized quantification of hierarchic level. In his thesis, D. Pol (1999) defined the index of generality, *IG*, to measure the hierarchic level of each node in a cladogram, given by the number of descendent nodes (terminal and inner nodes) subtended from the node in question, or,

$$IG = \frac{N_d - 1}{N - 1}$$

where N_d is the number of descendent nodes and *N* is the total number of nodes in the binary cladogram. The minimum *IG* is 0 for a terminal (autapomorphic) transformation, and the maximum *IG* is 1 (although that maximum is unattainable for unambiguous optimizations).

Using a modified macro written by D. Pol (pers. comm.), I calculated the *IG* of all unambiguous transformations in NONA for the following partitions: cytochrome *b*, cytochrome oxidase *c* I, mtDNA subunit H1, histone H3, rhodopsin, tyrosinase, seventh in absentia, recombination activating gene 1, and 28S. Further, I pooled the *IG* values for mtDNA and nuDNA. Alternative partitions could be explored (e.g., mtDNA subunit H1 could be partitioned into 12S, $tRNA^{val}$, and 16S fragments, or into stem and loop regions), and there is no scientific reason to explore these instead of others (see Siddall, 1997). Instead, these partitions were defined because they reflect distinctions commonly cited in phylogenetic studies. I calculated *IG* to 3 decimals, as that degree of precision is required to discriminate terminal (i.e., leaves, nodes of degree 1; $IG = 0.000$) transformations from minimal internal nodes (i.e., nodes of degree 2; $IG = 0.002$) for this cladogram.

The number of transformations at a particular hierarchic level is partially dependent on the frequency of that hierarchic level in the cladogram, which is determined by the shape of the particular cladogram. For example, few or no transformations may occur at a given hierarchic level simply because there are few or no instances of that hierarchic level in the particular topology and not because the data (partitioned or not) fail to provide resolution. I therefore calculated the "null"

distribution of *IG* values by generating the group inclusion matrix (Farris, 1973) for the binarized cladogram and calculating the *IG* values for that dataset. It should be noted that this is not intended as a null distribution for statistical tests.

Results

The number of unambiguously optimized transformations of each partition at each hierarchic level (*IG* value) is given in Table 8.1. Figures 8.2–8.12 show the frequency of *IG* values for each partition relative to (1) the null distribution for this topology and (2) the frequency of *IG* values for all DNA sequences combined. Figure 8.13 shows the relative contribution of each partition at each hierarchic level.

The results of this analysis demonstrate clearly that transformations of all partitions occur across vastly different hierarchic levels. The only partition that did not present unambiguously optimized transformations at both hierarchic extremes was the nuclear locus histone H3, for which no unambiguous changes were inferred at $GI > 0.496$. But even that locus exhibited transformations across all but eight of the hierarchic levels in this cladogram (Fig. 8.5). This finding suggests that any locus may provide evidence at any hierarchic level and thereby contradicts the commonly held view that loci are level- or rank-specific. Note that this finding is also consistent with the way evolution must proceed: all change necessarily occurs at the level of terminals, and it is only subsequent cladogenetic events that cause changes to characterize more inclusive hierarchic levels.

Nevertheless, the observation that transformations occur across all or most hierarchic levels for all loci does not imply that the relative frequencies at each

Table 8.1. Number of unambiguous transformations of each data partition at each hierarchic level of the optimal cladogram. Hierarchic level is given as the Index of Generality (*IG*) ×1000. Terminal transformations (*IG* = 0) are omitted. "Null" reports the number of nodes of different hierarchic levels that occur in the binarized cladogram.

IG	**Null**	**28S**	**COI**	**Cytochrome *b***	**H3**	**Mt Subunit H1**	**RAG1**	**Rhodopsin**	**SIA**	**Tyrosinase**	**All DNA**	**mtDNA**	**nuDNA**
2	131	25	424	400	10	2453	9	46	10	7	3384	3277	107
4	60	19	197	275	21	1454	21	23	14	18	2042	1926	116
7	46	24	258	173	10	1124	20	18	7	25	1659	1555	104
9	31	8	57	106	9	692	11	16	1	8	908	855	53
12	16	11	146	104	6	544	6	10	6	1	834	794	40
14	15	5	41	45	5	373	7	3	6	4	489	459	30
17	13	8	105	41	16	380	7	8	1	2	568	52	42
19	5	1	33	12	10	112	0	0	3	0	171	157	14
21	7	7	12	13	1	142	0	2	0	2	179	167	12
24	6	1	178	61	0	402	0	2	4	0	648	641	7
26	11	2	53	50	0	199	8	4	13	6	335	302	33
29	4	3	43	19	0	179	6	3	10	0	263	241	22
31	4	0	0	15	0	27	0	3	0	4	49	42	7
34	5	1	30	26	3	108	3	1	3	4	179	164	15
38	4	0	32	26	0	122	1	4	1	0	186	180	6
41	3	14	2	22	2	91	5	2	3	0	141	115	26
46	3	1	27	19	1	120	5	2	2	0	177	166	11
48	2	0	46	12	0	135	7	8	0	0	208	193	15
51	1	0	8	1	0	27	0	0	0	0	36	36	0
53	1	3	0	6	0	17	0	1	0	0	27	23	4
58	4	3	14	18	0	82	0	4	0	0	121	14	7
60	1	0	0	0	0	4	0	0	0	0	4	4	0
68	1	0	3	1	0	1	1	0	0	0	6	5	1
75	1	0	3	1	0	18	0	2	0	0	24	22	2
77	2	10	5	3	0	21	0	2	1	1	43	29	14
80	1	0	5	2	0	42	0	0	0	0	49	49	0

87	1	5	0	0	0	16	0	2	0	0	23	16	7
97	1	0	4	5	0	16	0	0	0	0	25	25	0
102	2	12	10	5	1	39	0	2	5	0	74	54	20
111	1	16	8	15	1	84	12	6	4	15	161	107	54
126	1	2	16	7	3	92	1	0	3	0	124	115	9
131	1	1	11	2	1	33	1	0	2	0	51	46	5
136	1	5	5	3	0	17	1	2	1	0	34	25	9
143	1	5	9	5	1	39	2	2	3	10	76	53	23
153	1	3	7	4	0	31	1	1	2	0	49	42	7
163	1	1	1	3	0	41	1	2	3	5	57	45	12
189	1	2	2	5	1	14	0	0	0	3	27	21	6
197	1	2	10	4	2	44	8	0	1	7	78	58	20
238	1	0	0	0	0	22	0	0	0	0	22	22	0
243	1	0	0	0	0	33	0	0	0	0	33	33	0
260	1	0	2	3	1	27	0	3	1	0	37	32	5
267	1	1	6	5	0	43	1	0	2	0	58	54	4
272	1	0	6	7	0	45	0	0	0	0	58	58	0
274	1	0	5	2	0	30	0	2	3	0	42	37	5
296	1	3	2	3	2	17	1	0	1	0	29	22	7
318	1	1	9	2	0	22	2	0	0	0	36	33	3
496	1	5	3	1	2	30	0	0	0	4	45	34	11
610	1	2	4	3	0	52	3	1	3	3	71	59	12
931	1	0	6	7	0	22	0	0	0	0	35	35	0
936	1	0	8	7	0	44	0	1	0	9	69	59	10
944	1	4	13	6	0	23	0	0	1	0	47	42	5
970	1	0	8	6	0	19	0	1	3	0	37	33	4
975	1	9	10	3	0	14	2	0	0	0	38	27	11
982	1	5	15	11	0	41	0	0	0	0	72	67	5
985	1	0	27	19	0	75	0	0	0	0	121	121	0
Total	408	230	1929	1594	109	9894	153	189	123	138	14359	12843	942

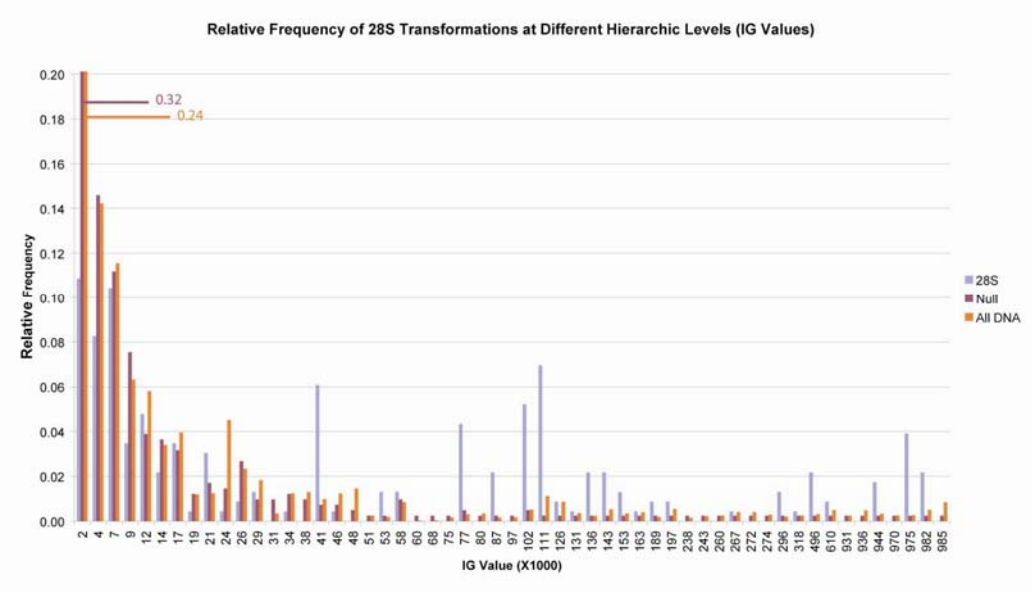

Figure 8.2. Relative frequency of unambiguous 28S transformations at different hierarchic levels (*IG* values ×1000) compared to the relative frequencies of nodes in the cladogram and unambiguous transformations for the unpartitioned DNA dataset. Frequencies are truncated at 0.20.

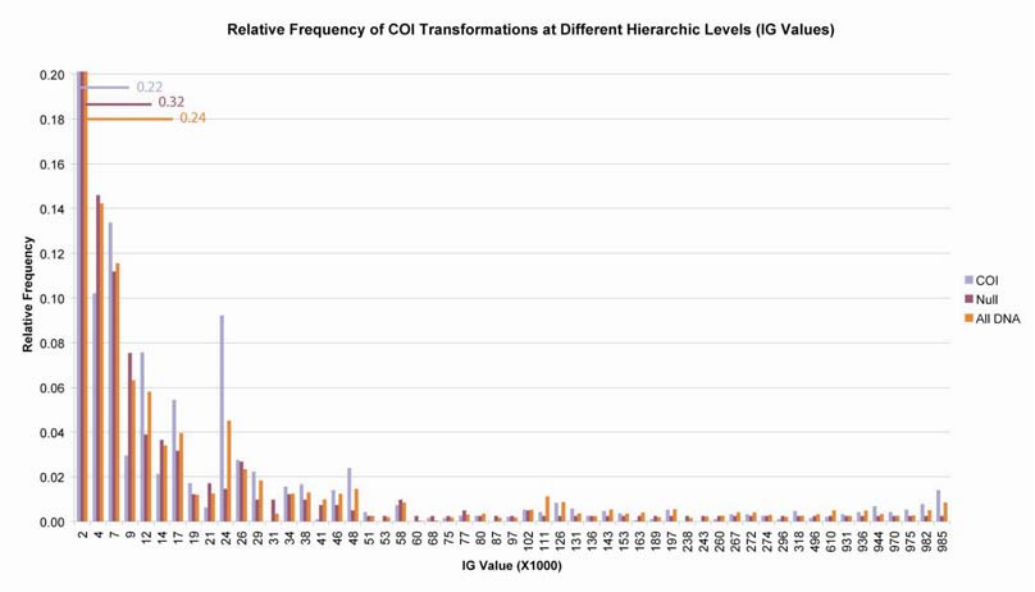

Figure 8.3. Relative frequency of unambiguous cytochrome *c* oxidase I transformations at different hierarchic levels (*IG* values ×1000) compared to the relative frequencies of nodes in the cladogram and unambiguous transformations for the unpartitioned DNA dataset. Frequencies are truncated at 0.20.

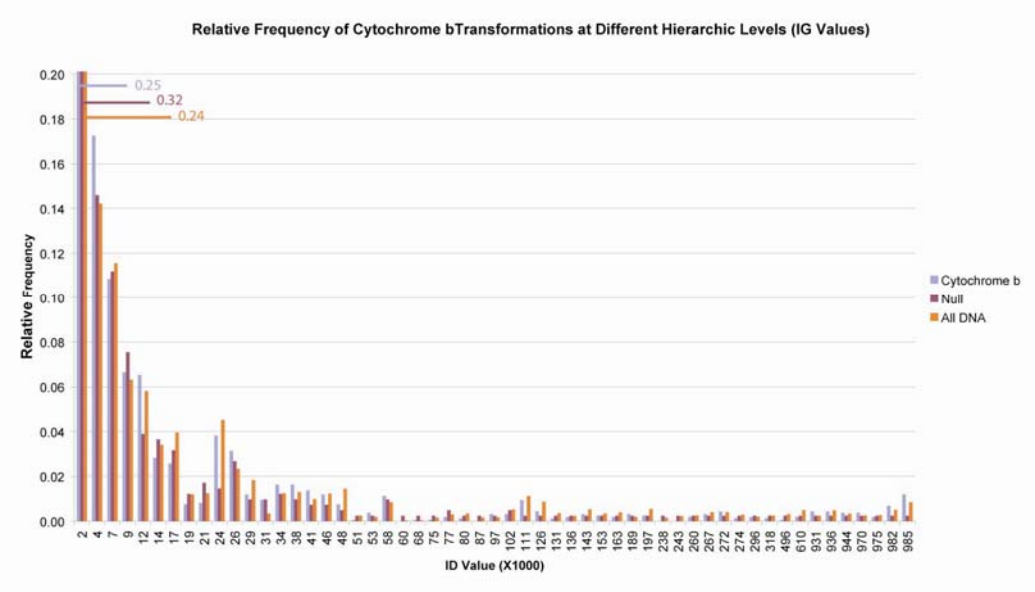

Figure 8.4. Relative frequency of unambiguous cytochrome *b* transformations at different hierarchic levels (*IG* values ×1000) compared to the relative frequencies of nodes in the cladogram and unambiguous transformations for the unpartitioned DNA dataset. Frequencies are truncated at 0.20.

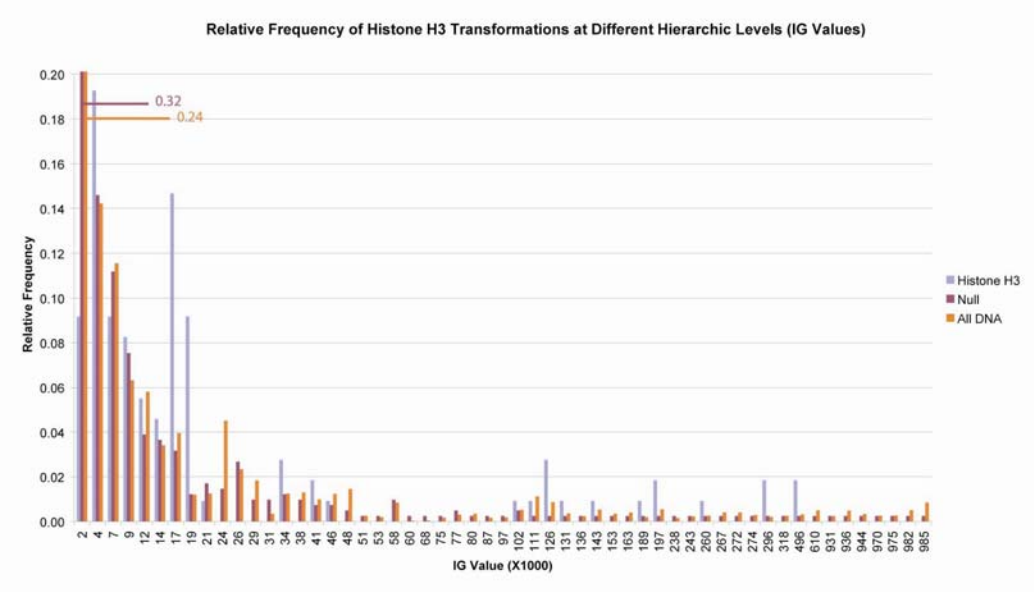

Figure 8.5. Relative frequency of unambiguous histone H3 transformations at different hierarchic levels (*IG* values ×1000) compared to the relative frequencies of nodes in the cladogram and unambiguous transformations for the unpartitioned DNA dataset. Frequencies are truncated at 0.20.

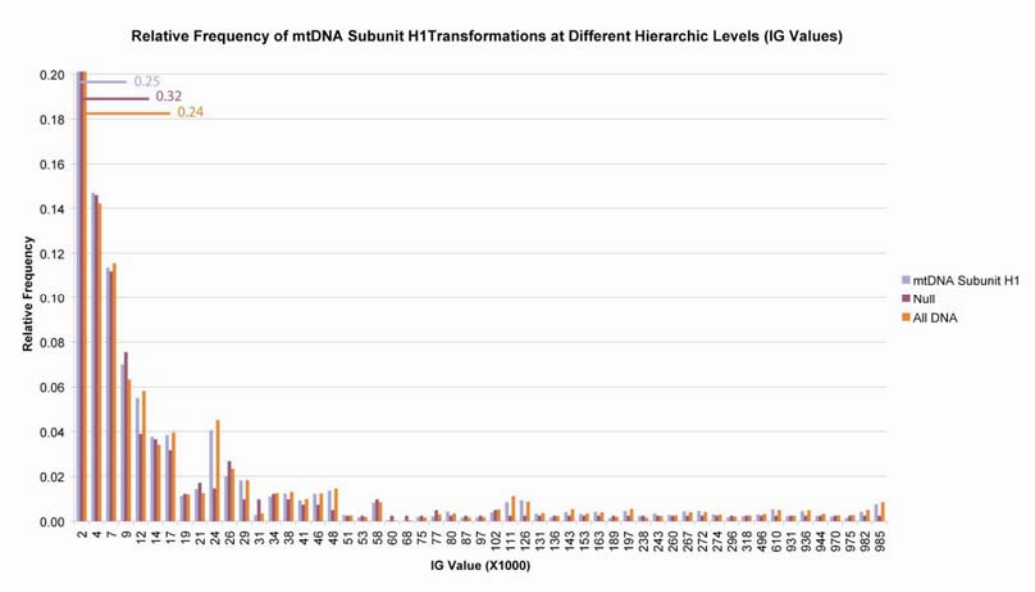

Figure 8.6. Frequency of unambiguous mtDNA subunit H1 transformations at different hierarchic levels (*IG* values ×1000) compared to the frequency of nodes in the cladogram and the frequency of unambiguous transformations for the unpartitioned DNA dataset. Frequencies are truncated at 0.20.

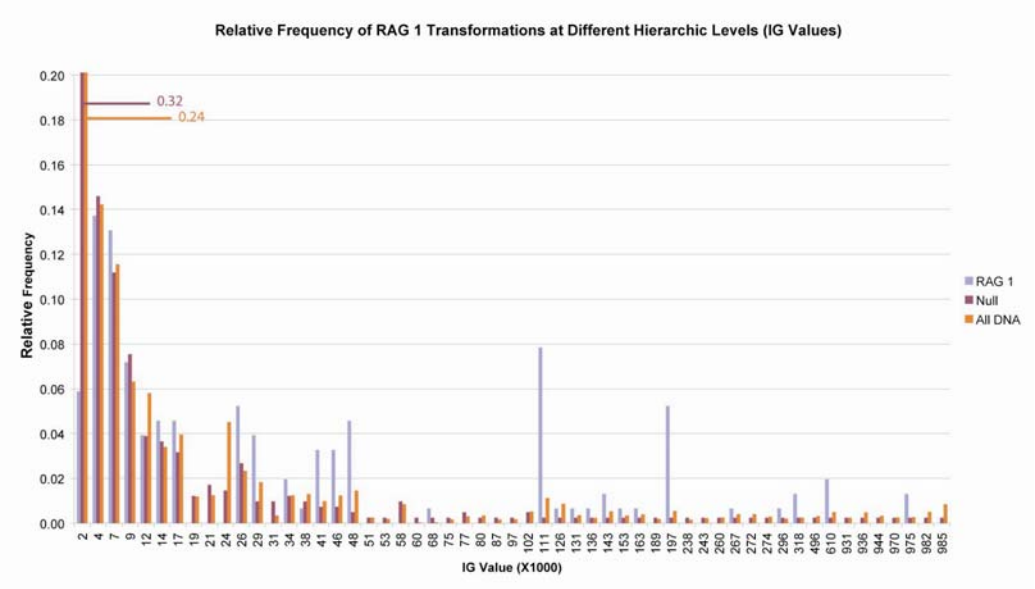

Figure 8.7. Frequency of unambiguous 28S transformations at different hierarchic levels (*IG* values ×1000) compared to the frequency of nodes in the cladogram and the frequency of unambiguous transformations for the unpartitioned DNA dataset. Frequencies are truncated at 0.20.

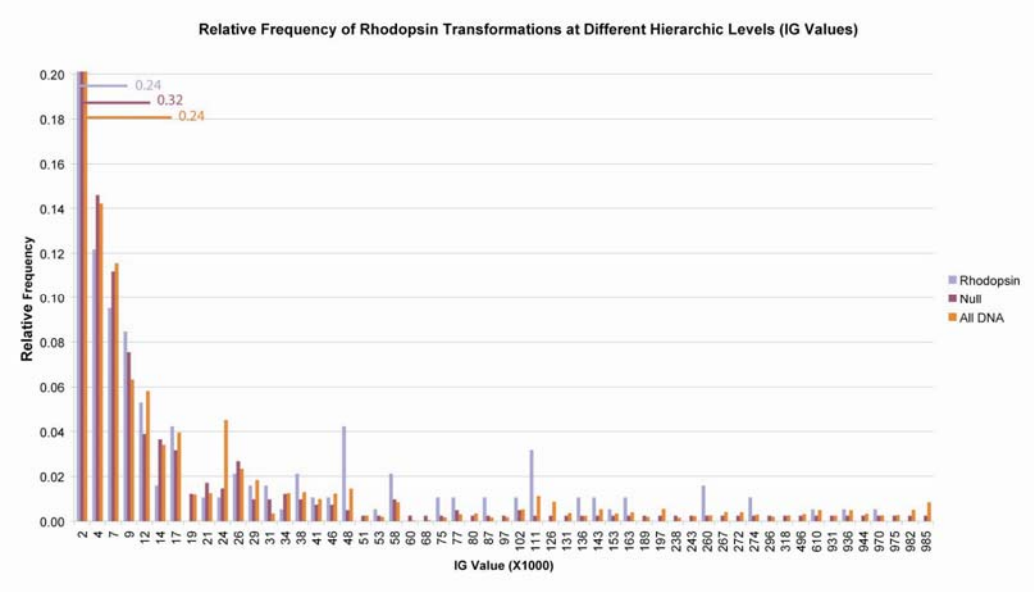

Figure 8.8. Frequency of unambiguous rhodopsin transformations at different hierarchic levels (*IG* values ×1000) compared to the frequency of nodes in the cladogram and the frequency of unambiguous transformations for the unpartitioned DNA dataset. Frequencies are truncated at 0.20.

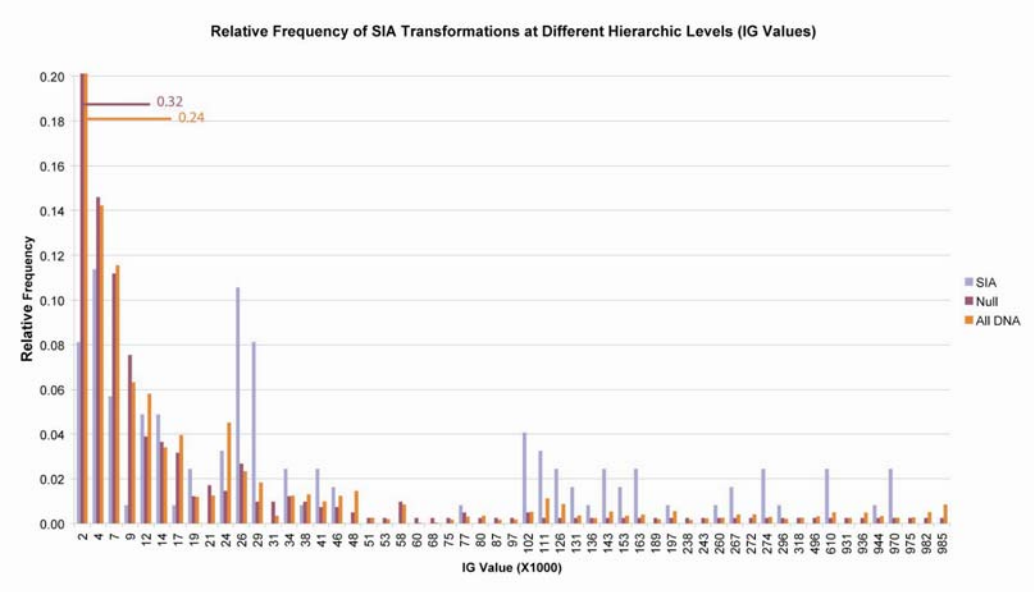

Figure 8.9. Frequency of unambiguous SIA transformations at different hierarchic levels (*IG* values ×1000) compared to the frequency of nodes in the cladogram and the frequency of unambiguous transformations for the unpartitioned DNA dataset. Frequencies are truncated at 0.20.

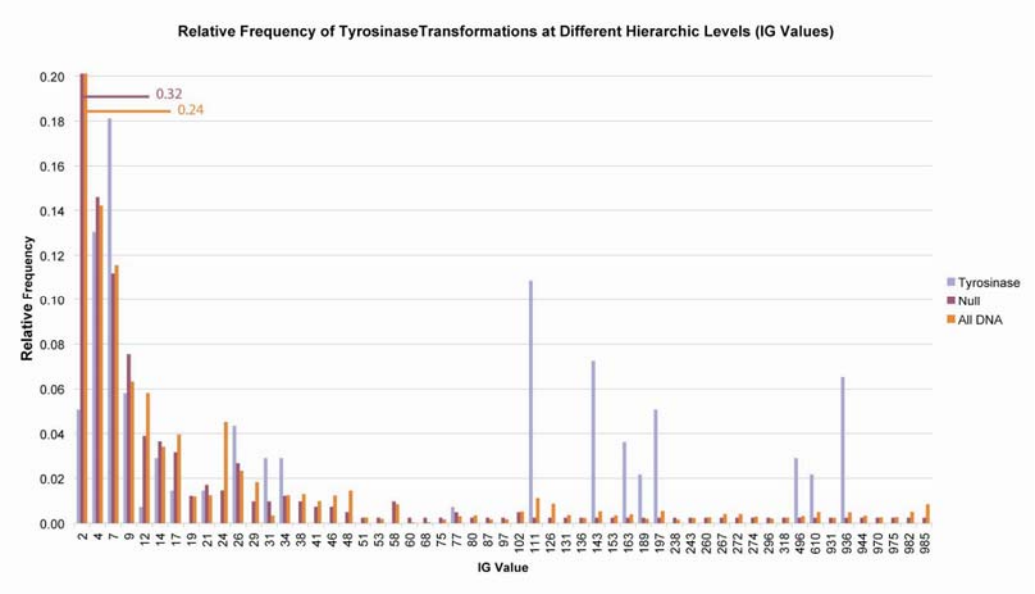

Figure 8.10. Frequency of unambiguous tyrosinase transformations at different hierarchic levels (*IG* values ×1000) compared to the frequency of nodes in the cladogram and the frequency of unambiguous transformations for the unpartitioned DNA dataset. Frequencies are truncated at 0.20.

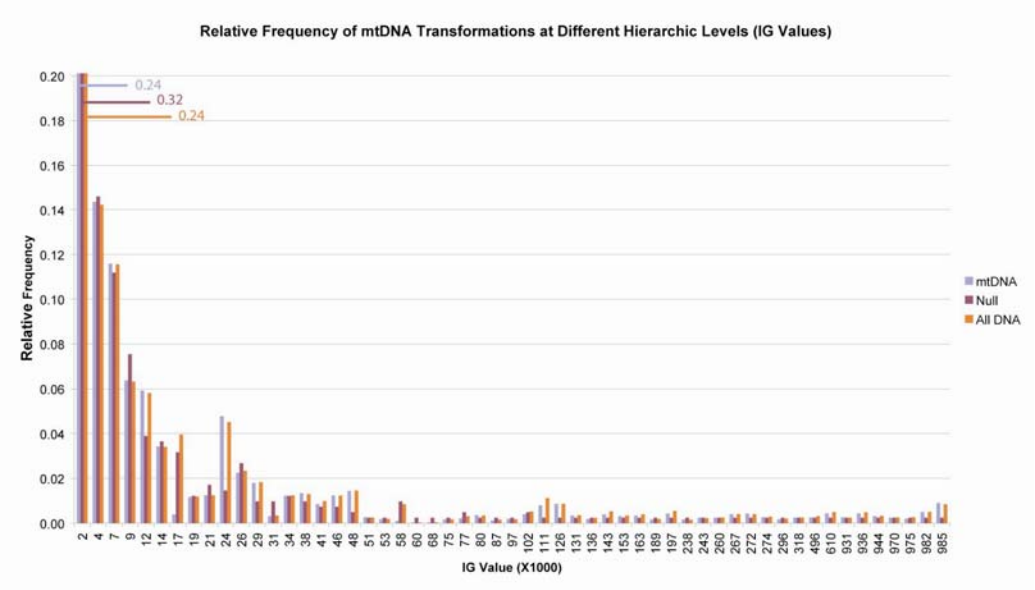

Figure 8.11. Frequency of unambiguous mtDNA transformations at different hierarchic levels (*IG* values ×1000) compared to the frequency of nodes in the cladogram and the frequency of unambiguous transformations for the unpartitioned DNA dataset. Frequencies are truncated at 0.20.

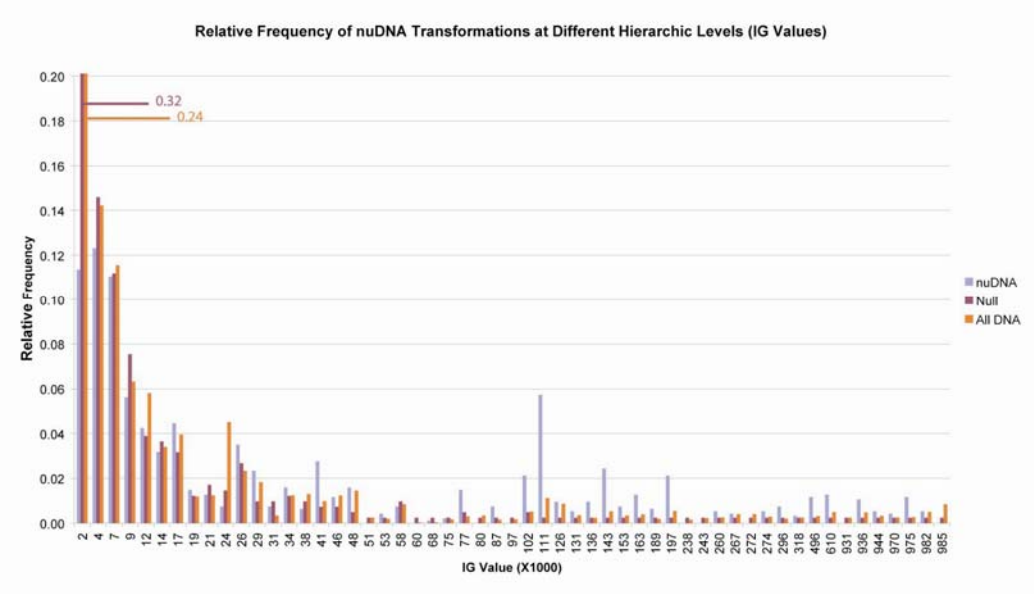

Figure 8.12. Frequency of unambiguous nuDNA transformations at different hierarchic levels (*IG* values ×1000) compared to the frequency of nodes in the cladogram and the frequency of unambiguous transformations for the unpartitioned DNA dataset. Frequencies are truncated at 0.20.

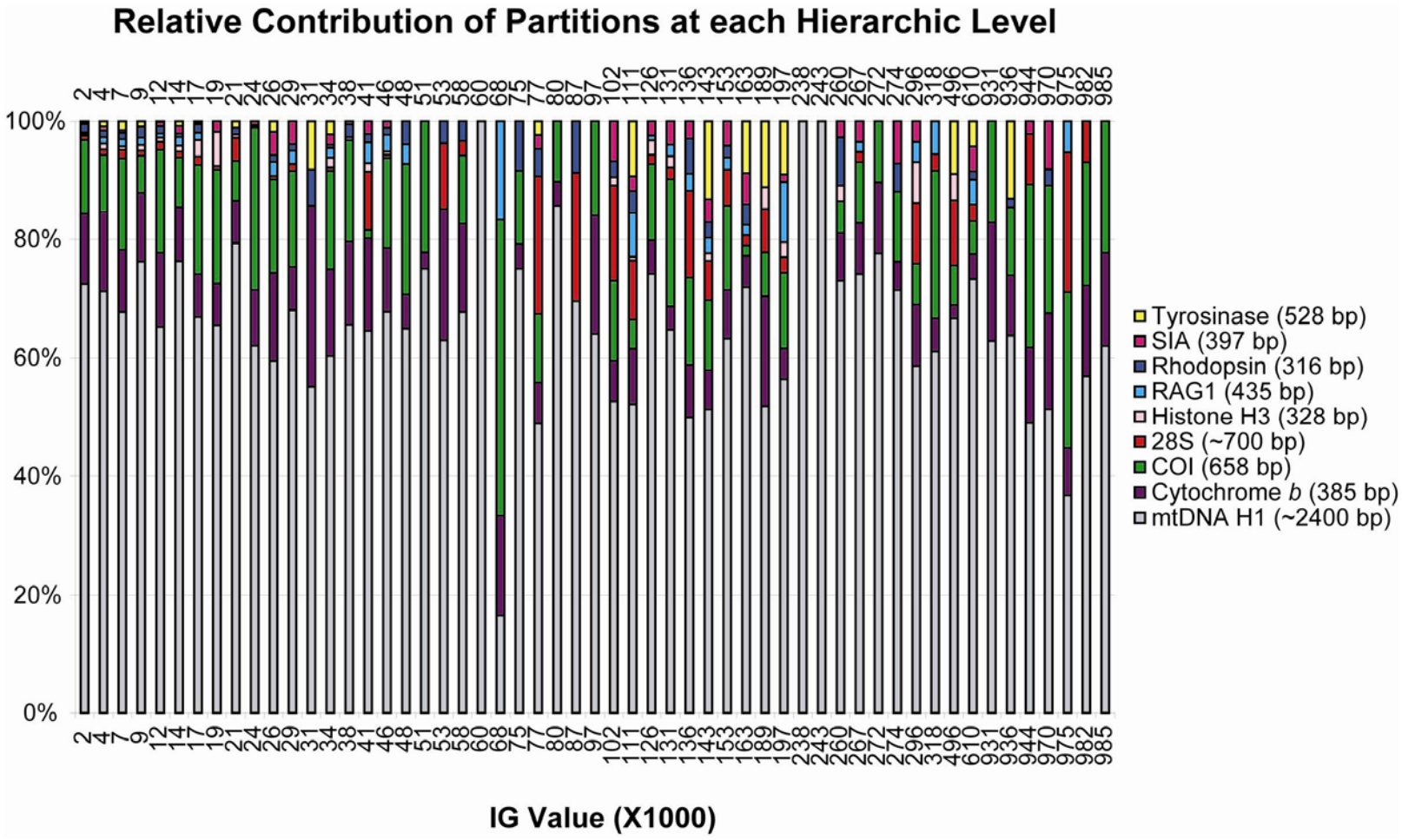

Figure 8.13. Relative contribution of each partition to the total number of unambiguous transformations at each hierarchic level of the cladogram, given by the *IG* value. Terminal transformations are excluded.

hierarchic level are identically distributed. As seen in Figs. 8.2–8.12, each partition has a unique distribution of relative frequencies, indicating that the evidential contribution of each partition to the total evidence solution varies across hierarchic levels. For example, whereas the combined mitochondrial partition tracks the null distribution quite closely, the combined nuclear partition has a greater proportion of transformations distributed among higher levels. To some degree this is undoubtedly due to the fact that I did not generate nuclear sequences for all terminals from the same localities. However, bias is likely to be minor, given that (1) the reason for not generating these sequences for all terminals is that preliminary sequencing showed variation in these sequences to be minor or absent in syntopic samples, which indicates inclusion of those sequences would not result in significantly more changes, and (2), the comparison holds even when the first several hierarchic levels are excluded. Further partitioning into smaller data sets revealed additional patterns, and this could be repeated to the level of individual transformation series, that being the only evidentially independent partition (Grant and Kluge, 2003).

In terms of raw number of changes, mtDNA subunit H1 is both the longest single partition (~2,400 bp) and requires the greatest number of transformations to explain its variation. Nevertheless, although this partition dominates at most hierarchic levels, the relative contributions of each partition vary across the hierarchic levels and is not directly proportional to fragment length. For example, the length of the cytochrome *b* fragment is 385 bp, or about 6% of the total length of nucleotides, yet it accounts for up to >20% of the transformations at some hierarchic levels.

Summary and Conclusions

The results of this analysis indicate that (1) all partitions contribute evidentially to the individuation of clades across vastly different hierarchic levels, (2) each partition differs in the frequency of unambiguous transformations at different hierarchic levels, and (3) the relative amount of evidence contributed by each partition varies across hierarchic levels. These finding lend themselves to investigations into the distinct histories, processes, and mechanisms that may operate for each partition. Of more direct concern in systematics, the different evidential contributions of each partition may be used to inform character sampling in future studies. More precise inferences about the hierarchic distribution of transformations among the different partitions will require the development of appropriate statistics to assess significance.

Prior attempts to discover and quantify differences among partitions relied on separate phylogenetic analysis of partitions and therefore failed to evaluate both the evolutionary and evidential aspects of the behavior of data partitions when analyzed simultaneously (Grant and Kluge, 2003). That is an important shortcoming of those methods, and a significant strength of the current approach, given that the results of separate analyses often differ notably from the globally optimal explanation for the evolution of those data.

Chapter 9: Summary and Future Research

General Results

DNA sequences totaling approximately 6,100 base pairs were generated for five mitochondrial and six nuclear loci, and 175 phenotypic characters were individuated from adult and larval morphology, alkaloid profiles, and behavior. The complete dataset included 412 terminals: 365 terminals of 152 ingroup species, and 47 outgroup terminals. Direct optimization phylogenetic parsimony analysis resulted in a single most parsimonious solution of 46,598 equally weighted transformations. Poison dart frogs were recovered as monophyletic a monophyletic group, identified as Dendrobatoidea, and the sister group was found to consist of *Crossodactylus*, *Hylodes*, and *Megaelosia*, recognized herein as Hylodidae. The latter finding disagrees with the results of Frost et al. (2005) but is based on greatly increased character sampling for directly relevant terminals and also included a large sample of taxa from Frost et al.'s study.

The sampled dendrobatoids were distributed approximately symmetrically in two clades: Dendrobatidae Cope, 1863 and Aromobatidae new family. Among aromobatids, a diverse clade of species that possess the median lingual process was discovered and named *Anomaloglossus* new genus. All included species of *Anomaloglossus* occur east of the Andes, but three species (*H. atopoglossus*, *H. chocoensis* auctorum [not *Hyloxalus chocoensis* Boulenger, 1912; see Grant et al., 1997)], and *H. lacrimosus*, are distributed in the Pacific slopes and lowlands of Colombia and Ecuador. Several species of *Anomaloglossus* possess unique

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 *Phyllobates palmatus* Werner, 1899 from the eastern Andes of Colombia, for which Newgenus1 was proposed.

The clade that includes those two genera was named Anomaloglossinae, and the clade of remaining aromobatids was dubbed Aromobatinae. *Colostethus saltuensis* 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 to *Nephelobates* La Marca, 1994. Consequently, *Nephelobates* was considered a junior synonym of *Aromobates*. *Aromobates* and *Mannophryne* are both 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 aromobatines form a clade of predominantly cis-Andean species referred to the existing name *Allobates* Zimmerman and Zimmerman, 1988. Within this clade is a complex of superficially similar species traditionally placed in Silverstone's (1976) *femoralis* group (or directly in *femoralis*; see below), including *Allobates zaparo* and *Allobates myersi* and *Allobates rufulus*. It is likely that further progress will allow additional clades in this group to be recognized formally and for *Allobates* to be restricted to the *femoralis* group. *Allobates nidicola* and *Allobates chalcopis* possess nidicolous and exoviviparous endotrophic larvae, respectively.

Dendrobatidae includes numerous well delimited clades, many of which can be referred to existing names. Colosethinae Cope, 1868 includes four genera. *Silverstoneia* new genus 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 for analysis) with highly modified larvae. The sister of *Silverstoneia* is *Epipedobates* Myers, 1987, which is here applied to the clade of species related to *Epipedobates tricolor*. All species of *Epipedobates* that have been tested have been shown to possess skin toxins, and it is predicted that future testing will demonstrate that this is shared with the remaining species as well.

The sister of those genera includes *Colostethus* Cope, 1866 and *Ameerega* Bauer, 1986. *Colostethus* is a non-toxic clade of species from the Andes of Colombia and Ecuador, the inter-Andean valleys of Colombia, and a single known species (*Colostethus fugax*) on the Amazon slope of the Ecuadorean Andes. Parental care varies among species of *Colostethus*; *C. pratti* and *C. panamensis* have female nurse frogs, whereas *C. fraterdanieli* and the undescribed C. *pratti*-like have male nurse frogs. *Ameerega* consists of most species previously referred to *Epipedobates*, and *Phyllobates* sensu Silverstone (1976) before that. The bulk of this radiation is cis-Andean, with only two species known to occur on the Pacific slopes of Colombia and Ecuador (*A. erythromos* and *A. andina*). Nevertheless, neither of those species was included explicitly in the present analysis, and it is possible that they will be found to be more closely related to a different group. Insofar as is known, all species of *Ameerega* are toxic.

Hyloxalus Jiménez de la Espada, 1871 “1870” includes a large number of non-toxic, primarily (but not exclusively) Andean species. 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 genera were included in the analysis, and both fall out in strongly supported clades. Nevertheless, inadequate knowledge of species not included in the present analysis prevents further refinement of the revised taxonomy. More specifically, the clade that would be referred to *Cryptophyllobates* is morphologically conspicuous, and referring species not explicitly analyzed (such as *Hyloxalus eleutherodactylus*) is unproblematic. Nevertheless, owing to its placement as the sister to the clade that includes the type species of *Phyllodromus* (*Phyllodromus pulchellum*), recognition of *Cryptophyllobates* necessitates the distinction between *Hyloxalus* and *Phyllodromus*, which is not possible given current knowledge of most species.

The remaining dendrobatids are all toxic and breed in phytotelmata. They include the five genera most commonly associated with poison dart frogs. Given the importance of this clade in many areas of biology, I recognized it as Dendrobatinae Cope, 1865. As such, I proposed Hyoxalinae New Subfamily for the sister group, i.e., *Hyloxalus*. This solution is not entirely satisfactory because it produces a redundant name. Nevertheless, as discussed above, within *Hyloxalus* available names exist and one conspicuous clade is known, and I anticipate that in the near future more genera will be recognized, thus making Hyloxalinae an informative name.

Phyllobates Duméril and Bibron, 1841 is identical to the group proposed by Myers et al. (1978) and is here recovered as the sister group to the remaining dendrobatines.

Ranitomeya Bauer, 1986 includes most of the diminutive species included in Silverstone's (1975) *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). Due to the placement of *Dendrobates steyermarki* (the type species of *Minyobates*) Myers's genus is inseparable from *Ranitomeya* (type species: *Dendrobates reticulatus*). Nevertheless, all other species previously included in *Minyobates* form a clade, and it is possible that expanding the relatively meager dataset for *R. steyermarki* will change its position and permit the recognition of a strictly Amazonian cis-Andean genus (*Ranitomeya*) and a primarily trans-Andean, montane genus (*Minyobates*; but note that *R. steyermarki* is a cis-Andean but montane species, curiously intermediate between the other species).

Oophaga Bauer, 1988 is applied to the *pumilio* 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.

A new genus referred to as Newgenus2 was proposed for the clade containing Newgenus2 *castaneoticus*, Newgenus2 *quinquevittatus,* and Newgenus2 *galactonotus*. The close relationships between Newgenus2 *castaneoticus* and Newgenus2 *quinquevittatus* was expected, but the placement of Newgenus2 *galactonotus* here is

somewhat heterodox (morphology alone would place it in *Dendrobates* Wagler, 1830, i.e., the *tinctorius* group of Silverstone, 1975) but was also found by Vences et al. (2003). Insofar as morphology was included for this species in the present analysis, there is no empirical basis to doubt its placement.

Finally, *Dendrobates* Wagler, 1830 was applied to the remainder of the *tinctorius* group of Silverstone (1975).

Data Exploration: Genotypic Process Partitions

The discovery of differences in both the evolutionary histories and evidential contributions of data partitions is of central concern for many systematists, due in part to its extensive heurism. Finding such differences suggests problems to be investigated (i.e., into the causes that underlie the differences among partitions) and are used to inform character sampling in future studies. Separate phylogenetic analysis of data partitions was previously considered necessary to detect such differences among partitions.

Grant and Kluge (2003) were critical of that position, arguing that heuristic inferences about character evolution and evaluations of evidential significance should be based on the objectively optimal phylogenetic hypothesis and not the suboptimal solutions that result from partitioned analysis. Herein, I developed an approach to explore data partitions based solely on the total evidence explanation, i.e., without the need for separate phylogenetic analysis. I applied this method to analyze the behavior of data partitions in the present study.

The results of this analysis showed that (1) all partitions contribute evidentially to the individuation of clades across vastly different hierarchic levels, (2) each partition differs in the frequency of unambiguous transformations at different hierarchic levels, and (3) the relative amount of evidence contributed by each partition varies across hierarchic levels. Further, more precise insights will require the development and application of appropriate statistical methods.

Future Research

Although including additional characters and species (especially type species to solve nomenclatural problems) for quantitative phylogenetic analysis is essential, it is secondary to the need to document the diversity of dendrobatoids. Several of the species included in this study were known to be undescribed from the outset, and many others (e.g., numerous species in the *Allobates femoralis* complex, *Ameerega* "*hahneli*" from Leticia) were discovered as a result of this study. As noted in the introductory chapters, the rate of discovery of new species of dendrobatids has been rapid, with most species being referred to the unwieldy and unnatural genus *Colostethus*. It is expected that improved knowledge of phylogeny will facilitate alpha taxonomic work by highlighting relevant comparisons. Such so-called descriptive work is far less appealing in today's climate of science as pop-culture, but it forms the foundation for all studies of diversity.

The need to accelerate work in this area is especially clear in light of the devastating amphibian declines that are extirpating the local diversity of anurans at an alarming rate (Young et al., 2001). Given the high levels of endemism of many species

of dendrobatoids, local loss is often equivalent to global extinction. One of the reasons *Anomaloglossus atopoglossus* was not included in this study is that it cannot be detected at its only known locality (Lynch and Grant, 1998; unpubl. data, 2004), despite once having been conspicuously abundant (Grant et al., 1997).

Field studies documenting the reproductive diversity of dendrobatoids are also needed. Detailed information is only available for a few species, but that is sufficient to reveal incredible variation. As discussed in Chapter 8, detailed developmental studies of closely and distantly related endotrophic species of *Anomaloglossus* and *Allobates* are likely to be extremely fruitful, as limited studies of other anurans have had surprising results. The close phylogenetic relationship between *Anomaloglossus stepheni* and *Anomaloglossus beebei* provides a unique opportunity to compare and contrast endotrophy and specialized oophagy as alternative evolutionary pathways to attain the same outcome. Also needed are basic data for the many species of *Anomaloglossus* for which larval habitat, and parental care have not been observed. Although predictions may be made from parsimonious optimizations, filling in these missing entries is crucial because they may result in the preference of alternative evolutionary scenarios. Likewise, *Colostethus pratti* and the undescribed species *Colostethus pratti*-like are morphologically indistinguishable but differ in DNA sequences and the sex of the nurse frog (female in *C. pratti*, male in *C. pratti*-like). Variation is known to occur within species, so it is possible that the male transport is atypical (in which case the mechanism for this variation poses a relevant research problem; e.g., Myers and Daly, 1983). Also relevant to this immediate problem, reproductive behavior is unknown in *Colostethus fugax*, *Colostethus inguinalis*, and

Colostethus imbricolus, which is key to determining the number of times sex role reversals occurred. Previous studies like these have made certain species model cases (e.g., *C. panamensis*, thanks to the studies by Wells, 1980a; 1980b).

A third area with great potential is the study of dendrobatid toxicity. Precise knowledge of the phylogenetic origins of alkaloid sequestration—both the general ability to sequester alkaloids and the differential uptake of different classes of alkaloids—enables the design of comparative studies that may elucidate the uptake mechanism(s). Similarly, knowledge of phylogeny provides a guide for both field studies in search of novel compounds and feeding experiments designed to increase our understanding of alkaloid uptake. For example, although it is predicted that all dendrobatines except *Phyllobates* possess pumiliotoxin 7-hydroxylase and are capable of converting PTX **251D** into aPTX **267A** (see Daly et al., 2003), the crucial feeding experiment has not yet been done. It was previously though that Newgenus2. *castaneoticus* and Newgenus2 *galactonotus* then placed in different species groups within *Dendrobates*) were distantly related and would provide appropriate reference points for feeding experiments. However, they are here found to be sister species, which severely limits the extrapolations that may be made defensibly. Instead, feeding experiments should be conducted on a species of *Ranitomeya*, with *Ranitomeya fulgurita* being the optimal candidate.

Also in need of detailed study are the biological implications of the results of this phylogenetic analysis. It is clear that Andean orogenesis has played a significant role in the evolution of dendrobatid frogs, as clear divisions between cis- and trans-Andean clades are evident. This is especially clear in the aromobatids, which are

entirely cis-Andean, with only two exceptions: *Allobates talamancae* and its undescribed sister species *A.* Magdalena-species. *Allobates* Magdalena-species occurs just across the Andes in the Magdalena valley of Colombia, while *C. talamancae* ranges from northwestern Ecuador through the Colombian Chocó to Nicaragua in Central America. Some taxa occur almost exclusively at mid- to higher elevations of the Andes (e.g., *Hyloxalus*), some are composed almost exclusively of lowland species (e.g., *Oophaga*), while yet others have considerable diversity at higher and lower elevations and on both sides of the Andes (particularly *Ranitomeya*). Thorough biogeographic analysis of these taxa promises considerable insights into dendrobatoid evolution and South American biogeography.

This study provides numerous insights into the diversification of dendrobatoids, but its most significant contribution will be in leading to new discoveries and corrections of prior errors. In a study of this size, accumulation of errors is inevitable. However, I have aimed to be as explicit as possible regarding data, methods, and the justifications for my decisions, all of which will hopefully facilitate criticism of my results and progress in understanding of these frogs.

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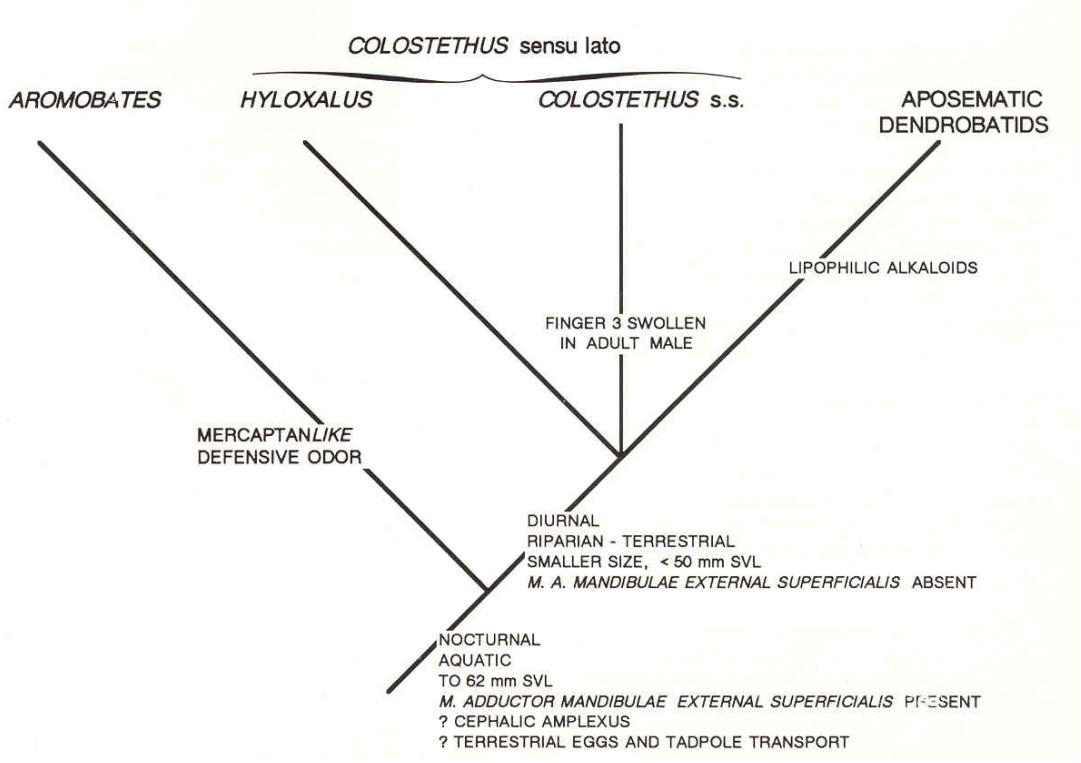
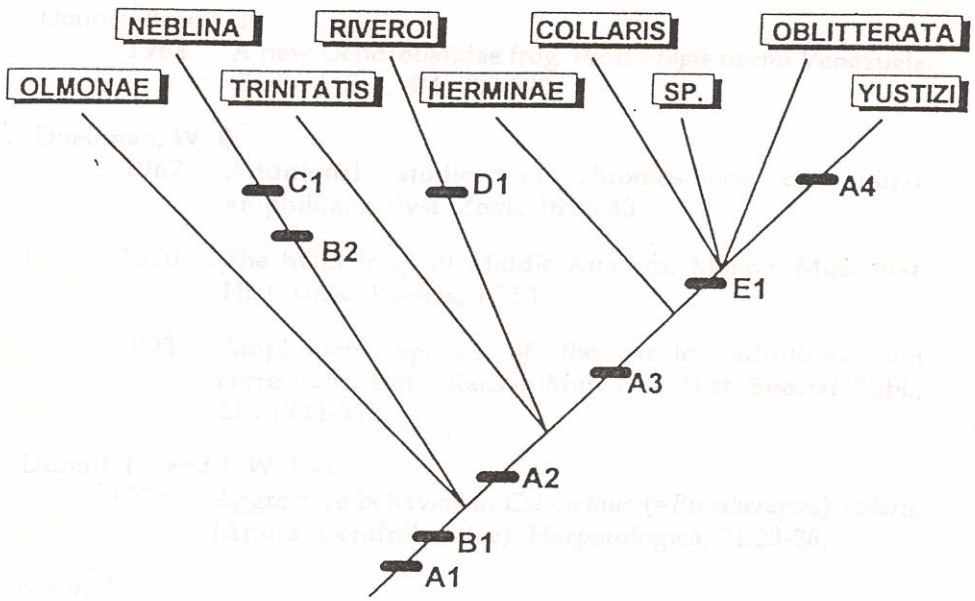
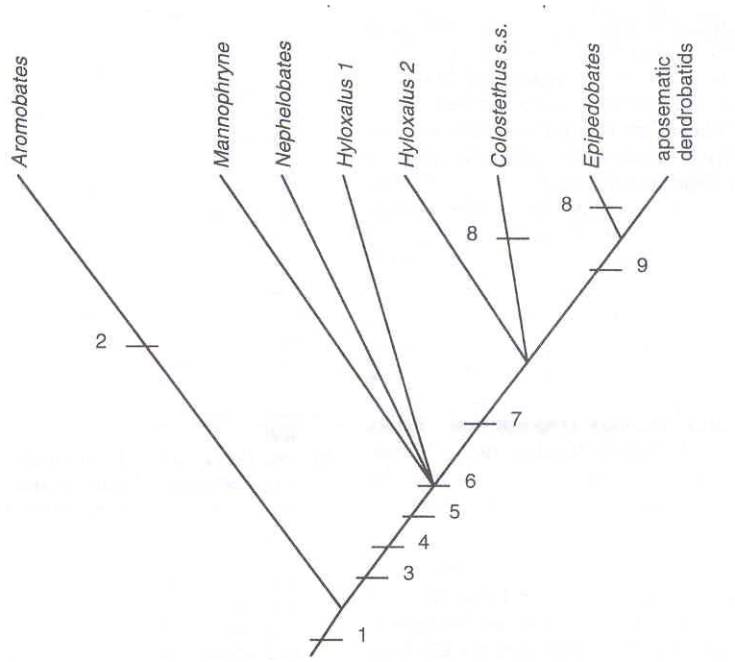
Appendix 1: Prior Phylogenetic Hypotheses



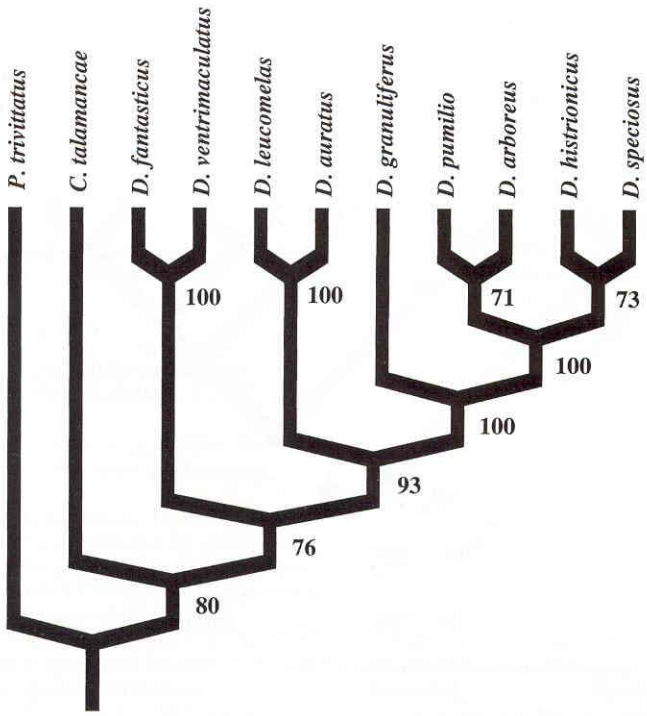
Myers et al., 1991: 29, Fig. 20.



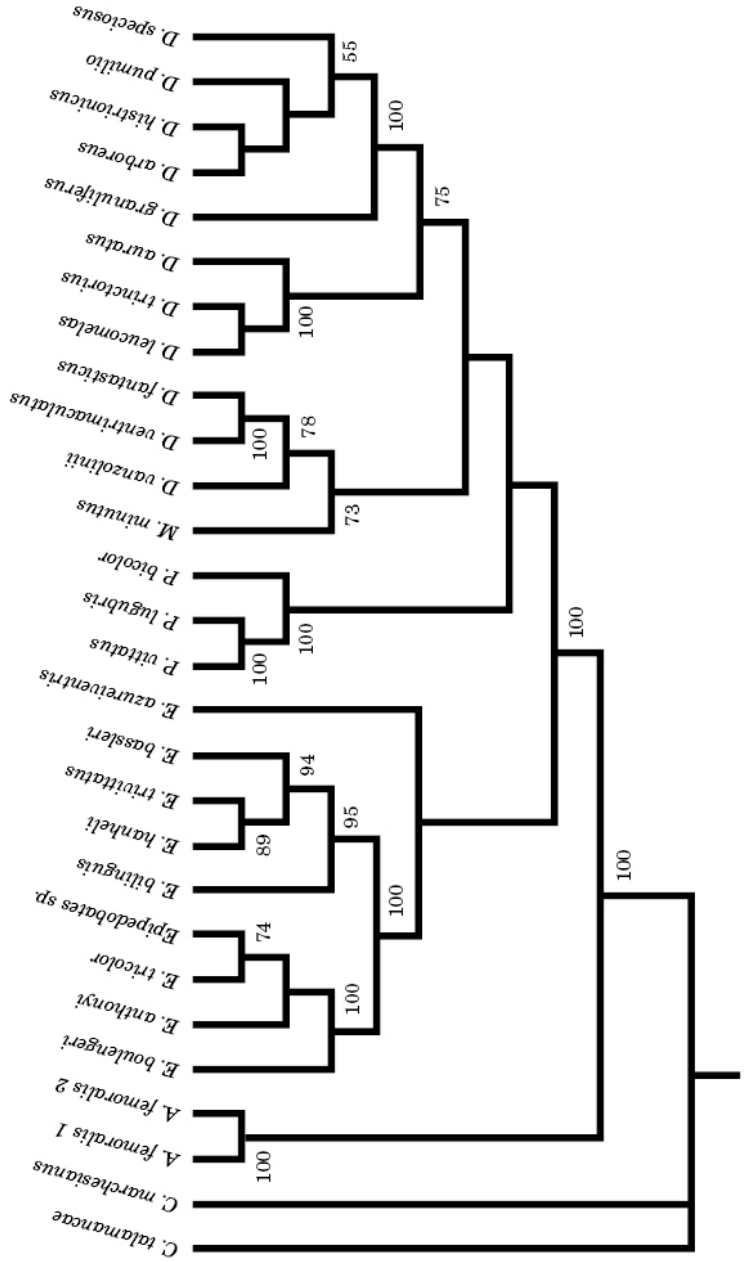
La Marca, 1995: 70, Fig. 11. Synapomorphies are: A1, narrow collar, uniformly colored; B1, tadpoles with small papillae [I have assumed that B1 on the cladorgram is in fact B0 from the text on p. 53]; B2, tadpoles with large papillae [B2 is undefined in the text on p. 53, so I have assumed it refers 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.



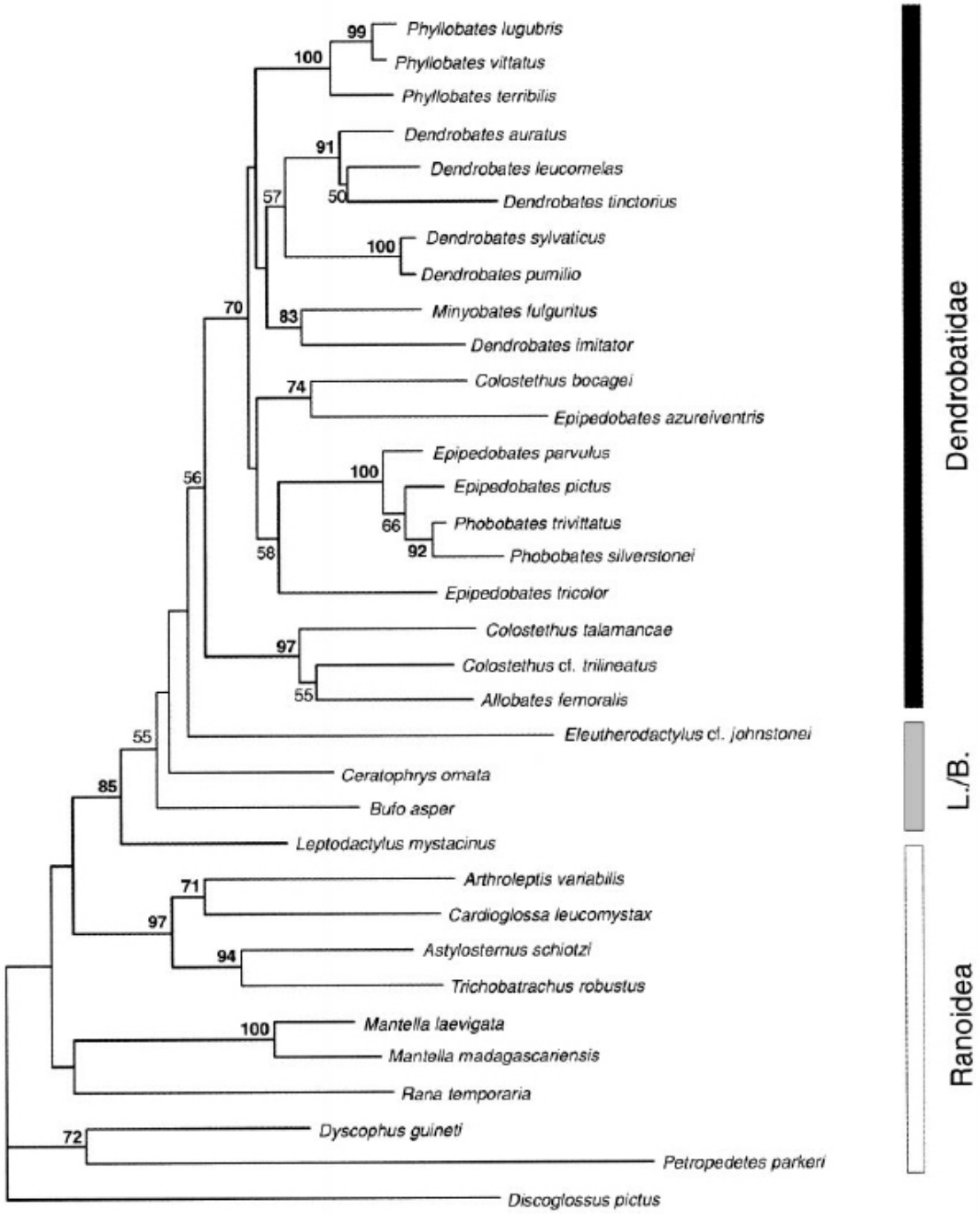
Kaplan, 1997:373, Fig. 3. Extended from Myers et al. (1991). Numbered synapomorphies are: (1) tympanum posterodorsally tilted under anterior edge of massive superficial slip of *m. depressor mandibulae*, (2) mercaptanlike defensive odor, (3) diurnal activity, (4) riparian-terrestrial habitat preference, (5) smaller size (<50 mm SVL), (6) *m. adductor mandibulae external superficialis* absent ("s" pattern), (7) neopalatines absent, (8) finger three of males swollen, and (9) lipophilic alkaloids present.



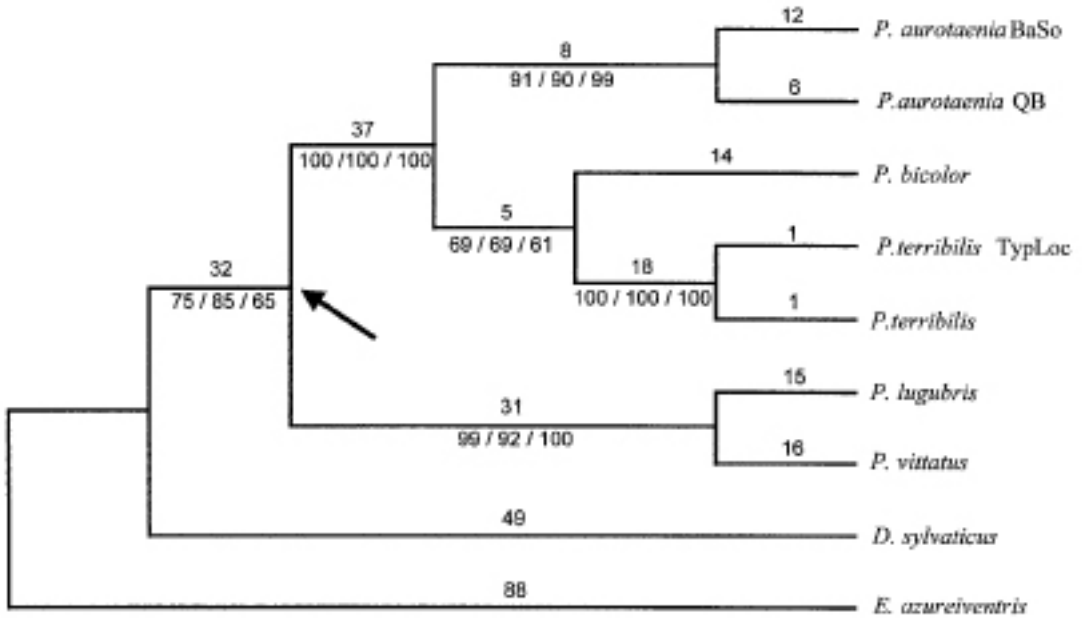
Summers et al., 1999:261, Fig. 1. Parsimony, bootstraps, cytochrome oxidase I, cytochrome *b*, 16S.



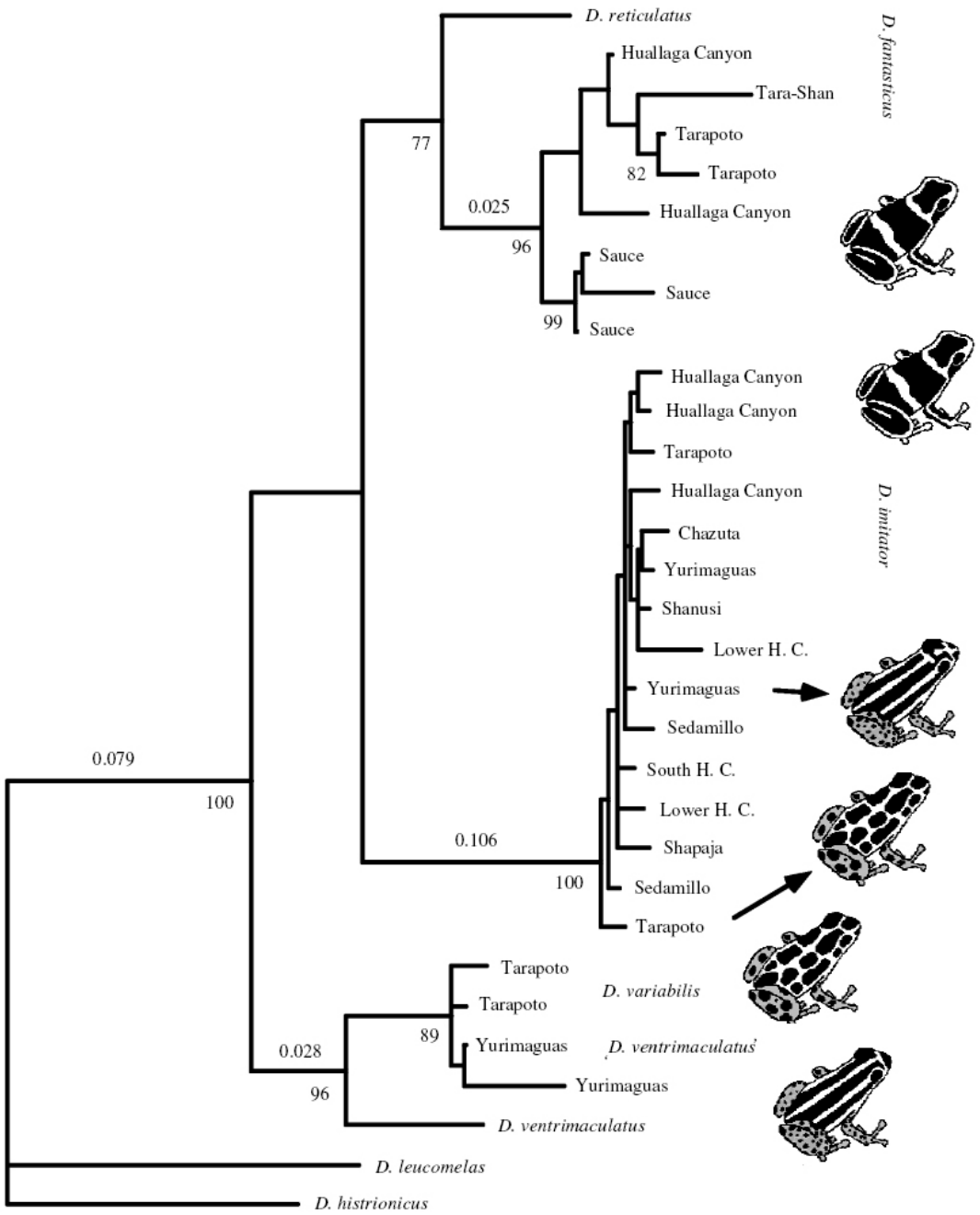
Clough and Summers, 2000:324, fig. 1. Parsimony, bootstrap frequencies, 12S, 16S, cytochrome *b*.



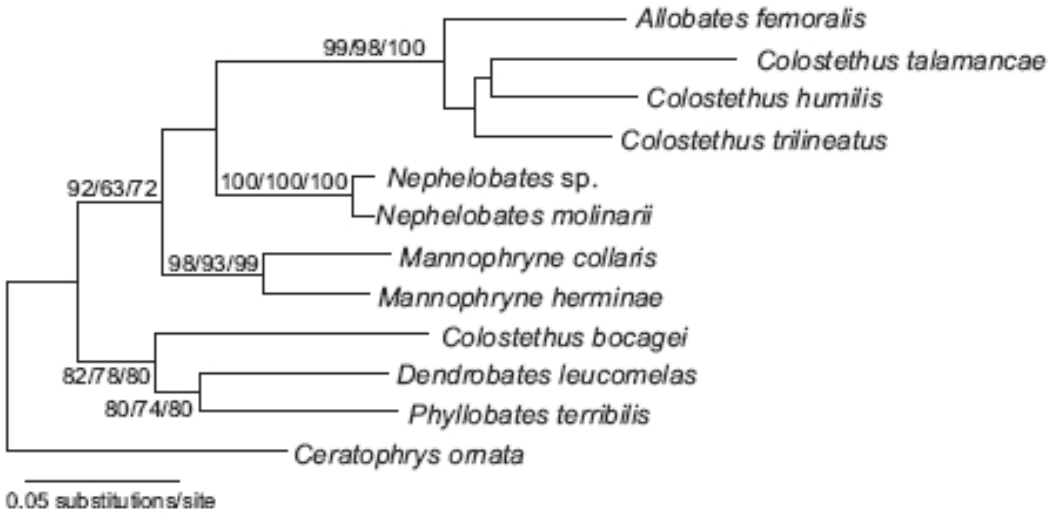
Vences et al., 2000: 37, Fig. 1. Neighbor-joining, bootstraps, 16S.



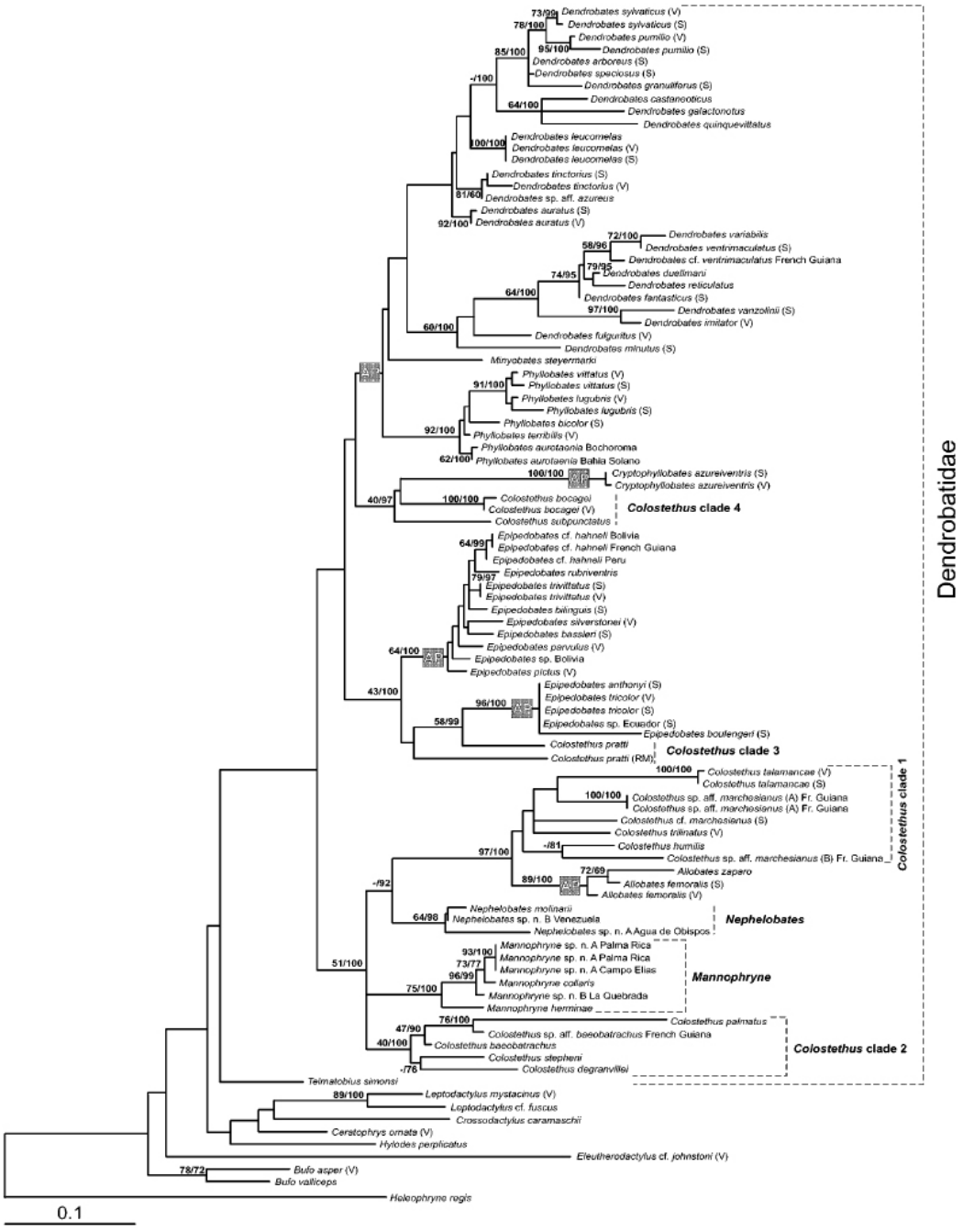
Widmer et al., 2000: 561, Fig. 2. Parsimony, branch length above (optimization not stated), bootstraps for parsimony, maximum likelihood, and neighbor-joining below, cytochrome *b*.



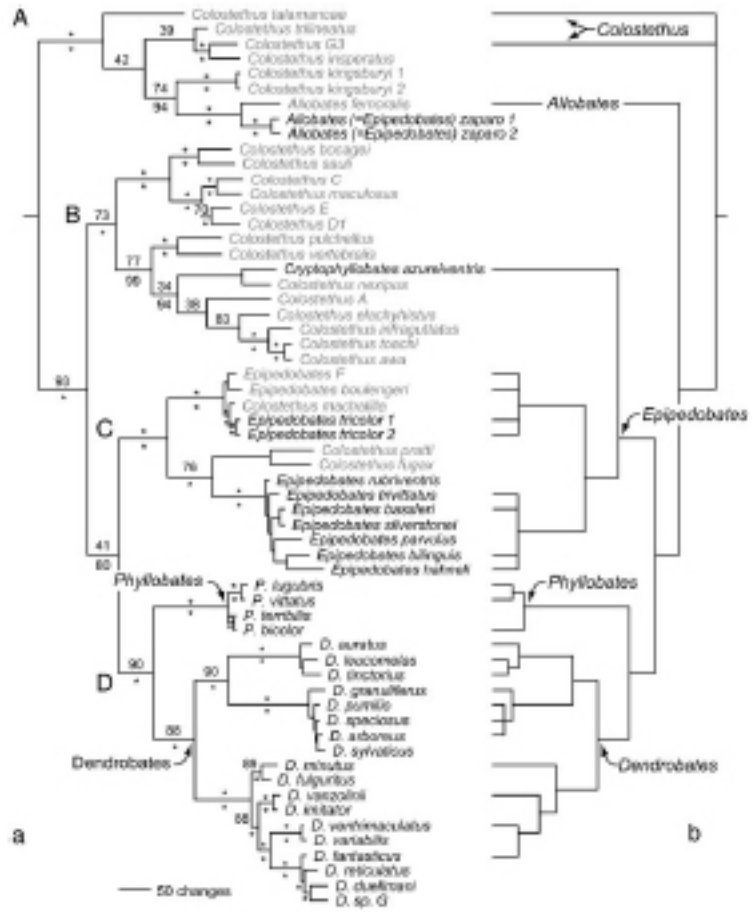
Symula et al., 2001:2419, Fig. 3. Maximum likelihood, branch lengths above, bootstrap frequencies from parsimony analysis below, cytochrome *b*, cytochrome occidase I, 12S, and 16S.



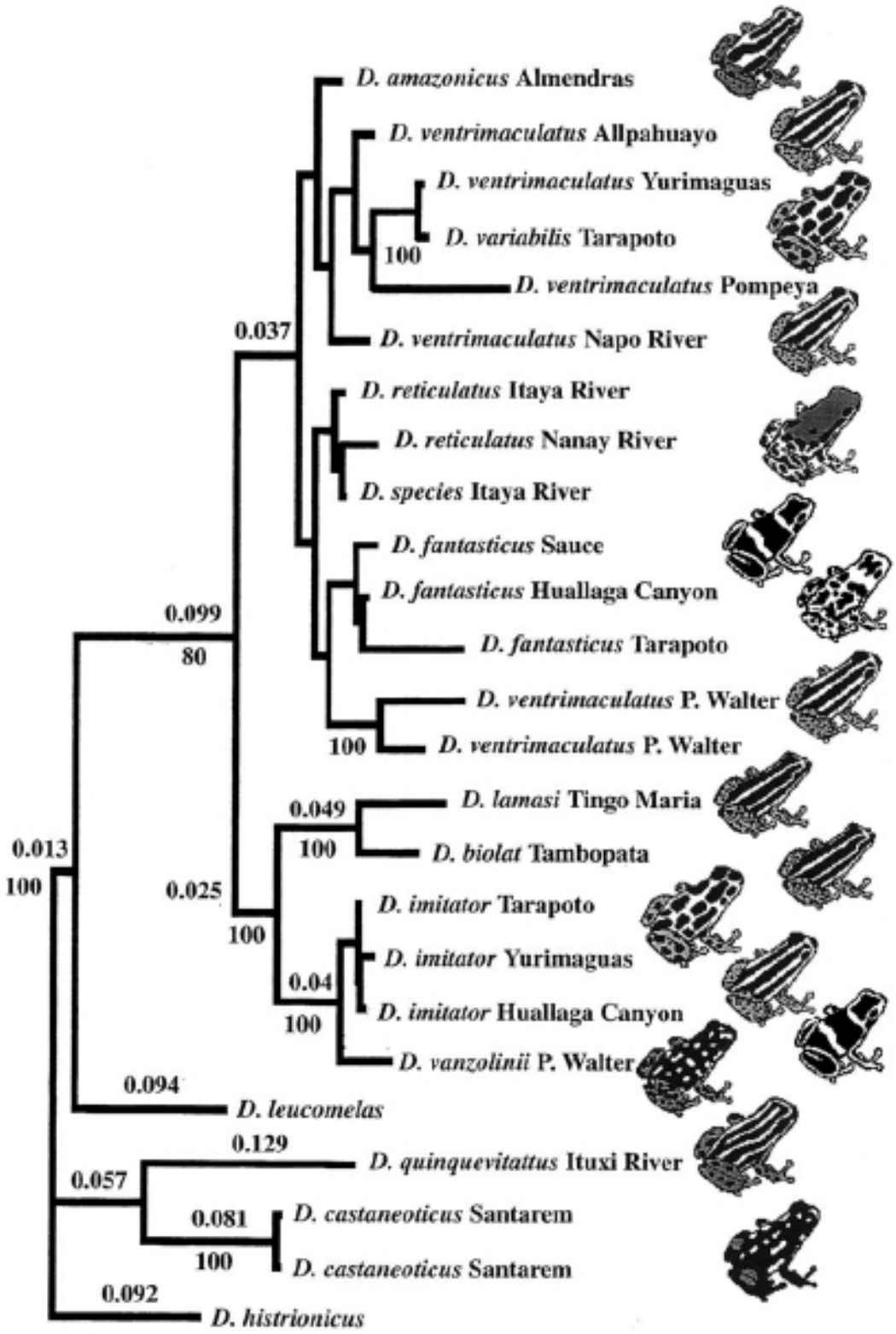
La Marca et al., 2002:239, Fig. 4. Maximum likelihood, bootstrap frequencies from maximum likelihood, parsimony, and neightbor-joining, 16S.



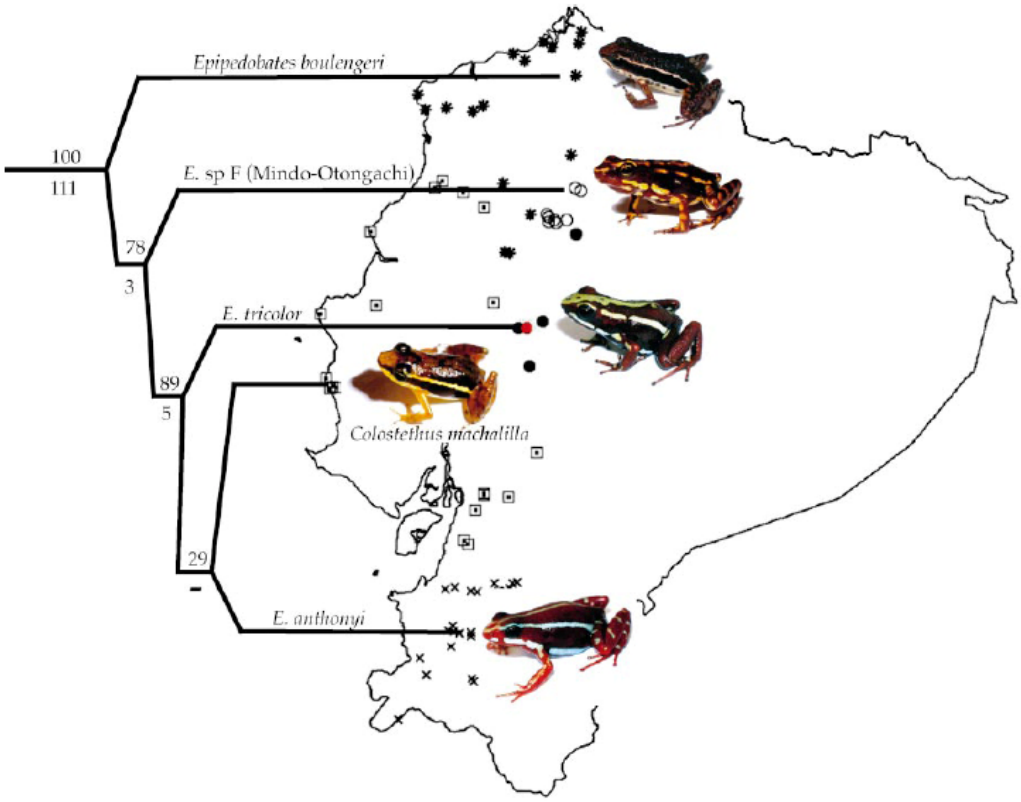
Vences et al., 2003:219, fig. 3. Maximum likelihood, 16S, bootstrap/Bayesian frequencies, 16S.



Santos et al., 2003: 12794, fig. 1. Parsimony, parsimony bootstraps above, Bayesian frequencies below, H1 mtDNA.



Symula et al., 2003: 459, Fig. 3. Maximum likelihood, branch lengths above, bootstrap frequencies below.



Graham et al., 2004, Fig. 2, maximum likelihood and parsimony, bootstrap above, Bremer below (fide Graham, *in litt*. 10/11/2004). Two equally parsimonious solutions were also found but not presented. Note that the crucial node for this hypothesis regarding the removal of *anthonyi* from the synonymy of *tricolor* has a Bremer value of 0, indicating that the *machalilla* + *anthonyi* clade is absent from at least one of the alternative most parsimonious solutions.

Appendix 2: Chronology of Dendrobatid 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

Appendix 3: Chronology of Available Genus-Group Names Proposed as or Currently Included in Dendrobatidae

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*

Appendix 4: Chronology of Available Species Names Proposed or Currently in Dendrobatidae, with Original, Current, and Proposed Generic Placement

Name	Authorship	Status	Original Genus	Current Genus	Revised Taxonomy
tinctorius	Cuvier, 1797		Rana	Dendrobates	Dendrobates
aurata	Wied, 1821	incertae sedis	Hyla		
nigerrima	Spix, 1824	trivittatus	Hyla		
trivittata	Spix, 1824		Hyla	Epipedobates	Ameerega
picta	Tschudi, 1838		Hylaplesia	Epipedobates	Ameerega
bicolor	Duméril and Bibron, 1841		Phyllobates	Phyllobates	Phyllobates
obscurus	Dumeril and Bibron, 1841	trivittatus	Dendrobates		
histrionicus	Berthold, 1845		Dendrobates	Dendrobates	Oophaga
lateralis	Guichenot, 1848	Batrachyla taeniata	Dendrobates	Leptodactylidae	
inhambanensis	Bianconi, 1849	Phrynomantis bifasciatus	Dendrobates	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	Eleutherodactylus limbatus	Phyllobates	Leptodactylidae	
glandulosus	Fitzinger, 1863	Physalaemus olfersi	Phyllobates	Leptodactylidae	
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	Newgenus2

leucomelas	Steindachner, 1864		Dendrobates	Dendrobates	Dendrobates
quinquevittatus	Steindachner, 1864		Dendrobates	Dendrobates	Newgenus2
ridens	Cope, 1866	Eleutherodactylus ridens	Phyllobates	Leptodactylidae	
peruensis	Steindachner, 1867	uncertain	Phyllobates	uncertain	
typographus	Keferstein, 1867	pumilio	Dendrobates		
inguinalis	Cope, 1868		Prostherapis	Colostethus	Colostethus
chocoensis	Posada Arango, 1869	bicolor	Phyllobates		
verruculatus	W. Peters, 1870	Eleutherodactylus verruculatus	Phyllobates	Eleutherodactylus	
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	Mantella betsileo	Dendrobates	Rhacophoridae	
madagascariensis	Grandidier, 1872	Mantella madagascariensis	Dendrobates	Rhacophoridae	
chalceus	W. Peters, 1873	Eleutherodactylus chalceus	Phyllobates	Leptodactylidae	
maculatus	W. Peters, 1873	trivittata	Dendrobates	Epipedobates	Ameerega
ignitus	Cope, 1874	pumilio	Dendrobates		
labialis	Cope, 1874		Dendrobates	Epipedobates	Ameerega
hylaeformis	Cope, 1875	Eleutherodactylus hylaeformis	Phyllobates	Leptodactylidae	
talamancae	Cope, 1875		Dendrobates	Colostethus	Allobates
cystignathoides	Cope, 1877	Eleutherodactylus cystignthoides	Phyllobates	Leptodactylidae	
ebenaui	Boettger, 1880	Mantella betsileo	Dendrobates	Rhacophoridae	
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	Dendrobates	Epipedobates	Ameerega
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	Newgenus1
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	Leptodactylidae	
boulengeri	Barbour, 1909		Prostherapis	Epipedobates	Epipedobates
chocoensis	Boulenger, 1912		Hylixalus	Colostethus	Hyloxalus
collaris	Boulenger, 1912		Hylixalus	Mannophryne	Mannophryne
huigrae	Fowler, 1913	Eleutherodactylus diastema	Hyloxalus	Leptodactylidae	
aurotaenia	Boulenger, 1914 "1913"		Dendrobates	Phyllobates	Phyllobates
coctaei	Boulenger, 1914 "1913"	histrionicus	Dendrobates		
paraensis	Boulenger, 1914 "1913"	galactonotus	Dendrobates		
walkeri	Ruthven, 1915	Geobatrachus walkeri	Geobatrachus	Leptodactylidae	
tarsalis	Werner, 1916	subpunctatus	Prostherapis		
kingsburyi	Boulenger, 1918		Phyllobates	Colostethus	Allobates
ranoides	Boulenger, 1918		Dendorbates	Colostethus	Allobates

granuliventris	Boulenger, 1919	palmatus	Hylixalus		
sylvaticus	Barbour and Noble, 1920		Phyllobates	Colostethus	Hyloxalus
anthonyi	Noble, 1921		Phyllobates	Epipedobates	Epipedobates
beatriciae	Barbour and Dunn, 1921	lugubris	Phyllobates		
beebei	Noble, 1923		Hyloxalus	Colostethus	Anomaloglossus
nubicola	Dunn, 1924		Phyllobates	Colostethus	Silverstoneia
		Eleutherordactylus			
nigriventris	A. Lutz, 1925	nigriventris	Hylaplesia	Leptodactylidae	
olfersioides	A. Lutz, 1925		Eupemfix	Colostethus	Allobates
tetravittatus	Miranda Ribeiro, 1926	trivittatus	Dendrobates		
		Crossodactylus			
brasiliensis	Witte, 1930	gaudichaudi	Phyllobates	Leptodactylidae	
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	unclear	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	Insertae 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 and Goin, 1970		Dendrobates	Epipedobates	Ameerega
thorntoni	Cochran, Goin, 1970		Phyllobates	Colostethus	Colostethus
walesi	Cochran and Goin, 1970	subpunctatus	Phyllobates	Colostethus	
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	Ranitomeya
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
abditus	Myers and Daly, 1976		Dendrobates	Minyobates	Ranitomeya
lehmanni	Myers and Daly, 1976		Dendrobates	Dendrobates	Oophaga
occultator	Myers and 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 and 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, Daly, and Malkin, 1978		Phyllobates	Phyllobates	Phyllobates
silverstonei	Myers and Daly, 1979		Dendrobates	Epipedobates	Ameerega
bombetes	Myers and Daly, 1980		Dendrobates	Minyobates	Ranitomeya
erythromos	Vigle and 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 and Burrowes, 1987		Dendrobates	Epipedobates	Ameerega
captivus	Myers, 1982		Dendrobates	Dendrobates	Newgenus2
edwardsi	Lynch, 1982		Colostethus	Colostethus	Hyloxalus
mysteriosus	Myers, 1982		Dendrobates	Dendrobates	Ranitomeya
ruizi	Lynch, 1982		Colostethus	Colostethus	Hyloxalus
syntomopus	Lynch & Ruiz-Carranza, 1982	Atopophrynus syntomopus	Atopophrynus	Leptodactylidae	
vanzolinii	Myers, 1982		Dendrobates	Dendrobates	Ranitomeya
olmonae	Hardy, 1983		Colostethus	Mannophryne	Mannophryne
arboreus	Myers, Daly, and Martínez, 1984		Dendrobates	Dendrobates	Oophaga
littoralis	Pefaur, 1984		Colostethus	Colostethus	Hyloxalus
agilis	Lynch & Ruiz-Carranza, 1985		Colostethus	Colostethus	Colostethus
azureiventris	Kneller and Henle, 1985		Phyllobates	Cryptophyllobates	Hyloxalus
duranti	Pefaur, 1985		Colostethus	Nephelobates	Aromobates
guatopoensis	Dixon and 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 and Simmons, 1988		Colostethus	Colostethus	Hyloxalus
variabilis	Zimmerman and Zimmerman, 1988		Dendrobates	Dendrobates	Ranitomeya
ardens	Jungfer, 1989	cainarachi	Epipedobates		Ameerega
bilinguis	Jungfer, 1989		Epipedobates	Epipedobates	Ameerega
cainarachi	Schulte, 1989		Epipedobates	Epipedobates	Ameerega
stepheni	Martins, 1989		Colostethus	Colostethus	Anomaloglossus
yustizi	La Marca, 1989		Colostethus	Mannophryne	Mannophryne
alacris	Rivero & Granados-Diaz, 1990 "1989"		Colostethus	Colostethus	Colostethus
castaneoticus	Caldwell and Myers, 1990		Dendrobates	Dendrobates	Newgenus2
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	bocagei	Colostethus	Colostethus	Hyloxalus
marmoreoventris	Rivero, 1991b		Colostethus	Colostethus	Hyloxalus
mittermieri	Rivero, 1991		Colostethus	Colostethus	Hyloxalus
nocturnus	Myers, Paolillo, & Daly, 1991		Aromobates	Aromobates	Aromobates
paradoxus	Rivero, 1991	tricolor	Colostethus		
parcus	Rivero, 1991b	exasperatus	Colostethus		
peculiaris	Rivero, 1991		Colostethus	Colostethus	Hyloxalus
poecilonotus	Rivero, 1991a		Colostethus	Colostethus	insertae 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 and 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 and Myers, 1993		Epipedobates	Epipedobates	Ameerega
chalcopis	Kaiser, Coloma, & Gray, 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 and Parmelee, 1996		Colostethus	Colostethus	Anomaloglossus
vicentei	Jungfer, Weygoldt and Juraske, 1996		Dendrobates	Dendrobates	Oophaga
atopoglossus	Grant, Humphrey, & Myers, 1997		Colostethus	Colostethus	Anomaloglossus
ayarzaguenai	La Marca, 1997 "1996"		Colostethus	Colostethus	Anomaloglossus
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, Debold, Henle, Glaw, and Kneller, 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 and Velazco, 1998		Epipedobates	Epipedobates	Ameerega
amazonicus	Schulte, 1999	igneus	Dendrobates		
baeobatrachus	Boistel and 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 and Serna, 2000 "1995"		Colostethus	Colostethus	Hyloxalus

cacerensis	Rivero and Serna, 2000 "1995"	inguinalis	Colostethus		
claudiae	Junger, Lötters, and Jorgens, 2000		Dendrobates	Dendrobates	Ranitomeya
dysprosium	Rivero and Serna, 2000 "1995"		Colostethus	Colostethus	Colostethus
erasmios	Rivero and Serna, 2000 "1995"		Colostethus	Colostethus	Silverstoneia
excisus	Rivero and Serna, 2000 "1995"		Colostethus	Colostethus	Hyloxalus
picachos	Ardila-Robayo, Acosta-Galvis, and Coloma, 2000 "1999"		Colostethus	Colostethus	Allobates
pseudopalmatus	Rivero and Serna, 2000 "1995"		Colostethus	Colostethus	Newgenus1
ramirezi	Rivero and Serna, 2000 "1995"		Colostethus	Colostethus	insertae sedis
simulans	Myers, Rodriguez, and Icochea, 2000		Epipedobates	Epipedobates	Ameerega
wayuu	Acosta, Cuentas, and Coloma, 2000 "1999"		Colostethus	Colostethus	Allobates
alessandroi	Grant & Rodríguez, 2001		Colostethus	Colostethus	Allobates
caeruleodactylus	Lima and Caldwell, 2001		Colostethus	Colostethus	Allobates
melanolaemus	Grant & Rodríguez, 2001		Colostethus	Colostethus	Allobates
undulatus	Myers and Donnelly, 2001		Colostethus	Colostethus	Allobates
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
nidicola	Caldwell & Lima, 2003		Colostethus	Colostethus	Allobates
patitae	Lötters, Morales, and Proy, 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
nubeculosus	Jungfer & Böhme, 2004	Dendrobates	Dendrobates	Dendrobates
pittieri	La Marca, Manzanilla, and Mijares-Urrutia, 2004	Colostethus	Colostethus	Allobates
pulcherrimus	Duellman, 2004	Colostethus	Colostethus	Hyloxalus
sordidatus	Duellman, 2004	Colostethus	Colostethus	Hyloxalus
spilotogaster	Duellman, 2004	Colostethus	Colostethus	Hyloxalus

Appendix 5: Tissue and Sequence Data

Sample ID	Voucher ID	Taxon	Sample ID	Voucher ID	Taxon
14	PK-437-1	baeobatrachus	537	V. Verdade	braccatus
42	PK-437-2	baeobatrachus	538	V. Verdade	olfersioides
43	PK-437-3	baeobatrachus	605	ROM 39631	beebei
44	PK-737-4	baeobatrachus	606	ROM 39637	tepuyensis
71	KU 220621	delatorreae	607	ROM 39639	Colostethus_ROM1
73	KU 220631	machalilla	608	ROM 39632	beebei
74	KU 215172	trilineatus	609	MVZ 199828	trinitatis
75	KU 211806	nexipus	611	Paulo Nuin	Megaelosia_goeldii
76	KU 219756	Phyllobates_sylvaticus	612	LSUMZ 15245	brunneus
77	KU 211885	idiomelus	613	LSUMZ 15186	brunneus
78	KU 215179	femoralis	614	LSUMZ 13743	Colostethus_PortoWalter1
79	KU 215183	pictus	615	LSUMZ 13785	Colostethus_PortoWalter1
105	KU 212522	elachyhistus	616	LSUMZ 17601	Colostethus_RioFormoso1
106	KU 212523	elachyhistus	617	LSUMZ 17424	Colostethus_RioFormoso2
107	KU 212524	elachyhistus	618	LSUMZ 17442	Colostethus_RioFormoso2
108	KU 219749	elachyhistus	619	LSUMZ 17556	Colostethus_RioFormoso3
109	KU 215185	pictus	620	LSUMZ 16928	Colostethus_Manaus1
110	KU 215184	pictus	621	LSUMZ 16955	caeruleodactylus
112	KU 215175	trilineatus	622	LSUMZ 15956	nidicola
113	KU 219757	Phyllobates_sylvaticus	623	LSUMZ 13733	Epipedobates_PortoWalter2
114	KU 212514	elachyhistus	624	LSUMZ 13723	Epipedobates_PortoWalter2
115	KU 212515	elachyhistus	625	LSUMZ 13778	Epipedobates_PortoWalter1
116	KU 212516	elachyhistus	626	LSUMZ 13723	Epipedobates_PortoWalter1
117	KU 212517	elachyhistus	627	LSUMZ 16912	trivittatus
118	KU 211947	pulcherrimus	628	LSUMZ 16908	trivittatus
119	KU 211948	pulcherrimus	645	Atlanta Bot. Gard.	leucomelas
120	KU 211908	idiomelus	646	Atlanta Bot. Gard.	silverstonei
121	KU 211109	idiomelus	647	Atlanta Bot. Gard.	galactonotus
122	KU 211110	idiomelus	657	BB557	Eupsophus_calcaratus
123	KU 212486	nexipus	838	Atlanta Bot. Gard.	anthonyi
124	KU 211877	insulatus	839	Atlanta Bot. Gard.	vittatus
125	KU 211878	insulatus	840	Atlanta Bot. Gard.	aurotaenia

126	KU 211886	idiomelus
127	KU 221841	zaparo
128	KU 215177	femoralis
129	KU 215180	femoralis
130	KU 211807	nexipus
131	KU 211808	nexipus
132	KU 220632	machalilla
133	KU 220633	machalilla
149	MLPA 1414	Crossodactylus_schmidti
217	MACN 38531	Melanophryniscus_klappenbachi
278	A [from Godfrey Bourne]	degranvillei
279	B [from Godfrey Bourne]	degranvillei
280	UMMZ 227952	boulengeri
313	AMNH A165110	Telmatobius_verrucosus
319	USNM 268846	trivittatus
320	USNM 269052	pictus
321	USNM 546404	zaparo
322	USNM 269052	pictus
323	USNM-FS 59979	claudiae
324	USNM-FS 59980	claudiae
325	USNM-FS 52055	talamancae
326	USNM-FS 59757	talamancae
327	USNM 313818	auratus
328	USNM 546405	zaparo
329	USNM-FS 195116	lugubris
330	USNM-FS 51785	claudiae
331	CWM 19715	undulatus
332	CWM 19718	undulatus
333	CWM 19719	undulatus
334	CWM 17698(A)	auratus
335	CWM 17698(B)	auratus
336	CWM 17661 ("unused" box)	histrionicus
337	CWM 19053	pulchripectus
338	CWM 19050	lehmanni
339	CWM 19044	granuliferus
889	249 (CFBH)	Hylodes_phyllodes
890	282 (CFBH)	Cycloramphus_boraceiensis
1039	UMFS 11492	Atelopus_zeteki
1115	IZUA 3504	Rhinoderma_darwinii
1132	CWM 18635	nocturnus
1133	LR 742	macero
1134	CWM 18634	nocturnus
1135	CWM 17658	terribilis
1139	CWM "#4"	espinosai
1141	CWM "III"	herminae
1142	SIUC 7652	nubicola
1143	SIUC 7657	flotator
1144	SIUC 7658	pratti
1145	SIUC 7664	flotator
1146	SIUC 7663	nubicola
1147	SIUC 7667	talamancae_Panama
1148	KRL 789	vicentei
1149	KRL 790	minutus
1150	SIUC 7666	panamensis
1151	Atlanta Bot. Gard.	truncatus
1152	MCL 00015	Hylodes_phyllodes
1186	CFBH-T 398	Thoropa_miliaris
1223	CH5546	panamensis
1224	CH5524	pratti_like
1225	MAR 095	Colostethus_Ibague
1226	TG 1487	fraterdanieli
1227	TG 1488	fraterdanieli
1228	TG 1491	fraterdanieli
1229	TG 1294	imbricolus
1230	MUJ to come	fraterdanieli_Acosta
1232	Marcus Breece	terribilis
1233	Marcus Breece	bicolor
1234	Marcus Breece	Phyllobates_sp
1235	LSUMZ 13742	Epipedobates_PortoWalter2
1236	LSUMZ 13677	Epipedobates_PortoWalter1

340	CWM 18636	arboreus
341	CWM 17826(D)	speciosus
342	CWM 17813(S)	pumilio
343	LSUMZ 12888	bocagei
344	LSUMZ 12908	bocagei
345	LSUMZ 12909	bocagei
346	LSUMZ 12921	marchesianus_Cuyabeno
347	LSUMZ 12969	marchesianus_Cuyabeno
348	LSUMZ 12970	marchesianus_Cuyabeno
349	LSUMZ 12971	marchesianus_Cuyabeno
350	LSUMZ 12972	marchesianus_Cuyabeno
351	LSUMZ 15176	marchesianus_Santarem
352	LSUMZ 15238	brunneus
353	LSUMZ 15299	marchesianus_Santarem
354	LSUMZ 15298	marchesianus_Santarem
355	LSUMZ 13690	Colostethus_PortoWalter2
356	LSUMZ 13790	Colostethus_PortoWalter2
357	LSUMZ 3081	marchesianus_RioItuxi
358	LSUMZ 15352	marchesianus_RioItuxi
359	LSUMZ 17419	Colostethus_RioFormoso1
360	LSUMZ 17420	Colostethus_RioFormoso3
361	LSUMZ 15094	talamancae_Nicaragua
362	LSUMZ 15095	talamancae_Nicaragua
363	LSUMZ 15209	castaneoticus
364	LSUMZ 14730	Dendrobates_sylvaticus
365	LSUMZ 15107	auratus_Nicaragua
366	LSUMZ 15096	lugubris_Nicaragua
367	LSUMZ 15103	pumilio_Nicaragua
368	LSUMZ 3093	quinquevittatus_RioItuxi
369	LSUMZ 13025	quinquevittatus_RioItuxi
370	LSUMZ 17435	quinquevittatus_RioFormoso
371	LSUMZ 17471	quinquevittatus_RioFormoso
372	LSUMZ 13652	vanzolinii
373	LSUMZ 13682	vanzolinii
374	LSUMZ 12919	ventrimaculatus_Sucumbios
375	LSUMZ 13755	ventrimaculatus_PortoWalter
1237	LSUMZ 17444	Colostethus_RioFormoso2
1260	LSU 15291	marchesianus_Santarem
1261	LSU 16926	caeruleodactylus
1262	LSU 12920	marchesianus_Cuyabeno
1263	LSU 17585	Colostethus_RioFormoso3
1264	LSU 15237	brunneus
1265	LSU 13792	Colostethus_PortoWalter2
1266	LSU 17555	Colostethus_RioFormoso3
1267	LSU 12910	bocagei
1268	LSU 15296	marchesianus_Santarem
1269	LSU 13789	Colostethus_PortoWalter2
1270	LSU 12936	marchesianus_Cuyabeno
1271	LSU 15227	marchesianus_Santarem
1272	LSU 17586	Colostethus_RioFormoso3
1273	LSU 13691	Colostethus_PortoWalter2
1274	LSU 17554	Colostethus_RioFormoso3
1275	TG	Atelopus_spurrelli
1276	LSU 17633	Colostethus_RioFormoso2
1277	LSU 15393	marchesianus_RioItuxi
1278	LSU 15208	brunneus
1279	LSU 17630	Colostethus_RioFormoso3
1280	LSU 15187	brunneus
1281	LSU 15218	brunneus
1282	LSU 17593	Colostethus_RioFormoso2
1283	LSU 12870	marchesianus_Cuyabeno
1284	LSU 15392	marchesianus_RioItuxi
1285	LSU 16941	nidicola
1286	LSU 15244	brunneus
1287	LSU 16957	caeruleodactylus
1288	LSU 17421	Colostethus_RioFormoso1
1289	LSU 17443	Colostethus_RioFormoso3
1290	CWM "#1"	anthonyi_sensu_Myers
1294	LSU 15212	brunneus
1295	LSU 17558	Colostethus_RioFormoso3
1296	LSU 17629	Colostethus_RioFormoso3
1297	LSU 13645	trivittatus

376	LSUMZ 15378	ventrimaculatus_RioItuxi
377	LSUMZ 15394	ventrimaculatus_RioItuxi
378	LSUMZ 12799	parvulus
379	JC 4787	Colostethus_sp_Neblina
380	RZ 12241	Colostethus_sp_Neblina
381	LSUMZ 13635	Epipedobates_PortoWalter1
382	LSUMZ 13639	Epipedobates_PortoWalter1
383	LSUMZ 13664	Epipedobates_PortoWalter2
384	LSUMZ 13686	Epipedobates_PortoWalter2
385	LSUMZ 16906	Epipedobates_sp.
386	LSUMZ 16923	Epipedobates_sp.
387	LSUMZ 13661	trivittatus
388	LSUMZ 13650	hahneli_PortoWalter
389	LSUMZ 13688	hahneli_PortoWalter
390	LSUMZ 13754	hahneli_PortoWalter
391	LSUMZ 16970	hahneli_Amazonas
392	LSUMZ 16931	hahneli_Amazonas
393	LSUMZ 17436	femoralis_RioFormoso
394	LSUMZ 17552	femoralis_RioFormoso
395	LSUMZ 15213	femoralis_Santarem
396	LSUMZ 15224	femoralis_Santarem
397	LSUMZ 13633	femoralis_PortoWalter
398	LSUMZ 13651	femoralis_PortoWalter
399	LSUMZ 12790	femoralis_Cuyabeno
400	LSUMZ 12834	femoralis_Cuyabeno
401	LSUMZ 12801	parvulus
402	LSUMZ 12938	marchesianus_Cuyabeno
403	LSUMZ 12950	marchesianus_Cuyabeno
404	LSUMZ 15435	Colostethus_RioItuxi2
405	LSUMZ 16910	Colostethus_Manaus1
406	LSUMZ 16929	caeruleodactylus
407	LSUMZ 16959	nidicola
408	LSUMZ 15097	talamancae_Nicaragua
496	TG1362	punctiventris
497	TG1363	punctiventris
498	TG1381	histrionicus
1298	LSU 15222	femoralis
1299	LSU 13712	Epipedobates_PortoWalter1
1300	LSU 13711	Epipedobates_PortoWalter1
1301	LSU 13660	Epipedobates_PortoWalter1
1302	LSU 13777	Epipedobates_PortoWalter1
1303	LSU 12800	parvulus
1304	LSU 16930	Epipedobates_sp
1305	LSU 13693	trivittatus
1306	LSU 12798	femoralis
1307	LSU 13646	Epipedobates_PortoWalter1
1308	LSU 13732	Epipedobates_PortoWalter1
1309	LSU 13667	femoralis
1310	LSU 16925	ventrimaculatus
1311	LSU 13770	ventrimaculatus
1312	LSU 15389	quinquevittatus
1313	LSU 15109	pumilio
1314	LSU 13658	vanzolinii
1315	LSU 15112	pumilio
1316	LSU 15211	brunneus
1317	LSU 12948	marchesianus_Cuyabeno
1318	LSU 16911	Colostethus_Manaus1
1319	LSU 17553	Colostethus_RioFormoso3
1321	WES 626	Nephelobates_sp
1322	WES 1034	Mannophryne_sp
1323	WES 1035	Mannophryne_sp
1324	WES 1036	Mannophryne_sp
1325	BPN 826	femoralis_Suriname
1326	BPN 837	Colostethus_BPN1
1327	BPN 840	tinctorius
1328	BPN 849	Colostethus_BPN2
1329	BPN 910	trivittatus_Suriname
1330	BPN 977	azureus
1331	BPN 1074	pictus_BPN
1332	BPN 1304	Colostethus_BPN3
1333	BPN 1305	Colostethus_BPN3
1334	CPI 10198	praderioi

499	TG1383	fulguritus	1335	CPI 10208	praderioi
514	MJH 3928	stepheni	1336	CPI 10209	degranvillei
515	MJH 3950	stepheni	1337	CPI 10216	roraima
516	MJH 3909	marchesianus_SaoFrancisco	1338	CPI 10217	roraima
517	MJH 3973	marchesianus_CurvaUna	1339	Tadpole (untagged)	roraima
518	MJH 7483	trivittatus	1345	ARA 2520	Colostethus_Ibague
519	MJH 3907	trivittatus	1346	ARA 2521	palmatus
520	MJH 3976	femoralis_Ducke	1347	MAR 105	Colostethus_Ibague
522	MJH 7041	petersi	1348	MUJ 3247	inguinalis
524	MJH 3988	marchesianus_Ducke	1349	JDL 24489	ventrimaculatus
525	MJH 3715	petersi	1350	JDL 24490	trivittatus_Leticia
526	MJH 7354	femoralis_Panguana	1351	JDL 26785	truncatus
527	MJH 7477	trilineatus	1352	JDL 26872	truncatus
528	MJH 3754	reticulatus	1354	JDL 24601	femoralis_Leticia
532	MJH 7095	Dendrophryniscus_minutus	1357	ARA 2394	juanii
533	V. Verdade	galactonotus	1358	MAR 159	Magdalena_species
534	V. Verdade	azureus	1359	MUJ to come	subpunctatus
535	V. Verdade	tinctorius	1360	MUJ to come	saltuensis
536	V. Verdade	flavopictus			

Appendix 6: Numbers and References for Sequences Obtained from Genbank

GenBank Identification	GenBank Number	Locus	Length	Reference
Colostethus awa	AY364544	12S, $tRNA^{val}$, 16S	2445	Santos et al., 2003
Colostethus baeobatrachus	AY263231	16S	535	Vences et al., 2003
Colostethus bocagei	AY364545	12S, $tRNA^{val}$, 16S	2435	Santos et al., 2003
Colostethus degranvillei	AY263260	16S	506	Vences et al., 2003
Colostethus degranvillei	AY263234	16S	542	Vences et al., 2003
Colostethus degranvillei	AY263213	12S	371	Vences et al., 2003
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., 2003
Colostethus pratti	AY263238	16S	499	Vences et al., 2003
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., 2003
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., 2003
Colostethus subpunctatus	AY263242	16S	448	Vences et al., 2003
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., 2003
Dendrobates imitator	AY263267	16S	492	Vences et al., 2003
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., 2003
Dendrobates sp. QCAZ16558	AY364568	12S, $tRNA^{val}$, 16S	2459	Santos et al., 2003
Dendrobates steyermarki	AY263244	16S	547	Vences et al., 2003
Dendrobates sylvaticus	AY364569	12S, $tRNA^{val}$, 16S	2449	Santos et al., 2003
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., 2003
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
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., 2003
Mannophryne herminae	AY263219	12S	358	Vences et al., 2003
Mannophryne herminae	AJ430676	16S	538	La Marca et al., 2002
Mannophryne sp. ULABG 4453	AY263221	16S	535	Vences et al., 2003

Mannophryne sp. ULABG 4458	AY263224	16S	538	Vences et al., 2003
Mannophryne sp. ULABG 4465	AY263222	16S	535	Vences et al., 2003
Mannophryne sp. ULABG 4481	AY263223	16S	535	Vences et al., 2003
Nephelobates molinarii	AY263263	16S	505	Vences et al., 2003
Nephelobates molinarii	AY263216	12S	368	Vences et al., 2003
Nephelobates molinarii	AJ430678	16S	546	La Marca et al., 2002
Nephelobates sp. ULABG 4445	AY263229	16S	540	Vences et al., 2003
Nephelobates sp. ULABG 4496	AJ430677	16S	543	La Marca et al., 2002
Phyllobates vittatus	AY263265	16S	473	Vences et al., 2003
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

Appendix 7: Specimens Examined

The following list of specimens examined includes only material used explicitly to score the character-states in Appendix 8. The extensive material examined to identify species and transformation series is not listed.

Outgroup Taxa

Telmatobius verrucosus: AMNH 165110

Atelopus spurrelli: AMNH 13597-98, 50983-84, 102065-68

Atelopus zeteki: AMNH 44687-91, 45995-96, 55533-44, 83920-22

Dendrophryniscus minutus: AMNH 93804-872

Melanophryniscus stelzneri: AMNH 51883-92, 76121-23; AMNH 77710 (skeleton)

Rhinoderma darwinii: AMNH 7567, 14441-45, 37813-14, 37848-50, 37852, 45331, 58082-91

Crossodactylus schmidti: JF 832, 850

Hylodes phyllodes: AMNH 103850-95, AMNH 103945-46 (larvae)

Megaelosia goeldii: AMNH 70249, 103947-53

Cycloramphus boraceiensis: AMNH 54546 (paratopotype)

Cycloramphus fuliginosus: KU 92789 (C&S)

Eupsophus roseus: AMNH 13979, 22102 22126, 22142, 22151, 23959, 23988, AMNH 22104 (skeleton), KU 207501 (C&S)

Thoropa lutzi: KU92850 (C&S)

Thoropa miliaris: AMNH 509, 17043-46, 17048-49, 17059, 20251-52, 20861, 36275-76, 52186, 70141, 20254.

Aromobatidae

Allobates femoralis: AMNH 116149, 140633-49, 164053-54; AMNH 87680-86, 909930-32; AMNH 103581, 85258, 85260 (C&S)

Allobates insperatus: KU 149663-149707, 175165, 175168-69, 175485, 182124; KU 149691 (C&S), KU 149671 (C&S), KU 109310 (C&S)

Allobates juanii: icn 39494-95, 15644-45; ICN 5097 (C&S),

Allobates kingsburyi: AMNH42282-83, 43604, 43606; UMMZ 89063-64, 90373 (X3), 90374 (X8), 90375-76, 90377 (X2); UMMZ 217617 (C&S)

Allobates Magdalena-species: MUJ 2897-2928, MAR 158-163

Allobates Neblina species: AMNH 118650-64, 118670, 118674-83, 118685-86, 118688-90; AMNH 118667 (C&S), 118669 (C&S), 118684 (C&S), 118687 (C&S)

Allobates olfersioides: AMNH 72445-47; UMMZ 127922 (X3); KU93161 (C&S), UMMZ 217618 (C&S)

Allobates talamancae: AMNH 113893-901, 124225, 124234-39, 124226-33 (carcasses), + uncatalogued carcasses; MUJ 808 (+ larvae); ICN 47972; UMMZ 193379 (C&S), AMNH 118380-81 (C&S)

Allobates trilineatus: USNM 343061, AMNH 153038-39

Allobates undulatus: AMNH 159118-38, 159139-40 (carcasses); AMNH 159141-42 (C&S)

Allobates zaparo: AMNH 52881-882, 96449-50, 94562-68, USNM 546404-405; AMNH 52882 (C&S), 52881 (C&S)

Anomaloglossus baeobatrachus: AMNH 140650-73; IRSNB-KBIN 12662, 12976, 12977; AMNH 140674 (larvae transported by AMNH 140654)

Anomaloglossus beebei: UMMZ 218880, 221371-74; ROM 39629-32; AMNH 18683 (holotype)

Anomaloglossus BPN1: BPN 837

Anomaloglossus BPN2: UTA 56469 (=BPN 849)

Anomaloglossus BPN3: UTA 56708 (=BPN 1299), UTA 56709-10 (=BPN 1304-05)

Anomaloglossus degranvillei: AMNH 90871-74, 878-881, 889-892; AMNH 90876(F), 90888(M), 90875(F)

Anomaloglossus praderioi: CPI 10198-205.

Anomaloglossus roraima: CPI 10212–17, + untagged larvae

Anomaloglossus ROM1: ROM 39639

Anomaloglossus stepheni: KU 129987–130145

Anomaloglossus tepuyensis: ROM 39637; AMNH 164817-833

Aromobates nocturnus: AMNH 13006-1, 130016-21, 130026-31, 130032-33, 130036-38

Aromobates molinarii: UMMZ 176208-211, 176220, 176222

Aromobates saltuensis: ICN 42512-16, 33587

Aromobates sp.: AMNH 129958-74.

Mannophryne collaris: AMNH 10512-16; USNM 291062-64; UMMZ 217615 (C&S)

Mannoprhyne herminae: AMNH 70761-87, 116941-977; USNM 259176 (larvae); AMNH 116978 (larvae); 116979 (larvae); UMMZ 139774-75 (larvae); UMMZ 210143-44 (C&S)

Mannophryne trinitatis: USNM 166302-342; USNM 166336 (male + larvae); UMMZ 167469, 167471, 167474; UMMZ 167465 (C&S); USNM 72474 (C&S); AMNH 118384 (C&S), 118389 (C&S)

Newgenus1 *palmatus*: ARA 2521; UTACV 4929, 8028-32, 39711--35, 39728-29, 39737; UTACV 4916, 39738-40 (larvae); UMMZ 149232, 149233 (skeletons)

Dendrobatidae

Ameerega bassleri: AMNH 42313, 42327, 42333, 42867, 42944; AMNH 43402 (C&S)

Ameerega braccatus: USNM 505750 (larvae)

Ameerega flavopicta: AMNH 88642, 158104-05; USNM 505751 (larvae)

Ameerega hahneli: AMNH 96185-96, 96751-54; AMNH 118421 (C&S); JDL 24628 (larvae)

Ameerega macero: AMNH 12973-74, 133205, 134159-63; AMNH 133207 (larvae)

Ameerega nexipus: USN 317147-85; USNM 317609 (larvae)

Ameerega parvula: AMNH 85200-208, 85210-14, 85216, 85224, 85226-27; AMNH 85215, 85219, 85221 (C&S)

Ameerega petersi: AMNH AMNH 17257 (paratype), 111000, 42179, 42505-07, 42546, 42790, 42945; AMNH 43016 (C&S)

Ameerega pulchripectus: AMNH 137280– 137293

Ameerega picta: AMNH 22637-38, 33959, 34075, 39562-63, 70151, 153546-73, 79196-211; UMMZ 184099 (C&S)

Ameerega rubriventris: AMNH 168494-97 (paratypes)

Ameerega silverstonei: AMNH 91845-46, 91851, 94803-05; AMNH 91847 (C&S), 91848 (C&S), 91849 (C&S)

Ameerega trivitatta: AMNH 77450, 9016-29, 90977-79; AMNH 42183-84, 43204, 42509, 42539-43, 42545, 42576; USNM 268845-47; AMNH 118428, 31 (C&S)

Colostethus fraterdanieli: AMNH 104361-68, 104375-92, 104397; AMNH 104399 (male + larvae), 104400 (male + larvae), 104401 (male + larvae)

Colostethus fugax: USNM282831 (holotype)

Colostethus imbricolus: AMNH 102082-85

Colostethus inguinalis: ARA 2360; LACM 42325-490, 72009-10; MUJ 3247; USNM 4349 (holotype)

Colostethus panamensis: IAvH 3337-70, 6206, 6208-09; UMMZ 167459 (C&S); AMNH 98317-18, 87293 (females + larvae)

Colostethus pratti: AMNH 108339, 162528, 118365-67, 118369-370, 117372; UMMZ 167514, 167506, 167460, 512, 515; ICN 47973-74, 47976, 47978; UMMZ 167503 (C&S); AMNH 118364 (C&S), AMNH 118371 (C&S)

Colostethus pratti-like: CH4052-47, 4650, 4702-03, 5524-25, 5598, 5601-02; CH5598 (larvae)

Dendrobates auratus: AMNH 97874, 9832540, 114588, 113904-912, +20 uncataloged skinned carcasses from Isla Tobago; AMNH 118524 (C&S), AMNH 118528 (C&S)

Dendrobates azureus: AMNH 88630, 88627,88628, 88626, 88629, 88631, + uncatalogued AMNH specimens

Dendrobates leucomelas: AMNH 23179, 23202, 23206, 23235, 46045-47, 46051, 75789, 81455, 90203-04, 90998, 137309-11; AMNH 137308 (larvae)

Dendrobates tinctorius: AMNH 49301-28, 140675-87; KU 93147 (C&S)

Dendrobates truncatus: AMNH 38820-21, 39087, 40309-12, 84381-83, 88578-79, 85229-36; ARA 2507; AMNH 118401 (C&S), AMNH 118403 (C&S); MUJ 3088 (larvae)

Epipedobates anthonyi: AMNH 104903-17; AMNH 118499 (C&S), 118502 (C&S)

Epipedobates boulengeri: USNM 145248-300 (topotypes); AMNH 50970-72 (topotypes); USNM 145248 (larvae); USNM 145253 (C&S)

Epipedobates espinosai: AMNH 89668-87, 104869-898, 162662, 162663-64; AMNH 118411 (C&S), 118417 (C&S)

Epipedobates machalilla: AMNH 89525-36, BM 98.3.1.4 to 98.3.1.7.; KU 220631, KU 220632, KU 220633; AMNH 89537 (male with 19 tadpoles)

Epipedobates tricolor: USNM 286082-83; AMNH 104946-54

Hyloxalus awa: AMNH 111541-44; UMMZ 217614 (C&S)

Hyloxalus azureiventris: AMNH 42186

Hyloxalus bocagei: AMNH 89570-71, 94043-73; UMMZ 182465 (C&S)

Hyloxalus delatorreae: KU 182197, 220618

Hyloxalus elachyhistus: AMNH 16262-303, 16305-13, 16315, 16317, 16321; KU120543 (C&S)

Hyloxalus Ibague species: ARA 2343-45, 2347-57, 2443-44, MAR 106, 111, 117, 123-24, 128-130 (+ untagged larvae, to be deposited at MUJ)

Hyloxalus infraguttatus: AMNH 89563-65, 91823-24, 104838-49; AMNH 85031

(male + larvae)

Hyloxalus pulchellus: AMNH 85018-21; AMNH 89538 (C&S)

Hyloxalus sauli: AMNH 85029, UMMZ 182478-79, 194745; UMMZ 182477(C&S)

Hyloxalus subpunctatus: ICN 26963, 7237, 11044, 4468, 31699, 26963, 7235, 7196, 10361, 3990, 11020, 27024 (+45777), 33686, 35672, 11868; ICN 45777 (larvae), 45778 (larvae), 45779 (larvae), 45780 (larvae); UMMZ 221158-59 (C&S)

Hyloxalus sylvaticus: KU 138071-79, 181667-79; KU 164093 (C&S)

Hyloxalus toachi: AMNH 89550-61, 111539-40; AMNH 89562 (male + larvae).

Hyloxalus vertebralis: AMNH 17458, 17604-08, 140977-141011; AMNH 89569 (male + larvae); USNM 282308-16, 282352-358; KU 120633-34 (C&S), UMMZ 217621 (C&S)

Newgenus2 *castaneoticus*: AMNH 133451-55 (paratypes)

Newgenus2 *galactonotus*: AMNH 128232-33

Newgenus2 *quinquevittatus*: AMNH 124068-71; AMNH 124072 (larvae)

Oophaga arborea: AMNH 116725–80; AMNH 116761-68 (C&S)

Oophaga granulifera: AMNH 134069, 134071-81, 118408-409, 86631; KU 110223 (C&S)

Oophaga histrionica: AMNH 88242-82; AMNH 118458, AMNH 118461-62 (C&S)

Oophaga lehmanni: AMNH 88154-95 (topoparatypes), 118435-37, 118439, 118441, 118443-45; AMNH 88231-34, 118438, 118442 (C&S)

Oophaga pumilio: AMNH 102256-63; AMNH 161152 (larvae); AMNH 118510,

118514 (C&S), + several hundred skinned carcasses from Bocas del Toro (uncatalogued) at AMNH

Oophaga speciosa: AMNH 124279-321, 124335-48, 124322-31, 12432-34, 161120, 161122-23; AMNH 124349 (larvae); AMNH 118447, 118454 (C&S)

Oophaga sylvatica: AMNH 85048-158, 86635-40; AMNH 89589-601; AMNH 85972, 88225-26 (C&S)

Oophaga vicentei: AMNH 97875, 98344-50, 114583-84, 114586; AMNH 98351-53 (C&S), 114587 (C&S); AMNH 98354 (larvae)

Phyllobates aurotaenia: AMNH 85238-45, 161109-111; AMNH 161108 (C&S); AMNH 85246 (male + larvae), AMNH 85247 (male + larvae), AMNH 85248(male + larvae), AMNH 85249 (male + larvae), AMNH 87167 (male + larvae) AMNH 87168 (male + larvae)

Phyllobates bicolor: AMNH 98209-236; AMNH 98256 (C&S)

Phyllobates lugubris: AMNH 113936-43, 124350-53, 55-56; AMNH86642 (male + larvae); AMNH 107237 (larva from AMNH 107231); AMNH 118554, 118557 (C&S)

Phyllobates terribilis: AMNH 162738-43; AMNH 86319-24 (C&S), AMNH 125831-35 (C&S); AMNH 118563 (skeleton)

Phyllobates vittatus: AMNH 82257, 86643–45, 114041, 118386, 118542-551

Ranitomeya biolat: AMNH 143908; USNM 537557-565; USNM 342882 (larvae)

Ranitomeya claudiae: AMNH 102307-68, 124255-65; AMNH 103514-523 (C&S)

Ranitomeya fulgurita: AMNH 89435-47; AMNH 89548 (C&S); AMNH 89448-53

Ranitomeya imitator: AMNH 127991-999 (topotypes), 128003-006 (topotypes);

AMNH 162723-727, 16278-730, 162731-732 (carcasses); KU209413 (C&S), KU 209412 (C&S)

Ranitomeya minuta: AMNH 59660-62, 84896-900, 87310, 118132, 89426-32

Ranitomeya reticulata: AMNH 103619-30, 103638-73; AMNH 103676, 80-81 (C&S)

Ranitomeya steyermarki: AMNH 100760-799; AMNH 118579, 118575-76, 118572, 118581 (C&S)

Ranitomeya vanzolinii: AMNH 43597-98, 108332

Ranitomeya ventrimaculata: ICN 47609, 47330-32, 47334-35; JDL 24314, 25447 (larvae); AMNH 103603-04 (C&S)

Silverstoneia flotator: AMNH 55509, 116781-83, 87300-01, 98323, 124210-15; AMNH 104229 (larvae); KU 77678 (C&S)

Silverstoneia nubicola: AMNH 94846-48 114574-77, 124249; AMNH 94849 (larvae); UMMZ 145585 (C&S)

Silverstoneia punctiventris: AMNH 102092-95, TG1362-63 (deposited at Universidad del Cauca)

Appendix 8: Phenotypic Character Matrix

TABLE 1. Characters 0 - 45

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                                  0    5    10   15   20   25   30   35   40   45
                                  |    |    |    |    |    |    |    |    |    |
Telmatobius verrucosus 313        2011030----0000000000-0110100-1-----1323654441
Atelopus spurrelli 1275           3000000----0000000000-0120100-0-----1545764551
Atelopus zeteki 1039              3000000----0000000000-0120100-0-----0545654450
Dendrophryniscus minutus 532      3011000----0000000000-00-0-00-0-----0411431230
Melanophryniscus klappenbachi 217 3011010----0000000000-00-0100-0-----0323433440
Rhinoderma darwinii 1115          1011000----0000000010-00-0100-0-----0213454540
Crossodactylus schmidti 149       1111011000000010100000-0101100-1011101221422111
Hylodes phyllodes 889             1111011122211111111100-0110100-1222211212322111
Hylodes phyllodes 1152            1111011122211111111100-0110100-1222211212322111
Megaelosia goeldii 611            1111031122211111111100-00-0100-1222221323443221
Cycloramphus boraceiensis 890     3011010----0011110000-00-0100-0-----1424564451
Eupsophus calcaratus 657          1011010----0000000000-0120100-0-----0000000000
Thoropa miliaris 1186             1010030----0000000000-0100100-0-----0000000000
awa                               11010$111120000000010-00-0101101222200000011000
baeobatrachus 14                  1100221111100101000013 00-0101201111112123221 11
baeobatrachus 42                  1100221111100101000013 00-0101201111112123221 11
baeobatrachus 43                  1100221111100101000013 00-0101201111112123221 11
baeobatrachus 44                  1100221111100101000013 00-0101201111112123221 11
beebei 605                        1101001122200000000000-00-0101001111102112310 00
beebei 608                        1101001122200000000000-00-0101001111102112310 00
bocagei 1267                      0101011222200101000 00-00-0101000110142455$43$0
bocagei 343                       0101011222200101000 00-00-0101000110142455$43$0
bocagei 344                       0101011222200101000 00-00-0101000110142455$43$0
bocagei 345                       0101011222200101000 00-00-0101000110142455$43$0
caeruleodactylus 406              1100231????0000000000-00-010120?????0001231000
caeruleodactylus 621              1100231????0000000000-00-010120?????0001231000
caeruleodactylus 1261             1100231????0000000000-00-010120?????0001231000
caeruleodactylus 1287             1100231????0000000000-00-010120?????0001231000
degranvillei 278                  1101021001100101 00*10-00-0101100222113123221 11
degranvillei 279                  1101021001100101 00*10-00-0101100222113123221 11
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praderioi 1336                  110102100110010100*10-00-010110022211312322111
delatorreae 71                  110???1????0000000000-00-0101?0??????000000000
elachyhistus 108                1101011$1110010100010-00-010110000001$234$$$11
elachyhistus 115                1101011$1110010100010-00-010110000001$234$$$11
elachyhistus 116                1101011$1110010100010-00-010110000001$234$$$11
elachyhistus 114                1101011$1110010100010-00-010110000001$234$$$11
elachyhistus 117                1101011$1110010100010-00-010110000001$234$$$11
elachyhistus 106                1101011$1110010100010-00-010110000001$234$$$11
elachyhistus 105                1101011$1110010100010-00-010110000001$234$$$11
elachyhistus 107                1101011$1110010100010-00-010110000001$234$$$11
flotator 1143                   1101231111100000000001200-0101200222100000011000
flotator 1145                   1101231111100000000001200-0101200222100000011000
fraterdanieli 1226              1101031111100000000011200-0101100222000000011000
fraterdanieli 1227              1101031111100000000011200-0101100222000000011000
fraterdanieli 1228              1101031111100000000011200-0101100222000000011000
fugax                           1101131????0000000001200-010120?????????????????
humilis                         1101?11111200?0?000?0-00-0101001222?1?????????
Colostethus Ibague 1225         1101121111100000000000-00-0111200111000000000000
Colostethus Ibague 1345         1101121111100000000000-00-0111200111000000000000
Colostethus Ibague 1347         1101121111100000000000-00-0111200111000000000000
idiomelus 77                    1101?3100000000000?0-00-0101?0??????00000000?
idiomelus 121                   1101?3100000000000?0-00-0101?0??????00000000?
idiomelus 120                   1101?3100000000000?0-00-0101?0??????00000000?
idiomelus 122                   1101?3100000000000?0-00-0101?0??????00000000?
idiomelus 126                   1101?3100000000000?0-00-0101?0??????00000000?
imbricolus 1229                 1101021111100101000112 00-0101001111131343 2101
infraguttatus AY326028          1101021001100000000000-00-0101100011003 1$$2000
inguinalis 1348                 1101131112$00101?00*1200-010100222221$2$$3$2$1
insperatus                      11002311$110000000001100-0101200122100012 11000
insulatus 124                   110??31?????????????0-00-010110?????0221411000
insulatus 125                   110??31?????????????0-00-010110?????0221411000
juanii 1357                     110*13111110000000000-00-0101201222200012 11000
kingsburyi AY364549             1101031111100101000 0-00-0101201222200000000000
machalilla 73                   1101131001100000000001200-0101200011000012 11000
machalilla 132                  1101131001100000000001200-0101200011000012 11000
Colostethus Magdalena 1358      010*2311111000000000 1200-0101200$2200001231000
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nexipus 75                      0100011112200101000000-00-0100001222114245534 51
nexipus 123                     0100011112200101000000-00-0100001222114245534 51
nexipus 130                     0100011112200101000000-00-0100001222114245534 51
nexipus 131                     0100011112200101000000-00-0100001222114245534 51
nidicola 407                    1100231????0000000000-00-010120????????????????
nidicola 622                    1100231????0000000000-00-010120????????????????
nidicola 1285                   1100231????0000000000-00-010120????????????????
Colostethus BPN3 1332           1101111111100101000??0?-01?110222221424443331
Colostethus BPN3 1333           1101111111100101000??0?-01?110222221424443331
nubicola 1142                   1101131111100101000012 00-0101201$$210000011000
nubicola 1146                   1101131111100101000012 00-0101201$$210000011000
olfersioides 538                1100221000000000000011 00-0101200111000000 11000
palmatus 1346                   1101011111100101000 10-00-01010012$21142466$$51
panamensis 1150                 1101031111100101000112 00-010100122211$12432221
panamensis 1223                 1101031111100101000112 00-010100122211$12432221
praderioi 1335                  1101021111100000000013 00-0101201222113134320 00
Colostethus 1334                1101021111100000000013 00-0101201222113134320 00
pratti 1144                     1101131111100000000012 00-0101201222100000000 00
pratti like 1224                1101131111100000000012 00-0101201222100000000 00
pulchellus                      1101111000000000000 00-00-0101200122200000000 00
pulcherrimus 118                010??31????????????0-00-010110?????0000000000
pulcherrimus 119                010??31????????????0-00-010110?????0000000000
punctiventris 496               1101131111100101000012 00-0101201222100000110 00
punctiventris 497               1101131111100101000012 00-0101201222100000110 00
roraima 1337                    1101011111100000000011 00-0101200111000000000 00
roraima 1338                    1101011111100000000011 00-0101200111000000000 00
roraima 1339                    1101011111100000000011 00-0101200111000000000 00
Colostethus ROM1 607            1101021111100000000013 00-?101201122100000000 00
saltuensis 1360                 1101031111100*0*00000-00-0101001222112123321 11
sauli AY364555                  1101011111100101000 00-00-0101101122113234332 21
stepheni 514                    110*2310000001010000130 0-0101100000012123221 11
stepheni 515                    110*2310000001010000130 0-0101100000012123221 11
subpunctatus 1359               1101111000000000000 00-00-0101200$$$00000000000
Phyllobates sylvaticus 113      11010?1????????????0-00-0101?0????????????????
Phyllobates sylvaticus 76       11010?1????????????0-00-0101?0????????????????
talamancae Nicaragua 361        1101131111100101000 00-00-0101201222100012110 00
```

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talamancae Nicaragua 362          1101131111110010100000-00-01012012221000121100O
talamancae Nicaragua 408          1101131111110010100000-00-01012012221000121100O
talamancae Panama 1147            1101131111110010100000-00-01012012221000121100O
talamancae 325                    1101131111110010100000-00-01012012221000121100O
talamancae 326                    1101131111110010100000-00-01012012221000121100O
tepuyensis 606                    1101011222200101000O0-00-0101002222114245443310
toachi                            1101131111100000000O0-00-0101201222100O$$$$000
trilineatus 74                    110*2311001000000000120O-0101200122100000110O0
trilineatus 112                   110*2311001000000000120O-0101200122100000110O0
trilineatus 527                   110*2311001000000000120O-0101200122100000110O0
undulatus 331                     1101131111100000000011O-0101201222100000110O0
undulatus 332                     1101131111100000000011O-0101201222100000110O0
undulatus 333                     1101131111100000000011O-0101201222100000110O0
vertebralis                       1101011000000000000O0-00-0101100000000000000O
arboreus 340                      0101001023200000000O0-00-0101300112100000000O
auratus 327                       0101011033300000000O0-00-0101000222100000000O
auratus 334                       0101011033300000000O0-00-0101000222100000000O
auratus 335                       0101011033300000000O0-00-0101000222100000000O
auratus Nicaragua 365             0101011033300000000O0-00-0101000222100000000O
azureus 1330                      0101011022200000000l0-00-0001300111000000000O
azureus 534                       0101011022200000000l0-00-0001300111000000000O
biolat                            0101001033300000000O0-00-0100-0022220000000000
castaneoticus 363                 0101011033300000000O0-00-0001300111000000000O
galactonotus 533                  0101011033300000000l0-00-0101200111000000000O
galactonotus 647                  0101011033300000000l0-00-0101200111000000000O
granuliferus 339                  210100102$20000000000-00-0101300112000000000O
histrionicus 336                  010101112$$0000000000-00-0101301222100000000O
histrionicus 498                  010101112$$0000000000-00-0101301222100000000O
imitator                          0100001033300000000O0-00-0100-0012220000000000
lehmanni 338                      01010111$220000000000-00-0101300111000000000O
leucomelas 645                    0101011022200000000O0-00-000*3001110000000000O
pumilio Nicaragua 367             0101001023300000000O0-00-0001300111000000000O
pumilio 1313                      0101001023300000000O0-00-0001300111000000000O
pumilio 1315                      0101001023300000000O0-00-0001300111000000000O
quinquevittatus 1312              0101011023300000000O0-00-0001300122000000000O
quinquevittatus RioFormoso 370    0101011023300000000O0-00-0001300122000000000O
```

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quinquevittatus RioFormoso 371    0101011023300000000000-00-0001300122000000000000
quinquevittatus RioItuxi 368      0101011023300000000000-00-0001300122000000000000
quinquevittatus RioItuxi 369      0101011023300000000000-00-0001300122000000000000
reticulatus 528                   0100001012200000000000-00-0101300111000000000000
speciosus 341                     0101011022200000000000-00-01013001$$10000000000
Dendrobates sylvaticus 364        0101011122200000000000-00-0101300111100000000000
tinctorius 1327                   0101011133300000000010-00-0001300111000000000000
tinctorius 535                    0101011133300000000010-00-0001300111000000000000
truncatus 1151                    0101011023300000000010-00-0101300111000000000000
truncatus 1351                    0101011023300000000010-00-0101300111000000000000
truncatus 1352                    0101011023300000000010-00-0101300111000000000000
vanzolinii 372                    0100001033300000000000-00-0101300022200000000000
vanzolinii 373                    0100001033300000000000-00-0101300022200000000000
vanzolinii 1314                   0100001033300000000000-00-0101300022200000000000
ventrimaculatus 1349              0101001033300000000000-00-01013000$220000000000
ventrimaculatus 1310              0101001033300000000000-00-01013000$220000000000
ventrimaculatus RioItuxi 376      0101001033300000000000-00-01013000$220000000000
ventrimaculatus RioItuxi 377      0101001033300000000000-00-01013000$220000000000
ventrimaculatus Sucumbios 374     0101001033300000000000-00-01013000$220000000000
ventrimaculatus 1311              0101001033300000000000-00-01013000$220000000000
ventrimaculatus PortoWalter 375   0101001033300000000000-00-01013000$220000000000
vicentei 1148                     0101001023300000000000-00-0001300000000000000000
anthonyi 838                      0101131111100000000001200-0101200111$0001211000
anthonyi sensu Myers 1290         0101131111100000000001200-0101200111$0001211000
azureiventris                     2101021112200000000000-00-?1012012221000000000000
bassleri                          2101131001000000000001100-0101300000000000000000
boulengeri 280                    1101131111100000000001200-0101200111100000011000
espinosai 1139                    1101131111100000000001200-0101200111000$011000
femoralis 78                      2101131222200000000000-00-0101202222200000011000
femoralis 128                     2101131222200000000000-00-0101202222200000011000
femoralis 129                     2101131222200000000000-00-0101202222200000011000
femoralis RioFormoso 393          2101131222200000000000-00-0101202222200000011000
femoralis RioFormoso 394          2101131222200000000000-00-0101202222200000011000
femoralis Santarem 395            2101131222200000000000-00-0101202222200000011000
femoralis Santarem 396            2101131222200000000000-00-0101202222200000011000
femoralis PortoWalter 397         2101131222200000000000-00-0101202222200000011000
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femoralis PortoWalter 398         21011312222000000000-00-01012022222000011000
femoralis Cuyabeno 399            21011312222000000000-00-01012022222000011000
femoralis Cuyabeno 400            21011312222000000000-00-01012022222000011000
femoralis Ducke 520               21011312222000000000-00-01012022222000011000
femoralis Panguana 526            21011312222000000000-00-01012022222000011000
femoralis 1298                    21011312222000000000-00-01012022222000011000
femoralis 1306                    21011312222000000000-00-01012022222000011000
femoralis 1309                    21011312222000000000-00-01012022222000011000
femoralis Suriname 1325           21011312222000000000-00-01012022222000011000
flavopictus 536                   21010310000000000001100-01011000000002331000
hahneli Amazonas 391              21010311111000000001100-01012002221000000000
hahneli Amazonas 392              21010311111000000001100-01012002221000000000
hahneli PortoWalter 389           21010311111000000001100-01012002221000000000
hahneli PortoWalter 390           21010311111000000001100-01012002221000000000
hahneli PortoWalter 388           21010311111000000001100-01012002221000000000
Epipedobates PortoWalter1 382     21010311111000000001100-01012002221000000000
femoralis Leticia 1354            21010311111000000001100-01012002221000000000
pictus 79                         21010311111000000001100-01012002221000000000
pictus 109                        21010311111000000001100-01012002221000000000
pictus 110                        21010311111000000001100-01012002221000000000
Epipedobates sp 386               21010311111000000001100-01012002221000000000
Epipedobates sp 1304              21010311111000000001100-01012002221000000000
macero 1133                       21011311111000000000-00-01010012221000000000
parvulus 378                      21011310011000000001100-01011001111000000000
parvulus 401                      21011310011000000001100-01011001111000000000
parvulus 1303                     21011310011000000001100-01011001111000000000
petersi 522                       21011311111000000001100-01010001221000000000
petersi 525                       21011311111000000001100-01010001221000000000
pictus SS                         21011310000000000001100-01011001110000000000
pulchripectus 337                 210113111$10000000000-00-01011001110000000000
silverstonei 646                  21011311111000000000-00-01010000000000000000
tricolor                          11011311111000000001200-010120$$11$0001211000
trivittatus 319                   21011311111000000000*0-00-0101$011111000$$$$000
trivittatus 387                   21011311111000000000*0-00-0101$011111000$$$$000
trivittatus 518                   21011311111000000000*0-00-0101$011111000$$$$000
trivittatus 519                   21011311111000000000*0-00-0101$011111000$$$$000
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trivittatus 628                  2101131111100000000*0-00-0101$011111000$$$$000
trivittatus 1297                 2101131111100000000*0-00-0101$011111000$$$$000
trivittatus 1305                 2101131111100000000*0-00-0101$011111000$$$$000
trivittatus Suriname 1329        2101131111100000000*0-00-0101$011111000$$$$000
trivittatus Leticia 1350         2101131111100000000*0-00-0101$011111000$$$$000
pictus 322                       2101131111100000000*0-00-0101$011111000$$$$000
Epipedobates PortoWalter2 384    2101131111100000000*0-00-0101$011111000$$$$000
Epipedobates sp 627              2101131111100000000*0-00-0101$011111000$$$$000
zaparo 321                       2101131122100000000000-00-0101201222100012110000
zaparo 328                       2101131122100000000000-00-0101201222100012110000
collaris                         1101021111100000000000-00-0101001111104134432310
herminae 1141                    1101021112200101000100-00-0101002222213$$33$$*
rubriventris                     2101131111100000000000-00-0101000111000000000000
trinitatis 609                   1101011111100000000000-00-0101001122103$11211000
claudiae 323                     0100001010$$0000000000-00-0101300011000000000000
claudiae 324                     0100001010$$0000000000-00-0101300011000000000000
lugubris 330                     0100001010$$0000000000-00-0101300011000000000000
fulguritus 499                   0101001022200000000000-00-0001300011000000000000
minutus 1149                     0100001010$$0000000000-00-0101300111000000000000
steyermarki                      0100021002200000000000-00-0101300011000000000000
nocturnus 1132                   1101011111100101000000-00-0101001111114338677510
nocturnus 1134                   1101011111100101000000-00-0101001111114338677510
molinarii                        1101011111100101000000-00-0101001222113134332210
Nephelobates sp 1321             1101031000000000000011100-0101100111000000000000
aurotaenia 840                   0101131$111000000000-00-0101202222100000000000
bicolor 1233                     0101031111100000000000-00-0101200$$$00000000000
lugubris 329                     0101031111100000000000-00-0101201222100000000000
lugubris Nicaragua 366           0101031111100000000000-00-0101201222100000000000
terribilis 1135                  0101031111100000000000-00-0101200$$$00000000000
terribilis 1232                  0101031111100000000000-00-0101200$$$00000000000
vitattus 839                     0101031111100000000010-00-0101201111100000000000
Epipedobates PortoWalter2 383    21????11?22??????????????????????????????????
Epipedobates PortoWalter2 623    21????11?22??????????????????????????????????
Epipedobates PortoWalter2 624    21????11?22??????????????????????????????????
Epipedobates PortoWalter2 1235   21????11?22??????????????????????????????????
Epipedobates sp 385              21????11?22??????????????????????????????????
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Colostethus sp Neblina 379        2100231111100000000001100-01012122222000001100O
Colostethus sp Neblina 380        2100231111100000000001100-01012122222000001100O
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TABLE 2. Characters 46 - 91

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                                  46   51   56   61   66   71   76   81   86   91
                                  |    |    |    |    |    |    |    |    |    |
Telmatobius verrucosus 313        0000100000--0004233?0??00001101100-------?????
Atelopus spurrelli 1275           0000200000--0003411100000000--10-0-------?????
Atelopus zeteki 1039              0000$00000--0000000100000000--10-0-------13100
Dendrophryniscus minutus 532      0000400000--0004233102100000--00-0-------10000
Melanophryniscus klappenbachi 217 000010000**10005333102100000--10-0-------10110
Rhinoderma darwinii 1115          1000400020--0004233102100000001100-------10110
Crossodactylus schmidti 149       0000400001010000$000?0?000001002100-------10111
Hylodes phyllodes 889             0000400001100003411102000*01002100-------10101
Hylodes phyllodes 1152            0000400001100003411102000*01002100-------10101
Megaelosia goeldii 611            2000400000--0006144?020000010000-0-------10100
Cycloramphus boraceiensis 890     0000400000--00153001?0?000011010-0-------10000
Eupsophus calcaratus 657          0000400000--000530$102000001101100-------11000
Thoropa miliaris 1186             0000400000--0005300?001000010010-0-------?????
awa                               10004000011$1004$33100111011111110-------10??0
baeobatrachus 14                  1000400001110006000100111011111111110101110100
baeobatrachus 42                  1000400001110006000100111011111111110101110100
baeobatrachus 43                  1000400001110006000100111011111111110101110100
baeobatrachus 44                  1000400001110006000100111011111111110101110100
beebei 605                        0000403000--0000000120111011111111000101??????
beebei 608                        0000403000--0000000120111011111111000101??????
bocagei 1267                      100040000*01001$$1$100111011111110-------?????
bocagei 343                       100040000*01001$$1$100111011111110-------?????
bocagei 344                       100040000*01001$$1$100111011111110-------?????
bocagei 345                       100040000*01001$$1$100111011111110-------?????
caeruleodactylus 406              0000400011020000000?01?????????0-------00120
caeruleodactylus 621              0000400011020000000?01?????????0-------00120
caeruleodactylus 1261             0000400011020000000?01?????????0-------00120
caeruleodactylus 1287             0000400011020000000?01?????????0-------00120
degranvillei 278                  2001403001100006144100011011111111110101?12---
```

```
degranvillei 279                2001403001100006144100011011111111110101?12---
praderioi 1336                  2001403001100006144100011011111111110101?12---
delatorreae 71                  000040001110002?301?0???????????0-------10100
elachyhistus 108                200040000110101$$3$100111011111110-------10100
elachyhistus 115                200040000110101$$3$100111011111110-------10100
elachyhistus 116                200040000110101$$3$100111011111110-------10100
elachyhistus 114                200040000110101$$3$100111011111110-------10100
elachyhistus 117                200040000110101$$3$100111011111110-------10100
elachyhistus 106                200040000110101$$3$100111011111110-------10100
elachyhistus 105                200040000110101$$3$100111011111110-------10100
elachyhistus 107                200040000110101$$3$100111011111110-------10100
flotator 1143                   10014000211000-$000112111011111110-------11001
flotator 1145                   10014000211000-$000112111011111110-------11001
fraterdanieli 1226              100040000110001 3$00102111011111110-------10000
fraterdanieli 1227              100040000110001 3$00102111011111110-------10000
fraterdanieli 1228              100040000110001 3$00102111011111110-------10000
fugax                           000140001110000000?????????????????????????????
humilis                         ??004000010200 14?0?1???????????1??0-------?????
Colostethus Ibague 1225         100040001110000202010011101?111??0-------10100
Colostethus Ibague 1345         100040001110000202010011101?111??0-------10100
Colostethus Ibague 1347         100040001110000202010011101?111??0-------10100
idiomelus 77                    ?000400001101006144 1?0????????1??0-------10100
idiomelus 121                   ?000400001101006144 1?0????????1??0-------10100
idiomelus 120                   ?000400001101006144 1?0????????1??0-------10100

idiomelus 122                   ?000400001101006144 1?0????????1??0-------10100
idiomelus 126                   ?000400001101006144 1?0????????1??0-------10100
imbricolus 1229                 2000413001010005333100?11011111110-------?????
infraguttatus AY326028          100040000110101$$33100111011111110-------10100
inguinalis 1348                 200040002100000405010111101111111 0-------?????
insperatus                      100140302102000202010011101111111 0-------10100
insulatus 124                   000?400001101 0???001?0???????????0-------10100
insulatus 125                   000?400001101 0???001?0???????????0-------10100
juanii 1357                     100140302102001600010011101111111 0-------?????
kingsburyi AY364549             100040302100000$130100111011111110-------10110
machalilla 73                   000140002110000000010211101111111 0-------10100
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machalilla 132                  00014000211000000001021110111111110-------10100
Colostethus Magdalena 1358      00014030210200040$01001110l?111??0-------?????
nexipus 75                      00004030110$000212310011101?111??0-------?????
nexipus 123                     00004030110$000212310011101?111??0-------?????
nexipus 130                     00004030110$000212310011101?111??0-------?????
nexipus 131                     00004030110$000212310011101?111??0-------?????
nidicola 407                    00014000110200020201?0???????11??0-------12---
nidicola 622                    00014000110200020201?0???????11??0-------12---
nidicola 1285                   00014000110200020201?0???????11??0-------12---
Colostethus BPN3 1332           11004020010l0?1?0?01?????????????1110101?????
Colostethus BPN3 1333           11004020010l0?1?0?01?????????????1110101?????
nubicola 1142                   10014000211000040001121110111111110-------11001
nubicola 1146                   10014000211000040001121110111111110-------11001
olfersioides 538                10014000110200020000?00111011111110-------?11?0
palmatus 1346                   20004000$10$0015$$0100111011111110-------10100
panamensis 1150                 200*400021000000400102111011111110-------?0100
panamensis 1223                 200*400021000000400102111011111110-------?0100
praderioi 1335                  1001403000--000$0$0?10111011111111010101?????
Colostethus 1334                1001403000--000$0$0?10111011111111010101?????
pratti 1144                     10014030210000060O$110111011111110-------?0100
pratti like 1224                10014030210000060000?10111011111110-------?0100
pulchellus                      100040000110*0-5$1$100111011111110-------?0100
pulcherrimus 118                000?400001100O?33331?0???????????0-------?????
pulcherrimus 119                000?400001100O?33331?0???????????0-------?????
punctiventris 496               10014000111000034111l?111011111110-------?????
punctiventris 497               10014000111000034111l?111011111110-------?????
roraima 1337                    0000400000--001$1$4110?110111111111000101?10100
roraima 1338                    0000400000--001$1$4110?110111111111000101?10100
roraima 1339                    0000400000--001$1$4110?110111111111000101?10100
Colostethus ROM1 607            0001403000--0002??2?10????????1??1000101?????
saltuensis 1360                 00004030010100051201001110l?111??0-------?????
sauli AY364555                  2000400001*000020201001110111111110-------?0100
stepheni 514                    20014000011000061400?0?11101111111111010l?12---
stepheni 515                    20014000011000061400?0?11101111111111010l?12---
subpunctatus 1359               10004000011000120$$100111011111110-------10100
Phyllobates sylvaticus 113      000040000010*0000001?0????????1??0-------10100
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Phyllobates sylvaticus 76          000040000010*0000001?0????????1??0-------10100
talamancae Nicaragua 361           1000403020--0004$$0100111011111110-------10100
talamancae Nicaragua 362           1000403020--0004$$0100111011111110-------10100
talamancae Nicaragua 408           1000403020--0004$$0100111011111110-------10100
talamancae Panama 1147             1000403020--0004$$0100111011111110-------10100
talamancae 325                     1000403020--0004$$0100111011111110-------10100
talamancae 326                     1000403020--0004$$0100111011111110-------10100
tepuyensis 606                     200040000101000$$$$1001110111111111101011101-?
toachi                             1000400011100006000102111011111110-------10100
trilineatus 74                     1001403021020002000100111011111110-------10100
trilineatus 112                    1001403021020002000100111011111110-------10100
trilineatus 527                    1001403021020002000100111011111110-------10100
undulatus 331                      1001400000--0012000100111011111110-------10100
undulatus 332                      1001400000--0012000100111011111110-------10100
undulatus 333                      1001400000--0012000100111011111110-------10100
vertebralis                        100040000110*0020$0110111011111110-------10100
arboreus 340                       0000$00000--0005333002011011111110-------20010
auratus 327                        100000$000--0003411002111011111110-------20000
auratus 334                        100000$000--0003411002111011111110-------20000
auratus 335                        100000$000--0003411002111011111110-------20000
auratus Nicaragua 365              100000$000--0003411002111011111110-------20000
azureus 1330                       0000100000--0004252002111011111110-------?0000
azureus 534                        0000100000--0004252002111011111110-------?0000
biolat                             000000010-100003411?0?111011111110-------10110
castaneoticus 363                  0010100000--0005333000111011111110-------20100
galactonotus 533                   1000100000--0004252000111011111110-------?????
galactonotus 647                   1000100000--0004252000111011111110-------?????
granuliferus 339                   1000100000--0004252002111011111110-------20010
histrionicus 336                   0000$00000--0005333002111011111110-------20010
histrionicus 498                   0000$00000--0005333002111011111110-------20010
imitator                           0000000*$0--000341100$111011111110-------?????
lehmanni 338                       0000200000--000$$33001111011111110-------?????
leucomelas 645                     0000000000--000$$5$000111011111110-------20100
pumilio Nicaragua 367              0000$00000--000$$$$002111011111110-------20010
pumilio 1313                       0000$00000--000$$$$002111011111110-------20010
pumilio 1315                       0000$00000--000$$$$002111011111110-------20010
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quinquevittatus 1312              0010000120--00032110021110111111110-------20000
quinquevittatus RioFormoso 370    0010000120--00032110021110111111110-------20000
quinquevittatus RioFormoso 371    0010000120--00032110021110111111110-------20000
quinquevittatus RioItuxi 368      0010000120--00032110021110111111110-------20000
quinquevittatus RioItuxi 369      0010000120--00032110021110111111110-------20000
reticulatus 528                   0000000000--00034110221110111111110-------?????
speciosus 341                     0000300000--00000000021110111111110-------20010
Dendrobates sylvaticus 364        0000$00000--000$$$$002110111111110-------?????
tinctorius 1327                   000010$000--00034110001110111111110-------20000
tinctorius 535                    000010$000--00034110001110111111110-------20000
truncatus 1151                    1000203020--00054330021110111111110-------20000
truncatus 1351                    1000203020--00054330021110111111110-------20000
truncatus 1352                    1000203020--00054330021110111111110-------20000
vanzolinii 372                    0000000000--00032330021110111111110-------?????
vanzolinii 373                    0000000000--00032330021110111111110-------?????
vanzolinii 1314                   0000000000--00032330021110111111110-------?????
ventrimaculatus 1349              000000012*00000$$110221110111111110-------20000
ventrimaculatus 1310              000000012*00000$$110221110111111110-------20000
ventrimaculatus RioItuxi 376      000000012*00000$$110221110111111110-------20000
ventrimaculatus RioItuxi 377      000000012*00000$$110221110111111110-------20000
ventrimaculatus Sucumbios 374     000000012*00000$$110221110111111110-------20000
ventrimaculatus 1311              000000012*00000$$110221110111111110-------20000
ventrimaculatus PortoWalter 375   000000012*00000$$110221110111111110-------20000
vicentei 1148                     0000$00000--00040000221110111111110-------?0010
anthonyi 838                      1000$10001100015333102110111111110-------?????
anthonyi sensu Myers 1290         1000$10001100015333102110111111110-------?????
azureiventris                     1000003021000004$$$000?11011111110-------10100
bassleri                          0000200001100002?2?2?0?1??????????0-------?????
boulengeri 280                    0000400011100012 5$$00?111011111110-------10100
espinosai 1139                    00014000$10000025$$112111011111110-------10100
femoralis 78                      1000$00120--00042111$0111011111110-------10100
femoralis 128                     1000$00120--00042111$0111011111110-------10100
femoralis 129                     1000$00120--00042111$0111011111110-------10100
femoralis RioFormoso 393          1000$00120--00042111$0111011111110-------10100
femoralis RioFormoso 394          1000$00120--00042111$0111011111110-------10100
femoralis Santarem 395            1000$00120--00042111$0111011111110-------10100
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femoralis Santarem 396            1000$00120--00042111$0111011111110-------10100
femoralis PortoWalter 397         1000$00120--00042111$0111011111110-------10100
femoralis PortoWalter 398         1000$00120--00042111$0111011111110-------10100
femoralis Cuyabeno 399            1000$00120--00042111$0111011111110-------10100
femoralis Cuyabeno 400            1000$00120--00042111$0111011111110-------10100
femoralis Ducke 520               1000$00120--00042111$0111011111110-------10100
femoralis Panguana 526            1000$00120--00042111$0111011111110-------10100
femoralis 1298                    1000$00120--00042111$0111011111110-------10100
femoralis 1306                    1000$00120--00042111$0111011111110-------10100

femoralis 1309                    1000$00120--00042111$0111011111110-------10100
femoralis Suriname 1325           1000$00120--00042111$0111011111110-------10100
flavopictus 536                   0000500001100013411?00?11011111110-------10100
hahneli Amazonas 391              0000110011100004233?02111011111110-------10110
hahneli Amazonas 392              0000110011100004233?02111011111110-------10110
hahneli PortoWalter 389           0000110011100004233?02111011111110-------10110
hahneli PortoWalter 390           0000110011100004233?02111011111110-------10110
hahneli PortoWalter 388           0000110011100004233?02111011111110-------10110
Epipedobates PortoWalter1 382     0000110011100004233?02111011111110-------10110
femoralis Leticia 1354            0000110011100004233?02111011111110-------10110
pictus 79                         0000110011100004233?02111011111110-------10110
pictus 109                        0000110011100004233?02111011111110-------10110
pictus 110                        0000110011100004233?02111011111110-------10110
Epipedobates sp 386               0000110011100004233?02111011111110-------10110
Epipedobates sp 1304              0000110011100004233?02111011111110-------10110
macero 1133                       0000100001000000$$$$102111011111110-------10110
parvulus 378                      0000110001000000$$$$100111011111110-------?????
parvulus 401                      0000110001000000$$$$100111011111110-------?????
parvulus 1303                     0000110001000000$$$$100111011111110-------?????
petersi 522                       1000100001100000$$$$100111011111110-------10100
petersi 525                       1000100001100000$$$$100111011111110-------10100
pictus SS                         0000-1001110000$333102111011111110-------10100
pulchripectus 337                 1000100011100004411012111011111110-------10100
silverstonei 646                  0000$10000--001425$100111011111110-------10100
tricolor                          1000210001100015333?02111011111110-------?????
trivittatus 319                   $000$000$1100004233112111011111110-------10100
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trivittatus 387                  $000$000$1100004233112111011111110-------10100
trivittatus 518                  $000$000$1100004233112111011111110-------10100
trivittatus 519                  $000$000$1100004233112111011111110-------10100
trivittatus 628                  $000$000$1100004233112111011111110-------10100
trivittatus 1297                 $000$000$1100004233112111011111110-------10100
trivittatus 1305                 $000$000$1100004233112111011111110-------10100
trivittatus Suriname 1329        $000$000$1100004233112111011111110-------10100
trivittatus Leticia 1350         $000$000$1100004233112111011111110-------10100
pictus 322                       $000$000$1100004233112111011111110-------10100
Epipedobates PortoWalter2 384    $000$000$1100004233112111011111110-------10100
Epipedobates sp 627              $000$000$1100004233112111011111110-------10100
zaparo 321                       1000--0*20--000423310011101111110-------?????
zaparo 328                       1000--0*20--000423310011101111110-------?????
collaris                         10004030010$010212410011101111110-------10100
herminae 1141                    000040301100011202410011101111110-------10100
rubriventris                     100011000110000533310?111011111110-------10100
trinitatis 609                   000040300100010202010011101111110-------?????
claudiae 323                     000050300100000$$$$022111011111110-------?????
claudiae 324                     000050300100000$$$$022111011111110-------?????
lugubris 330                     000050300100000$$$$022111011111110-------?????
fulguritus 499                   000050300100000$$$$022111011111110-------?????
minutus 1149                     000010300*0$0005333?22111011111110-------10110
steyermarki                      0000000000--001614402$111011111110-------?????
nocturnus 1132                   200040300101000614410011l*11111110-------10100
nocturnus 1134                   200040300101000614410011l*11111110-------10100
molinarii                        1000403000--001$333100111011111110-------10100
Nephelobates sp 1321             1000403000--000203310011101111110-------?????
aurotaenia 840                   1000203000--000425200011101111110-------20100
bicolor 1233                     1000$01000--000400000011101111110-------?????
lugubris 329                     0000203000--00042$$000111011111110-------10100
lugubris Nicaragua 366           0000203000--00042$$000111011111110-------10100
terribilis 1135                  1000301000--000200000011101111110-------10100
terribilis 1232                  1000301000--000200000011101111110-------10100
vitattus 839                     1000103010--000425200011101111110-------10100
Epipedobates PortoWalter2 383    ?0002?3010--???????0?????????????-------?????
Epipedobates PortoWalter2 623    ?0002?3010--???????0?????????????-------?????
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Epipedobates PortoWalter2 624     ?0002?3010--???????0?????????????-------?????
Epipedobates PortoWalter2 1235    ?0002?3010--???????0?????????????-------?????
Epipedobates sp 385               ?0002?3010--???????0?????????????-------?????
Colostethus sp Neblina 379        2001403010--00000001000110111111110-------10100
Colostethus sp Neblina 380        2001403010--00000001000110111111110-------10100
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TABLE 3. Characters 92 - 137

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                                  92   97   102  107  112  117  122  127  132  137
                                  |    |    |    |    |    |    |    |    |    |
Telmatobius verrucosus 313        ???????????1???0-???00001??????????????????
Atelopus spurrelli 1275           ?????????????????????101100??0----????1001???
Atelopus zeteki 1039              123110?????????????????101100??0----??????????
Dendrophryniscus minutus 532      123010?????10000-00-2100112?????????4????????
Melanophryniscus klappenbachi 217 12301??????10000-00-1100112010----?0700101211
Rhinoderma darwinii 1115          00$110??????1?110-?3-1?0?10100110 20?0200100001
Crossodactylus schmidti 149       023011????????0?0-00-100??2101120 20?1????????
Hylodes phyllodes 889             023011?0?00?10000-00-2100021211100201201001001
Hylodes phyllodes 1152            023011?0?00?10000-00-2100021211100201201001001
Megaelosia goeldii 611            023011???????????00-11010????1??????8?1001001
Cycloramphus boraceiensis 890     023??0??????1011?-0??1?00123201102001121000000
Eupsophus calcaratus 657          000100??????100?0003-1001121201100000011011000
Thoropa miliaris 1186             ?23??????????0110-?????000232110000?1211000001
awa                               02301???000???131200-11?1000111200101400011111
baeobatrachus 14                  022010?????????????????21???????????????????????
baeobatrachus 42                  022010?????????????????21???????????????????????
baeobatrachus 43                  022010?????????????????21???????????????????????
baeobatrachus 44                  022010?????????????????21???????????????????????
beebei 605                        ??????70?000202110120 21???????????????????????
beebei 608                        ??????70?000202110120 21???????????????????????
bocagei 1267                      ?????????????????????11?1000111200101601001111
bocagei 343                       ?????????????????????11?1000111200101601001111
bocagei 344                       ?????????????????????11?1000111200101601001111
bocagei 345                       ?????????????????????11?1000111200101601001111
caeruleodactylus 406              023010?000000011100 0?21???????????????????????
caeruleodactylus 621              023010?000000011100 0?21???????????????????????
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caeruleodactylus 1261          023010?0000000111000?21?????????????????????
caeruleodactylus 1287          023010?0000000111000?21?????????????????????
degranvillei 278               -00?0???????????10-3?11??????????????3????????
degranvillei 279               -00?0???????????10-3?11??????????????3????????
praderioi 1336                 -00?0???????????10-3?11??????????????3????????
delatorreae 71                 02301?????????????100??21?????????????????????
elachyhistus 108               02301??????????110???11??0000012001O?500001111
elachyhistus 115               02301??????????110???11??0000012001O?500001111
elachyhistus 116               02301??????????110???11??0000012001O?500001111
elachyhistus 114               02301??????????110???11??0000012001O?500001111
elachyhistus 117               02301??????????110???11??0000012001O?500001111
elachyhistus 106               02301??????????110???11??0000012001O?500001111
elachyhistus 105               02301??????????110???11??0000012001O?500001111
elachyhistus 107               02301??????????110???11??0000012001O?500001111
flotator 1143                  0000100?????????10???21?1000001200l1?400000111
flotator 1145                  0000100?????????10???21?1000001200l1?400000111
fraterdanieli 1226             02301?0??????????1000-21?????????????????????
fraterdanieli 1227             02301?0??????????1000-21?????????????????????
fraterdanieli 1228             02301?0??????????1000-21?????????????????????
fugax                          ????????????????????????????????????????????

humilis                        ??????????????????????21?????????????????????
Colostethus Ibague 1225        023010???????????1????21?????????????????????
Colostethus Ibague 1345        023010???????????1????21?????????????????????
Colostethus Ibague 1347        023010???????????1????21?????????????????????
idiomelus 77                   02301????????????1000-11?????????????????????
idiomelus 121                  02301????????????1000-11?????????????????????
idiomelus 120                  02301????????????1000-11?????????????????????
idiomelus 122                  02301????????????1000-11?????????????????????
idiomelus 126                  02301????????????1000-11?????????????????????
imbricolus 1229                ??????0??????????????11?????????????????????
infraguttatus AY326028         023010???????????10?????????????????????????
inguinalis 1348                ??????????????????????11?????????????????????
insperatus                     02301?0?????????100??21?10001110001113000011111
insulatus 124                  02301?????????????00-11?????????????????????
insulatus 125                  02301?????????????00-11?????????????????????
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juanii 1357                    ??????0??????????????21?10000112011015010000010
kingsburyi AY364549            023011?????????1????11?10001011001015000011000
machalilla 73                  023010??????????100????1000101?01111?00??????
machalilla 132                 023010??????????100????1000101?01111?00??????
Colostethus Magdalena 1358     ????????????????????21????????????????????
nexipus 75                     ???????????????10???1*????????????????????
nexipus 123                    ???????????????10???1*????????????????????
nexipus 130                    ???????????????10???1*????????????????????
nexipus 131                    ???????????????10???1*????????????????????
nidicola 407                   -00100????????1?0-23-21????????????????????
nidicola 622                   -00100????????1?0-23-21????????????????????
nidicola 1285                  -00100????????1?0-23-21????????????????????
Colostethus BPN3 1332          ??????????????????????11????????????????????
Colostethus BPN3 1333          ??????????????????????11????????????????????
nubicola 1142                  0$00103?????????10???21?10000012101015000011111
nubicola 1146                  0$00103?????????10???21?10000012101015000011111
olfersioides 538               02301???????????10?????10000111001114001111111
palmatus 1346                  023011010110?00111000-111?0???????????2?1001000
panamensis 1150                023010?1010?2?1?1100-11110000012001015000011111
panamensis 1223                023010?1010?2?1?1100-11110000012001015000011111
praderioi 1335                 ????????????????????21????????????????????
Colostethus 1334               ????????????????????21????????????????????
pratti 1144                    02301???????????11???21?10000112001014000011111
pratti like 1224               023010??????????10????1????????????????????
pulchellus                     02301?1?????????100??2??10000012001013000011111
pulcherrimus 118               ??????????????????????11????????????????????
pulcherrimus 119               ??????????????????????11????????????????????
punctiventris 496              ??????0??????????????21????????????????????
punctiventris 497              ??????0??????????????21????????????????????
roraima 1337                   023010???????????1??21????????????????????
roraima 1338                   023010???????????1??21????????????????????
roraima 1339                   023010???????????1??21????????????????????
Colostethus ROM1 607           ????????????????????21????????????????????
saltuensis 1360                ????????????????????21????????????????????
sauli AY364555                 02301?0???????????00?11?10001012111015010000000
stepheni 514                   -0011??0?10?2?100-23-21????????????????????
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stepheni 515                    -0011??0?10?2?100-23-21?????????????????????
subpunctatus 1359               023010????????111000-21?10000112001103100110 11
Phyllobates sylvaticus 113      02301???????????1000-11?1000001??010?501010000
Phyllobates sylvaticus 76       02301???????????1000-11?1000001??010?501010000
talamancae Nicaragua 361        0230100??????????11???21?1000$11200$*1300011111
talamancae Nicaragua 362        0230100??????????11???21?1000$11200$*1300011111
talamancae Nicaragua 408        0230100??????????11???21?1000$11200$*1300011111
talamancae Panama 1147          0230100??????????11???21?1000$11200$*1300011111
talamancae 325                  0230100??????????11???21?1000$11200$*1300011111
talamancae 326                  0230100??????????11???21?1000$11200$*1300011111
tepuyensis 606                  023011??-??-??-???00?11--???????????????----
toachi                          023010???????????10???21?????????????????????
trilineatus 74                  0230100??????????12???21?????????????????????
trilineatus 112                 0230100??????????12???21?????????????????????
trilineatus 527                 0230100??????????12???21?????????????????????
undulatus 331                   023011????????????00-21?10000012001113000111 11
undulatus 332                   023011????????????00-21?10000012001113000111 11
undulatus 333                   023011????????????00-21?10000012001113000111 11
vertebralis                     0230100???????1?100??21?10000111001105000011 11
arboreus 340                    01111?40010001 2???12121?10001110000116001012 11
auratus 327                     02311?10??0001110$1-2111000011$*0$00600001211
auratus 334                     02311?10??0001110$1-2111000011$*0$00600001211
auratus 335                     02311?10??0001110$1-2111000011$*0$00600001211
auratus Nicaragua 365           02311?10??0001110$1-2111000011$*0$00600001211
azureus 1330                    02311?????????11101??211?????????????????????
azureus 534                     02311?????????11101??211?????????????????????
biolat                          023110???????????1??21?????????????????????
castaneoticus 363               023*1?????????????11-211?????????????????????
galactonotus 533                ??????????????????????211?????????????????????
galactonotus 647                ??????????????????????211?????????????????????
granuliferus 339                01111?40000?01$1111212111000011??001?600101211
histrionicus 336                01111?4?0100012211121211100001 0----10600001211
histrionicus 498                01111?4?0100012211121211100001 0----10600001211
imitator                        ????????????????????211100001100000160001 1211
lehmanni 338                    ??????4???? 001?211121211100001*0003104000*1211
leucomelas 645                  023110???????111000-211??????0??????????????
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pumilio Nicaragua 367             01111040000101131112121110000011000$10600101211
pumilio 1313                      01111040000101131112121110000011000$10600101211
pumilio 1315                      01111040000101131112121110000011000$10600101211
quinquevittatus 1312              023111?????????????1???21?????????????????????
quinquevittatus RioFormoso 370    023111?????????????1???21?????????????????????
quinquevittatus RioFormoso 371    023111?????????????1???21?????????????????????
quinquevittatus RioItuxi 368      023111?????????????1???21?????????????????????
quinquevittatus RioItuxi 369      023111?????????????1???21?????????????????????
reticulatus 528                   ????????????????3101$0211100011120010*600101211
speciosus 341                     011110?????100?311121211000111000$10600011211
Dendrobates sylvaticus 364        ??????????????????????21?1000010----10400001211
tinctorius 1327                   02311??????1??1110???211?000011????0?600001211
tinctorius 535                    02311??????1??1110???211?000011????0?600001211
truncatus 1151                    023111????????1110$??211100001100010160000 1211
truncatus 1351                    023111????????1110$??211100001100010160000 1211
truncatus 1352                    023111????????1110$??211100001100010160000 1211
vanzolinii 372                    ????????????????2?101$021?????????????????????
vanzolinii 373                    ????????????????2?101$021?????????????????????
vanzolinii 1314                   ????????????????2?101$021?????????????????????
ventrimaculatus 1349              023110????????21101$0211100011100021160000 1211
ventrimaculatus 1310              023110????????21101$0211100011100021160000 1211
ventrimaculatus RioItuxi 376      023110????????21101$0211100011100021160000 1211
ventrimaculatus RioItuxi 377      023110????????21101$0211100011100021160000 1211
ventrimaculatus Sucumbios 374     023110????????21101$0211100011100021160000 1211
ventrimaculatus 1311              023110????????21101$0211100011100021160000 1211
ventrimaculatus PortoWalter 375   023110????????21101$0211100011100021160000 1211
vicentei 1148                     0??110?000010011111212 1?1000110----10600011211
anthonyi 838                      ???????0010?20?312???211100000120010150000 1111
anthonyi sensu Myers 1290         ???????0010?20?312???211100000120010150000 1111
azureiventris                     02301?30000100111000-21?????????????????????
bassleri                          ????????????????110????11?000011$00111600001111
boulengeri 280                    023010???????????10????21??0???????????-00001001
espinosai 1139                    02301????????????10????21?10000112001015000 1111
femoralis 78                      02301????????????12$??211100000120010130001 1111
femoralis 128                     02301????????????12$??211100000120010130001 1111
femoralis 129                     02301????????????12$??211100000120010130001 1111
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femoralis RioFormoso 393          02301????????????12$??211100000120010130001111
femoralis RioFormoso 394          02301????????????12$??211100000120010130001111
femoralis Santarem 395            02301????????????12$??211100000120010130001111
femoralis Santarem 396            02301????????????12$??211100000120010130001111
femoralis PortoWalter 397         02301????????????12$??211100000120010130001111

femoralis PortoWalter 398         02301????????????12$??211100000120010130001111
femoralis Cuyabeno 399            02301????????????12$??211100000120010130001111
femoralis Cuyabeno 400            02301????????????12$??211100000120010130001111
femoralis Ducke 520               02301????????????12$??211100000120010130001111
femoralis Panguana 526            02301????????????12$??211100000120010130001111
femoralis 1298                    02301????????????12$??211100000120010130001111
femoralis 1306                    02301????????????12$??211100000120010130001111
femoralis 1309                    02301????????????12$??211100000120010130001111
femoralis Suriname 1325           02301????????????12$??211100000120010130001111
flavopictus 536                   023010????????1?10???11??????????????????????
hahneli Amazonas 391              012010??????????112????21?10000111001006000111111
hahneli Amazonas 392              012010??????????112????21?10000111001006000111111
hahneli PortoWalter 389           012010??????????112????21?10000111001006000111111
hahneli PortoWalter 390           012010??????????112????21?10000111001006000111111
hahneli PortoWalter 388           012010??????????112????21?10000111001006000111111
Epipedobates PortoWalter1 382     012010??????????112????21?10000111001006000111111
femoralis Leticia 1354            012010??????????112????21?10000111001006000111111
pictus 79                         012010??????????112????21?10000111001006000111111
pictus 109                        012010??????????112????21?10000111001006000111111
pictus 110                        012010??????????112????21?10000111001006000111111
Epipedobates sp 386               012010??????????112????21?10000111001006000111111
Epipedobates sp 1304              012010??????????112????21?10000111001006000111111
macero 1133                       0230106??????????1000-21??????????????0???????
parvulus 378                      ????????????????110????211000011200101400001111
parvulus 401                      ????????????????110????211000011200101400001111
parvulus 1303                     ????????????????110????211000011200101400001111
petersi 522                       02301????????????12???????0???????????????111
petersi 525                       02301????????????12???????0???????????????111
pictus SS                         02301?0??????????10???211100000120010140001111
pulchripectus 337                 023010??????????110???211?????????????????????
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silverstonei 646                02301?5????????11000-2111000001??010?300000000
tricolor                        ??????????????????????21?????????????????????
trivittatus 319                 02301?5????????11000-211100001120010140001l011
trivittatus 387                 02301?5????????11000-211100001120010140001l011
trivittatus 518                 02301?5????????11000-211100001120010140001l011
trivittatus 519                 02301?5????????11000-211100001120010140001l011
trivittatus 628                 02301?5????????11000-211100001120010140001l011
trivittatus 1297                02301?5????????11000-211100001120010140001l011
trivittatus 1305                02301?5????????11000-211100001120010140001l011
trivittatus Suriname 1329       02301?5????????11000-211100001120010140001l011
trivittatus Leticia 1350        02301?5????????11000-211100001120010140001l011
pictus 322                      02301?5????????11000-211100001120010140001l011
Epipedobates PortoWalter2 384   02301?5????????11000-211100001120010140001l011
Epipedobates sp 627             02301?5????????11000-211100001120010140001l011
zaparo 321                      ??????????????????????21?????????????????????
zaparo 328                      ??????????????????????21?????????????????????
collaris                        023011??1???????10???111100001120010020100????
herminae 1141                   023010??????????10???1??100000110010030l001111
rubriventris                    02311?????????????????????1?????????????????????
trinitatis 609                  ???????01?????111000-111100001120010130l001111
claudiae 323                    ??????????????????????21?1000111$*0101600101211
claudiae 324                    ??????????????????????21?1000111$*0101600101211
lugubris 330                    ??????????????????????21?1000111$*0101600101211
fulguritus 499                  ??????1????100?1101??21?100001120010150001l111
minutus 1149                    02311?1??????????1?1???21?100010110010l$00101211
steyermarki                     ????????????2???10???21?1000001$00$0*600101111
nocturnus 1132                  023010????????????00-00?100001111010020l011000
nocturnus 1134                  023010????????????00-00?100001111010020l011000
molinarii                       02301?????????????00-1??100000120000030l000000
Nephelobates sp 1321            ??????????????????????21?????????????????????
aurotaenia 840                  0230103??????????10???211100000120010050001000l
bicolor 1233                    ??????3?????0??010???211100001120010050001l111
lugubris 329                    0230103??????????101??2111000111100101600000111
lugubris Nicaragua 366          0230103??????????101??2111000111100101600000111
terribilis 1135                 0230103???????0010???211100001121O?016000**111
terribilis 1232                 0230103???????0010???211100001121O?016000**111
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vitattus 839                        023010??????0??1101??21?10000012*010*300001111
Epipedobates PortoWalter2 383       ????????????????????????1????????????????????
Epipedobates PortoWalter2 623       ????????????????????????1????????????????????
Epipedobates PortoWalter2 624       ????????????????????????1????????????????????
Epipedobates PortoWalter2 1235      ????????????????????????1????????????????????
Epipedobates sp 385                 ????????????????????????1????????????????????
Colostethus sp Neblina 379          02301???????????10???21?10000112001013000011111
Colostethus sp Neblina 380          02301???????????10???21?10000112001013000011111
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TABLE 4. Characters 138 - 174

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                                    138  143  148  153  158  163  168  173
                                    |    |    |    |    |    |    |    |
Telmatobius verrucosus 313          1?10????????--????--?-?-????-???-???4
Atelopus spurrelli 1275             0-002???0--------------------------1?
Atelopus zeteki 1039                0-002???0--------------------------12
Dendrophryniscus minutus 532        ????????0--------------------------0?
Melanophryniscus klappenbachi 217   0-00200010011111110001000001000000002
Rhinoderma darwinii 1115            0-002100??????????????????????????????4
Crossodactylus schmidti 149         1000????0--------------------------?4
Hylodes phyllodes 889               101010000--------------------------?4
Hylodes phyllodes 1152              101010000--------------------------?4

Megaelosia goeldii 611              1010????0--------------------------?$
Cycloramphus boraceiensis 890       1010????????????????????????????????4
Eupsophus calcaratus 657            10101000????????????????????????????6
Thoropa miliaris 1186               10101000????????????????????????????4
awa                                 10011000????????????????????????????
baeobatrachus 14                    1?0????????????????????????????????
baeobatrachus 42                    1?0????????????????????????????????
baeobatrachus 43                    1?0????????????????????????????????
baeobatrachus 44                    1?0????????????????????????????????
beebei 605                          1?0????????????????????????????????
beebei 608                          1?0????????????????????????????????
bocagei 1267                        11010000????????????????????????????
bocagei 343                         11010000????????????????????????????
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bocagei 344                 11010000??????????????????????????????
bocagei 345                 11010000??????????????????????????????
caeruleodactylus 406        1?0??????????????????????????????????2
caeruleodactylus 621        1?0??????????????????????????????????2
caeruleodactylus 1261       1?0??????????????????????????????????2
caeruleodactylus 1287       1?0??????????????????????????????????2
degranvillei 278            1?0-????????????????????????????????
degranvillei 279            1?0-????????????????????????????????
praderioi 1336              1?0-????????????????????????????????
delatorreae 71              1?0-????????????????????????????????
elachyhistus 108            11011000????????????????????????????
elachyhistus 115            11011000????????????????????????????
elachyhistus 116            11011000????????????????????????????
elachyhistus 114            11011000????????????????????????????
elachyhistus 117            11011000????????????????????????????
elachyhistus 106            11011000????????????????????????????
elachyhistus 105            11011000????????????????????????????
elachyhistus 107            11011000????????????????????????????
flotator 1143               110100000--------------------------??
flotator 1145               110100000--------------------------??
fraterdanieli 1226          1?01????0--------------------------03
fraterdanieli 1227          1?01????0--------------------------03
fraterdanieli 1228          1?01????0--------------------------03
fugax                       ??????????????????????????????????????
humilis                     1?0??????????????????????????????????
Colostethus Ibague 1225     ??????????????????????????????????????
Colostethus Ibague 1345     ??????????????????????????????????????
Colostethus Ibague 1347     ??????????????????????????????????????
idiomelus 77                1?0??????????????????????????????????
idiomelus 121               1?0??????????????????????????????????
idiomelus 120               1?0??????????????????????????????????
idiomelus 122               1?0??????????????????????????????????
idiomelus 126               1?0??????????????????????????????????
imbricolus 1229             1?0?????0--------------------------0?
infraguttatus AY326028      1?0?????0--------------------------0?
inguinalis 1348             ??????????????????????????????????????
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insperatus                  11010000??????????????????????????????
insulatus 124               ????????????????????????????????????????
insulatus 125               ????????????????????????????????????????
juanii 1357                 10010000??????????????????????????????
kingsburyi AY364549         11011000??????????????????????????????
machalilla 73               1?0??000??????????????????????????????
machalilla 132              1?0??000??????????????????????????????
Colostethus Magdalena 1358  ????????????????????????????????????????
nexipus 75                  ????????????????????????????????????????
nexipus 123                 ????????????????????????????????????????
nexipus 130                 ????????????????????????????????????????
nexipus 131                 ????????????????????????????????????????
nidicola 407                1?0?????????????????????????????????????2
nidicola 622                1?0?????????????????????????????????????2
nidicola 1285               1?0?????????????????????????????????????2
Colostethus BPN3 1332       1?0????????????????????????????????????
Colostethus BPN3 1333       1?0????????????????????????????????????
nubicola 1142               110100000-------------------------??
nubicola 1146               110100000-------------------------??
olfersioides 538            11010000??????????????????????????????3
palmatus 1346               11011000??????????????????????????????3
panamensis 1150             110110100-------------------------13
panamensis 1223             110110100-------------------------13
praderioi 1335              ????????????????????????????????????????
Colostethus 1334            ????????????????????????????????????????
pratti 1144                 11011000??????????????????????????????
pratti like 1224            1?0????????????????????????????????????
pulchellus                  11011000??????????????????????????????
pulcherrimus 118            ????????????????????????????????????????
pulcherrimus 119            ????????????????????????????????????????
punctiventris 496           1?0????????????????????????????????????
punctiventris 497           1?0????????????????????????????????????
roraima 1337                1?0????????????????????????????????????
roraima 1338                1?0????????????????????????????????????
roraima 1339                1?0????????????????????????????????????
Colostethus ROM1 607        1?0????????????????????????????????????
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saltuensis 1360                 ???-??????????????????????????????????
sauli AY364555                  11010000??????????????????????????????
stepheni 514                    ????????????????????????????????????3
stepheni 515                    ????????????????????????????????????3
subpunctatus 1359               110100000-------------------------?3
Phyllobates sylvaticus 113      11010000??????????????????????????????
Phyllobates sylvaticus 76       11010000??????????????????????????????
talamancae Nicaragua 361        110100000-------------------------03
talamancae Nicaragua 362        110100000-------------------------03
talamancae Nicaragua 408        110100000-------------------------03
talamancae Panama 1147          110100000-------------------------03
talamancae 325                  110100000-------------------------03
talamancae 326                  110100000-------------------------03
tepuyensis 606                  1?0?-??????????????????????????????????
toachi                          1?0?????????????????????????????????????
trilineatus 74                  ??0?????????????????????????????????????
trilineatus 112                 ??0?????????????????????????????????????
trilineatus 527                 ??0?????????????????????????????????????
undulatus 331                   11010000??????????????????????????????
undulatus 332                   11010000??????????????????????????????
undulatus 333                   11010000??????????????????????????????
vertebralis                     11011000????????????????????????????????3
arboreus 340                    0-01$**1100110001101100000000000001??
auratus 327                     0-0100**10111111111111100111010000 1?0
auratus 334                     0-0100**10111111111111100111010000 1?0
auratus 335                     0-0100**10111111111111100111010000 1?0
auratus Nicaragua 365           0-0100**10111111111111100111010000 1?0
azureus 1330                    ?????000101010100101110000100000001??
azureus 534                     ?????000101010100101110000100000001??
biolat                          0-0?????????????????????????????????????
castaneoticus 363               0-0?????10100011000010000000000000 1??
galactonotus 533                0-0??0001??1??1?????????????????????1??
galactonotus 647                0-0??0001??1??1?????????????????????1??
granuliferus 339                0-011101101110111101111011010000001?1
histrionicus 336                0-011**11011101111011101110000000 1?1
histrionicus 498                0-011**11011101111011101110000000 1?1
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imitator                          0-0110001010011110011000100000000???
lehmanni 338                      0-0111*1101111010111111011000000001??
leucomelas 645                    0-0??000101110010000110000000000001??
pumilio Nicaragua 367             0-0111*1101111111111111101101010000101
pumilio 1313                      0-0111*1101111111111111101101010000101
pumilio 1315                      0-0111*1101111111111111101101010000101
quinquevittatus 1312              0-0?????101111111101000000000000001??
quinquevittatus RioFormoso 370    0-0?????101111111101000000000000001??
quinquevittatus RioFormoso 371    0-0?????101111111101000000000000001??
quinquevittatus RioItuxi 368      0-0?????101111111101000000000000001??
quinquevittatus RioItuxi 369      0-0?????101111111101000000000000001??
reticulatus 528                   0-01000*1011101010001100000000000001??
speciosus 341                     0-0111011011101111011110010000000001??
Dendrobates sylvaticus 364        0-0111011011101111011100101000000001?1
tinctorius 1327                   0-0110*0101110111101110000100100001??
tinctorius 535                    0-0110*0101110111101110000100100001??
truncatus 1151                    0-0100*0101000110101100000000000000??0
truncatus 1351                    0-0100*0101000110101100000000000000??0
truncatus 1352                    0-0100*0101000110101100000000000000??0
vanzolinii 372                    0-0?????101000101010000001000000000??1
vanzolinii 373                    0-0?????101000101010000001000000000??1
vanzolinii 1314                   0-0?????101000101010000001000000000??1
ventrimaculatus 1349              0-0110001011101110011000000000000001??
ventrimaculatus 1310              0-0110001011101110011000000000000001??
ventrimaculatus RioItuxi 376      0-0110001011101110011000000000000001??
ventrimaculatus RioItuxi 377      0-0110001011101110011000000000000001??
ventrimaculatus Sucumbios 374     0-0110001011101110011000000000000001??
ventrimaculatus 1311              0-0110001011101110011000000000000001??
ventrimaculatus PortoWalter 375   0-0110001011101110011000000000000001??
vicentei 1148                     0-0101011001100001011100010000000001??
anthonyi 838                      1101000010011010010111000000101000??
anthonyi sensu Myers 1290         1101000010011010010111000000101000??
azureiventris                     1?0?????0-------------------------??
bassleri                          1101000010111011010111000100000000??
boulengeri 280                    11010000??????????????????????????????
espinosai 1139                    1101000010111000010111000000001001??
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femoralis 78                    110100000-------------------------?3
femoralis 128                   110100000-------------------------?3
femoralis 129                   110100000-------------------------?3
femoralis RioFormoso 393        110100000-------------------------?3
femoralis RioFormoso 394        110100000-------------------------?3
femoralis Santarem 395          110100000-------------------------?3
femoralis Santarem 396          110100000-------------------------?3
femoralis PortoWalter 397       110100000-------------------------?3
femoralis PortoWalter 398       110100000-------------------------?3
femoralis Cuyabeno 399          110100000-------------------------?3
femoralis Cuyabeno 400          110100000-------------------------?3
femoralis Ducke 520             110100000-------------------------?3
femoralis Panguana 526          110100000-------------------------?3
femoralis 1298                  110100000-------------------------?3
femoralis 1306                  110100000-------------------------?3
femoralis 1309                  110100000-------------------------?3
femoralis Suriname 1325         110100000-------------------------?3
flavopictus 536                 0?0?????10110110000000000000000000?3
hahneli Amazonas 391            1101100010100010000000000000000100??3
hahneli Amazonas 392            1101100010100010000000000000000100??3
hahneli PortoWalter 389         1101100010100010000000000000000100??3
hahneli PortoWalter 390         1101100010100010000000000000000100??3
hahneli PortoWalter 388         1101100010100010000000000000000100??3
Epipedobates PortoWalter1 382   1101100010100010000000000000000100??3
femoralis Leticia 1354          1101100010100010000000000000000100??3
pictus 79                       1101100010100010000000000000000100??3
pictus 109                      1101100010100010000000000000000100??3
pictus 110                      1101100010100010000000000000000100??3
Epipedobates sp 386             1101100010100010000000000000000100??3
Epipedobates sp 1304            1101100010100010000000000000000100??3
macero 1133                     1?011000101010110100000000000010000???
parvulus 378                    1101$000101100100100000000000000000???
parvulus 401                    1101$000101100100100000000000000000???
parvulus 1303                   1101$000101100100100000000000000000???
petersi 522                     1?011000101100100100000000000000000???
petersi 525                     1?011000101100100100000000000000000???
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pictus SS                          1101000010111001010100000011010000??3
pulchripectus 337                  0-0?????10110010010100000000010000???
silverstonei 646                   1101000010011001010100000000001000??
tricolor                           1?0?????10011000010001000000000100???
trivittatus 319                    0-0100001010001001000000100010000-?3
trivittatus 387                    0-0100001010001001000000100010000-?3
trivittatus 518                    0-0100001010001001000000100010000-?3
trivittatus 519                    0-0100001010001001000000100010000-?3
trivittatus 628                    0-0100001010001001000000100010000-?3
trivittatus 1297                   0-0100001010001001000000100010000-?3
trivittatus 1305                   0-0100001010001001000000100010000-?3
trivittatus Suriname 1329          0-0100001010001001000000100010000-?3
trivittatus Leticia 1350           0-0100001010001001000000100010000-?3
pictus 322                         0-0100001010001001000000100010000-?3
Epipedobates PortoWalter2 384      0-0100001010001001000000100010000-?3
Epipedobates sp 627                0-0100001010001001000000100010000-?3
zaparo 321                         ????????????????????????????????????
zaparo 328                         ????????????????????????????????????
collaris                           1101?100????????????????????????????
herminae 1141                      11011000????????????????????????????3
rubriventris                       1?0????????????????????????????????
trinitatis 609                     110100000-------------------------03
claudiae 323                       0-011*011001101001000100010000000001??
claudiae 324                       0-011*011001101001000100010000000001??
lugubris 330                       0-011*011001101001000100010000000001??
fulguritus 499                     0-010001100110000100000000000000001??
minutus 1149                       0-011*011001101101011100000000000001??
steyermarki                        0-01$000100110000000110000000000001??
nocturnus 1132                     110110000-------------------------0?
nocturnus 1134                     110110000-------------------------0?
molinarii                          1101000?????????????????????????????
Nephelobates sp 1321               ????????0-------------------------0?
aurotaenia 840                     1101000011110010100000000000000010??
bicolor 1233                       1101001011110010110000000000000100?
lugubris 329                       1101000011011110000100000100000000??3
lugubris Nicaragua 366             1101000011011110000100000100000000??3
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terribilis 1135                  11010000110000001100000000000001011-??
terribilis 1232                  11010000110000001100000000000001011-??
vitattus 839                     11010000110001111100000100010000000-??
Epipedobates PortoWalter2 383    ????????0------------------------???
Epipedobates PortoWalter2 623    ????????0------------------------???
Epipedobates PortoWalter2 624    ????????0------------------------???
Epipedobates PortoWalter2 1235   ????????0------------------------???
Epipedobates sp 385              ????????0------------------------???
Colostethus sp Neblina 379       11010000??????????????????????????????
Colostethus sp Neblina 380       11010000??????????????????????????????
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CHARACTER LIST (only named characters listed!)

0. Dorsal skin texture: smooth = 0; posteriorly granular = 1;
    strongly granular = 2; spiculate = 3. [nonadditive].
1. Paired dorsal digital scutes: absent = 0; present = 1. .
2. Supernumerary tubercles on hand: absent = 0; present = 1. .
3. Distal tubercle on finger 4: absent = 0; present = 1. .
4. Finger IV length:
    surpassing distal subarticular tubercle of finger III = 0; reaching distal 1/2 of subarticular tubercle of finger III (II=IV) = 1;
    not reaching distal subarticular tubercle of finger III = 2. [additive].
5. Finger 1 vs. Finger 2 (sensu Kaplan, 1997: 370):
    1<<2 (1.2 or more times longer) = 0; 1<2 = 1; 1=2 = 2; 1>2 = 3. [additive].
6. Digital discs: absent = 0; present = 1. .
7. Finger disc I: not/very weakly expanded = 0; weakly expanded = 1;
    moderately expanded = 2. [additive].
8. Finger disc II: unexpanded expanded = 0; weakly expanded = 1;
    moderately expanded = 2; very expanded = 3. [additive].
9. Finger disc III: unexpanded expanded = 0; weakly expanded = 1;
    moderately expanded = 2; very expanded = 3. [additive].
10. Finger disc IV: unexpanded expanded = 0; weakly expanded = 1;
    moderately expanded = 2; very expanded = 3. [additive].
11. Finger fringe: I preaxial: absent = 0; fringe = 1. .
12. Finger fringe: I postaxial: absent = 0; fringe = 1. .

13. Finger fringe: II preaxial: absent = 0; fringe = 1. .
14. Finger fringe: II postaxial: absent = 0; fringe = 1. .
15. Finger fringe: III preaxial: absent = 0; fringe = 1. .
16. Finger fringe: III postaxial: absent = 0; fringe = 1. .
17. Finger fringe:IV preaxial: absent = 0; fringe = 1. .
18. Finger fringe: IV postaxial: absent = 0; fringe = 1. .
19. Metacarpal ridge/fold: absent = 0; present = 1. .
20. Finger III swelling in adult males: absent = 0; present = 1. .
21. Morphology of swollen third finger in males: weak preaxial swelling = 1;
    strong preaxial swelling = 2; swelling extending from wrist, mainly preaxial on digit = 3.
[nonadditive].
22. Carpal pad: absent = 0; present = 1. .
23. Male nuptial excrescenses on thumb: absent = 0; present = 1. .
24. Morphology of male nuptial excrescenses on thumb:
    large, cornified spines = 0; small, uncornified spines = 1; nonspinous asperities = 2. [additive].
25. Female nuptial excrescences on thumb: absent = 0; present = 1. .
26. Thenar tubercle: absent or small, inconspicuous swelling = 0;
    large, conspicuous, well defined tubercle = 1. .
27. Black arm gland in adult males: absent = 0; present = 1. .
28. Tarsal keel: absent = 0; present = 1. .
29. Morphology of tarsal keel:
    straight or weakly curved, ext. from inner mt tub to center of tarsus = 0; strong, tuberclelike
(=enlarged, curved) proximally, ext. from mt tub = 1;
    short, tuberclelike, not ext. from mt tub = 2; weak, short dermal thickening, not ext. from mt. tub.
= 3. [additive].
30. Tarsal fringe: absent = 0; present = 1. .
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. 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].
38. Webbing: Toe II Preaxial: absent = 0; 2.5 = 1; 2 = 2; 1 = 3; 0 = 4. [additive].
39. Webbing: Toe II Postaxial: absent = 0; 2 = 1; 2 (with fringe) = 2; 1.5 = 3; 1 = 4; 0 = 5. [additive].
40. Webbing: Toe III Preaxial: absent = 0; fringe = 1; 3.5 = 2; 3.5 (with fringe) = 3; 3 = 4; 2.5 = 5; 2 = 6; 1.5 = 7; 1 = 8. [additive].
41. Webbing: Toe III Postaxial: absent = 0; 3 = 1; 3 (with fringe) = 2; 2.5 = 3; 2 = 4; 1.5 = 5; 1 = 6. [additive].
42. Webbing: Toe IV Preaxial: absent = 0; 4 = 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].
44. Webbing: Toe V Preaxial: absent = 0; fringe = 1; 2.5 = 2; 2 = 3; 1.5 = 4; 1 = 5. [additive].
45. Webbing: Toe V Postaxial: absent = 0; fringe = 1. .
46. Metatarsal fold: absent = 0; weak = 1; strong = 2. [additive].
47. Cloacal tubercles: absent = 0; present = 1. .
48. Iridescent orange or golden spot at dorsal limb insertions: absent = 0; present = 1. .
49. Pale paracloacal mark : absent = 0; present = 1. .
50. Thigh dorsal coloration:
    pale w/ dark spots (forming retic. when spots close together) = 0; solid dark (black, brown, blue-green) = 1; dark w/ pale spots/bands = 2;
    solid pale = 3; brown with dark brown bands/blotches = 4;
    dark with pale longitudinal stripe = 5. [nonadditive].
51. Pale proximoventral calf spot: absent = 0; present = 1. .
52. Dorsolateral stripe A (does not drop to thigh): absent = 0;
    present in juveniles only (i.e., lost ontogenetically) = 1; anterior, faint, weakens ontogenetically (but present nonetheless) = 2;
    complete = 3. [additive].
53. Dorsolateral stripe B (drops to top of thigh, not groin): absent = 0;
    present = 1. .

54. Ventrolateral stripe: absent = 0; wavy series of elongate spots = 1;
straight = 2. [nonadditive].
55. Oblique lateral stripe: absent = 0; present = 1. .
56. Oblique lateral stripe length: partial = 0; complete = 1. .
57. Oblique lateral stripe structure: solid = 0; series of spots = 1;
diffuse = 2. [nonadditive].
58. Gular-chest markings: absent = 0; present = 1. .
59. Dermal collar: absent = 0; present = 1. .
60. Dark lower labial stripe: absent = 0; present = 1. .
61. Male throat (vocal sac) color:
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].
62. Female throat and chest color:
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: pale, free or almost free of melanophores = 0;
pale with discrete dark spotting/reticulation/marbling = 1; evenly stippled = 2;
dark with discrete pale spotting/reticulation/marbling = 3; irregular (clumped) stippling or faint, diffuse spotting = 4; solid dark = 5.
[nonadditive].
64. Female abdomen color: 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. [nonadditive].
65. Iris coloration: lacking metallic pigmentation and pupil ring = 0;
with metallic pigmentation and pupil ring = 1. .
66. Large intestine color: unpigmented = 0; pigmented anteriorly = 1;
pigmented entirely = 2. [additive].
67. Adult testis (mesorchium) color : unpigmented = 0;
pigmented medially only = 1; entirely pigmented = 2. [additive].

68. Color of mature ova : unpigmented white or yellowish) = 0;
pigmented (animal pole brown) = 1. .
69. M. semitendinosus insertion: "bufonid type" (ventrad) = 0;
"ranid type" (dorsad) = 1. .
70. M. semitendinosus binding tendon: absent = 0; present = 1. .
71. M. adductor mandibulae externus superficialis : absent = 0; present = 1. .
72. M. depressor mandibulae dorsal flap: dorsal flap absent = 0;
dorsal flap 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. .
75. Tympanum and m. depressor mandibulae relation:
tympanum superficial to m. depressor mandibulae = 0; tympanum covered superficially by m. depressor
mandibulae = 1. .
76. Vocal sac (structure sensu Liu, 1935): absent = 0; median, subgular = 1;
paired lateral = 2. [nonadditive].
77. M. intermandubularis supplementary element occurrence: absent = 0;
present = 1. .
78. M. intermandibularis supplementary element orientation: anterolateral = 0;
anteromedial = 1. .
79. Median lingual process (MLP): absent = 0; present = 1. .
80. MLP shape: short, bumplike = 0; elongate = 1. .
81. MLP tip: blunt = 0; tapering to point = 1. .
82. MLP texture: smooth = 0. .
83. MLP orientation when protruded: posteriorly reclined = 1. .
84. MLP retractility: nonretractile = 0. .
85. MLP associated pit: present = 1. .
86. MLP epithelium: nonglandular = 1. .
87. Larval caudal coloration: vertically striped = 0;
scattered melanophores clumped to form diffuse blotches and retic = 1; evenly pigmented = 2.
[additive].
88. Larval oral disc: "normal" = 0; umbelliform = 1; absent = 2; suctorial = 3.
[nonadditive].
89. Lateral indentation of larval oral disc: absent (not emarginate) = 0;

present (emarginate) = 1. .
90. Larval marginal labial papillae size: short = 0; enlarged = 1;
greatly enlarged = 2. [additive].
91. Submarginal papillae of larval oral disc: absent = 0; present = 1. .
92. Median break in marginal papillae of lower labium: absent = 0; present = 1. .
93. Anterior larval tooth rows: 0 = 0; 1 = 1; 2 = 2. [additive].
94. Posterior larval tooth rows: 0 = 0; 1 = 1; 2 = 2; 3 = 3. [additive].
95. Larval anus: dextral = 0; median = 1. .
96. Spiracle: absent = 0; present = 1. .
97. Lateral line stitches: absent = 0; present = 1. .
98. Advertisement calls: peep = 0; buzz = 1; croak = 2; trill = 3; chirp = 4;
retarded trill = 5; harsh peep train = 6; whistled trill = 7. [nonadditive].
99. Male courtship: Stereotyped strut: absent = 0; present = 1. .
100. Male courtship: Jumping up and down: absent = 0; present = 1. .
101. Female courtship: Crouching: absent = 0; present = 1. .
102. Female courtship: Sliding under male: absent = 0; present = 1. .
103. Timing of sperm deposition: After oviposition = 0; Prior to oviposition = 1. .
104. Copulatory amplexus: absent = 0; axillary = 1; cephalic = 2. [nonadditive].
105. Cloaca-cloaca touching: absent = 0; present = 1. .
106. Egg deposition site: aquatic = 0;
terrestrial: leaf litter, soil, on or under stones = 1; terrestrial: above ground in vegetation
(bromelias etc) = 2. [additive].
107. Egg attendance: none = 0; male = 1; female = 2; both = 3. [nonadditive].
108. Dorsal tadpole transport: absent = 0; present = 1. .
109. Sex of nurse frog: male = 0; female = 1; both = 2. [nonadditive].
110. Larval habitat: pool or stream = 0; phytotelmata = 1; nidicolous = 2.
[nonadditive].
111. Larval diet: detritivorous = 0; predaceous = 1; oophagous = 2;
endotrophic = 3. [nonadditive].
112. Egg provisioning for larval oophagy: both sexes involved = 0;
female only = 1. .
113. Adult habitat selection: aquatic = 0; riparian (<3 m from water) = 1;
independent of streams (up to ca. 30 m or more from water) = 2. [additive].
114. Diel activity: nocturnal = 0; diurnal = 1. .
115. Toe trembling: absent = 0; present = 1. .
116. Hyalia anterior process: absent = 0; present = 1. .

117. Shape of terminal phalanges: T-shaped = 0; knobbed = 1. .
118. Epicoracoid fusion in adults: entirely fused (Kaplan's E) = 0;
anteriorly fused, posteriorly free (Kaplan C) = 1; fused at anterior exteme, free posteriorly (Kaplan A) = 2. [additive].
119. Epicoracoid overlap in adults: no overlap (Kaplan's B) = 0;
partial overlap (Kaplan's E) = 1; partial overlap (Kaplan's C) = 2; partial overlap (Kaplan's A) = 3. [nonadditive].
120. Angle of procoracoid element: laterad, perpendicular to sagittal plane = 0;
directed posteriorly = 1; directed anteriorly = 2. [nonadditive].
121. Acromion process: cartilaginous, distinct = 0;
calcified/ossified fully, continuous with clavicle and scapula = 1. .
122. Prezonal element (omosternun): absent = 0; present = 1. .
123. Prezonal element (omosternum) anterior expansion:
not expanded distally, tapering to tip = 0; weakly expanded, to 2.5x style at base of cartilage or equivalent = 1;
extensively expanded distally, 3.5x or greater = 2. [additive].
124. Prezonal element (omosternun) shape of anterior terminus:
rounded or irregularly shaped = 0; distinctly bifid = 1. .
125. Prezonal element (omosternum) shape of posterior terminus: simple = 0;
notched, forming two struts = 1; continuous with epicoracoid cartilage = 2. [nonadditive].
126. Prezonal element (omosternum) ossification: entirely cartilaginous = 0;
medially ossified (cartilaginous base and tip) = 1; basally ossified (cartilaginous tip) = 2; entirely ossified = 3. [nonadditive].
127. Suprascapula anterior projection: cartilaginous = 0; heavily calcified = 1. .
128. Sternum shape: simple, ovoid, or irregular = 0; medially divided, bifid = 1. .
129. Zygomatic ramus of squamosal: 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, hook-like = 6; miniscule bump = 7;
robust, elongate, in broad contact with the maxilla = 8. [nonadditive].
130. Orientation of alary process of premaxilla: tilted anteriorly = 0;
directed dorsally (vertical, not tilted) = 1; tilted posteriorly = 2. [additive].
131. Palatines: absent = 0; present = 1. .
132. Quadratojugal-maxilla relation: overlapping = 0; separated = 1. .

133. Nasal-maxilla relation: separated = 0; in contact = 1. .
134. Nasal-sphenethmoid relation: separate = 0; overlapping or fused = 1. .
135. Frontoparietal fusion: entirely free (articulating, but not fused) = 0;
fused posteriorly = 1; fused along entire length = 2. [additive].
136. Frontoparietal-otoccipital relation : free, articulating but not fused = 0;
fused = 1. .
137. Exoccipitals: free, separate = 0; fused sagitally = 1. .
138. Maxillary teeth: absent = 0; present = 1. .
139. Maxillary tooth structure: pedicelate = 0; nonpedicelate = 1. .
140. Vomerine teeth: absent = 0; present = 1. .
141. Retroarticular process of mandible: absent = 0; present = 1. .
142. Expansion of sacral diapophyses: unexpanded = 0;
weakly expanded (1.5-2.5X) = 1; strongly expanded = 2. [additive].
143. Sacrum and vertebra 8: free = 0; fused = 1. .
144. Vertebae 1 and 2: free = 0; fused = 1. .
145. Vertebae 2 and 3: free = 0; fused = 1. .
146. Ability to sequester liophilic alkaloids: absent = 0; present = 1. .
147. 1 Batrachotoxins (BTX): absent = 0; present = 1. .
148. 2 Histrionicotoxins (HTX): absent = 0; present = 1. .
149. 3A Pumiliotoxins (PTX): absent = 0; present = 1. .
150. 3B Allopumiliotoxins: absent = 0; present = 1. .
151. 4 Homopumiliotoxins: absent = 0; present = 1. .
152. 5 Decahydroquinolines (DHQ): absent = 0; present = 1. .
153. 6 3,5-pyrrolizidines: absent = 0; present = 1. .
154. 7 3,5-disubstituted indolizidines: absent = 0; present = 1. .
155. 8 5,8-disubstituted indolizidines: absent = 0; present = 1. .
156. 9 Dehydro-5,8-indolizidines: absent = 0; present = 1. .
157. 10 5,6,8-indolizidines: absent = 0; present = 1. .
158. 11 4,6-quinolizidines: absent = 0; present = 1. .
159. 12 1,4-quinolizidines: absent = 0; present = 1. .
160. 13 Lehmizidines: absent = 0; present = 1. .
161. 14 Epiquinamide: absent = 0; present = 1. .
162. 15 2,5-pyrrolidines (PYR): present = 0; absent = 1. .
163. 16 2,6-piperidines: absent = 0; present = 1. .
164. 17 Gephyrotoxins (GTX): absent = 0; present = 1. .
165. 18 Coccinelline-like tricyclics, 193C, 205B, 207J, 209G: absent = 0;

present = 1. .
166. 19 Cyclopentylquinolizidine: absent = 0. .
167. 20 Spiropyrrolizidines: absent = 0; present = 1. .
168. 22 Indolic alkaloids: absent = 0; present = 1. .
169. 23 Epibatidine: absent = 0; present = 1. .
170. 24 Pyridine alkaloids: absent = 0; present = 1. .
171. Noranabasamine (=pyridyl-piperidine): absent = 0; present = 1. .
172. Pumiliotoxin 7-hydroxylase: absent = 0; present = 1. .
173. Tetrodotoxin (TTX): absent = 0; present = 1. .
174. Chromosome number (2n): 18 = 0; 20 = 1; 22 = 2; 24 = 3; 26 = 4; 28 = 5; 30 = 6.
[nonadditive].