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Evolution of Ecomorphological Variation and Acoustic Diversity in Mate-Recognition Signals of Southeast Asian Forest Frogs (subfamily Platymantinae)

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Evolution of Ecomorphological Variation and Acoustic Diversity in Mate-Recognition Signals of Southeast Asian Forest Frogs (subfamily Platymantinae)

by

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Dedication

This one goes out to all my homies, the fallen rappers—cut down in the streets, taken out in the drive-bys, ganked by their own brothers, beat down by The Man.

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Evolution of Ecomorphological Variation and Acoustic Diversity in Mate-Recognition Signals of Southeast Asian Forest Frogs (subfamily Platymantinae)

Publication No._______

Rafe Marion Brown, Ph.D.
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Supervisors: David Cannatella and David Hillis

I estimated evolutionary relationships of frogs of the subfamily Platymantinae (genera *Platymantis, Batrachylodes, Palmatorappia, Discodeles, Ceratobatrachus*) and their relatives (genus *Ingerana* and various SE Asian ranids) using mitochondrial gene sequences. Various methods of phylogenetic inference all suggested that platymantines consist of two reciprocally monophyletic clades, one composed of Philippine *Platymantis* and the other containing all Papuan-Solomon-Bismarck archipelago taxa. Non-*Platymantis* genera are nested within *Platymantis* and fall basal to SW Pacific island archipelago species.

I recognized 51 evolutionary lineages of Philippine platymantines and attempted to statistically define morphological, ecological, and acoustic classes of species.

Multivatiate analyses of continuous morphological characters suggested that species diversity falls into five classes: (1) canopy frogs, (2) shrub frogs, (3) ground frogs, (4) giants, and (5) miniaturized species. Analyses of 10 acoustic characters similarly distinguished five call types: (1) simple single pulse ("tink") calls, (2) pure tone calls, (3) frequency sweeps, (4) amplitude-modulated pulsed calls, and (5) complex calls. Although the correlation of morphological and call types was not perfect, their general association with each other and with specific microhabitat preferences suggests selection for suites of associated morphological, ecological, and behavioral traits.

I also tested the Acoustic Adaptation Hypothesis (AAH) and the prediction that species should produce acoustic signals in the environments where those calls transmit best. I used playback experiments in which I broadcasted calls into different forest types, re-recorded calls along distance transects and statistically compared these experimentally degraded calls to non-degraded exemplars. I found moderate support for the predictions of the AAH and the general prediction that species may evolve advertisement calls that maximize transmission efficacy in preferred microhabitats.

Finally, I mapped call characters on the phylogeny and asked whether "morphological" call characters (e.g., dominant frequency) and "behavioral" call characters (e.g., call rate) have evolved at different rates. Results suggested that some characters evolved more rapidly than others, but there was no clear-cut distinction between morphological and behavioral classes. Nevertheless, patterns of repeated evolution of call types and differential performance of calls in various environments

suggest repeated evolutionary convergence on morphological, ecological, and behavioral traits across replicated radiations of platymantine frogs.

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Chapter 1:

Cryptic species diversity in a large oceanic island frog radiation: partial taxonomic review of Philippine forest frogs of the genus *Platymantis* (Amphibia: Ranidae).

Summary

In this chapter I partially review the Philippine species of the frog genus *Platymantis* with an effort to apply new systematic characters to the problem of species boundaries. I recognize 51 putative independent evolutionary lineages, 26 of which I suspect will eventually be described as new species. The resulting taxonomic changes will represent a doubling of the numbers of Philippine platymantines and a 26% percentage increase in the total amphibian fauna for this country.

The history of recognition and rate of discovery of species diversity in this remarkable island radiation is notable when we consider that only seven species were recognized following the first comprehensive review of Philippine frogs (Inger, 1954), that 12 were recognized as late as the early 1990s (Alcala, 1986), and only 24 were recognized by the year 2000 (Alcala and Brown, 1998, 1999). Philippine *Platymantis* species are characterized by extremely high levels of local endemism (i.e., single island and/or mountaintop endemics) and an extraordinarily high degree of morphological

conservatism. Most of the new discoveries are cryptic species that have only been recognized with increasing attention to advertisement calls and biogeographical predictions. Philippine *Platymantis* species are one of the earth's major oceanic island archipelago frog radiations; I expect that many new species will be discovered in the near future and that many others may have recently gone extinct (before their discovery) due to activities of humans, specifically the destruction of low elevation habitats in the Philippines.

"My impression is that there are more undescribed species of Philippine *Platymantis* than you, Angel and Arvin can describe if you worked non-stop for the next 10 years. Rather than view it as a problem of 'dividing up' the new species, why not consider it a question of how much you can all accomplish together?" (Walter Brown, 1998, *pers. comm.*).

Introduction

The platymantine ranids are a diverse assemblage of frogs endemic to SE Asia, and the SW Pacific (Inger, 1954; Frost, 1985; Dubois, 1981, 1987, 1992; Allison, 1996; Inger and Tan, 1996; Brown, 1997). Platymantines are noted for their unusual geographic distribution (Fig. 1.1; Allison, 1996; Brown, 1997), highly variable and unique morphology (Noble, 1931; Inger, 1954; Gorham, 1965), direct larval development (Tyler, 1979; Brown and Alcala, 1982b; Brown et al, 1997a), and their ability to colonize habitats that otherwise conspicuously lack ranid frogs (Inger, 1954; Ota and Matsui, 1985). Additionally, species of *Platymantis* have been noted for their microhabitat diversity in various rainforest strata and their complex and unusual advertisement calls (Menzies, 1982; Boistel and Sueur, 1997; Brown et al., 1997a, 1997b, 1997c; Alcala et al. 1998).

The Philippine frogs of the genus *Platymantis* have suffered considerable taxonomic instability since their first descriptions appeared in print (e.g., Tschudi, 1838; Brown and Inger, 1964; Zweifel, 1967, 1969). Although Taylor (1920, 1922a, 1922b, 1923, 1925) recognized nearly 20 species, Inger (1954) submerged many of these and argued that only seven species were valid at the time of his review of Philippine frogs (Inger, 1954). Brown and Alcala (1963, 1970a, 1970b, 1974, 1982) increased that number to 12 by the early 1990s with new species descriptions of morphologically distinct forms, most of which were single-island endemics (Alcala, 1986). Discoveries in the early to mid-1990s (Brown et al, 1997a, 1997b, 1997c, 1997d, 1998, 1999a, 1999b; Alcala et al., 1998; Allison, 1996; Brown, 1997) drastically increased the number of species from the Philippines, and as many as 24 species were recognized by the year 2000 (Alcala and Brown, 1998, 1999).

Over the course of my dissertation fieldwork in collaboration with Arvin Diesmos and Angel Alcala, we have identified an additional 26 putative new taxa in the genus *Platymantis* from the Philippines. It is the purpose of this paper to partially review that fauna, such that an understanding of the lineage diversity in this group will be possible for related phylogenetic and biogeographic analyses and comparative studies of the tempo of call character evolution.

A major challenge for identification of lineages of Philippine *Platymantis* is the apparent lack of salient morphological characters on which to base diagnoses of species identity. The apparent presence of morphological conservatism and prevalence of cryptic speciation in this group has clearly been the major source of disagreement among earlier authors (e.g., Taylor 1920; Inger, 1954) and the major reason behind Brown and Alcala's (e.g., Alcala 1986; Brown, 1997) conservative approach to appraisal of the Philippine species. In the current study, I bring new characters to bear on the problem of species identification in Philippine *Platymantis* and provide a partial review of the group such that related phylogenetic and comparative studies can be carried out (Chapts. 4–6). It is not the purpose of this chapter to provide a thorough technical taxonomic review of Philippine *Platymantis* but rather to enumerate what I consider independent lineages for the purposes of my larger study of acoustical and functional variation in advertisement call variation in the group. Because of my perspective, I do believe that all will be recognized eventually as independent evolutionary lineages (Frost and Hillis, 1990; de Queiroz 1998, 1999), worthy of taxonomic rank. But the task of providing exhaustive and comprehensive technical descriptions of each species will have to await a thorough review of the genus in the Philippines, and that is a work in progress (Brown, Diesmos, and Alcala, unpublished data).

Materials and Methods

I conducted fieldwork targeted at estimating *Platymantis* species diversity between the years 1998 and 2002 throughout the Philippines (Fig. 1.2). Some observations and natural history data I used were accumulated between the late 1950s and early 1990s as part of Angel Alcala's and Walter Brown's collaborative research program in Philippine herpetology, and some were taken as part of my own Masters fieldwork between 1995 and 1997 (Brown and Guttman, 2002).

During nocturnal fieldwork and data collection, emphasis was placed on preliminarily identifying putative species by diagnostic elements (spectral or temporal characteristics of the advertisement call, unique notes, syllables, or call prefixes) of the advertisement call and then attempting to confirm species identity by quantifying behavior, microhabitat preference, activity patterns, reproductive characteristics, and diagnostic morphological characteristics in life and, later, in preserved specimens. I collected a series of specimens per putative species, described color in live animals before preservation, collected tissue samples for molecular studies, and preserved specimens for subsequent morphometric studies.

I examined live and fluid-preserved specimens now deposited in the collections at the California Academy of Sciences (CAS), the Harvard University Museum of Comparative Zoology (MCZ), the Field Museum of Natural History (FMNH), the United States National Museum (USNM), the National Museum of the Philippines (PNM), the Carnegie Museum of Natural History (CM), the Cincinnati Museum of Natural History

(CMNH), the Silliman University Biology Museum (SUBM), and the Texas Natural History Collections at the Texas Memorial Museum (TNHC) at the University of Texas (museum acronyms follow Leviton et al., 1985). Data on diagnostic morphological character states were scored from specimens (including types of as many species as possible), and mensural character measurements (Matsui, 1984; Chapter 2) were taken for univariate and multivariate analyses of morphological variation (not presented here).

Other qualitative morphological characteristics considered include color pattern, dermal ornamentation, and size and shape of subdigital tubercles on hands and feet. All measurements were taken to the nearest 0.1 mm (with digital calipers and microscope when necessary) from sexually mature adults, and sex was determined by gonadal inspection when necessary and possible. Only data scored by myself were used in an effort to reduce inter-measurer inconsistencies (Lee, 1982, 1990; Hayek et al., 2001). Analyses of morphological characters were performed using Statview^{TM} (Abacus concepts, 1992) software.

Advertisement calls were recorded with a Sony™ WM DC6 Professional Walkman with a Sennheiser™ ME80 condenser microphone (equipped with K3U power module). Calls were recorded at distances of approximately 1.5 m, and temperatures (ambient, substrate, and cloacal) were recorded immediately after recording. Calls were digitized and analyzed using Soundedit$^{©}$ (Macromedia, 1995) and analyzed using Canary$^{©}$ (Charif et al., 1996) software. I examined oscillograms (waveforms), audiospectrograms (sonograms), and results of the Fast Fourier Transformation (FFT;

power spectrum) for a variety of temporal and spectral characters (Chapt. 3) and used these to form the basis of initial diagnoses for each species.

Molecular data (12S and 16S ribosomal RNA mitochondrial gene sequences (Chapt.4) were also useful for distinguishing between cryptic species when two morphologically or acoustically similar forms did not fall out together in phylogenetic analysis (Wiens, 1993; Brown and Guttman, 2002; Evans et al., 2003; see Chapter 4). Thus, phylogenetic information also contributed to lineage diagnoses in several cases (McGuire & Kiew, 2001; Brown and Guttman, 2002) where cryptic variants were not sister species or divergence levels between previously-considered conspecifics were unexpectedly high (Chapt. 4).

For the purpose of this partial review I relied heavily on expectations based on an understanding of the biogeography of the Philippines (Heaney, 1985, 1986; Hall, 1996; Brown and Diesmos, 2002; Brown and Guttman, 2002; Evans et al., 2003). Recent studies have shown that the distributions of amphibians and reptiles in the Philippines have been strongly influenced by the mid- to late-Pleistocene formation of aggregate island complexes, as well as by climatic variation associated with elevational gradients. Each Pleistocene Aggregate Island Complex (PAIC; Brown and Diesmos, 2002) is a major center of biological diversity, and within these major (and several other minor) land mass amalgamations, there exist numerous sub-centers of endemism (review: Brown et al., 2002a; Evans et al., 2003). Because of the known geological history of the Philippines, predictions concerning the patterns and processes behind the generation of biodiversity can made with reasonable confidence (Brown and Diesmos, 2002; Brown et al., 2002a; Brown and Guttman, 2002). As such, colleagues and I have looked for new species where we have expected to find them—on isolated and unsurveyed islands and mountains. I adopt the General Lineage Concept (de Queiroz 1998, 1999; see also Simpson [1961] Wiley [1978], and Frost & Hillis [1990]) and consider a species a lineage of ancestor-descendant populations with a unique evolutionary history and predictable evolutionary future or fate. Recently, de Queiroz (1998, 1999) demonstrated that all modern species concepts are consistent with a simple, unified principal of species as population-level lineage segments. De Queiroz (1998, 1999) suggested that species be described by the properties they acquire during the process of speciation (i.e., not by rigid, formulaic, predetermined criteria). I agree with the advantages of this general framework and find it particularly appropriate in the context of the insular nature of populations in the Philippines (McGuire and Alcala, 2000; Brown & Diesmos, 2001). Accordingly, taxa that I propose as independent lineages possess fixed and diagnostic phenotypes (morphology, color, advertisement calls) and either occur sympatrically (with no evidence of intergradation) or allopatrically on separate PAICs. Each PAIC is separated by deep water (≥ 120 m) channel depths (Heaney, 1985; Hall, 1996; Evans et al., 2003), and each possesses a known history of isolation, precluding recent dry-land connections (Hall, 1996).

For the purposes of this chapter, I consider as distinct lineages populations that are (1) geographically isolated as insular endemics that are morphologically, behaviorally, acoustically, and genetically distinct and (2), sympatric, reliably diagnosable populations for which the hypothesis of conspecificity confidently can be rejected by analyses of morphological, genetic, and advertisement call data (Frost & Hillis, 1990; Wiens, 1993).

Results

I recognize a total of 51 Philippine species in the genus *Platymantis*. In all but a few cases, I have no doubt as to the validity of each as a separate, diagnosable evolutionary lineage with clear ancestor-descendant lineage integrity/cohesion and a lack of any evidence of intergradation with similar forms.

The following enumeration of proposed lineages is presented in several forms. First, I present a brief species account with information on each putative species. I also present a series of tabular summaries (Table 1.1) of each putative species by "species group" (*sensu* Brown et al., 1997a; see Ecomorphology Chapt. 2). I include a convenient onomatopoeic reference (Table 1.1) for each putative species, focusing on the advertisement call as one of the most convenient means of diagnosing platymantines.

Species accounts included here are not intended to provide full technical information or species descriptions. Instead I provide a list of specimens examined, a skeletal diagnosis that emphasizes only the morphological and acoustic characteristics that distinguish the species from other phenotypically similar forms, and information on the current known distribution of the species. Full species descriptions, synonymies, comparisons sections, and justifications for the recognition of each species will be provided elsewhere (Brown, Diesmos, and Alcala, unpublished data).

Although I recognize the non-phylogenetic nature of “species groups” based on gestalt and not explicitly phylogenetic or derived character statements, I organize species accounts that follow into the general groups described by Brown et al. (1997a) for convenience.

Species accounts

Litter frogs – the *P. dorsalis* group

Platymantis cagayanensis, Brown, Alcala, and Diesmos, 1999b.

Holotype.—PNM 6691. Type locality: "disturbed Dipterocarp forest in Taggat Forest Reserve in Santa Praxedes Town, Central Cordillera, Cagayan Province, Luzon, at 50-100 m elevation", Philippines.

Paratypes.—CAS 207447–451, PNM 6692–93, and SUBM 2321–22, collected with Holotype on the same date.

Referred specimens.— Palaui Isl., Cagayan Prov., Municipality of Santa Anna, Barangay, Palaui: PNM 7508 (RMB 4242), PNM 7506-07 (RMB 4241-42), PNM 7525-

26 (RMB 4259-60), PNM 7496-99 (RMB 4230-33), PNM 7522 (RMB 4256), PNM 7564 (ACD 1447). Luzon Isl., Ilocos Norte Prov., Municipality of Pagudpud, Barangay Pansian: PNM 7578 (ACD 1461).

Definition.—A moderately-sized member of the *P. dorsalis* group, SVL 26.4–30.8 mm for seven males and 34.7–37.4 mm for two females (Brown et al., 1999b). Advertisement call: "Cree-eek…cree-eek." Dorsum deep reddish brown, with darker pigmentation associated with short dorsal ridges in scapular region; limbs barred dark brown; dorsal edge of tympanum with crescent-shaped black marking.

Comment.—Among Philippine *Platymantis*, this species' advertisement call is quite unique. There is no other known species possessing a similar advertisement call.

Ecology.—Males of this species call from limestone rocks and other low perches above ground level in primary and mature secondary forest along the north coast of Luzon and Palaui islands. On Palaui, calling activity begins before sunset and lasts until well past 2200 hr (Brown and Diesmos, unpubl. data)

Platymantis corrugata, (A. Duméril, 1853).

Hylodes corrugatus A. Duméril, 1853, Ann. Sci. Nat., Paris, (3)19: 176.

Platymantis corrugata Günther, 1999, Mitt. Mus. Naturkd., Berlin, Zool., 75: 327-328, by implication.

Platymantis corrugatus corrugatus Loveridge, 1948, Bull. Mus. Comp. Zool., 101: 406; Zweifel, 1967, Copeia, 1967.

Rana (Platymantis) rugata Van Kampen, 1923, Amph. Indo-Aust. Arch.: 190.

Platymantis corrugata. Boulenger, 1918, Ann. Mag. Nat. Hist., (9)1: 373.

Hylodes (Batrachyla) corrugatus Cope, 1862, Proc. Acad. Nat. Sci. Philadelphia, 14: 154.

Halophila (Platymantis) plicifera Peters, 1863, Monatsber. Preuss. Akad. Wiss. Berlin, 1863: 176.

Platymantis plicifera Günther, 1858, Arch. Naturgesch., 24: 327. Syntypes: BM (4 specimens) according to Günther, 1859 "1858", Cat. Batr. Sal. Brit. Mus.: 95. Type locality: "Philippinen". Synonymy by Peters, 1873, Monatsber. Preuss. Akad. Wiss. Berlin, 1873: 611; Boulenger, 1882, Cat. Batr. Sal. Brit. Mus.; 110; Van Kampen, 1923, Amph. Indo-Aust. Arch.: 190; Inger, 1954, Fieldiana: Zool., 33: 351-352.

Cornufer corrugatus Boulenger, 1882, Cat. Batr. Sal. Brit. Mus.: 110; Brown, 1965, Breviora, 218: 2.

Platymantis corrugata Peters, 1873, Monatsber. Preuss. Akad. Wiss. Berlin, 1873: 611; Boulenger, 1918, Ann. Mag. Nat. Hist.,1: 373.

Holotype.—MNHNP 4884, according to Guibé, 1950 "1948", Cat. Types Amph. Mus. Natl. Hist. Nat.: 40. Type locality: "Java," in error, according to Inger, 1954, Fieldiana: Zool., 33: 351-352, who suggested that the holotype originated in the Philippines. Placed on the Official List of Specific Names in Zoology by Opinion 1104, 1978, Bull. Zool. Nomencl., 34: 223.

Referred specimens.—Philippines, **Negros** Isl., Negros Oriental Prov., Cuernos de Negros (female, DSR col): FMNH 1731174; Negros Isl., Negros Occidental Prov., Canlaon Volcano: FMNH 22508 (m, EHT Dec 1915); Philippines, Negros Isl., Negros Oriental Prov., Municipality of Valencia, Barangay Bongbong, Camp Lookout, Cuernos de Negros Mt. Range, Mt. Talinis, 500 m: TNHC 61972 (RMB 3232-F), TNHC 61973 (RMB 3233-F), TNHC 61974 (RMB 3234-F), TNHC 61975 (RMB 3235), TNHC 61976 (RMB 3260); **Luzon** Isl, Sorsogon Prov., Municipality of Bulusan Barangay San Roque, Bulusan Volcano (12°24’40”N, 124°2’E) 600 m: FMNH 251646–47, 251649; 750 m: FMNH 251651; Camarines Sur Prov., Municipality of Naga City, 4 km N, 18 km E Naga City(13°40’N, 123°20’E), Mt. Isarog, 450 m: FMNH 251654–55, 251657; Philippines, Catadnduañes Isl., Catanduañes prov., Municipality of Gigmoto, 1 km S, 4 km W Gigmoto Town (13°40’N, 124°21’E), 450 m: FMNH 24802; Philippines, Luzon Isl., Zambales Prov., Municipality of Olongapo, Subic Bay Metro Authority Naval Base, “Nav-Mag” area, Ilanin Forest, Triboa Bay: TNHC 61988 (RMB 4489); Philippines, Luzon Isl., Sorsogon Prov., Municipality of Irosin, Barangay San Roque, Mt. Bulusan National Park, Lake Bulusan, Mt. Bulusan 350 m: TNHC 61986 (RMB 4008); 700 m: TNHC 61987 (RMB 4046), TNHC 61985 (RMB 3968 – f); Philippines, Luzon Isl., Quezon Prov., Municipality of Atimonan, Barangay Malinao Ilaya, boundary of Quezon National Park: TNHC 62177 (RMB 4069), PNM XXXX (RMB 4098); Philippines, Luzon Isl., Camarines Sur Prov., Municipality of Naga City, Barangay Panicuason, Mt. Isarog National Park, Mt. Isarog, 450 m: CMNHXXXX (RMB 208, 214, 213); TNHC 61977 (RMB 3330), PNM XXXX (RMB 3331), TNHC 61978 (RMB 3332), TNHC 61979 (RMB 3333), PNM XXXX (RMB 3414), TNHC 61980 (RMB 3416), PNM XXXX (RMB 3417); Philippines, Luzon Isl., Albay Prov., Municipality of Tobaco, Barangay, Bongabong: TNHC 61981 (RMB 3606); Philippines, Luzon Isl., Quezon Prov., Municipality of Tayabas, Barangay Lalo, Mt. Banahao : TNHC 61982 (RMB 3633), TNHC 61983 (RMB 3634), PNM XXXX (RMB 3659); Barangay Tagoytoy, Sitio Kumangingking, Area Mina-abaga, Mt. Malinao 700 m: TNHC 61984 (RMB 3869); **Siquijor** Isl., Siquijor Prov., Municipality of Siquijor, Barangay Kang-Adiang: TNHC 56440 (RMB 1112), TNHC 56441 (RMB 1113), TNHC 56442 (RMB 1114), TNHC 56443 (RMB 1115), TNHC 56444 (RMB 1116), TNHC 56445 (RMB 1117), TNHC 56446 (RMB 1118), TNHC 56447 (RMB 1119), TNHC 56448 (RMB 1120 – f), TNHC

56449 (RMB 1121), TNHC 56450 (RMB 1122), TNHC 56451 (RMB 1123), TNHC 56452 (RMB 1124), TNHC 56453 (RMB 1125), TNHC 56454 (RMB 1126), TNHC 56455 (RMB 1127), TNHC 56456 (RMB 1128), TNHC 56458 (RMB 1130), TNHC 56459 (RMB 1131).

Definition.—A moderately-sized member of the *P. dorsalis* group, SVL 23.3–27.8 for 14 males and 35.6–47.3 for seven females. Advertisement call: "Whaah…whaah…whaah." Dorsum flat homogeneous blond to gray with occasional black pigmentation associated with short dorsal ridges in scapular region; entire lateral side of head black, giving the appearance of a dark mask.

Comment.—With little locality data other than "Philippinen" available for this name, I somewhat indiscriminately apply the name *P. corrugata* to the closest population to Manila: the low elevation masked frog of Luzon. Frogs of this species assemblage (includes *P. corrugata, P*. sp. cf "jagori," and *P*. n. sp. cf corrugata (Mindoro) differ morphologically from other Philippine species by the possession of a distinctly prominent jaw in ventral aspect and the variable presence of a dark mask or partial mask covering lateral portions of the head and snout (see below).

Ecology.—Males of this species concentrate calling activity into a 30–45 m period at dusk. They call singly from underneath dry leaves on the forest floor or within crevices in limestone.

Platymantis sp. cf "*jagori*" (Peters, 1863).

Halophila jagorii Peters, 1863, Monatsber. Preuss. Akad. Wiss. Berlin, 1863: 456; Brown and Inger, 1964 , Copeia, 1964: 450-451.

Cornufer jagorii Boulenger, 1882, Cat. Batr. Sal. Brit. Mus.: 109

Holotype.—ZMB 4914 according to Bauer, Günther, and Klipfel, 1995, Herpetol. Contrib. W. C. H. Peters: 48; Type locality: "Insel Samar," Philippines; formerly tentatively identified as a senior synonym of *Platymantis meyeri* by Inger, 1954, Fieldiana: Zool., 33: 354.

Referred specimens.— Philippines, **Mindanao**, "Cotobato, Saub:" FMNH: 106190-91, 174338; Samar Isl., Samar Prov., "Matuquinao, Tarabucan:" FMNH 96240, 96242, 96254; Mindanao, Cotobato Prov., "Buayan, Conel, 100': FMNH 50567; Davao City Prov., Municipality of Todaya, Mt. Apo 2800': FMNH 50532–34, 50536, 50538–41, 50543; Davao City Prov., "Tagum, Sitio Taglawig" near sea level: FMNH

50544–45; Cotobato Prov.,”Upi, Burungkot:” FMNH 50547; Cotobato Prov., “Buayan, Conel:” FMNH 50550; Sarangani Prov., Municipality of Kiamba: PNM/CMNH H2065; New Bataan Prov., Mt. Puting Bato: PNM/CMNH H2346; S. Cotobato Prov., Municipality of Kiamba, Barangay Binati, Mt. Busa, 950 m.: PNM/CMNH H1548, H1585; **Leyte** Isl., Leyte Prov., : Inayupan, near Abuyog:” FMNH 42885; Leyte Isl., Leyte Prov., Municipality of Baybay, Barangay Guadalupe, Visayan State University, Forestry Department Nursery area: PNM 7694 (RMB 4336), PNM 7695 (RMB 4337), PNM 7696 (RMB 4338), PNM 7697 (RMB 4339), PNM 7698 (RMB 4340), PNM 7699 (RMB 4341), PNM 7724 (RMB 4366 – f), PNM 7791 (ACD 1498), PNM 7792 (ACD 1499 – f), PNM 7802 (ACD 1509 – f), PNM 7790 (ACD 1497), PNM 7813 (ACD 1520); **Bohol Isl.**, Bohol Prov., Municipality of Carmen, Barangay Riverside: TNHC 56425 (RMB 1039 – f), TNHC 56426 (RMB 1040), TNHC 56427 (RMB 1041 – f), TNHC 56428 (RMB 1042), TNHC 56429 (RMB 1043), TNHC 56870 (RMB 1044); Barangay Villa Aurora (near boundary with Bilar): TNHC 56360 (RMB 1095 – f), TNHC 56361 (RMB 1096), TNHC 56362 (RMB 1097 – f), TNHC 56363 (RMB 1098 –f), TNHC 56364 (RMB 1099 – juv), TNHC 56365 (RMB 1100), TNHC 56366 (RMB 1101), TNHC 56367 (RMB 1102).

<u>Definition</u>.—A moderately-sized member of the *P. dorsalis* group, SVL 24.6–28.8 for 21 males and 36.9–42.1 for seven females. Advertisement call: “Weeah-weeah-weeah… weeah-weeah- weeah….” Dorsum flat dark gray with black streaks associated with longitudinal dorsal ridges across dorsal surfaces of body; supra-tympanic fold and

canthus rostralis bordered ventrally with black, giving the appearance of an incomplete, thin dark mask.

Comment.—The frog from the Mindanao PAIC that has been referred to *P. corrugata* for the past 40+ years clearly is a distinct species from that found on S. Luzon (presumably true *P. corrugata*). *P. jagori* and *P. plicifera* are the names available for this population. For the present, I refer to this population as *P. jagori* because the description (Peters 1863) matches observed variation, although *P. plicifera* (Gunther, 1858) may be the appropriate name if the type locality can be traced.

Ecology.—Males of this species concentrate calling activity into a 30–45 m period at dusk. They call singly from underneath dry leaves on the forest floor.

Platymantis, n. sp. cf corrugata, Mindoro

Holotype.— Philippines, Mindoro Isl., Oriental Mindoro Prov., Municipality of XXXX, Barangay XXXX, Dulanan River, Mt. Halcon, 1350 m: PNM XXXX (H876, formerly CMNH 5176), collected by R. M. Brown and R. V. Sison 3 June 1992.

Paratopotypes.— PNM 2777 (H861 30 May), PNM 2778 (H835 28 May), PNM 2779 (H864 31 May), PNM 2780 (PNM/CMNH H817), PNM 2781 (H819 28 May), PNM

2782 (H860 – f 30 May), PNM 2783 (H805 27 May), PNM 2784 (H809 27 May), PNM 2785 (H843 29 May), PNM 2786 (H830 28 May), PNM 2787 (H844 29 May), PNM 2788 (H828 28 May), PNM 2790 (H851 – juv 29 May), PNM 2791 (H833 28 May), PNM 2792 (H868 31 May), PNM 2797 (H831 28 May), PNM 2794 (28 May), PNM 2795 (H873 30 April), PNM 2797 (H805 26 May), CMNH 5160–5171 (H834 28 May)

Referred Specimens.—Philippines, Mindoro Isl., Oriental Mindoro Prov., "near edge of San Jose, 500 yrds from Bugsanga River:" FMNH 60827–28 (small males, E. S. Ross col, 16 March 1945); TNHC 54941 (JAM 878); Lantuyan: PNM 2796 (H965 – juv 15 June), PNM 2798 (H914 8 June)

Definition.— A larger member of the *P. dorsalis* group, SVL 34.4–41.3 for 31 males and 38.7–47.2 for eight females; Advertisement call: "Whak-whak…whak-whak," dorsal surfaces of body uniformly light, with slightly darker streaks associated with longitudinal ridges, stretching across most of body; limbs usually unbarred, lips barred, slightly darker dorsal mask, reminiscent of *P. corrugata* but much lighter, usually incomplete.

Comment.—This species is larger, more variable in color pattern, and possesses a less distinct dark mask than *P. corrugata*. It also appears to have far fewer dorsal dermal ridges and its skin appears smoother to the unaided eye.

Ecology.—This species calls in large, loose congregations in valleys surrounding small streams primary forest and in a variety of conditions in secondary or disturbed forest.

Platymantis dorsalis (A. Duméril, 1853)

Cornufer dorsalis A. Duméril, 1853, Ann. Sci. Nat., Paris, (3)19: 174.

Platymantis dorsalis Zweifel, 1967, Copeia, 1967: 120.

Cornufer dorsalis Brown, 1965, Breviora, 218: 2.

*Rana (Platymantis) dorsali*s Guibé, 1950 "1948," Cat. Types Amph. Mus. Natl. Hist. Nat.: 41.

Cornufer jagorii Boulenger, 1882, Cat. Batr. Sal. Brit. Mus.: 109.

Halophila jagorii Peters, 1863, Monatsber. Preuss. Akad. Wiss. Berlin, 1863: 456

Halophila platydactyla Günther, 1864, Proc. Zool. Soc. London, 1864: 49; Boulenger, 1882, Cat. Batr. Sal. Brit. Mus.: 108.

Hylodes (Batrachyla) dorsalis Cope, 1862, Proc. Acad. Nat. Sci. Philadelphia, 14: 154.

Holotype.—MNHNP 4880. Type locality: "Java;" in error according to Barbour, 1923, Proc. Acad. Nat. Sci. Philadelphia, 75: 112, who corrected the type locality to Fiji.

Referred specimens.— **Negros** Isl**.**, Negros Oriental Prov., Municipality of Valencia, 3.5 km S and 6.5, km W Valencia Town (9°16’N, 123°12’E), Mt. Talinus 1450 m: FMNH 247742, 247746–48; Cuernos de Negros, Camp Lookout, 1500–4500’: FMNH 77890–02, 77727; “Talong, Naliong:” FMNH 62904–06; Negros Oriental Prov., Municipality of Valencia, Barangay Bongbong, Cuernos de Negros, Mt. Range, Mt. Talinis, Camp Lookout, 500 m: TNHC 62099 (RMB 3236), TNHC 62097 (RMB 3239), TNHC 62098 (RMB 3242), TNHC 62095 (RMB 3258), TNHC 62088 (RMB 3259), TNHC 62096 (RMB 3261), TNHC 62086 (RMB 3238), TNHC 62087 (RMB 3240), TNHC 62085 (RMB 3241), TNHC 62084 (RMB 3243), TNHC 62090 (RMB 3244), TNHC 62100 (RMB 3262), TNHC 62394 (RMB 3271), TNHC 62393 (RMB 3237-F); Negros Oriental Prov., Municipality of Valencia, Sitio Nasuji, Cuernos de Negros Mountain Range, PNOC-EDC Watershed Area, Mt. Talinis, 1150 m: TNHC 62089 (RMB 3327), TNHC 62101 (RMB 3328); Lake Balinsasayo, 3000’: FMNH 61603; Negros Oriental Prov., Municipality of Sibulan, Barangay Janay-janay, Sitio Balinsaysayo, Cuernos de Negros Mountain Range, Lake Balinsasayo, 850 m: TNHC 62128 (RMB 4115); Municipality of Bais, Barangay Pagyabunan, 1000’: FMNH 61412 (m, DS Rabor, 10 May 1949; 61601–02 (m, DS Rabor 8 May 1949); “Amio, Pamoat:” FMNH 57277 (m, DS Rabor, 5

May 1948); **Panay** Isl., Antique Prov., Municipality of Valderrama, Barangay Lublub, Mt. Baloy, 600 m.: TNHC 56347 - TNHC 56350 (RMB 1012-1015); Panay Isl., Antique Prov., Municipality of Culasi, Barangay Alojipan, “Hangud Tubig,” Mt. Madja-as, 600-900 m: CMNH 4964 (H509), CMNH 4965 (H598), CMNH 4966 (H595), CMNH 4967 (H457), CMNH 4968 (H541), CMNH 4969 (H505), CMNH 4970 (H456), CMNH 4971 (H506), CMNH 4972 (H465), CMNH 4973 (H511), CMNH 4974 (H463), CMNH 4975 (H462), CMNH 4976 (H460), CMNH 4977 (H628), CMNH 4978 (H629), CMNH 4979 (H512), CMNH 4980 (H508), CMNH 4981 (H507), CMNH 4982 (H592), CMNH 4983 (H602), CMNH 4984 (H591), CMNH 4985 (H599), CMNH 4986 (H555), CMNH 4987 (H626), CMNH 4988 (H469), CMNH 4989 (H461), CMNH 4990 (H459), CMNH 4991 (H593), CMNH 4992 (H510), CMNH 4993 (H630), CMNH 4994 (H603), CMNH 4995 (H610), CMNH 4996 (H464); **Luzon** Isl., Laguna Prov., Municipality of Los Baños, Barangay Batong Malake, Mt. Maquiling, 800 m: FMNH 260354; 1000 m: FMNH 51311; Mt. Makiling: 22000, 22507, 110364, 110368, 110370–71; PNM/CMNH H2118, RMB 2240, 2185-87, 2803-2804; Luzon Isl., Sorsogon Prov., Municipality of Irosin, Barangay Manban, Sitio San Benon, 4 km NNE Irosin Centro, Mateo Hot and Cold Springs Resort, edge of Mt. Gapayao: TNHC 54934 (JAM 757), TNHC 54935 (JAM 758), TNHC 54936 (JAM 759), TNHC 54937 (JAM 760), TNHC 54938 (JAM 761), TNHC 54939 (JAM 762), TNHC 54940 (JAM 764); Luzon, Aurora Prov., Municipality of San Luis, Dipiningan branch of the Cobatangan (= ”Kabatangan” of Brown et al., 1999b) River drainage; 1.2 km S, 1.3 km E of Barangay Villa Aurora; 15° 40.2 N, 121° 20.8 E; *ca* 410–650 m above sea level: CMNH XXXX (JWF 97125, RMB 966, 714, 775, 733, 915, 702, 777, 779, 776, 851, 848, 833, JWF 97154); Camarines Sur Prov., Municipality of Goa, Baraangay Hiwacloy, Mt. Isarog: FMNH 251667; Municipality of Naga Cit (4 km N, 18 km E Naga City (13°40'N, 123°20'E), Mt. Isarog, 450 m: FMNH 256158, 251656; Municipality of Naga City, Barangay Panicuason, Mt. Isarog National Park, Mt. Isarog, 450 m.: TNHC 62093 (RMB 3334), TNHC 62092 (RMB 3335), PNM XXXX (RMB 3433), CMNH XXXX (RMB 185, 182, 126, 184, 180, 186, 178, 130, 188, 183, 181, 179, 127, 187, 125, 176, 128, 177, 215, 126; Mt. Isarog, 825 m: TNHC 62091 (RMB 3369), TNHC 62094 (RMB 3370); Luzon Is., Sorsogon Prov., Municipality of Irosin, Barangay San Roque, Mt. Bulusan Natural Park, Lake Bulusan, Mt. Bulusan, 325 m.: PNM XXXX (RMB 3966), PNM XXXX (RMB 3967), TNHC 62173 (RMB 4006), TNHC 62121 (RMB 3929), TNHC 62123 (RMB 3930), TNHC 62119 (RMB 3931), TNHC 62122 (RMB 3932), TNHC 62124 (RMB 3960), TNHC 62120 (RMB 3965), TNHC 62118 (RMB 3985), TNHC 62125 (RMB 4007); Mt. Balusan, 700 m: PNM XXXX (RMB 4053); Luzon Isl., Albay Prov., Municipality of Tiwi, Barangay Banhaw, Sitio Purok 7, Mt. Malinao, 550 m: TNHC 62103 (RMB 3558), TNHC 62104 (RMB 3560), TNHC 62102 (RMB 3557), PNM XXXX (RMB 3553), PNM XXXX (RMB 3556), PNM XXXX (RMB 3559); Municipality of Malinao, Barangay Togoytoy, Sitio Kumangingking, Mt. Malinao, 700 m: TNHC 62115 (RMB 3826), TNHC 62116 (RMB 3837), TNHC 62112 (RMB 3880), TNHC 62113 (RMB 3884), TNHC 62117 (RMB 3828), PNM XXXX (RMB 3823), PNM XXXX (RMB 3844), PNM XXXX (RMB 3867); Albay Prov., Municipality of Tobaco, Barangay Bongabong: TNHC 62111 (RMB 3605), TNHC 62108 (RMB 3604), PNM XXXX (RMB 3607); Luzon Isl, Quezon Prov., Municipality of Tayabas, Barangay Lalo, “Camp 1,” Mt. Banahao, 600 m: TNHC 62107 (RMB 3613), TNHC 62109 (RMB 3614), TNHC 62110 (RMB 3617), TNHC 62105 (RMB 3618), TNHC 62106 (RMB 3619), PNM XXXX (RMB 3635); Luzon Isl, Quezon Prov., Municipality of Atimonan, Barangay Malinao Ilaya, boundary of Quezon National Park: PNM XXXX (RMB 4081, 4087), PNM XXXX (ACD 1250), PNM XXXX (ACD 1251), PNM XXXX (ACD 1253), TNHC 62126 (RMB 4073), TNHC 62127 (RMB 4074); **Polillo** Isl., Quezon Prov., Municipality of Polillo, Barangay Sibucan, Sitio Tambangin: TNHC 54942 (JAM 965).

Definition.—A moderately-sized member of the *P. dorsalis* group, SVL 22.6–26.9 for 18 males and 31.2–38.7.1 for 14 females. Advertisement call: “Sweet!…sweet!” Dorsum highly variable in color and with raised longitudinal dorsal ridges.

Comment.—Although the type locality for this species is unclear or unknown, I suspect that this name applies to the common low-mid elevation frog found on S. Luzon. This species can be found close to Manila and was accessible to early collectors who based their efforts nearly exclusively in the (now destroyed) forests immediately surrounding Manila Bay. I refer numerous questionable populations to this species and hold in abeyance taxonomic designation of these forms until further study. For the present study, all frogs possessing typical frequency sweep calls (including the frogs with paired sweeps from the Visayan islands) are referred to *P. dorsalis* with the expectation that future studies will prove many of these to be distinct.

Ecology.—Males of this species call from the ground and perches (≤ 2 m) on stumps, stream banks, and large vines encircling larger trees. Calling activity can last from sunset until 02:00 hr the next morning.

Platymantis indeprensus Brown, Alcala, and Diesmos, 1999.

Platymantis indeprensus Brown, Alcala, and Diesmos, 1999, Proc. California Acad. Sci., 51: 455

Holotype.—CAS 201196. Type locality: "submontane forest on Mt. Banahao, Luzon Island at about 1,080 m," Philippines.

Paratypes.—CAS 201013–14, 201178–83, 201185, 207452–54, PNM 6685–86, SUBM 2325.

Referred specimens.— Philippines, Luzon Isl., Quezon Prov., Municipality of Tayabas, Barangay Lalo, Mt. Banahao, “Hasaan” area, 1275 m: PNM XXXX (RMB 3710), PNM XXXX (RMB 3738), PNM XXXX (RMB 3754), TNHC 61958 (RMB 3712 – f), TNHC 61959 (RMB 3739), TNHC 61960 (RMB 3752); “Camp 1,” Mt. Banahao, 600 m: TNHC 61956 (RMB 3643), TNHC 61957 (RMB 3644).

Definition.—A moderately-sized member of the *P. dorsalis* group, SVL 21.5–27.3 for 14 males and 29.2–33.3 for three females. Advertisement call: "eeyak…eeyak-eeyak….eeyak…eeyak-eeyak." Dorsum highly variable in color and with raised tubercles but no ridges.

Comment.—This species appears most phenotypically and acoustically similar to *P. pseudodorsalis* from 100 m below on the slopes of Mt. Banahao. It differs from that species by the presence of a generalized perching microhabitat preference (vs. ravine bank preference in *P. pseudorsalis*) and by the possession of an advertisement call with both tonal ("eee") and vibrational ("yak") syllables (vs. entirely tonal, and wavering in frequency modulation in *P. pseudodorsalis*).

Ecology.—Males of this species prefer higher perches (1.5–2.0 m), such as broken tree fern stumps, and calling lasts for several hours following sunset.

Platymantis sp., cf "laticeps" (Taylor 1920) Mindanao-Malagos soft frequency sweep frog.

Holotype.— EHT 197, Type locality: "Bunawan, Agusan, Mindanao," not yet traced.

Referred specimens.— Philippines, Mindanao Isl., Davao City Prov., "Davao:" FMNH 172815 (m, EHT col, no date SVL=31.6 mm). Philippines, Mindanao Isl., Davao City Prov., Municipality of Calinan, Barangay Malagos, Malagos Eagle Station: TNHC 59874 (RMB 587), PNM XXXX (RMB 3774, 3781, 3795); Mindanao Is., S. Cotobato Prov., Municipality of Kiamba, Barangay Binati, Mt. Busa, 900 m.: PNM/CMNH H1502, H1595, H1620-F, H1640-F, H1689-F.

Definition.—A moderately-sized member of the *P. dorsalis* group, SVL 24.6–28.3 for seven males and 26.2–31.1 for two females . Advertisement call: "Soo-it…soo-it…soo-it…." Dorsum highly variable in color and with raised tubercles and short, longitudinally oriented ridges.

Comment.—Of the three names applicable to Mindanao PAIC ground frogs, I suspect Taylor's (1920) *P. laticeps* is the most appropriate appellation for this form. The other available names (*P. jagori* and *P. plicifera*) seem to apply to *P. corrugata* group frogs. Additionally, this species has a characteristically wide head that is visible in Taylor's (1920) illustrations of *P. laticeps*. The only other frog that could be confused with this name is the Mindanao n. sp. 1 ("clicker") frog, which is somewhat smaller, and has a narrow head and a limited calling activity pattern concentrated for 30 minutes right at dusk. Thus, this species is much more common and one that I would suspect would be collected by any generalist herpetologist working in central Mindanao.

Ecology.—Males of this species call immediately following the fall of darkness and appear to call for less than two hours following sunset.

Platymantis levigata Brown and Alcala, 1974

Platymantis levigatus Brown and Alcala, 1974, Occas. Pap. California Acad. Sci., 113: 4. Holotype

Platymantis levigata Günther, 1999, Mitt. Mus. Naturkd., Berlin, Zool., 75: 327-328, by implication.

Holotype.—CAS 136097. Type locality: "along stream in secondary forest at about 650 feet elevation, Dubduban, San Agustin, Tablas Island."

Referred specimens.— Philippines, Sibuyan Isl., Romblon Prov., Municipality of Magdiwang, Barangay Tampayan: PNM XXXX-XX (RMB 2928, 2958-59).

Definition.—A larger member of the *P. dorsalis* group, SVL 29.2–37.8.3 for 16 males and 31.2–35.1 for six females . Advertisement call: "Shree-er-ee…shree-er-ee." Dorsum unusually smooth (unique among all terrestrial Philippine *Platymantis*), lacking all tubercles or dermal ridges.

Comment.—This species can be distinguished from all other Philippine terrestrial forms by possession of an entirely smooth dorsum, completely devoid of dermal ornamentation or ridges. In some respects, its wavery tonal advertisement call is most similar to that of *P. pseudodorsalis* from Luzon Island.

Ecology.—Males of this species call in primary and secondary forest, usually in close proximity to stream banks. Calling activity lasts for several hours following sunset.

Platymantis pseudodorsalis Brown, Alcala, and Diesmos, 1999

Platymantis pseudodorsalis Brown, Alcala, and Diesmos, 1999, Proc. California Acad. Sci., 51: 454.

Holotype.—PNM 6689. Type locality: "upper Dipterocarp forest on Mt. Banahao, Luzon Island, Philippines."

Definition.—A moderately-sized member of the *P. dorsalis* group, SVL 22.4–31.5 for 10 males and 28.7–37.2 for four females . Advertisement call: a wavery tonal frequency modulation in two syllables: “Tseeo-lek…Tseeo-lek.” Dorsum unusually lighter than lateral surfaces of body, with dark bars on hindlimbs only.

Comment.—This species is morphologically similar to, and occurs in near parapatry with, *P. indeprensus*. It differs from *P. indeprensus* however, by its distinct, wavering, tonal advertisement call and a unique microhabitat preference.

Ecology.—Males of this species call just before sunset for a period of 30 minutes or slightly more. *Platymantis pseudodorsalis* calls only from the banks of small, dry, arroyo-like creek beds above 900 m (100 m above the range of *P. indeprenssus*) on Mt. Banahao.

Platymantis spelaea, Brown and Alcala, 1982a.

Brown and Alcala, 1982, Proc. Biol. Soc. Washington, 95: 386.

Platymantis spelaea Günther, 1999, Mitt. Mus. Naturkd., Berlin, Zool., 75: 327-328, by implication.

Holotype.—CAS 153469. Type locality: "limestone cave, Tiyabanan Barrio, Basay, southern Negros Oriental, Philippines."

Paratypes.—CAS 153470–83; USNM 221838–39, FMNH 213331, BM 1981.9, MCZ-A 100300, SUBM 2288–92, AMNH 109454.

Referred specimens.—Negros Island, Negros Oriental Prov., Municipality of Basay, Tiyabanan Barrio: PNM 6901–02, CAS 153481; SUBM XXXX-XX (uncatalogued RMB and EA specimens).

Definition.—The largest member of the *P. dorsalis* group, SVL 42.6–52.5 for 11 males and 28.4–58.9 for three females . Advertisement call: “Pee-coh, pee-coh… pee-coh, pee-coh” (Brown et al., 2003a).

Ecology.—*Platymantis spelaea* calls in large, loosely-congregated choruses situated on limestone outcrops, with the greatest concentration of courtship behavior and reproductive activity in the evenings, following heavy rains (Brown et al., 2003a).

Platymantis taylori, Brown, Alcala, and Diesmos, 1999b

Platymantis taylori Brown, Alcala, and Diesmos, 1999, Proc. California Acad. Sci., 51: 451

Holotype.—PNM 6684. Type locality: "disturbed lowland rain forest in eastern Sierra Madre Mountains in Sitio Natapdukan, Barangay Didian, Municipality of Palanan, Isabela Province, Luzon Island," Philippines.

Paratypes.—PNM 6512–13, 6524, 6525–29, 6671, 6674–75, 6687–88, CAS 207440—207446, SUBM 2327.

Definition.—A moderately-sized member of the *P. dorsalis* group, SVL 27.6–28.3 for three males and 37.3 for one female (Brown et al., 1999). Advertisement call: "Kraak….kraaak…kraaaak." Dorsum medium brown, with darker lateral surfaces; ventral surfaces cream with darker reticulum. Canthus and anterior half of tympanum below the supratympanic fold, black. Lips heavily barred with vertical black crossbars.

Ecology.—This species is rare at the type locality and calls singly on the forest floor in leaf litter on nights when atmospheric conditions are humid and quiet.

Platymantis, n. sp. ("clicker;" Malagos + Leyte)

Holotype.— Philippines, Mindanao Isl., Davao City Prov., Municipality of Calinan, Barangay Malagos, Malagos Eagle Station, alt. ??: PNM XXXX RMB (3797), collected by R. Brown and A. Diesmos 9 November 2001 (1800 hr).

Paratopotypes.— PNM XXXX (RMB 3775), same data as holotype except collected 7 November 2001 (2320 hr), PNM XXXX (RMB 3785), same data as holotype except collected 8 November 2001 (1800 hr), PNM XXXX (RMB 3786), same data as holotype except collected 8 November 2001 (2030 hr), PNM XXXX (RMB 3796), same data as holotype except collected 1730 hr, PNM XXXX (RMB 3801), same data as holotype except collected 8 November 2001 (1745 hr); Leyte Isl., Leyte Prov., Municipality of Baybay, Barangay Guadalupe, Leyte State University campus, Calbiga-a Creek: PNM 7712? (RMB 4354), PNM 7800 (RMB 1507), PNM 7801 (ACD 1508).

Referred Specimens.— Philippines, Mindanao Is., S. Cotobato Prov., Municipality of Kiamba, Barangay Banate, Mt. Busa, 900 m.: PNM/CMNH H1616; CMNH XXXX (PNM/CMNH H1489, 22 March 1993).

Definition.—A moderately-sized member of the *P. dorsalis* group, SVL 22.6–25.4 for seven males and 25.4–29.8 for four females. Advertisement call: “Tiktiktiktik.” Dorsum and lateral surfaces medium gray with black flecks; ventral surfaces yellow with dark brown throat.

Comment.—The only other sympatric species with which this form can be confused include *P.* sp. cf “laticeps,” a wide-headed species with a soft, tonal call and a different pattern of calling activity.

Ecology.—This species concentrates the entirety of its calling effort into a narrow period of less than 30 minutes at sunset on days following heavy rains. I observed calling males in leaf litter in secondary forest only on nights following rainy days.

Platymantis n. sp., Sibuyan sp. 1 (bank frog)

Holotype.— Philippines, Sibuyan Isl., Romblon Prov., Municipality of Magdiwang, Barangay Tampayan: PNM XXXX (RMB 2929), collected 31 December 2000 (2300 hr) by R. Brown and A. Diesmos.

Paratopotypes.— PNM XXXX (RMB 2930, 2945, 2955, 2956) (ACD 1066), same data as above, except RMB 2945, 2955, 2956, ACD 1066, collected 1 Jan 2001 (2230-2400 hr).

Definition.—A smaller member of the *P. dorsalis* group, SVL 24.2–29.6 for 11 males and 34.2–37.3 for three females. Advertisement call: "Sweet-sweet…sweet-sweet." Dorsum dark brown to black, with dark lateral surfaces and highly variable, irregular light flecks; ventral surfaces dark red; dorsum with numerous raised dermal ridges and scattered tubercles.

Comment.—The only two other species with which this form could possibly be confused are *P. levigata* from Sibuyan and *P. dorsalis* of Luzon, Negros, and Panay. From *P. levigata* this species differs by the presence of dermal ornamentations and advertisement call, and from *P. dorsalis* this species differs by the presence of a loud, paired frequency sweep advertisement call (vs. single sweeps) and a unique microhabitat preference.

Ecology.—This species calls exclusively from stream banks and has not been observed more than a meter from actively-flowing water. This species appears to be unique among Philippine *Platymantis* in that it calls exclusively from high-ambient sound level environments.

Platymantis n. sp., Guttaran "yokyok"

Holotype.— Philippines, Luzon Isl., CagayanProv., Municipality of Guttaran, Barangay Nassiping, near border of Municipality of Alcala: PNM 7479 (RMB 4213), collected 10 August 2002 by R. Brown, R. E. Fernandez, and A. Diesmos (20-2300 hr).

Paratopotypes.— PNM 7560 (ACD 1443), PNM 7561 (ACD 1444), PNM 7579 (ACD 1462 – f) 7480-76 (RMB 4214 – f, 4215, 4216 – f, 4217-20), PNM 7493-95 (RMB 4227-29), same data as holotype.

Definition.—A smaller member of the *P. dorsalis* group, SVL 23.9–29.2 for eight males and 34.2 for one female. Advertisement call: "yahk…yahk…yahk…." Dorsum and lateral surfaces light gray, lacking darker pigmentation; ventral surfaces immaculate white; dorsum with scattered tubercles.

Comment.—This species could probably most easily be confused with *Platymantis* n. sp "seeyok" but differs from that form in having consistently light coloration and a single note (vs. dual note) advertisement call.

Ecology.—This species has only been observed in disturbed secondary forests and plantations in the Municipality of Guttaran, calling from low perches (logs, suspended debris) following light rains.

Platymantis n. sp., cf *indeprensus* – Mt. Isarog

Holotype.— Philippines, Luzon Isl., Camarines Sur Prov., Municipality of Naga City, Barangay Panicuason, Mt. Isarog National Park, Mt. Isarog 825 m: PNM XXXX (RMB 3364), collected by R. Brown and R. E. Fernandez 28 July 2001 (1845 hr).

Paratopotypes.— PNM XXXX (RMB 3348), same data as holotype except collected 27 July (2230 hr), PNM XXXX (RMB 3381 – f), same data as holotype except collected 29 July 2001 (2130 hr), TNHC 62146 (RMB 3383 – f), same data as holotype except collected 30 July 2001 (1600 hr), TNHC 62144 (RMB 3347), TNHC 62145 (RMB 3349), same data as holotype except collected 27 July 2001 (1830 hr), TNHC 62147 (RMB 3399), TNHC 62148 (RMB 3400), same data as holotype except collected 31 July 2001 (2045 and 2115 hrs, respectively).

Referred Specimens.—Philippines, Luzon Isl., Municipality of Naga City, 4 km N, 21 km E Naga City (13°40'N, 123°22'E), Mt. Isarog, 1300 m: FMNH 256159 (m, DS Balete, 22 March 2004, 1350 m) 251662 (1500 m, female, DS Balete, 27 April, 1994), 251660, 251663 (females, 800 m, DS Balete 3 may 1994, 13°49'N, 123°20'50" E), 251665 (1300m, male, R. V. Penas, 30 April 1993), 251666 (f D Balete, 17 June 1992).

Definition.—A large member of the *P. dorsalis* group, SVL 31.3–38.2 for four males and 45.6 for one female. Advertisement call: "Wheeeeeee-ahhhhhh." Dorsum dark brown with thick ,light yellow dorsolateral stripes; ventral surfaces dark gray with darker throat; dorsum lacking raised dermal ridges or scattered tubercles.

Comment.—This species is most similar in some respects to *Platymantis indeprensus* but differs by its longer, husky, ethereal sounding advertisement call, its activity pattern, low local abundance, and its unique microhabitat preference.

Ecology.—The new species calls singly from high banks and ledges at mid elevations (900-1100 m) on Mt. Isarog and can be heard for up to 0.5 km due to its extremely loud vocalization.

Platymantis n. sp "seeyok"

Holotype.— PNM XXXX (RMB XXXX) collected at Baragay Balbala.n, Municipality of Balbalan, Kalinga Prov., Luzon Isl. by Rafe Brown and Arvin Diesmos.

Referred specimens .— Luzon Isl., Cagayan Prov., Municipality of Claveria, Barangay Mabnang, Mabnang Falls: PNM 7575 (ACD 1458), PNM 7522 (RMB 4256). Luzon Isl., Ilocos Norte Prov., Municipality of Pagudpud, Barangay Pansian: PNM 7529-31 (RMB 4263-65), PNM 7533 (RMB 4267). Luzon Isl., Calinga Prov., Municipality of Balbalan, Barangay Balbalasang, Sitio Magdallao, 1600 m: FMNH 259031 (RMB 2232), FMNH 259029 (ACD 980); Sitio/Area Mapga, 900 m: FMNH 259539 (RMB 3134), FMNH 259540 (RMB 3135), FMNH 25941 (RMB 3136), FMNH 25942 (RMB 3140), FMNH 259543 (RMB 3141), FMNH 259548 (RMB 3165), FMNH 259549 (RMB 3176), FMNH 259551 (ACD 1151), FMNH 259553 (ACD 1152), FMNH 259554 (ACD 1153), FMNH 259556 (ACD 1167), FMNH 259538 (ACD 1191), FMNH 259550 (ACD 1192); Philippines, Luzon Is., Nueva Viscaya Prov., Municipality of Santa Fe, Barangay Imugan, Imugan River, 800 m.: PNM 7461 (RMB 4195-F), PNM 7462 (RMB 4196-F), PNM 7463 (RMB 4197), PNM 7464 (RMB 4198), PNM 7465 (RMB 4199-F), PNM 7466 (RMB 4200), PNM 7467 (RMB 4201), PNM 7554 (ACD 1437-F), PNM 7549 (ACD 1432), PNM 7552 (ACD 1435), PNM 7553 (ACD 1436-F), PNM 7555 (ACD 1438), Collected by R.M. Brown, R.E. Fernandez, and A.C. Diesmos, 7-August 2002, (1830-2200 hr.); Nueva Ecija Prov., Dalton Pass, 800 m.: PNM 7453 (RMB 4187), Collected by R.E. Fernandez, 5-August 2002, (1900 hr.); Ilocos Norte Prov., Municipality of Pagudpud, Barangay Pansian, near boundary of Cagayan Prov.: PNM

7529-31 (RMB 4263-65), PNM 7533 (RMB 4267), Collected by R.M. Brown, A.C. Diesmos, and R.E. Fernandez, 14-August 2002, (1830-2130 hr.); Banguet Prov., 8km. W. Baguio city, on road to Bauang, "near Burgos": PNM 7545 (RMB 4279), Collected by R.E. Fernandez, 15-August 2002, (2000 hr.).

Definition.—A moderately-sized member of the *P. dorsalis* group, SVL 23.3–32.6 for 17 males and 27.8–35.4.3 for four females. Advertisement call: "See-yok…see-yok." Dorsal color highly variable; ventral torso white, throat bluish gray; dorsum with numerous raised dermal ridges and scattered tubercles.

Comment.—I refer several populations to this species with some hesitation due to the tremendous variation in the appearance of specimens and the impression that different populations have on the human ear. Despite the large degree of variability in these characters, I feel that at present we lack sufficient data to discriminate between geographical variants, and so I refer all species that generally produce the two-note "see-yok" call to this species with the caveat that further studies will be required to determine if, in fact, all are conspecific.

Ecology.—As presently understood, this species appears to have a fairly wide geographical and elevational distribution and has been observed or heard calling in primary forest, disturbed forest, secondary forests, and tree plantations. It calls on the ground or on low (≤ 0.5 m) perches.

Platymantis n. sp. (QNP sp. 1 – tonal soft caller)

Holotype.— Philippines, Luzon Isl., Quezon Prov., Municipality of Atimonan, Barangay Malinao Ilaya, boundary of Quezon National Park: TNHC 62176 (RMB 4062), collected by R. M. Brown, A. C. Diesmos, G. V. A. Gee, and M. Leonida on 28 November 2001 (1800 hr).

Paratopotypes.— TNHC 62174 (RMB 4059), TNHC 62175 (RMB 4060), 27 November 2001 (2330 hr); TNHC 62054 (RMB 4061), 28 November 2001 (1730 hr).

Definition.—A moderately-sized member of the *P. dorsalis* group, SVL 25.3–34.2 for six males, females unknown. Advertisement call a slowly-delivered plaintive "Whoo…whoo…whoo." Dorsal color highly variable; ventral surfaces cream, throat black; dorsum with dermal ridges, concentrated in scapular region.

Comment.—This species can probably most easily be confused with *P. dorsalis*, which is found sympatrically, and syntopically, in Quezon National Park. However, observing these two species sympatrically assured me that the two are separate forms with distinct microhabitat preferences and advertisement calls.

Ecology.—This species has only been observed calling from atop leaf-strewn boulders, 1-2 m above the ground near the Municipality of Atimonan.

Platymantis n. sp. (QNP sp. 2 – limestone frog)

Holotype.— Philippines, Luzon Isl., Quezon Prov., Municipality of Atimonan, Barangay of Malinao Ilaya, boundary of Quezon National Park: PNM XXXX (RMB 4067), collected by R. Brown 28 November 2001 (2245 hr).

Paratopotypes.— PNM XXXX (ACD 1260), PNM XXXX (RMB 4099), TNHC 61992 (RMB 4066), same data as holotype except collected 29 November 2001 (21-2400 hr); TNHC 61989 (RMB 4063), TNHC 61990 (RMB 4064), TNHC 61991 (RMB 4065), same data as holotype, TNHC 61993(RMB 4068), 28 November 2001 (2245 hr), TNHC 61994 (RMB 4085), 29 November 2001 (22-2300 hr).

Definition.—A moderately large member of the *P. dorsalis* group, SVL 33.4–42.2 for seven males, 43.3 for one female. Advertisement call: "Eahhh….eahhh." Dorsal color dark greenish gray with distinct irregular black spots; ventral surfaces light gray, throat dark gray; dorsum smooth.

Comment.—This species' call sounds most like the morphologically-distinct *P. corrugata* but differs from that form by a larger body size, greenish coloration, a less prominent jaw in vental aspect, and the absence of a dark face mask.

Ecology.—This species calls exclusively from limestone crevices atop large (4-6 m) cliff-sheer boulders and from thin ledges in limestone cliffs at the Municipality of Atimonan and in Quezon National Park.

Platymantis n. sp. (sp. 3 Malinao cliff frog)

Holotype.—PNM XXXX (field no. RMB 3525), an adult male collected at 20:00 hr at "Tamagong," 950 m above sea level, Mt. Malinao, Sitio Purok 7, Barangay Banhaw, Municipality of Tiwi, Albay Province, Luzon Island, Philippines by Renato B. Fernandez and Rafe M. Brown.

Paratopotypes.—TNHC 62040 (RMB 3524), 62041 (RMB 3526), and 62042 (RMB 3527), same data and locality as holotype.

Definition.—A large member of the *P. dorsalis* group, SVL 39.4–46.2 for four males, females unknown. Advertisement call: "Yeer-yeer…yer-yer-yer" (final notes very closely-spaced). Dorsal color black with distinct light spots; lateral surfaces of head medium brown with light bars on lips; ventral surfaces white, throat black; dorsum with longitudinal ridges stretching the length of torso.

Comment.—This species is generally morphologically similar to *P. insulata* from Gigante Island but differs from that species by (and is referred to the *P. dorasalis* species group because of) the absence of widely-expanded terminal phalanges, its unique microhabitat preference, and unique advertisement call.

Ecology.—This species calls exclusively from the lips of high, (>50 m) steep cliffs along ravines at mid elevations on Mt. Malinao.

Small ground frogs – the *P. mimula* group

Platymantis mimula Brown, Alcala, and Diesmos, 1997c

Platymantis mimulus Brown, Alcala, and Diesmos, 1997, Proc. Biol. Soc. Washington, 110: 19.

Platymantis mimula Günther, 1999, Mitt. Mus. Naturkd., Berlin, Zool., 75: 327-328, by implication.

Holotype.—Holotype: CAS 196362. Type locality: "Mt. Maquiling, Los Banos, Laguna Province, Luzon Island, at an elevation of about 400 m," Philippines.

Referred specimens.— Philippines, Luzon Isl., Laguna Prov., Municipality of Los baños, Barangay Batong Malake, University of the Philippines at Los Baños campus, Mt. Maquiling, 700 m: FMNH 260355–56. Paratopotypes?; Mt. Makiling: FMNH 110365; Los Baños: 110372. Philippines, Luzon Isl., Laguna Prov., Municipality of Los Baños, Barangay Batong Malake, University of the Philippines at Los Baños campus, 400 m: TNHC 54930-34 (JAM 976, 725-27), TNHC XXXX (RMB 2791-99, 2802); Luzon Isl., Rizal Prov., Municipality of Tanay, Barangay Sampaloc: PNM 7636-41 (RMB 4167-72); Philippines, Luzon, Aurora Prov., Municipality of San Luis; Dipiningan branch of the Cobatangan (= ”Kabatangan” of Brown et al., 1999b) River drainage; 1.2 km S, 1.3 km E of Barangay Villa Aurora; 15° 40.2 N, 121° 20.8 E; *ca* 410–650 m above sea level: CMNH XXXX (RMB 797, 849, 946).

Definition.—A typical member of the *P. mimula* species group, SVL 19.2–24.5 for 28 males, 22.3–27.5 mm for 14 mature females. Advertisement call: “osek…sek…sek.” Dorsal color flat gray with darker pigment associated with dermal ridges and tubercles;

lateral surfaces of head medium brown with dark bars on lips; ventral surfaces white, throat gray; dorsum with longitudinal ridges and tubercles.

Comment.—The most common species on the University of the Philippines at Los Baños campus (Brown et al., 1997c), this species was not recognized until 1997 but was often collected and presumed to be a juvenile of *P. dorsalis* (Taylor, 1920, 1922b). This species is most similar to *P. naomiae* from high elevations of Mt. Banahao, and *P.* n. sp. Subic Bay, but differs from these by characteristics of the advertisement call.

Ecology.—This species calls from a variety of forest types from primary to disturbed secondary forest and even the edges of agricultural clearings and plantations.

Platymantis naomiae Alcala, Brown, and Diesmos, 1998

Platymantis naomii Alcala, Brown, and Diesmos, 1998, Proc. California Acad. Sci., 50: 383.

Platymantis naomiae Frost 2003. Amphibian Species.

Holotype.—CAS 204746. Type locality: "montane forest on southeast slope of Mt. Banahao (Tayabas side), Luzon Island at about 1400 m," Philippines.

Referred specimens.— Philippines, Luzon Isl., Quezon Prov., Municipality of Tayabas, Barangay Lalo, Mt. Banahao 900 m: TNHC 62169 (RMB 3662), TNHC 62170 (RMB 3729), TNHC 62171 (RMB 3743).

Definition.—A typical member of the *P. mimula* species group, SVL 20.3–23.9 for 14 males, 21.6–28.0 mm for 14 mature females (Alcala et al., 1998). Advertisement call: "psik…psik." Dorsal color dark purplish brown; lateral surfaces of head black; dorsal surfaces of forearms bright red; ventral surfaces yellow throughout; dorsum with longitudinal ridges and tubercles.

Comment.—The resemblance of this species to *P. mimula* does not convince me that the two are conspecific. *P. naomiae* occurs only at very high elevations (above 1000–2150 m) on Mt. Banahao, in very different environmental conditions and temperature regimes than those faced by the habitat generalist *P. mimula,* which occurs only below 600 m on a separate mountain massif. Additionally, the advertisement call is distinct, and this species appears to have more and more densely-congregated dorsal tubercles (Alcala et al., 1998).

Ecology.—This species calls the forest floor at high elevations on Mt. Banahao.

Platymantis pygmaea Alcala, Brown, and Diesmos, 1998

Platymantis pygmaeus Alcala, Brown, and Diesmos, 1998, Proc. California Acad. Sci., 50: 382

Platymantis pygmaea Günther, 1999, Mitt. Mus. Naturkd., Berlin, Zool., 75: 327-328, by implication.

Holotype.—PNM 6255. Type locality: "disturbed Dipterocarp Forest at 55-65 m in the Northern Sierra Madre Natural Park in Sitio Natapdukan, Barangay Didian, Municipality of Palanan, Isabela Province (16° 57.93´ N, 122° 24.23´ E), Luzon Island," Philippines.

Referred specimens.— Philippines, Luzon Isl., Cagayan Prov., Municipality of Calveria, Barangay Mabnang, Mabnang Falls: PNM 7523 (RMB 4257).

Definition.—A typical member of the *P. mimula* species group, SVL 14.1–15.7 for 10 mature males, 15.0–16.5 mm for four mature females (Alcala et al.,1998; Brown and Diesmos, unpubl. data). Advertisement call: a very high frequency "tik…tik…tik." Dorsal color light gray with a few black spots in scapular region, head markedly darker gray to brown; lateral surfaces of head and body black with white areolations; ventral surfaces light gray with a darker throat.

Comment.—The smallest form in the archipelago, this species in unlike any other in the Philippines except for the new species from Sibuyan Island, which is very similar in size but differs slightly in coloration, scansorial microhabitat preferences, and some characteristics of the advertisement call.

Ecology.—This species appears to be intolerant of disturbance and is now only known from a few pristine areas with primary forest in the Sierra Madres and on the north coast of Luzon. It calls on the forest floor in leaf litter and does not climb vegetation or perch like most other species.

Platymantis n. sp “Redor’s frog”

Holotype.— Philippines, Luzon Isl., Municipality of Tayabas, Barangay Lalo, “Camp 1,” Mt. Banahao, 725 m: PNM XXXX (RMB 3693), collected by R. M. Brown and A. C. Diesmos, 28 August 2001 (2030 hr).

Paratopotypes.— PNM XXXX (RMB 3697), PNM XXXX (RMB 3699), same data as holotype; TNHC 62073 (RMB 3694), TNHC 62072 (RMB 3695), TNHC 62068 (RMB 3696), TNHC 62053 (RMB 3698), collected by R. M. Brown and V. Yngente 28 August 2001 (2100-2130 hr); TNHC 62070 (RMB 3641), TNHC 62074 (RMB 3642), TNHC 62069 (RMB 3660 – f), 26 August 2001 (20-2300 hr).

Referred Specimens.—Philippines, Luzon Isl., Sorsogon Prov., Municipality of Bulusan, Barangay San Roque, Bulusan Volcano (12°46'N, 124°2'E), 600 m: FMNH 251648, 251650, 251652–53 (f, DS Balete, 18 June 1992, 750 m); Barangay San Roque, Mt. Bulusan Natural Park, ridge above Lake Bulusan, Mt. Bulusan, 700 m: PNM XXXX (RMB 4047), PNM XXXX (RMB 4049), PNM XXXX (RMB 4054), PNM XXXX (RMB 4056), TNHC 62052 (RMB 4042), TNHC 62055 (RMB 4043), TNHC 62057 (RMB 4044), TNHC 62056 (RMB 4045), TNHC 62075 (RMB 4052), collected by R. M. Brown and R. E. Fernandez 24 November 2001 (18-1900 hr). Philippines, Luzon Isl., Albay Prov., Municipality of Tiwi, Barangay Banahaw, Sitio Purok 7, "Tamagong" area, Mt. Malinao, 900 m: PNM XXXX (RMB 3491 – f), PNM XXXX (RMB 3494-juv), PNM XXXX (RMB 3499), PNM XXXX (RMB 3502), TNHC 62058 (RMB 3487), TNHC 62051 (RMB 3488), TNHC 62049 (RMB 3489), TNHC 62050 (RMB 3490), TNHC 62048 (RMB 3492 – f), TNHC 62066 (RMB 3500), TNHC 62061 (RMB 3501), TNHC 62065 (RMB 3503), collected by R. M. Brown and R. E. Fernandez 9 August 2001 (18-2100 hr); PNM XXXX (RMB 3507), TNHC 62064 (RMB 3506), TNHC 62059 (RMB 3508), TNHC 62060 (RMB 3509 – f), 10 August 2001 (1745 hr); PNM XXXX (RMB 3515), TNHC 62062 (RMB 3516), TNHC 62063 (RMB 3517), 11 August 2001 (1820 hr), PNM XXXX (RMB 3519 – f), PNM XXXX (RMB 3523 – juv) collected 2100 hr; Barangay Tagoytoy, Sitio Kumangingking, Area Mina-abaga, Mt. Malinao, 700 m: TNHC 62071 (RMB 3827), TNHC 62067 (RMB 3868), TNHC 62114 (RMB 3825).

Definition.—A larger member of the *P. mimula* species group, SVL 23.1–24.9 for 26 males, 24.6–26.6 mm for 12 mature females. Advertisement call: “choo-rink, choo-rink” at the type locality (Mt. Banahao) and “kee-oo-lee…kee-oo-lee” on Mt. Malinao and Mt. Bulusan. Head characteristically wide for this species group; dorsal color homogeneous medium brown; dorsal surfaces of forearms orange; ventral surfaces white with bluish gray throat; dorsum with longitudinal ridges and tubercles.

Comment.—It is with some hesitation that I refer all known populations to this single species. At the type locality, this species calls in two-note calls (“chu-rink, chu-rink”) from the ground or from low perches for some time after dark; calling activity lasts from 1800 to 2200 hr. On Mt. Malinao and Mt. Bulusan, this species calls in three-note calls (“kee-oo-lee…kee-oo-lee”) for approximately one hour following sunset, and frogs perch at a variety of heights (0–1.6 m) in suspended litter. Nevertheless, I refer them all to the same species pending further analysis because of the shared distinctive appearance of these populations and because of the general sound of the advertisement call.

Ecology.—This species is found in disturbed habitats throughout its range. It occurs from disturbed forest edges at 600+ m to approximately 950 m on Mt. Banahao and in similar elevational ranges on Mt. Malinao and Mt. Bulusan.

Platymantis n. sp. (“Katipunan frog”)

Holotype.— Philippines, Luzon Isl., Municipality of Tayabas, Barangay Lalo, “Camp 1,” Mt. Banahao, 600 m: PNM XXXX (RMB 3671), collected 27August 2001 by R. Brown and A. Diesmos (1845 hr).

Paratopotypes.—Philippines, Luzon Isl., Municipality of Tayabas, Barangay Lalo, “Camp 1,” Mt. Banahao, 600 m: PNM XXXX (RMB 3616, 3631), TNHC 62037 (RMB 3611), TNHC 62038 (RMB 3612), TNHC 62032 (RMB 3615), TNHC 62028 (RMB 3625 - f), TNHC 62029 (RMB 3632 - f), TNHC 62036 (RMB 3636), TNHC 62039 (RMB 3637), TNHC 62033 (RMB 3371), TNHC 62031 (RMB 3673), TNHC 62034 (RMB 3674), TNHC 62035 (RMB 3675), TNHC 62030 (RMB 3676), same data as holotype except collected 25 August 2001 (2130 hr); PNM XXXX (RMB 3672, 3677), PNM 7325-7331 (RMB XXXX-XX), same data as holotype; PNM XXXX (RMB 3692), same data as holotype except collected 28 August 2001 (2000 hr).

Other paratypes.— Philippines, Luzon Isl., Quezon Prov., Municipality of Atimonan, Barangay Malinao Ilaya, boundary of Quezon National Park: TNHC 62026 (RMB 4057), TNHC 62025 (RMB 4086), TNHC 62027 (RMB 4089), collected 28 November 2001 by R. Brown and A. Diesmos (21-2300 hr).

Referred specimens.—Three uncatalogued specimens from the Watershed Area, Polillo Town, Polillo Island, deposited at PNM.

Definition.—A moderately-sized member of the *P. mimula* species group, SVL 20.2–23.2 for 22 males, 21.7–26.1 mm for nine mature females. Advertisement call: "Zzzz-zzzz-zzzz." Head relatively narrow for this species group; dorsal color homogeneous dark brown to black, occasionally lighter and/or with a thin vertebral line; ventral surfaces gray with a reddish brown throat; dorsum with delicate, longitudinal ridges.

Comment.—This species differs from all members of the *P. mimula* group by possession of a narrow head and long, pointed snout and by its unique advertisement call. It can not readily be confused with any other Philippine species.

Ecology.—This species is found in disturbed habitats throughout its range. It occurs from disturbed forest edges at 600 on Mt. Banahao, is found at forest edges on Polillo Island, and was found in road-side clearings along roads passing through primary forest in Quezon National park.

Platymantis n sp. ("Benedict frog")

Holotype.— Philippines, Luzon Isl., Calinga Prov., Municipality of Balbalan, Barangay Balbalasan, Sitio Magdallao/Mt. Magdallao, 1600 m: FMNH 259034 (RMB 2226), collected by R. M. Brown, A. C. Diesmos, and G. V. A. Gee on 28 March 2000 (2000 hr).

Paratopotypes.— FMNH 259027 (RMB 2212), collected 30 March 2000 (1845 hr); FMNH 259035 (RMB 2217), collected 31 March 2000 (1800 hr); FMNH 259002 (RMB 2222), collected 1 April 2000 (2000 hr); FMNH 259028 (RMB 2223 – f), collected 1 April 2000 (2030 hr); FMNH 259036 (RMB 2224), collected 1 April 2000 (1845 hr); FMNH 259003 (RMB 2227), collected 2 April 2000 (1930 hr); FMNH 259033 (RMB 2230), collected 3 April 2000 (1630 hr); FMNH 259007 (RMB 2231), collected 3 April 2000 (1700 hr); FMNH 259032 (RMB 2236), collected 4 April 2000 (1800 hr); FMNH 259025 (ACD 979), FMNH 259026 (ACD 978), FMNH 259030 (ACD 977), collected by A. C. Diesmos 30 March 2000 (time ?); Area Am-Licao, 1800 m: FMNH 259600 (GVAG 215), collected by G. V. A. Gee on 21 March 2001 (1910 hr), FMNH 259601 (GVAG 216), FMNH 259602 (GVAG 217), collected 21 March 2001 (1910 hr); FMNH 259544 (ACD 1188 – f), FMNH 259545 (ACD 1189), FMNH 259546 (ACD 1190), collected by N. Nantoque on 22 March 2001 (time ?); FMNH 259547 (ACD 1173), collected by R. E. Fernandez 19 March 2001 (time ?); FMNH 259557 (ACD 1170), collected by L. R. Heaney 19 March 2001 (time ?); FMNH 259558 (ACD 1174), collected by R. E. Fernandez 19 March 2001 (time ?).

Definition.—A larger member of the *P. mimula* species group, SVL 22.2–27.1 for 16 males, 24.7–29.1 mm for six mature females. Advertisement call:

"Benedict!…Benedict!" Dorsal color highly variable, light brown to black, occasionally with a thin vertebral line; ventral surfaces white with a dark purple throat; dorsum with numerous dermal ornamentations, wavy ridges, and tubercles.

Comment.—This species differs from all members of the *P. mimula* group by its highly unique advertisement call and diurnal habits.

Ecology.—This species is found only at high elevations (1250+ m) in mid-montane forest where it is diurnally active and calls from creek beds and small valleys in primary forest.

Platymantis n. sp. (cf *pygmaea* – Sibuyan)

Holotype.— Philippines, Sibuyan Isl., Romblon Prov., Municipality of Magdiwang, Barangay Tampayan, Area Logdeck, boundary of Guiting-guiting National Park: PNM XXXX (RMB 2946), collected 1 January, 2001 (2030 hr) by R. Brown, A. Diesmos, M. Leonida, and G. Gee.

Paratopotypes.— Philippines, Sibuyan Isl., Romblon Prov., Municipality of Magdiwang, Barangay Tampayan, Area Logdeck, boundary of Guiting-guiting National Park: PNM XXXX-xxxx (RMB 2947, 2950-54, 2960), same data as holotype.

Referred Specimens.—Philippines, Sibuyan Isl., Romblon Prov., Municipality of Magdiwang, 5.25 km S & 3.5 km E Magdiwang Town (12°27'N, 122°33'E), Mt. Guitinguiting, 725 m: FMNH 236141 (m, S. Goodman col, 23 May 1989).

Definition.—A small member of the *P. mimula* species group, SVL 14.5–16.7 for seven males, 17.6 mm for one mature female. Advertisement call: "Syk-syk…syk-syk…." Dorsal color light gray with a few black spots in scapular region, head markedly darker gray to brown; lateral surfaces of head and body black with white areolations; ventral surfaces light gray with a darker throat.

Comment.—One of the smallest species in the archipelago, this frog in unlike any other in the Philippines except for *P. pygmaea*. It differs form this species by the absence of dark coloration of the head, the presence of an enlarged post axial tubercle behind the forearm insertion, a tendency towards scansorial habits, and a paired advertisement call.

Ecology.—This species appears to be intolerant of disturbance and is now only known from pristine forest on Sibuyan Island. This frog calls while perched on low vegetation (≤ 1 m).

Platymantis n. sp (Balblan sp. 2 – "shek-shek-shek…")

Holotype.— CAS XXXX, collected 8 July 1998 by Rafe M. Brown and A. C. Diesmos at Barangay Balbalan, Municipality of Balbalan, Kalinga Province, Luzon Island, Philippines.

Paratopotypes.—CAS XXXX-XX, collected at same locality and date as holotype.

Definition.—A typical member of the *P. mimula* species group, SVL 19.0–21.2 for three males, females unknown. Advertisement call: "Shek-shek-shek-shek-shek-shek-shek…;" rapid, harshly modulated call. Dorsal color light gray, dorsal edge of tympanum black; lateral surfaces of head and body fade to white ventrally; ventral surfaces immaculate white.

Comment.—This species has only been observed once and recorded twice on a single night. Very little is known about its biology, but the highly distinctive advertisement call can not be assigned to any other form.

Ecology.—This species is known only from a disturbed tiny forest fragment on a low ridge across the valley from the town of Balbalan proper ("Old Balbalan"). We observed calling males on the ground after sunset following rain and, on subsequent nights when no precipitation was forthcoming, no further calling activity was observed. Further studies at and around the type locality are needed to establish the distribution of this potentially highly endangered (or possibly now extinct) new species.

Platymantis n. sp. ("Rizal's Frog", Mt. Palaypalay)

Holotype.— Philippines, Luzon Isl., Cavite Prov., Mt. Palay-palay Natural Park: PNM 7646 (RMB 4288), collected by R. Brown and A. Diesmos 22 August 2002 (1845-2230 hr).

Paratopotypes.— PNM 7647 (RMB 4289), same data as above for holotype.

Definition.—A typical member of the *P. mimula* species group, SVL 17.6–23.7 for 13 males, 20.1–25.5 mm for 11 mature females. Advertisement call: "Psu-rot…psu-rot;" a husky, lower frequency version of *P. mimula* call. Dorsal color dark brown with black associated markings with dermal ridges; lateral surfaces of head medium dark gray with alternating dark and light bars on lips; ventral surfaces cream, throat yellow; dorsum with longitudinal ridges but lacking tubercles.

Comment.—This species is perhaps most phenotypically and acoustically similar to *P. mimula* but differs by possession of a two-syllable, lower-frequency advertisement call, absence of dorsal tubercles, and darker coloration.

Ecology.—This species calls from disturbed primary and secondary forest on the Cavite Peninsula and is common in Mt. Palay-palay National Park. This species calls from suspended debris and prefers dry leaf perches ≤ 2 m from the ground.

Platymantis n. sp. (Subic)

Holotype.— Philippines, Luzon Isl., Zambales Prov., Municipality of Olongapo, Subic Bay Metro Authority Naval Base, "Nav-Mag" area, Ilanin Forest, Triboa Bay: PNM XXXX (RMB 4425), collected by R. M. Brown, 15 September 2002 (1830 hr).

Paratopotypes.— PNM XXXX (RMB 4427 – f), same data as holotype; TNHC 62047 (RMB 4470), 18 September 2002 (1900-2230 hr); PNM 7757 (RMB 4175), 28 July 2002 (18-1930 hr), Nabasan River: PNM XXXX (RMB 4490), PNM XXXX (RMB 4491) (2 juveniles), 20 September 2002 (10-1400 hr); TNHC 62043 (RMB 4423), TNHC 62044 (RMB 4424), TNHC 62045 (RMB 4426), 15 September 2002 (1830-1930 hr); Boton Falls area: TNHC 62046 (RMB 4451) 17 September 2002 (19-2300 hr).

Definition.—A moderately-sized member of the *P. mimula* species group, SVL 24.5–27.3 for 11 males, 25.2–27.5 mm for six mature females. Advertisement call: "Psk…psk…psk…." Dorsal color yellowish-brown, lacking darker pigment on dermal ridges; lateral surfaces of head medium brown with dark brown bars on lips; ventral surfaces white, throat bluish-gray; dorsum with longitudinal ridges stretching the length of torso.

Comment.—This species appears to be closely-related to *P. mimula* but differs in the sound of the advertisement call and microhabitat preference.

Ecology.—This species in known only from coastal native bamboo forests of Subic Bay. An extremely arid forest type, the bamboo forests of Subic Bay are characterized by highly sandy soil and lack of standing water in small streams. This species calls from rolled, dead bamboo leaves in contact with the forest floor or suspended in vegetation slightly above it.

Rain frogs: the *P. guntheri* group

Platymantis guentheri (Boulenger, 1882)

Cornufer guentheri Boulenger, 1882, Cat. Batr. Sal. Brit. Mus.: 108.

Platymantis guentheri Zweifel, 1967, Copeia, 1967: 120, by reference to Brown, 1965, Breviora, 218: 2-3

Platymantis ingeri Zweifel, 1967, Copeia, 1967: 120, by reference to Brown, 1965, Breviora, 218: 2-3.

Cornufer guentheri Brown, 1965, Breviora, 218: 2

Cornufer ingeri Brown, 1965, Breviora, 218: 2

Cornufer ingeri Brown and Alcala, 1963, Copeia, 1963: 672; Brown, Alcala, Diesmos, and Alcala, 1997, Proc. California Acad. Sci., 50: 4.

Holotype.—BM 1947. 2. 31-34 (formerly 77. 10. 9. 52); Type locality: "Dinagat Island," Philippines.

Referred specimens.— Philippines, Mindanao Isl., Davao City Prov., “Tagum, Sitio Taglawig, near sea level.” FMNH 50571 (m, 27.2 svl) 50572 (juv male., D. Heneyman) 50573 (f, 37.3 SVL); H. Hoogstral col., 12 Oct 1946; Cotobato Prov., “Cotobato, near Milbuk:” FMNH 106656–57; Mindanao Isl., New Bataan Prov., Mt. Putting Bato: PNM/CMNH H-2350. Philippines, Bohol Isl., Bohol Prov., Municipality of Bilar, Barangay Logarito, boundary of Raja Sikatuna National Park: PNM XXXX (RMB 2889, 2894-98, 2908); Municipality of Carmen, Barangay Riverside: TNHC 56407 (RMB 1048).

Definition.—A moderately-sized member of the *P. guentheri* species group, SVL 24.5–33.3 for 29 males, 27.6–40.5 mm for nine females. Advertisement call: “Sweeet…sweeet…sweet.” Dorsal color yellowish-brown, gray, or dark gray, with reddish brown mottling and indistinct blotches; tympanum black, postrictal tubercles white, lips barred dark gray; ventral surfaces white with dark spots near groin, throat with dense dark gray pigmentation; dermal ornamentation extensive.

Comment.—There is, at present, no reason to doubt the taxonomic assignment of this name to populations from Mindanao, Bohol, Leyte, Samar, Dinagat, and Biliran, but this distribution is unusually extensive among Philippine platymantines. This member of the *P. guentheri* species complex possesses the narrowest terminal phalange expansion of any member of the group.

Ecology.—This species is often found in leaf litter on the forest floor but calls exclusively from suspended debris and understory vegetation in primary and secondary forest.

Platymantis banahao Brown, Alcala, Diesmos, and Alcala, 1997

Holotype.— CAS 201208. Type locality: "original forest at 1100 m on the NE slope of Mt. Banahao at Lucban, Quezon Province, Luzon Island", Philippines.

Paratypes.—CAS 201003–07, 201209–10, 201231, 201531–32, 201554, same location and conditions of collection as holotype; CAS 201015 (Mt. San Cristobal).

Referred specimens.— Philippines, Luzon Isl., Quezon Prov., Municipality of Tayabas, Barangay Lalo, “Camp 1,” Mt. Banahao, 600 m: PNM XXXX (RMB 3640); “Hasaan,” Mt. Banahao 1275 m: PNM XXXX (RMB 3711), TNHC 61968 (RMB 3713), TNHC 61969 (RMB 3723), TNHC 61970 (RMB 3741), TNHC 61971 (RMB 3744).

Definition.—A moderately-sized member of the *P. guentheri* species group, SVL 27.8–39.4 for 29 males, 34.6–47.5 mm for five females (Brown et al., 1997b; Brown and Diesmos, unpubl. data). Advertisement call: “Tut-tut-tut-tut-tut-tut-tut-tut….” Dorsal color yellowish to brown, with darker lateral surfaces of the body; ventral surfaces tan with dark spots throughout all ventral surfaces; dermal ornamentation absent; skin smooth.

Comment.—This species differs from all other members of the *P. guentheri* species group by a heavily mottled venter, smooth dorsal skin, reduced digital webbing of the toes (Brown et al, 1997b) and except for *P. cornuta*, by an extremely rapidly-pulsed advertisement call.

Ecology.—This species is limited to high elevations (1000–1700 m) on Mt. Banahao and Mt. San Cristobal in the Banahao massif. Males usually call from high perches (pandanus fronds and high in trees) across forest gaps on cold nights following heavy rains. Females tend to large clutches (60–155 eggs) of large, jelly-coated eggs, wedged in the bases of fronds of pandanus plants.

Platymantis luzonensis Brown, Alcala, Diesmos, and Alcala, 1997

Holotype.—Holotype: CAS 196368. Type locality: "forest at about 600 m elevation, Mt. Maquiling, Laguna Province, Luzon Island", Philippines.

Paratypes.—CAS 196364, 196369–70, 200404–08, 210544-45, 201538–39 from Mt. Makiling; CAS 201218–21from Mt. Banahao.

Referred specimens.— Philippines, Luzon Isl., Laguna Prov., Municipality of Los Baños, Barangay Batong Malake, University of the Philippines at Los Baños campus, Mt. Maquiling, 700 m: FMNH 26057–60; Camarines Sur Prov., Municipality of Naga City, Mt. Isarog, 1000 m: FMNH 251643–44, 251661, 251664; 825 m: PNM XXXX (RMB

3355, 3367, 3384, 3398), TNHC 62008 (RMB 3351), TNHC 62006 (RMB 3356), TNHC 62016 (RMB 3368), TNHC 62009 (RMB 3393 – f), TNHC 62007 (RMB 3396), TNHC 62010 (RMB 3397); 450 m: TNHC 62014 (RMB 3336), TNHC 62015 (RMB 3337), TNHC 62003 (RMB 3415), TNHC 62002 (RMB 3478 – f); Philippines, Luzon Isl., Quezon Prov., Municipality of Tayabas, Barangay Lalo, "Camp 1," Mt. Banahao, 600 m: PNM XXXX (RMB 3622, 3623, 3678), TNHC 62005 (RMB 3621), TNHC 62004 (RMB 3624), TNHC 62012 (RMB 3701), TNHC 62013 (RMB 3702); Albay Prov., Municipality of Malinao, Barangay Tagoytoy, Sitio Kumangingking, Area Mina-abaga, Mt. Malinao, 700 m: PNM XXXX (RMB 3824), TNHC 62017 (RMB 3881 – f); Municipality of Tiwi, Barangay Banhaw, Sitio Purok 7, Area "Tamagong," Mt. Manlinao, 950 m: TNHC 62011 (RMB 3518); Luzon Isl., Sorsogon Prov., Municipality of Irosin, Barangay San Roque, Mt. Bulusan Natural Park, Lake Bulusan, Mt. Bulusan, 325 M: TNHC 62018 (RMB 4005), TNHC 62019 (RMB 4055); Philippines, Luzon Isl., Quezon Prov., Municipality of Atimonan, Barangay Malinao Ilaya, boundary of Quezon National Park: TNHC 62020 (RMB 4058), TNHC 62022 (RMB 4083), TNHC 62021 (RMB 4079), TNHC 62023 (RMB 4084), TNHC 62024 (RMB 4088). Municipality of Naga City, Barangay Panicuason, Mt. Isarog National Park, Mt. Isarog, 450 m.: CMNHXXXX JWF 94079.

<u>Definition</u>.—A typical member of the *P. guentheri* species group, SVL 27.1–36.4 for 15 mature males, 35.6–46.5 mm for 10 females (Brown et al., 1997b; Brown and Diesmos,

unpubl. data). Advertisement call: “Kwenk…kwenk…kwenk .“ Dorsal color usually tan to dark brown, with light dorsolateral lines, a think vertebral line, or dorsum immaculate, with darker lateral surfaces; ventral surfaces cream with some dark reddish brown pigmentation on the throat; dermal ornamentation absent; skin smooth.

Comment.—This species differs from all other members of the *P. guentheri* species group by a combination of morphological and advertisement call characters (Brown et al, 1997b). I suspect that several cryptic species current reside under the name *P. luzonensis* but that study of the infrequent forested habitats throughout S. Luzon will be required to distinguish between phenotypically and acoustically similar forms. At present I refer frogs from Mt. Makiling to the southern tip of Bicol peninsula to this species.

Ecology.—This species ranges widely for a *P. guentheri* group species. Colleagues and I have observed this species throughout S. Luzon island, from sea level to 1200 m, in a variety of habitats, from disturbed second growth to pristine primary forest. This species does appear to require some degree of forest cover, as evinced by its absence in deforested areas, but among *P. guentheri* group species, *P. luzonensis* appears most tolerant of disturbance and habitat degradation.

Platymantis negrosensis Brown, Alcala, Diesmos, and Alcala, 1997.

Holotype.—CAS 137416. Type locality: "original forest at lake Balingsasayao, Negros Oriental Province, Negros Island," Philippines.

Paratypes.—Lake Balinsasayo: CAS 137286–415, 137417–28: Cuernos de Negros Mountains: CAS-SU17996–18002, 18434–35, 18487, CAS 89804.

Definition.—A smaller member of the *P. guentheri* species group, SVL 27.1–36.4 for 15 mature males, 29.8–39.3 mm for 25 females (Brown et al., 1997b; Brown and Diesmos, unpubl. data). Advertisement call: "Kwek-kwek-kwek… ." Dorsal color dark brown, with light dorsolateral lines, or a single thin vertebral line; ventral surfaces cream with some dark reddish brown pigmentation on the throat and pectoral region and in groin; dermal ornamentation extensive; dorsal skin with numerous, enlarged tubercles and tubercles present on snout.

Comment.—This species is probably most easily confused with *P. luzonensis* but differs from that species by characteristics of the advertisement call, by a much more tuberculate dorsum, by the presence of enlarged tubercles on the snout, and by a much more restricted (high elevation, pristine forest) habitat preference.

Ecology.—This species appears limited to high elevation habitats on the higher volcanoes of Negros and Panay islands. It occurs now in low densities and calls exclusively following heavy rain. In the case of heavy fog cover, *P. negrosensis* occasionally calls before sunset.

Platymantis cornuta (Taylor, 1922)

Cornufer cornutus Taylor, 1922, Philippine J. Sci., 21: 175.

Platymantis cornuta Günther, 1999, Mitt. Mus. Naturkd., Berlin, Zool., 75: 327-328, by implication

Platymantis cornutus Zweifel, 1967, Copeia, 1967: 120. By reference to Brown, 1965, Breviora, 218: 2-3; Brown, Brown, and Alcala, 1997a.

Cornufer cornutus Brown, 1965, Breviora, 218: 2.

Holotype.—Holotype: CAS 61476 (originally EHT 764) according to Slevin and Leviton, 1956, Proc. California Acad. Sci., (4)28: 536. Type locality: "Balbalan, Kalinga, Mountain Province, Luzon," Philippines.

Referred specimens.— Aurora CMNH 8128 (RMB 1007), Two uncatalogued specimens at CAS, collected at Balbalan Town, Kalinga Province, Luzon Island.

Definition.—A smaller member of the *P. guentheri* species group, SVL 23.1–26.6 mm for two mature males, 29.8–39.3 mm for a single known female (the holotype; Brown et al., 1997a; Brown and Diesmos, unpubl. data). Advertisement call: "tututututut…." The fastest amplitude-modulated call of all Philippine platymantines; dorsal color tan, with light cream dorsolateral lines; ventral surfaces cream with dark brown spots on the throat and in groin; dermal ornamentation limited to two enlarged triangular fleshy tubercles (sometimes flap-like) above the eyelids.

Comment.—This species is unique among Philippine platymantines by virtue of its extremely rapid call repetition rate and fleshy dermal horns/flaps on the eyelids.

Ecology.—This species appears limited to mid elevation forested habitats in Balbalan and Balbalasang (800-1100 m) and calls following heavy rains in the late afternoon and early evening.

Redescription of Holotype.—The holotype is a female with convoluted oviducts. This species is referable to the *guentheri* group on the basis of the following: (1) ratio of head width to length falls within range for that species group (2), subarticular tubercles are large and protruding, some pointed (possibly but less strongly than for some *guentheri* group species), plus, the poor state of preservation makes Brown et al.'s tentative assignment understandable, (3) terminal phalanges and disks widely expanded, the penultimate portions not subtending or flanged to width of disk (4), first finger shorter than second but not as relatively short as in some other *hazelae* group species (its disk reached to just short of midway between 2nd finger's subarticular tubercle and its disk), (5) toe disks are not as broad as finger disks but the specimens is desiccated, disenabling this comparison, (6) digits of fingers not much broader than deep, dermal flanges wider than some *guentheri* group species but not as wide as most *hazelae* group species (7) venter is smooth, except for extreme posterior portions and is not entirely or predominantly glandular as in *hazelae* group species.

Head barely wider than body; snout rounded in dorsal and lateral aspect, not sloping (lateral view); dorsal surface of head fairly flat, eyes protruding dorsally only slightly, oriented anterolaterally; snout barely protruding beyond lower lips; nares much closer to tip of snout (width of tympanum) than to eye; distance from nares to eye equal to width of eye; loreal region strongly concave; labial region clearly visible in dorsal aspect; canthus strongly angular, medially when viewed from above; labial region full and swollen; tympanic annulus visible through skin, its dorsal edge covered by supratympanic fold extending from eye to postrictal region.

Dermal ornamentation includes large flap like triangular extension of skin from eye lid (oriented anterolaterally), a cluster of tubercles on posterior edge of palpebra, numerous small tubercles on back of head, supratympanic region, and supraxial region, a pair of postrictal tubercles (pointed) on both sides of head, a postocular tubercle on both sides of head, pectoral region tubercles, a small tubercle at the rictis of the lower lip (both sides), and sacral region small tubercles. Venter is nearly smooth, becoming increasingly glandular in groin; ventral surfaces of femoral segments of limbs coarsely glandular.

Disks of fingers with circummarginal grooves, inner two disks rounded, outer squared; first finger reaches just beyond subarticular tubercle of finger 2; finger formula from shortest to longest 1, 2, 4, 3, each with large, raised and pointed subarticular tubercles, one on inner digits I and II and two on each outer digit; fingers II, III, IV with distinct, round, and slightly pointed supernumerary tubercles; inner metacarpal tubercle large and oval (at base of finger I), separated from larger suboval outer metacarpal tubercles at base of finger III; small, elongate tubercle at base of finger 4 not separated from tubercle most medial to it.

Tubercles of pes I(1), II(1), III(2) IV(3), V(2), basal tubercle of 4th toe much smaller than distal, inner metatarsal tubercle barely perceptible, evidently limited to preaxial edge of heel, outer a small pointed point; slight webbing between toes I, II, III, and especially between III and IV.

<u>Coloration</u> <u>in</u> <u>preservative</u>.— dorsum faded dark orange-brown, with two slightly lighter dorsolateral lines, bordered laterally by slightly darker color, and medially by darker color in pectoral region interorbital bar light, contrasting with darker coloration on posterior portions of head; snout considerably lighter brown than posterior portions of

head; lateral portions of head not much darker than anterior portions, save for thin line of darker coloration extending from snout, along lateral edges of canthus, through eye, and under supratympanic fold and across dorsal edge of tympanum; slightly dark brown spot on dorsal edge of tympanum dark canthal stripe curves posteriorly at nares, and extends to upper lip where it fades in integrity slightly; upper lips barred with darker brown; lower lips spotted slightly dark brown; several dark brown spots beyond tympanum and above insertion of arm; flanks with posteroventrally sloping broad upside down acute triangle of light gray on brown back ground; this wedge of light color ends in the groin where its apex is rounded and very light (presumably white or yellow in life), reminiscent of areolations in the groin.

Dorsal surfaces of limbs gray-brown with dark brown bars (2 on forearms, 2 on femur, 3 on tibia, 1 on tarsa); dorsal surface of digits brown with slightly lighter brown at joints and terminal disks.

Ventral surface of throat and body light orange-brown in preservative, without darker spots; ventral surfaces of limbs slightly darker, faintly marbled or blotched with darker orange-brown; ventral surface of tibia and tarsals more strongly marbled; ventral surface of manus and pes brown with slightly lighter tubercles.

Remarks.—Brown et al. (1997a) placed this species in the *hazelae* group tentatively, noting (1) the head was broader relative to its length than for other species in the group

(2), dermal orientation distinguished it from all other *haelae*-group species (3), the tentative placement of this species in this group was troubled by small sample size (1) for *P. cornutus*. In fact, dermal flanges on this specimen *are* wider than most *P. guentheri* group frogs, especially on fingers II, III and IV (another reason that probably led Brown et al., [1997a] to place it in the *P. hazelae* group).

Platymantis insulata Brown and Alcala, 1970.

Platymantis insulatus Brown and Alcala, 1970, Occas. Pap. California Acad. Sci., 84: 2.

Platymantis insulata Günther, 1999, Mitt. Mus. Naturkd., Berlin, Zool., 75: 327-328, by implication.

Holotype.—CAS 117441. Type locality: "South Gigante Island," Philippines.

Definition.—A large member of the *P. guentheri* species group, SVL 37.6–44.7 mm for 12 mature males, 39.2–49.1 mm for four females. Advertisement call: “Tik…tik...tik..tik-tik-tik,” with terminal pulses becoming increasingly rapid (Brown et al., 2003a); dorsal color brown or greenish brown with dark, W-shaped chevrons; ventral surfaces cream; dermal ornamentation absent; dorsal skin smooth.

Comment.—This species differs from other members of the *guentheri* species group by the combination of its large size, color pattern, unusual advertisement call, and unique microhabitat preference.

Ecology.—This species occurs only on Gigante Island where it lives an entirely terrestrial existence and calls from limestone crevices at dusk and dawn when humidity is high (Brown and Alcala, 2000). This is the only species of Philippin *Platymantis* that I have observed calling as extensively at dawn as it does at dusk or after sunset.

Platymantis rabori Brown, Alcala, Diesmos, and Alcala, 1997

Platymantis rabori Brown, Alcala, Diesmos, and Alcala, 1997, Proc. California Acad. Sci., 50: 8

Holotype.—CAS 136889. Type locality: "Cantaub, Sierra Bullones, Bohol Island," Philippines.

Paratypes.—CAS-SU 17284, 21721, 21623, 21733, 21738–39, 21741, 21748, 21756, 21775–81, 23148–64, 23166–68, 23170–82, 23184–212, 23222–23, 23425; CAS 136888, 136890–137006, 138169–70, 139019–21, 145697, 145699, 186065; FMNH 134987–88; MCZ 39052–53; PNM 5283.

Referred specimens.— Philippines, Mindanao Isl., New Bataan Prov., Mt. Puting Bato: PNM/CMNH H-2305; Davao City Prov., Municipality of Toril, Barangay Baracatan, Sitio Upper Baracatan: PNM/CMNH H-1462 – f; Municipality of Calinan, Barangay Malagos, Malagos Eagle Station: PNM XXXX (RMB 3779-80); Leyte Isl., Leyte Prov., Municipality of Abuera, Barangay Danao, Lake Danao, 650 m: PNM 7693 (RMB 4335), PNM 7776 (ACD 1483).

Definition.—A large member of the *P. guentheri* species group, SVL 27.5–35.7 mm for 23 mature males, 38.2–49.1 mm for 27 females; Advertisement call: "Chur-enk…chur-enk…", a slow, two-note pulsed call. Dorsal color dark brown to black, with slightly lighter dorsolateral lines; ventral surfaces cream; dorsum with low ridges and tubercles; venter highly glandular.

Comment.—This species differs from other members of the *P. guentheri* species group by its large size, slow, two-note pulsed call, and extremely widely-expanded terminal digits of the fingers. Often when conditions are suboptimal (limited humidity, before sunset), colleagues and I heard this species calling in single, widely spaced calls ("Chur-enk"), reminiscent of *P. hazelae* group frogs. Only on high-humidity nights at high elevations did we hear full trains of calls that convinced us of this species identity.

Ecology.—This species is common but sparsely distributed in tree tops on Bohol, Leyte, Mindanao, and Samar. Individuals call singly after sunset when rain is absent and pulse trains can be heard when heavy afternoon rains have just stopped. This species appears to congregate in trees surrounding forest gaps, and its loud call can be heard often in open areas in the forest.

Platymantis n. sp ("fast caller" – Polillo, Bulusan, Tobaco)

Holotype.— Philippines, Polillo Isl., Quezon Prov., Watershed Area, near Polillo Town: PNM XXXX (collected by J. A. McGuire, R. I. Crombie, and V. Yngente).

Paratopotypes.—Philippines, Polillo Isl., Quezon Prov., Watershed Area, near Polillo Town: TNHC 54976–80 (JAM 966–70); five males, collected XX date, by J. McGuire, V, Yngente, and R. Crombie.

Other paratypes.— Philippines, Luzon Isl., Sorsogon Prov., Municipality of Irosin, Barangay San Roque, Mt. Bulusan National Park, Lake Bulusan, Mt. Bulusan 350 m: PNM XXXX (RMB 4019), PNM XXXX (RMB 4050), TNHC 62081 (RMB 3948), TNHC 62082 (RMB 4009), TNHC 62079 (RMB 4016), TNHC 62080 (RMB 4017), TNHC 62083 (RMB 4018); Philippines, Luzon Isl., Albay Prov., Municipality of

Tobaco, Barangay, Bongabong: TNHC 62078 (RMB 3601), TNHC 62077 (RMB 3602), TNHC 62076 (RMB 3603).

Definition.—A moderately-sized member of the *P. guentheri* species group, SVL 27.5–32.7 mm for nine mature males, 31.1–39.1 mm for three females. Advertisement call: "Klu-klu-klu-klu-klu…", a notably rapid pulse train. Dorsal color light brown-reddish brown, with yellow dorsolateral lines; ventral surfaces immaculate cream (Polillo, Tobaco) to cream with dark chocolate spots (Bulusan); dorsum with few low ridges.

Comment.—This species is perhaps most easily confused with *P. luzonensis* but differs from that species in having a less variable dorsal coloration, a much more rapidly pulsed advertisement call, and a low-elevation distribution limited to coastal forests and low-elevation dipterocarp forests. This species' elevational range overlaps with that of *P. luzonensis* only at Mt. Bulusan, Sorsogon Prov., but it is assumed that before most of Luzon's lowland forests were destroyed that these two species were frequently paripatric. I suspect that a few species may eventually be recognized from the range of variation I currently refer to this lineage.

Ecology.—This species is common in moist coastal forests of Polillo Island and Luzon Island, Bicol Peninsula Municipalities of Tobaco and Sorsogon (Mt. Bulusan) when low-elevation forests are present. I assume that its patchy distribution is an artifact of forest degradation and that it does not survive the removal of forest cover.

Platymantis n. sp (“sp. F” tuberculate Sierra Madres frog)

Holotype.— ACD collection.

Paratypes.— ACD collection.

Referred Specimens.—Aurora Prov., Municipality of Maria Aurora: CMNH 8129 (RMB 729); Cagayan Prov., Municipality of Callao, Mt. Ceteceo 1450 m (17°42’N, 122°02’E): FMNH 251641–42.

Definition.—A small member of the *P. guentheri* species group, SVL 22.8–31.2 mm for three mature males, females unknown; Advertisement call: “tuuu..tu-tu…tu-tu…tu-tu….” Dorsal color very dark brown; ventral surfaces white with dark chocolate spots on throat; dorsum extensively ornamented with dermal tubercles and rows of pointed spicules.

Comment.—This species is most easily confused with the distantly allopatric *P. guentheri* by virtue of its tuberculate dorsum and narrowly-expanded digital disks (Brown et al., 2000b) but differs by its more extensively tuberculate dorsum, invariant dark dorsal coloration, a rapidly pulsed (vs. frequency sweep) advertisement call, and microhabitat preference.

Ecology.—This species has only been heard or collected a few times, and in each instance, calling males were located inside epiphytic fern axils, 2–3 m above the forest floor.

Cloud frogs: the *P. hazelae* group

Platymantis hazelae (Taylor, 1920).

Philautus hazelae Taylor, 1920, Philippine J. Sci., 16: 298.

Platymantis hazelae Zweifel, 1967, Copeia, 1967: 120. By reference to Brown, 1965, Breviora, 218: 2-3.

Cornufer hazelae Brown, 1965, Breviora, 218: 2

Platymantis hazelae Inger, 1954, Fieldiana: Zool., 33: 367-370

Rhacophorus (Philautus) hazelae Ahl, 1931, Das Tierreich, 55: 67

Holotype.—CM 3427 (formerly EHT F293), according to McCoy and Richmond, 1966, Ann. Carnegie Mus., 38: 247. Type locality: "at an elevation of about 1,000 meters, on CanlaonVolcano, central northern Negros," Philippines.

Referred specimens.—Philippines, Negros Isl., Negros Occidental Prov., “Mt Canlaon:” FMNH 22512; Municipality of Pula Pinto, SE slope Makawili Peak, Mt. Canloan, 3600’: FMNH 95871–72; Municipality of Valencia, 3.5 km S and 6 km W Valencia Town (9°16’N, 123°12’E) Mt. Talinis, 1250 m: FMNH 247736, 247743–45, 250818; Mt. Canlaon: CMNH 5804 (RSK 3918), CMNH 5805 (RSK 3939); Negros Isl., Negros Oriental Prov., Municipality of Valencia, Sitio Nasuji, Mt. Talinis Range, PNOC-EDC Watershed Area, 1150 m: TNHC 62159 (RMB 3307), TNHC 62160 (RMB 3316) TNHC 62161 (RMB 3317), TNHC 62162 (RMB 3318), TNHC 62163 (RMB 3319), TNHC 62164 (RMB 3320), TNHC 62165 (RMB 3321), TNHC 62166 (RMB 3323), TNHC 62167 (RMB 3324), TNHC 62168 (RMB 3325).

Definition.—A typical member of the *P. hazelae* species group, SVL 21.8–28.2 mm for 21 mature males, 26.2–25.2 for 21 adult females. Advertisement call: “Ting…ting…ting,” a ringing, unmodulated, tonal call with calls delivered in groups of 8–12. Dorsal color very light yellow to light brown, sometimes with a thick vertebral stripe; ventral surfaces white with light brown spots on venter but not throat; dermal ornamentation limited to one or two flesh tubercles per eyelid.

Comment.—This species is most easily confused with the distantly allopatric *P. polillensis* (Polillo Island and southern Sierra Madres of Luzon Island), *P*. sp., cf "rivularis" (Cordillera of northern Luzon; Taylor 1922b; Brown et al, 1997a) and related cloud frogs that lack areolations in the groin (*P*. n. sp. "Enteng's Frog," (in part: *P. sierramadrensis*), *P*. n. sp. "plaintive cf. *montana*", and *P*. cf. "rivularis sweep frog"). It differs from these by combinations of color pattern, tonal advertisement call, and exclusively cloud-forest habitat preference.

Ecology.—This species is nearly completely limited to high elevation stunted forests of the volcanic mountains of Negros Island. It breeds in arboreal ferns, and males call from fern fronds or large leaves in high humidity environments.

Platymantis n. sp "cf *montana* –Plaintive Banahao frog"

Holotype.— Philippines, Luzon Isl., Quezon Prov., Municipality of Tayabas, Barangay Lalo, Mt. Banahao 800 m: ACD XXXX, deposited in PNM.

Paratopotypes.— Philippines, Luzon Isl., Quezon Prov., Municipality of Tayabas, Barangay Lalo, Mt. Banahao 800 m: TNHC 62172 (RMB 3763); four specimens deposited in PNM.

Definition.—A typical member of the *P. hazelae* species group, SVL 22.7–26.4 mm for 21 five mature males, 27.2 for a single female; Advertisement call: “Tu-ting…tu-ting…tu-ting,” a ringing, paired, two-note tonal call. Dorsal color very light yellow to light brown, sometimes with a thick vertebral stripe; ventral surfaces white with light brown spots on venter but not throat; dermal ornamentation limited to one or two flesh tubercles per eyelid.

Comment.—This species was previously confused with *P. montana* on Mt. Banahao until A. C. Diesmos found a single locality (Hasaan Area, 800 m) where the two forms can be observed syntopically. It has since been determined that *P. montana* occurs at 800+ m on Mt. Banahao and the new species can be found only below this limit, between 725 and 800 m on the south face. The call is a much more deliberate, softer, slower two-note tonal call, delivered in groups of six to eight.

Ecology.—The new species is known only from stream-side vegetation in a very limited area along a single stream on the Tayabas side of Mt. Banahao and at similar elevations on the Lucban side of the mountain.

Platymantis isarog Brown, Brown, Alcala, and Frost, 1997

Platymantis reticulatus Brown, Brown, and Alcala, 1997, Proc. California Acad. Sci., 49: 416. Primary homonym of *Platymantis reticulatus* Zhao and Li, 1984

Platymantis isarog Brown, Brown, Alcala, and Frost, 1997, Herpetol. Rev., 28: 131.

Holotype.—CAS 197218. Type locality: "Mt. Isarog (1200-1300 m), Camarines Peninsula, southeastern Luzon Island," Philippines.

Paratopotypes.— Philippines, Luzon Isl., Camarines Sur Prov., Municipality of Naga City, Barangay Panicuason, Mt. Isarog National Park, Mt. Isarog 825 m: PNM XXXX (RMB 3360, 3365, 3376, 3420-21), TNHC 61961 (RMB 3359), TNHC 61962 (RMB 3361), TNHC 61963 (RMB 3362), TNHC 61964 (RMB 3363), TNHC 61965 (RMB 3366), TNHC 61966 (RMB 3419), TNHC 61967 (RMB 3422).

Referred specimens.— Philippines, Luzon Isl., Albay Prov., Municipality of Tiwi, Barangay Banahaw, Sitio Purok 7, Area Tamagong, Mt. Malinao 900 m: TNHC 62131 (RMB 3496), TNHC 62132 (RMB 3497), TNHC 62133 (RMB 3498), TNHC 62130 (RMB 3520), TNHC 62134 (RMB 3521), TNHC 62135 (RMB 3522); Barangay Tagoytoy, Sitio Kumangingking, Area Mina-abaga, Mt. Malinao 700 m: TNHC 62136 (RMB 3848), TNHC 62129 (RMB 3849), TNHC 62137 (RMB 3852), TNHC 62138 (RMB 3854), TNHC 62139 (RMB 3856), TNHC 62140 (RMB 3859), TNHC 62141

(RMB 3861), TNHC 62142 (RMB 3897), TNHC 62143 (RMB 3899); PNM XXXX (RMB 3850, 3851, 3853, 3855, 3857, 3858, 3860, 3862, 3898).

Definition.—A moderately-sized member of the *P. hazelae* species group, SVL 23.3–27.7 mm for 17 mature males, 27.0–34.6 for nine females; Advertisement call: "Ting…ting…ting," a ringing, single tonal call delivered in groups of five to 11. Dorsal color tan to dark brown with lighter blotches; ventral surfaces white with a distinct dark brown reticulate network on torso, dark gray with white spots on throat and undersurfaces of the limbs; light cream colored areolations in groin; dermal ornamentation limited to one or two flesh tubercles per eyelid.

Comment.—This species can be confused with *P. montana* on Mt. Banahao but differs from that species by a distinct reticulate brown network on an otherwise white venter. I suspect that future taxonomic works may recognize the Mt. Malinao population as a separate species on the basis of dorsal coloration (brown reticulum on yellow background) and slight differences in advertisement call rate. At present, I treat them as a single species due to a lack of statistically significant differences between the advertisement calls.

Ecology.—This species calls from herb and shrub layer vegetation between 900 and 1400 m on Mt. Isarog and Mt. Malinao.

Platymantis lawtoni Brown and Alcala, 1974

Brown and Alcala, 1974, Occas. Pap. California Acad. Sci., 113: 2. Holotype

Holotype.—CAS 135732. Type locality: "in forest at about 800 feet elevation, Dubduban, Tablas Island," Philippines.

Referred specimens.— Philippines, Sibuyan Isl., Romblon Prov., 5.25 km S and 3.5 km E Magdiwang (12°27'N 122°33'E) 725 m above sea level, Mt. Guitingguiting: FMNH 236092, 232096, 236142, 236146, 249701.

Definition.—Possibly the largest member of the *P. hazelae* species group, SVL 31.2–33.4 mm for five mature males, 39.2–44.2 for six females; Advertisement call: Cherenk-cherenk….cherenk-cherenk…," a paired two-note tonal call delivered in groups of two to four. Dorsal color tan to dark greenish brown with lighter blotches; ventral surfaces white with dark flecks on throat and thighs; white or yellow areolations present in groin and on anterior surfaces of the thighs; dermal ornamentation limited to one or two flesh tubercles per eyelid.

Comment.—This large, distinctive species is not easily confused with any other member of the *P. hazelae* species group and is the only cloud frog present on the Romblon PAIC (Brown and Diesmos, 2002 – Romblon, Tablas, and Sibuyan Islands).

Ecology.—This species calls from herb and shrub layer vegetation between 650 and 1200 m on Mt. Guitingguiting.

Platymantis montana (Taylor, 1922)

Cornufer montanus Taylor, 1922, Philippine J. Sci., 21: 272.

Platymantis montana Günther, 1999, Mitt. Mus. Naturkd., Berlin, Zool., 75: 327-328, by implication.

Platymantis montanus Zweifel, 1967, Copeia, 1967: 120 (by reference to Brown, 1965, Breviora, 218: 2-3); Brown, Brown, and Alcala, 1997, Proc. California Acad. Sci., 49: 405-421 [412].

Holotype.—CAS 61179 (formerly EHT 861) according to Slevin and Leviton, 1956, Proc. California Acad. Sci., (4)28: 536. Type locality: "at an elevation of about 1,500 meters on Mount Banahao, Laguna Province, Luzon," Philippines.

Referred specimens.— Philippines, Luzon Isl., Zambales Prov., Municipality of Masinloc, Barangay Coto, Mt. Highpeak, 1600 m: CMNH 4326 (PNM/CMNH H319), CMNH 4325 (PNM/CMNH H326); Philippines, Luzon Isl., Quezon Prov., Municipality of Tayabas, Barangay Lalo, Mt. Banahao, 900 m: PNM XXXX (RMB 3716 – f, 3717 – f, 3725, 3745, 3746, 3750, 3753), TNHC 62149 (RMB 3661), TNHC 62150 (RMB 3663), TNHC 62151 (RMB 3664); Area Hasaan, 1275 m: TNHC 62152 (RMB 3715), TNHC 62153 (RMB 3720 – f), TNHC 62154 (RMB 3728 – f), TNHC 62155 (RMB 3740), TNHC 62156 (RMB 3747), TNHC 62157 (RMB 3748), TNHC 62158 (RMB 3749).

Definition.—A typical member of the *P. hazelae* species group, SVL 23.9–27.8 mm for 28 mature males, 26.2–33.0 mm for six females; Advertisement call: Twenk…twenk…twenk,” single-note call produced in groups of six to 14. Dorsal color highly variable, from tan to dark brown, with vertebral stripes absent or present; ventral surfaces white with dark spots; yellow areolations present in groin and flanks; dermal ornamentation limited to one or two flesh tubercles per eyelid.

Comment.—This species is probably most easily confused with *P. isarog* but differs from that species by characteristics of the advertisement call and by the absence of a ventral reticulum.

Ecology.—This species calls from shrub layer and understory vegetation between 800 and 1600 m on Banahao. This is the most common tree frog on the mid-elevation slopes of Mt. Banahao.

Platymantis panayensis Brown, Brown, and Alcala, 1997

Holotype.—PNM 2495. Type locality: "northwest ridge approach to Mt. Madja-as (about 1410 m), Libacao, Aklan Prov., Panay Island," Philippines.

Paratypes.—Panay Island, Aklan Prov., Municipality of Nabas: CAS 137641–42; Antique Prov., Mt. Madja-as, Municipality of Culiasi, Barangay Allojipan, "Hungud Tubig" Area: CMNH 4113–18, 4120, PNM 2314–120.

Definition.—A typical member of the *P. hazelae* species group, SVL 24.5–28.0 mm for seven mature males, 28.4–32.3 mm for seven mature females. Advertisement call: Pinnggg… pinnggg … pinnggg," single, ringing-note tonal calls with extensive harmonic structure, produced in groups of eight to 10. Dorsal color from yellow or tan to dark brown, with light vertebral stripes absent or present; ventral surfaces white with dark pigment in clusters of flecks on throat; yellow areolations present in groin and flanks; dermal ornamentation limited to one or two flesh tubercles per eyelid.

Comment.—This species was confused for years with *P. hazelae* from the nearby Negros Island, probably in part based on expectations of shared species between Panay and Negros. It differs from *P. hazelae* by its variable coloration, the presence of areolations in the groin, and the elaborate ringing advertisement call.

Ecology.—This species calls from shrub layer and understory vegetation between 950 m and the peak (2100 m) of Mt. Madja-as. This is the most common tree frog on the upper slopes of Mt. Madja-as and the only frog occurring at the peak.

Platymantis polillensis (Taylor, 1922)

Philautus polillensis Taylor, 1922, Philippine J. Sci., 21: 171.

Platymantis polilloensis Brown, Brown, and Alcala, 1997a, Proc. California Acad. Sci., 49: 409; Alcala and Brown, 1999. Incorrect spelling.

Platymantis polillensis Zweifel, 1967, Copeia, 1967: 120. By reference to Brown, 1965, Breviora, 218: 2-3.

Cornufer polillensis Inger, 1954, Fieldiana: Zool., 33: 365; Brown, 1965, Breviora, 218: 2.

Rhacophorus polillensis Ahl, 1931, Das Tierreich, 55: 107.

Platymantis sierramadrensis (part) Brown, Alcala, Ong, Diesmos (1999a) Proc. Biol. Soc. Washington 112:510.

Holotype.—CAS 62250 (formerly EHT 351) according to Slevin and Leviton, 1956, Proc. California Acad. Sci., (4)28: 536. Type locality: "near the southern end of Polillo Island," Philippines.

Referred specimens.— Philippines, Luzon, Aurora Prov., Municipality of San Luis; Dipiningan branch of the Cobatangan (= ”Kabatangan” of Brown et al., 1999b) River drainage; 1.2 km S, 1.3 km E of Barangay Villa Aurora; 15° 40.2 N, 121° 20.8 E; *ca* 410–650 m above sea level: PNM 5780, 5808; CMNH 5678–79, 5904; Philippines, Luzon Isl., Nueva Viscaya Prov., Municipality of Santa Fe, Barangay Imugan, Imugan River, 800 m: PNM 7468 (RMB 4202), PNM 7469 (RMB 4203).

Definition.—A small member of the *P. hazelae* species group, SVL 20.2–22.1 mm for five mature males, 25.5–26.2 mm for three mature females; Advertisement call: “Plink…plink…plink,” single-note tonal calls, produced in groups of eight to 14. Dorsal color white to little or no dark pigment or markings; ventral surfaces immaculate white; dermal ornamentation limited to one or two flesh tubercles per eyelid.

Comment.—This species has been the source of much taxonomic confusion throughout the years. Recently, with increasing attention to advertisement calls, it has become clear that *P. polillensis* is not endemic to Polillo, and, not surprisingly, also occurs in the southern Sierra Madres Mountains of nearby Luzon. This species is virtually indistinguishable from the populations in the northern Sierra Madres except that it has a pure tone single advertisement call (vs. modulated chirp in northern populations). I refer the chirping frogs of the north to a new species (*P*. n. sp "Enteng's frog") and assemble all available Polillo + S. Sierra Madres localities under the name *P. polillensis*. Because Brown et al. (1999a) declared a southern Sierra Madres locality (Sitio Mapidjas, Barangay Umiray, Municipality of General Nakar, Quezon Province) as the type locality for their *P. sierramadrensis* and this population is preoccupied by the name *P. polillensis*, I recommend that the name *P. sierramadrensis* be submerged and placed in the synonymies of both *P. polillensis* and *P*. n. sp. "Enteng's Frog."

Ecology.—On Polillo Island this species is critically endangered. Males call from ferns and shrub layer vegetation following rains, and abundances are low and the known distribution patchy. Along the E coast of Luzon this species is common in some localities and can be found in suitable habitat from 300–900 m in Quezon and Aurora Provinces.

Platymantis subterrestris (Taylor, 1922)

Cornufer subterrestris Taylor, 1922, Philippine J. Sci., 21: 274.

Holotype.—CAS 61518 (formerly EHT 707) according to Slevin and Leviton, 1956, Proc. California Acad. Sci., (4)28: 536. Type locality: "near kilometer 101, on the Mountain Trail, Mountain Province, Luzon," Philippines

Referred specimens.— Philippines, Luzon Isl., Ifugao Prov., Municipality of Banaue, approx. 12 km NW Banaue, ca 6500': FMNH 172392, 173165.

Philippines, Luzon Isl., Mountain Prov., Municipality of Bauko, Barangay Sinto, Mt. Data, Mt. Data Hotel vicinity, 2200 m: PNM 7547 (RMB 4281), PNM 7548 (RMB 4282), PNM 7524 (RMB 4283), PNM 7587 (ACD 1470); Philippines, Luzon Isl., Kalinga Prov., Municipality of Balbalan, Barangay Balbalasang, Area “Am-Licao,” 1700 m: FMNH 259505 (RMB 3180), FMNH 259589 (RMB 3178), FMNH 259590 (RMB 3182), FMNH 259591 (RMB 3183), FMNH 259592 (RMB 3184), FMNH 259593 (RMB 3185), FMNH 259594 (RMB 3186), FMNH 259595 (RMB 3188), FMNH 259596 (RMB 3189), FMNH 259597 (RMB 3190), FMNH 259598 (RMB 3191), FMNH 259577 (ACD 1171), FMNH 259578 (ACD 1172), FMNH 259579 (ACD 1176), FMNH 259580 (ACD 1177), FMNH 259581 (ACD 1178), FMNH 259583 (ACD 1180), FMNH 259509 (ACD 1181), FMNH 259584 (ACD 1183), FMNH 259585 (ACD 1184), FMNH 259586 (ACD 1185), FMNH 259588 (ACD 1186).

Definition.—A large member of the *P. hazelae* species group, SVL 24.2–26.0 mm for 17 mature males, 25.5–29.2 mm for three mature females. Advertisement call: "Whip…whip…whip…," a single-note slight frequency sweep, produced in groups of six to 12. Dorsal color gray or tan with dark brown blotches; ventral surfaces heavily patterned in black partial reticula on white; jaw very prominent in ventral aspect; bold yellow areolations present on black flanks; dermal ornamentation limited to one or two flesh tubercles per eyelid.

Comment.—This species was known from a single specimen until it was recently rediscovered on Mt. Data by Alcala and party (Alcala and Brown, 1999; Brown et al., 2003b) and again on the Am-Licao peak, above Balbalasang (Diesmos et al., in press). It can not be confused with any other Philippine species by virtue of its ventral coloration, the presence of areolations, and its extremely prominent jaw in ventral aspect.

Ecology.—This species calls from shrub and understory vegetation of the peaks of Mt. Data (Mountain Prov.) and Mt. Am-Licao (Balbalasang, Kalinga Prov.). It has been observed only between 1750 and 2200 m.

Platymantis sp., cf "real rivularis" (Taylor, 1922)

Cornufer rivularis Taylor, 1922, Philippine J. Sci., 21: 270. Synonymy by Inger, 1954, Fieldiana: Zool., 33: 367. Synonymy considered provisional by Brown, Brown, and Alcala, 1997, Proc. California Acad. Sci., 49: 408.

Holotype.—CAS 61477 (formerly EHT 761) according to Slevin and Leviton, 1956, Proc. California Acad. Sci., (4)28: 536. Type locality: "Balbalan, Kalinga Sub province, northern Luzon," Philippines.

Paratype.— an immature male, similar to holotype in all respects but with several small rounded "spots" of absence of melanophores in the groin - possibly areolations, but too faded (as Holotype) to be sure.

Referred specimens.— Philippines, Luzon Isl., Kalinga Prov., Municipality of Balbalan, Barangay Balbalasan, Sitio Magdallao, 1600 m: FMNH 259000 (RMB 2218), FMNH 259009 (RMB 2220), FMNH 258999 (RMB 2233).

Definition.—A moderately-sized member of the *P. hazelae* species group, SVL 21.0–23.6 mm for four mature males, 26.2 mm for a single mature female. Advertisement call: “Sweeet…sweeet…sweeet…,” single frequency sweep calls, produced in groups of six to 10. Dorsal color dark brown with blotches or dorsolateral stripes; ventral surfaces dirty gray; areolations absent; dermal ornamentation limited to one or two flesh tubercles per eyelid.

Comment.—Until a revisit to the type locality (Diesmos et al., in press; Brown and Diesmos, unpublished data, 1998) and recent work in the Balbalasang National Park, this species had been included (with reservation) in the synonymy of the distantly-allopatric *P. hazelae* (Brown et al., 1997a). This decision was based primarily on the fact that a single, older specimen was available, and it clearly lacked areolations. Biogeographically, this action was untenable, and Brown et al. (1997a) clearly stated that they included this species in the synonymy of *P. hazelae* with reservations. Observations at the type locality proved that the populations at mid elevations (850-1250 m) in Balbalan and Balbalasang are distinct by virtue of their size, coloration, and advertisement call (Diesmos et al., in press).

Ecology.—This species calls from pandanus fronds and nettle thickets on extremely steep slopes of the mountains above Balbalasang. Its elevational range is restricted to mid-elevation forests below 1200 m, and it is replaced at higher elevations by *P.* n. sp. cf "rivularis sweep frog."

Description of holotype.—CAS 61477; the male holotype, an apparent male, is poorly preserved and not hardened; body small, head slightly wider than widest portion of trunk; dorsal surface of head rounded, eyes protruding dorsally and oriented anterolaterally; snout barely protruding beyond lower lip symphysis of upper jaws, barely protruding anteriorly beyond most anterior point of nares (snout barely sloping anteroventrally) lores slightly concave; labial regions clearly visible in dorsal aspect; canthus moderately angular, only slightly concave medially from above, labial region full and swollen, slight postrictal swelling but no tubercles; tympanum's position evident through skin, its dorsal edge covered by supratympanic fold running from corner of orbit to behind rictus; nares laterally protuberant when viewed from above but not dorsally or anteriorly protuberant. Ventral surfaces of manus and pes smooth save for well-developed subarticular tubercles (typical *hazelae*-group), one on inner two digits of manus, two on each outer digit; supernumerary tubercles clearly evident on digits 2, 3, and 4; all digits with widened terminal disks and some with slight lateral flanges of skin (strongest on third finger); palmar metacarpal tubercles barely evident, flat; inner metatarsal tubercle elongate and oval, outer a single rounded low point; subarticular tubercles of pes 1 (I), II(1), III (2), IV (3), V(2); first finger much shorter than second, order of length (shortest to longest) 1, 2, 4, 3; toes: 1, 2, 3=5, 4; posterior 2/3 of venter and ventral surfaces of femoral segments of legs coarsely glandular; dorsal body surfaces smooth, without tubercles or asperities. Tongue subcircular, with medial papilla and deep posterior notch; change very small, widely separated, oval, their longer axis oriented anteromedially; dentigerous process small, oval, separated by more than width of one process, distant from choanae by distance of one choana, oval, longer axis oriented anterolaterally, each with four teeth.

Coloration of type.—mid-dorsal color and dorsal surface of head and snout grayish brown with irregular distinct dark brown flecks; dorsal is divided from lateral portions of the body by a stratified (light above, dark below) pair of dorsolateral boundaries between light grayish brown above and dark brown laterally; lateral dark color is continuous with darker coloration of tympanic region, lateral head, and dark lateral portions of canthus and to tip of snout; lips not barred with dark; dorsal surfaces of limbs darker brown than mid-dorsal region, barred or blotches with dark brown; dorsal surfaces of digits brown, with lighter bands at joints and on dorsal surfaces of terminal disks; venter faded gray with network of small irregularly shaped brown spots on venter but not on throat (immaculate), becoming more congregated, and overall appearance darkens in groin; ventral surfaces of legs dark gray on femur, lighter on tibia, darker again on tarsals; ventral surfaces of manus and pes orange-brown with slightly lighter tubercles; posterior flanks and anterior surfaces of femoral segments of legs without dark pigment, giving the appearance of a possible areolation (not sure as it is not distinctly round, but networks of darker pigment are arranged in a vague reticulum in these areas, not unlike some species with clear areolations); cloacal region with larger round dark brown spot.

Platymantis n. sp., “sp. 2 Balbalasang”(cf *rivularis* higher elevation, sweep frog)

Holotype.— Philippines, Luzon Isl., Calinga Prov., Municipality of Balbalan, Barangay Balbalasan, Area Am-Licao, 1750 m: FMNH 259587 (ACD 1186), collected by A. C. Diesmos, G. V. A. Gee, and R. M. Brown on 21 March 2001.

Paratopotypes.— FMNH 259582 (ACD 1179 – f), FMNH 259510 (ACD 1182), FMNH 259508 (ACD 1175), same data as holotype; Sitio Magdallao/Mt. Magdallao, 1600 m: FMNH 259002 (RMB 2211), collected on 30 March 2000 (1745 hr), FMNH 259022 (ACD 981), collected 31 March 2000 at 1580 m, FMNH 259016 (RMB 2204), collected 28 March 2000 (1900 hr), FMNH 259015 (RMB 2205), collected on 28 March 2000 (2000 hr), FMNH 259023 (RMB 2206), collected on 29 March 2000 (1900 hr), FMNH 259017 (RMB 2207), collected on 29 March 2000 (1900 hr), FMNH 259011 (RMB 2208), collected on 29 March 2000 (1945 hr), FMNH 259020 (RMB 2209), collected on 29 March 2000 (2030 hr), FMNH 259012 (RMB 2214), collected on 31 March 2000 (2020 hr), FMNH 259001 (RMB 2215), collected on 31 March 2000 (2050 hr), FMNH 259010 (RMB 2216), collected on 31 March 2000 (2130 hr), FMNH 259014 (RMB 2221), collected on 1 April 2000 (1930 hr), FMNH 259013 (RMB 2228), collected on 2 April 2000 (1930 hr), FMNH 259021 (RMB 2229), collected on 2 April 2000 (2045 hr), FMNH 259004 (RMB 2237), collected on 5 April 2000 (1000 hr); Area Am-Licao, 1700 m: FMNH 259503 (RMB 3177), FMNH 259504 (RMB 3179), FMNH 259506 (RMB 3187), collected on 19 March 2001 (1930-2230 hr).

Definition.—A moderately-sized member of the *P. hazelae* species group, SVL 19.7–25.3 mm for 16 mature males, 23.1–28.2 mm for a single mature female; Advertisement call: “Pi-ing…pi-ing…pi-ing…,” two-note tonal calls, produced in groups of three to six. Dorsal color variable, tan to light brown , with yellow dorsolateral or vertebral stripes; ventral surfaces cream with distinct dark gray spots throughout, congregated heavily on throat and thighs; areolations absent but groin bright yellow; dermal ornamentation limited to one or two flesh tubercles per eyelid.

Comment.—Specimens of this new species are nearly indistinguishable from those of *P*. sp., cf "real rivularis" (especially after preservation), but the two species are paripatrically distributed and differ markedly by advertisement call (sweeps vs. tonal pings).

Ecology.—This species calls from the tops of giant ferns, understory and shrub layer vegetation, and tree holes and bamboo trunks at Magdallao, Am-Licao, and Mt. Bali-it, Balbalasang National Park.

Platymantis n. sp, "Enteng's Frog" (=Palanan "sierramadrensis")

Platymantis sierramandrensis Brown, Alcala, Ong, and Diesmos, 1999 (part) Proc. Biol. Soc. Washington 112:510.

Holotype.— PNM XXXX (ACD 703).

Paratopotypes.—.Philippines, Luzon Isl., Isabella Prov., Municipality of Palanan (Sierra Madre Mountains) CAS 204739–41, PNM 6464, 6470–74.

Definition.—A small member of the *P. hazelae* species group, SVL 19.8–23.4 mm for nine mature males, 21.1–23.0 mm for two mature females. Advertisement call: "Cheerp…cheerp…cheerp…," a single-note, amplitude-modulated chirp, produced in groups of six to 12. White to bright yellow, devoid of all dark pigment; ventral surfaces immacculaate white; areolations absent; dermal ornamentation limited to one fleshy tubercle per eyelid.

Comment.—Specimens of this new species are nearly indistinguishable from those of *P. polillensis, P.* n. sp. cf "polillensis Imugan," *P.* n. sp., "plaintive *montana*," and some light examples of *P. hazelae* but differ from all by the amplitude-modulated chirp advertisement call.

Ecology.—This new species is common at the type locality and calls from shrub layer vegetation from 550 to 1150 m in the Palanan forest of the northern Sierra Madres.

Discussion

The recent flood of Philippine *Platymantis* species descriptions that began with the discovery of *P. panayensis* in 1994 (Brown et al., 1997a) has continued unabated to this day (Brown et al, 1997b, 1997c; Alcala and Brown, 1998, 1999; Brown et al., 2000b; Brown and Diesmos, 2002; Diesmos et al., in press). Virtually every time herpetologists get into the field in a new remote area of Luzon, a handful of taxa are discovered. Clearly, close attention to advertisement calls has had a profound impact on our understanding of the diversity of Philippine *Platymantis* (Alcala and Brown, 1998, 1999; Diesmos et al., in press). Additionally, attention to observing each species in life has provided additional impetus for taxonomic decisions that have led to increases in species diversity (Brown et al., 2002a).

It is clear that the formation of Pleistocene aggregate island complexes (Heaney, 1985, 1986; Hall, 1996; W. C. Brown et al.,1999a, 1999b; R. M. Brown et al., 2000b, 2001a, 2001b; Brown and Diesmos, 2002;) and climatic gradients associated with elevation (Brown and Alcala, 1961, 1963a, 1986; Heaney and Rickart, 1990; Ruedas et al., 1994; Dickinson and Kennedy, 1991; Brown and Alcala, 1994; Brown et al., 2002) are two major geological phenomena that have profoundly affected Philippine platymantine species diversity. At one extreme, diversity is partitioned among PAICs, according to what one would expect to find (Brown et al., 1997a; Brown et al., 1999a, 1999b; Brown and Diesmos, 2002; Brown and Guttman, 2002; Evans et al, 2003): unique faunal assemblages and replicated community assemblages endemic to each of the deep-water island platforms (Fig. 1.1), with forest or high-elevation species seldom shared between PAICs (Evans et al., 2003). At another extreme, we find closely-related species and species complexes finely-partitioned on different montane massifs (sensu Auffenberg, 1988; Hall, 1996) and stratified (Custodio, 1986; see also Brown et al, 1995a, 1995b, 1996, 1999a; Diesmos, 1998) up elevational gradients within the larger of the islands (e.g., Luzon) or on separate islands within a PAIC (e.g., *P. panayensis* of Panay vs. *P. hazelae* of Negros; see also Brown et al., 1999b; Diesmos et al, in press).

The case of species diversity on Mt. Banahao requires special consideration. We find between seven and 11 species sympatrically on this single mountain – the highest concentrated diversity of platymantines at any one site in the Philippines (Diesmos, 1998). Exactly which factors control regional vs. local species diversity are unclear, but the isolated nature of the Banahao massif, combined with its location at the southern extreme of the Sierra Madres might have contributed to the unusually high species diversity there (Brown et al., 1996, 2000b; Diesmos et al, 2002a). Other isolated mountains are less well surveyed (e.g., Mt. Isarog: Brown et al., 1995b, 2002; Brown et al, 1997a) and hold possibilities for similar intensive studies of altitudinal species succession of the kind that have been so fruitful on Mt. Banahao (Diesmos, 1998).

In addition to exploration and extensive faunal inventories needed on almost all of the larger islands in the Philippines, much work remains to be completed within the well-understood species complexes before a reasonable approximation of species diversity can be completed. Numerous taxonomic problems await biologists willing to closely study the natural history of suspected cryptic species. I note the following taxonomic areas of interest and stress that these are merely the most obvious and in need of immediate attention: (1) The frogs of the *P. corrugata* assemblage. This is a group of several species all masquerading under the "widespread species" *P. corrugata*. I recognize the Luzon PAIC, Mindanao PAIC, and Mindoro PAIC all as separate species, but frogs referred to this species that occur on several other aggregate island complexes (e.g., central Visayas) may also be distinct. (2) The frogs of the *P. polillensis* assemblage. Currently, the secretive and clearly imperiled frogs related to *P. polillensis* are poorly understood. The description of *P. sierramadrensis* (Brown et al., 1999a) further confused this situation, as has the insistence by conservation biologists working in the Philippines that this species is a "critically-endangered" Polillo endemic. The Mt. Banahao "Plaintive *montana*" population as well as the *P.* cf. *polillensis* Imugan population appear to be distinct, but before any reasonable understanding of species diversity in this group of frogs can be accomplished, southern Luzon, the S. Cordilleras, and all of the Sierra Madres will have to be extensively sampled for herpetofuna (Brown et al., 2000b). (3) Luzon vs. Visayan PAIC comparisons. Currently, several species are understood as occurring both on the Luzon PAIC and the Visayan PAIC – a situation contrary to expectations based on biogeography (Heaney, 1986; Hall, 1996) and to what is currently known from molecular systematics studies (Brown and Guttman, 2002; Evens et al, 2003). Many of these shared distributions have been satisfactorily resolved (e.g., *P. subterrestris, P. hazelae*, and *P.* sp., cf "rivularis"), but the shared presence of *P. dorsalis, P. corrugata* on Luzon and Negros+Panay makes little biogeographical sense (see also McGuire and Alcala, 2000; McGuire and Kiew, 2001; Brown and Diesmos, 2002). I suspect that Visayan populations currently referred to Luzon species will prove to be distinct taxa in on-going analyses (see Brown et al., 1999a, 2001). (4) Fine-scale differentiation within PAICs. Finally, I suspect that there is much room for improvement in our understanding of patterns of montane endemism and stratification of species ranges on larger mountains. Many large, isolated mountains have yet to be visited by herpetologists, and entire ranges (e.g., the Sierra Madres) have yet to be adequately surveyed (Auffenberg, 1988; Brown et al, 2000a, 2000b; Diesmos et al., in press; Diesmos et al., 2002a). (5) Small oceanic islands. Tne lesson of the past two decades is that smaller, land bridge islands lacking forest sometimes yield surprises. The discovery of the Gigante Island endemic (*P. insulata*) and the endemics of the Romblon PAIC (*P. levigata, P. lawtoni*) are fine examples of potential diversity that awaits biologists willing to travel to small oceanic islands far from usual commercial hubs in the Philippines. I would expect that the deep water islands would be the best candidates for additional species diversity (Maestre de Campo, Semira, Lubang, Babuyans, Burias, etc.). (6) Lowland forests. In the past 70 years, virtually all of the last remaining lowland forests of the Philippines have been removed (Lewis, 1988; Quinnell and Balmford, 1988; Dickinson and Kennedy, 1991; Kummer, 1992; Heaney and Mittermeier, 1997; Heaney and Regalado, 1998; Heaney et al., 1999). Thus, virtually all lowland dipterocarp forest (Whitmore, 1984) obligate frog species should be considered at risk of extinction (Brown and Alcala, 1994). One corollary of this prevailing trend is that any forest fragment located at or near sea level could harbor threatened, now rare, or undecided species. Every effort should be made to preserve and exhaustively inventory these remaining fragments. Unfortunately, with increasing bureaucracy, and increasingly restrictive laws governing access to biological resources in the Philippines (La Viña et al., 1997), opportunities for such studies are becoming fewer and fewer at exactly the time when liberal policies that promote scientific inquiry are needed most (Brown et al., 2002a).

Chapter 2:

Ecological morphology of platymantine frogs (Ranidae) of SE Asia and the SW Pacific

Summary

In this chapter I characterize and statistically define the naturally-occurring morphological and ecological classes (ecomorphs) of platymantines. I consider ecological traits (perch type and height from ground), meristic characters (presence/absence of morphological specializations), and analysis of continuous variables (measurements of external morphology) while defining morphological types among the extensive range of variation in platymantines. I use multivatiate analyses to assess taxonomic/group structure in continuous variables and to compare the results of these explorations of morphometric space to previously existing, non-phylogenetic "species group" taxonomies of earlier authors.

Analysis of continuous morphological data reveal that platymantine diversity falls into three convenient morphological classes: tree/canopy frogs, shrub/cloud frogs, and ground frogs. Within "ground frogs," diversity can be further subdivided into typical ground frogs, giants, and miniaturized species, for a total of five ecomorphs recognized

here. There is some evidence of sub-partitioning of typical “ground frog” ecomorphs into small- (e.g., *P. mimula*) and large-bodied (e.g., *P. dorsalis*) species, but data do not warrant formally recognizing a sixth ecomorph. It should be noted that these quantitatively-characterized ecomorph classes do not correspond exactly to either of the previously existing supraspecific classification attempts. Thus, neither the platymantine generic classifications (i.e., *Platymantis, Palmatorappia, Ceratobatrachus, Discodeles, Batrachylodes,* and *Ingerana*) nor the species groups within *Platymantis* (*dorsalis*, *mimula*, *hazelae*, and *guentheri* species groups) perfectly correspond to the natural groupings of species according to variation in continuous morphometric data or ecological types. In contrast to expectations based on classification schemes of previous authors, platymantines fall into five distinct ecomorph classes. The existence of these non-monophyletic groups suggests repeated evolution of specializations via selection for similar suites of morphological and associated ecological traits in replicated radiations of island archipelago frogs.

“Phylogenetic patterns are just that; without an understanding of the biology of the organisms, usually gained by study of extant forms, little more can be said. The phylogenetic approach to *Anolis*…is only fruitful because the biology of these lizards has been so thoroughly studied"—Losos, 1992:361.

"The least specialized of [several SE Asian genera of frogs] seems to be *Platymantis*…"—Noble, 1931:522.

Introduction

The remarkable degree of morphological variation within platymantine ranids has more often been the source of taxonomic distinctions than the impetus for hypothesizing relationships (Tschudi, 1838; Boulenger, 1884, 1886; Günther, 1859; Taylor, 1920; Noble, 1931; Inger, 1954; Zweifel, 1969; Gorham, 1965; Dubois, 1981). Platymantines range in form from the tiny shrub frogs and large tree frogs of the genera *Platymantis* and *Palmatorappia*, to robust scrub frogs and terrestrial forest frogs (also *Platymantis*), to the giant bull frogs of the genus *Discodeles*, to elaborately-colored forest frogs of the genus *Batrachylodes*, to the bizarre leaf litter mimics of the genus *Ceratobatrachus* (Günther, 1859; Schmidt, 1932; Parker, 1939). Given the degree of morphological and ecological specialization exhibited in these unusual SE Asian and SW Pacific island frogs (Allison, 1996; Brown, 1997), it is perhaps understandable that various authors of the last two centuries assigned these frogs to different genera, and even different families (Tschudi, 1838; Boulenger 1884, 1886, 1887, 1888, 1890, 1918; Günther, 1859; Brown, 1952; Gorham, 1965).

Within the Philippines, where three or four major classes of morphological/ecological foms can be found, taxonomists have attempted to further subdivide the classes of specializations and have erected supra-specific classifications (species groups) that represent hypothesized monophyletic groups of closely-related phenotypically similar species (Brown et al.,1997a, 1997b, 1997c). With the proliferation of numerous species descriptions in subsequent years (e.g., Alcala, 1986; Alcala et al., 1998; Brown et al., 1999a, 1999b), it has become necessary to expand on Brown et al.'s (1997a) original analysis and define further classes of Phillippine frogs, in order to accommodate perceived diversity (Brown et al., 2002a). Thus, in addition to Brown et al.'s (1997a) *P. hazelae* (cloud forest/shrub frogs), *P. guentheri* (canopy tree frogs), and *P. dorsalis* (leaf litter/terrestrial) species groups, Philippine biologists have begun to consider frogs of the *P. mimula* (small terrestrial frogs) and *P. pygmaea* (terrestrial miniature frogs) groups as separate complexes of phenotypically similar and possibly monophyletic species assemblages (W. C. Brown, A. C. Alcala, A. C. Diesmos, R. I. Crombie, *pers. comm.*).

Finally, although taxonomists have not erected the same kind of supra-specific classification for SW Pacific island species (Papuan, E. Indonesian, Solomon, Bismarck, and Admiralty archipelagoes) as has been developed in the Philippines (Alcala and Brown, 1998, 1999), frogs of the Solomon–Bismarck archipelagoes exhibit a similar range of morphological variation, occupy the same ecological niches, and produce similar vocalizations, and, thus, could conveniently be subjected to the same species group diagnoses outlined by Brown et al. (1997a; R. Brown, *unpubl. data*).

Consequently, it has been suspected by anuran systematists that a comprehensive review of platymantines that would consider all diversity in this group might uncover evidence for phylogenetic affinities of morphologically similar forms on either sides of the SW Pacific (R. Zweifel, A. Allison, W. C. Brown, G. Zug, *pers. comm.*). One might suspect, for example, that terrestrial forms from the Solomons and the Philippines might share recent common ancestors, as might the large tree frogs of each region. In fact, the final, unfinished project outlined by Walter. C. Brown (who published on platymantine diversity between the years of 1948 and 2001) before his recent death was to provide a comprehensive generic classification for all platymantine ranids. Brown fully expected tree frogs of the SW Pacific to be close relatives of tree frogs of the Philippines and that ground frogs of the Philippines would be close relatives of ground frogs of the Solomons, Papua, and Bismarcks (*pers. comm.*). In fact, his confidence in the monophyly of each of these morphological types is reflected in his unpublished notes (archived at the California Academy of Sciences, San Francisco, USA) which contain manuscript names for several putative new genera that he intended to erect from within *Platymantis*.

Thus, although each of the classes of frogs discussed above was expected to have inherited its conspicuous, ecology-related structural characteristics from a common ancestor, an alternative scenario should be considered. Rather than a single evolutionary origin of each type, followed by dispersal or vicariance, could similar “eccomorphs” (Williams, 1972, 1983; Wainwright and Reilly, 1994) be produced independently in separate environments or on different island archipelagoes (Losos et al, 1998)? Might the taxonomy of earlier authors (and morphological structures on which it was based) be an indication of convergent or parallel evolution? Might each of the major radiations (Philippines, Solomons, E. Indonesia, Bismarcks, Fiji) of platymantines possess similar ecomorphs that are more closely-related to other species in the same island/island group than they are to morphologically-similar species on separate islands/island groups (Losos et al., 1998)?

An obvious question when faced with such an array of diversity coupled to an historically-complex and confusing taxonomic history is whether qualitatively-defined classifications of earlier taxonomists correspond to objectively or statistically continuous variation that can be characterized free of *a priori* assumptions of species affinities (Brown et al., 2000a , Brown and Diesmos, 2002; Brown and Guttman, 2002). In this chapter I attempt such an effort. I use multivariate analyses of morphology to objectively define morphological types and relate these to ecological variation and microhabitat preference. The resulting ecomorph (Williams, 1973, 1983; Karr and James, 1975; Losos,1990a, 1990b, 1994) classes are considered to be functional types free of hypotheses about ancestry. They are defined by suites of specializations that are linked in functional ways to the environment (see Whitmore, 1984; Dickinson and Kennedy, 1991; Diesmos, 1998) via microhabitat preferences and ecological or structural adaptations (Schoener, 1968; Schoener and Schoener, 1971a, 1971b; Losos, 1990a; Beuttell and Losos, 1999; Leal et al., 2002).

The goal of such an effort will be to determine if morphologically similar but geographically disparate types of species are monophyletic and deserving of taxonomic recognition, or whether similar ecomorphs have evolved numerous times in separate portions of the platymantine radiation, presumably in response to similar regimes in similar, but distinct, environments.

Materials and Methods

Analyses of morphological characters were performed using Statview^{TM} (Abacus concepts, 1992), SuperAnova^{TM} , Statistica^{TM} (StatSoft, 1994), and JMP (SAS institute, 2000) software. Specimens (including types of as many species as possible) were examined for diagnostic morphological character states, and mensural data were collected from preserved specimens using digital calipers (see species accounts, Chapt. 1). Only data scored by me were used in order to minimize potential inter-observer and other sources of bias (Lee, 1982, 1990; Hayek et al., 2001). Characters were selected from Matsui (1984) according to their obvious relation to habitat use by frogs (following Losos, 1990a, 1990b, 1992), and 10–20 males per species were measured when possible (see Appendix 1). Symmetrical characters were scored on the specimen's right side.

Characters (Matsui, 1984) measured to the nearest 0.1 mm included snout—vent length (SVL), head length (HL), snout length (SNL), interorbital distance at the midpoint of the orbits (IOD), head width at the widest point (HW), forearm length (FAL), tibia length (TBL), tarsus length (TSL), pes length (PL), manus length (ML), fourth toe length (Toe4L), first finger length (Fin1L), third finger length (Fin3L), third finger disk width (Fin3DW), fourth toe disk width (Toe4DW), and widths of penultimate phalanges of the third finger (PpFin3) and the fourth toe (PpToe4).

I qualitatively confirmed the assumptions of normality and homoscedasticity by examining frequency distributions of each variable (Sokal & Rohlf, 1981), and the data initially were explored and errors removed by examining graphs of each variable plotted against SVL (not shown). Principal component analyses (PCA) were performed on log-transformed data for males only.

Although I tentatively identified the ecomorph classes as groups of interest (Chapt. 1) on the basis of previous taxonomic arrangements, ecology, call type, discrete character differences, and body size, I applied principal component analysis using a correlation matrix to reduce data dimensionality and assess whether continuous morphometric character variation also could form the basis of qualitatively detectable structure (group separation without *a priori* species group designation) in the morphometric data. To guarantee orthogonal orientation among factors, I extracted nonrotated (i.e., non varimax transformed) factors from the correlation matrix. This procedure enables a relatively straightforward interpretation of the importance of each morphological variable to any given factor. I used the root curve criterion for factor extraction and retained the number of factors indicated before a qualitatively-characterized dramatic shift occurred in eigenvalues vs. rank plots (scree plots not shown). Throughout these procedures, factor scores were saved for subsequent analysis and visualization via standard bivariate plots of principal components.

Alternatively, I visualized the relative positions of each species (for which morphometric data were available) in morphometric space using the unweighted paired-group method using arithmetic averages (UPGMA) of Euclidean distances derived from

PC scores. Because UPGMA constrains networks to depict simple nested hierarchies (Beuttell and Losos, 1999) there is no actual depiction of morphological space but, rather, species positions are depicted as relative clusters. I followed Losos et al. (1998) and Buettell and Losos (1999) in simultaneously calculating Euclidean distances between all species and between each species and its group centroid as an alternative way of investigating a species' relative position in morphometric space.

Finally, I traced the evolution of ecomorph class on the phylogeny (Chapt. 4) for all platymantines, and in particular detail within the Philippines using MacClade (Maddison and Maddison, 2000).

Results

Using the root curve criterion, I extracted four principal components, together accounting for 92% of the total variation. Five groups are clearly discernable in the ordination of principal components 1 vs. 2 (Fig. 2.1). The loadings for PC 1 (Table 2.1) were all positive and generally large in magnitude (with the exception of SNL, PpFin3, PpToe4), indicating that this axis is primarily a body size component. Thus, PC 1 allows for a straightforward interpretation of body size variation (i.e., Philippine and Papuan miniatures at one extreme and giants at the other). Principal component 2 loads most heavily on digital characters (Toe4L, Fin1L, Fin3L, Fin3DW, Toe4DW), indicating high correlations with these variables. As such, PC 2 might best be viewed as an axis of terminal toe pad expansion. Thus, the two major axes that define the majority of platymantine morphological variation are predominated by body size and toe pad expansion variables. Components 3–4 did not form the basis of any detectable structure in the data (plots not shown) and so will not be discussed further.

With the exception of the Philippine miniatures, each of these morphological groupings consists of frogs from both the Philippine (see Chapt. 1, Table 1.1) and Papuan platymantine radiations (Fig. 2.1).

The Shrub/Cloud frogs ecomorph consists of Philippine species of the *Platymantis hazelae* group (Brown et al., 1997a: *P. hazelae, P. isarog, P. montana, P. panayensis, P. polillensis, P.* n. sp. cf *polillensis* Imugan, *P. subterrestris, P.* n. sp. “Enteng’s frog,” *P.* n. sp. “plaintive montanus,” *P.* sp. cf “rivularis,*” P. “*real” *rivularis*), plus small-bodied and delicate Solomon and Bismarck archipelago species that possess moderate degrees of digital expansion (*P. browni, P. parkeri*, *P. macrosceles, P.* n. sp “longnose,” P. n. sp. bamboo, and *Palmatorappia solomonis*).

The Tree/Canopy species ecomorph consists of frogs of the *P. guentheri* species group from the Philippines (Brown et al., 1997a; 1997b: *P. guentheri, P. banahao, P. luzonensis,* n. sp. “fastcaller,” *P. negrosensis, P. insulata, P. rabori,* n. sp. “species F”), large-bodied tree frogs of the Bismarcks and Solomon archipelagoes (*P. neckeri, P. guppyi, P. nexipus, P.* n. sp. “melodius,” *P.* n. sp. “little nexipus”) and the Fijian tree frog (*P. vitiensis*).

The Giants ecomorph class consists of large-bodied Bismarck/Solomon island species (e.g., *P. solomonis, P. weberi, P. myersi, P. boulengeri*, *P. punctata*), a single Philippine species (*P. spelea*) and a single Fijian species (*P. vitiana*).

The Miniatures ecomorph class consists of two tiny (11–13 mm SVL) Philippine species, *P. pygmaeus,* and *P.* n. sp. cf. *pygmaeus* (Sibuyan Isl.).

Finally, the default Ground frogs ecomorph class consists of numerous Philippine frogs of the *P. dorsalis* (*P. dorsalis, P.* sp. cf *"jagori,"* *P.* sp. cf *"laticeps,"* P. n. sp. "clicker," *P. corrugata,* n. sp. cf corrugata Mindoro, *P. levigata,* n. sp."bank frog," *P. cagayanensis,* n. sp. "yokyok," *P. taylori, P. pseudodorsalis, P. indeprensus,* n. sp. cf "whee-ahhh," n. sp. seeyok, n. sp "softcaller," n. sp. "limestone frog," n. sp. "cliff frog") and *"P. mimula"* (*P. mimula, P. naomiae,* n. sp. "Redor's frog," *P.* n. sp. (cf Redor's frog), *P.* n. sp. "Katipunan frog," *P.* n. sp."benedict," *P.* n. sp. "Balblan sp. 2," n. sp "Rizal's frog," *P.* n. sp. Subic) species groups (Brown et al., 1997a, 1997c, 1999b, Alcala et al., 1998; Alcala and Brown, 1998, 1999), and a wide variety of Papuan (Günther, 1999), Solomon, Admiralty, Palau, and Bismarck archipelago species (e.g., *P. papuensis, P. occcidentalis, P. pelewensis, P. schmidti, P. macrops, P. aculeodactyla, P. akarithyma, P. rhipiphalca, P. gillardi*, *P. cheesemanae,P. mimica, P. cryptotisis, P. bimaculata, P. batantae, P. macrops,* etc.). Within the Ground frog ecomorph class, a number of Philippine species cluster at the smaller body size spectrum end of this group (Fig. 1). These are frogs related to *P. mimulus* of the Philippines.

Finally, UPGMA analysis of Euclidean distances sorted perfectly with respect to ecomorph classes and the principal axes of variation (PC 1 and 2). In general UPGMA clustering reflects species' ordination of PC scores with respect to morphology (Fig. 2.2) and ecomorphs always cluster together irregardless of phylogenetic affinities (Chapt. 4). These results suggest that ecomorph classes cluster together in morphological space and that each species is more similar in overall gross morphology to other members of its own ecomorph class than to members of different ecomorph classes.

With a few exceptions (Philippine Miniatures and Philippine Cloud frogs; e.g., *P. hazelae* species group; Brown et al., 1997a), each ecomorph class is polyphyletic (Fig. 2.3), indicating the prevalence of multiple origins of morphological+ecological types and multiple evolutionary shifts between habitat and associated morphological types. Across both the Philippine and Papuan/Solomon/Bismarck radiations tree frogs have evolved from terrestrial forms (Fig. 2.3). One interesting difference with regard to the order of ecomorph evolution is that in Papuan radiations, Tree/Canopy ecomorphs have evolved exclusively from Shrub frogs, whereas in the Philippines Cloud/Shrub frogs have never given rise to Tree/Canopy specialists. Instead, these forms have evolved directly from ground frogs (Fig. 2.3). Aquatic frogs have re-evolved from terrestrial ancestors in the case of Solomon Island and Bismarck archipelago *Discodeles*; no aquatic platymantines are known from the Philippines (with the exception of the basal *Ingerana mariae* on the Sunda-Shelf land bridge island of Palawan (see Chapt. 1: Fig. 1.1). In the Philippines, terrestrial forms have re-arisen from within arboreal lineages twice: the Gigante Island limestone cave frog *P. insulata* (Brown and Alcala, 1970b) and the newly discovered Malinao frog *P.* n. sp. “cliff frog” (Fig. 2.3). Giants have evolved only once in the Philippines, but as many as six times in the Papuan/Solomon/Bismark radiation.

A fine-scale look at the Philippine radiation with dense taxonomic sampling reveals numerous evolutionary shifts in body size of ground frogs (Fig. 2.4). Most of these smaller frogs (associated with the *P. mimula* species group) have scansorial, semi-arboreal ecologies and call from elevated perches (fallen logs, stumps, steep banks, and suspended leaf litter).

Discussion

The presence of numerous non-monophyletic classes of morphological/ecological types suggests numerous instances of repeated ecomorph evolution across a series of replicated radiations of platymantine frogs. With the exception of Philippine miniatures (*P. pygmaeus* and *P.* n. sp. cf. *pygmaeus*), each ecomorph class has evolved in both the Philippine and Papuan/Solomon/Bismark archipelagoes. All members of an ecomorph class are more similar to their own ecomorph type than they are to others, but none are monophyletic. This pattern suggests that in each radiation of platymantines, frogs have evolved similar morphologies (and associated ecologies), presumably in response to similar selective regimes experienced within each archipelago as each radiation diversified and filled available niche space (Losos, 1990a, 1990b; Losos et al., 1998). Thus, within each major radiation, platymantines have evolved large-bodied Giant species, Ground frogs, Tree/Canopy frogs, and Cloud/Shrub frogs. The readily-available interpretation is that structurally similar, but geographically different, environments have produced the same structural morphological habitat specialists in a repeated and predictable fashion (Schoener, 1968, 1971a, 1971b; Williams, 1983; Beuttell and Losos, 1999).

Some instances of ecomorphological evolution are more pronounced than others. Within the Philippines, Cloud frogs (members of the *P. hazelae* species group) are a monophyletic group, yet outside of the Philippines, several species (previously considered miniatures; W. C. Brown, *pers. comm.*) are clearly convergent on this ecomorphological type, and fall among the Cloud/Shrub ecomorph (Fig. 2.1) type, clearly by virtue of their slightly expanded terminal disks of fingers and toes. These forms consist of small, scansorial forms that may have evolved arboreality in a "ground-up" fashion: *P. browni, P. parkeri, Palmatorappia solomonis*, etc. All are species found in moist forests; all call from shrubs and understory vegetation (Allison and Kraus, 1991; W. Brown, S. Richards and J. Foufopoulis, pers. comm.). These species call from shrub-layer vegetation in Philippine cloud forests or similar habitats in the Solomon/Bismarck archipelagoes.

The Giant Species ecomorph is a cohesive group of morphologically-similar forms, yet its members may have disparate phylogenetic origins—and may have arisen as many as seven times. This group consists of Solomon/Bismarck archipelago forms plus a single species from the Philippines (*P. spelea*; Brown and Alcala, 1982a; Brown et al., 2003a). These are all large-bodied ground forms that call on the ground, as exemplified by the giants *P. magna* (New Britain) and *P. vitiana* (Fiji). Although I lack morphometric data for the giant water frogs and leaf mimics (genera *Discodeles* and *Ceratobatrachus*), it is presumed that these species would be similar in some respects to the Giants ecomorph class but also that they represent unique ecomorphs due to their widely different ecologies (e.g., fully aquatic frogs in the case of *Discodeles*).

Truly miniaturized (11–13 mm SVL) species consist of two species (*P. pygmaea* and *P.* n. sp. cf. *pygmaea* Sibuyan), although it is suspected that numerous undescribed species in this group have escaped the attention of field biologists (Chapt. 2.1) because of their small size. These tiny frogs call from leaf litter of herb-layer vegetation (0.3–0.5 m), and it is likely that additional species will be discovered in both Philippine and Papuan/Solomon/Bismarck Island radiations.

Tree/Canopy frogs (Philippine species of the *P. guentheri* species group plus Solomon/Bismarck arboreal species) are a diverse group, ranging from the giant species *P. vitiensis*, to the small Philippine species *P. guentheri* (Brown and Alcala, 1963b; Brown et al., 1997b). These species exhibit widely-expanded terminal disks of the manus and pes (*P. nexipus, P.* n. sp. "little nexipus," *P. neckeri, P. guppyi,* and *P.* n. sp. "melodius"), and most are known to call from high perches (3–5 m) on the edges of forest gaps (i.e., calling across open spaces). This ecomorph has evolved as many as two to four times in the Papuan/Solomon/Bismarck archipelagoes and two to four times in the Philippines. The tendency for Tree/Canopy frogs to evolve from Shrub frogs in the islands of the SW Pacific but to evolve from Ground frogs in the Philippines (Fig. 2.3) may be a genuine evolutionary phenomenon, or possibly is an artifact of the tendency for semi-arboreal, scansorial Pacific island frogs to group with the Cloud frogs of the Philippines. In any case, large-bodied Tree/Canopy frogs have evolved numerous times in all major island archipelagoes, with as many as nine species in the Philippines, two to three in the Solomon Islands, two to three in the Bismarcks (none on Paua New Guinea), and one in Fiji.

Finally, "Ground frogs" consist of a heterogeneous group of species that range from the small-bodied ground frogs of the Philippines (*P. mimula* group) and small species of the Solomon/Bismarck archipelago (*P. mimica, P. batantae, P. akarithyma, P. aculeodactyla*) to large-bodied terrestrial generalist forms (*P.gillardi, P. schmidti, papuensis, P. occidentalis, P. pelewensis, P. dorsalis* group, etc.). Numerous evolutionary transitions in body size are apparent in distal clades of Philippine *Platymantis* (Fig. 4b), but the (Chapt. 4) poorly-supported relationships of these forms prevent rigorous interpretation of numbers and orders of transitions in these species.

The absence of congruence between UPGMA clustering patterns and phylogenetic relationships suggests that platymantine radiations are characterized by extensive ecomorphological evolution and repeated origins of morphological and ecological species types across replicated radiations of frogs of SE Asia and the SW Pacific. The fact that, with a single exception (Philippine Miniatures), each ecomorph type is represented by species from both the Philippine and Papuan/Solomon/Bismarck Island radiations (Fig. 2.1) and that each of these quantitatively-defined morphological types is widely polyphyletic (with the exceptions of Philippine Miniatures and Cloud/Shrub frogs, Chapt. 4), further emphasizes the extensive degree of ecomorph evolution in this diverse group of frogs.

Although relationships of apical Philippine clades (Fig. 2.4b) are not satisfactorily resolved by 12S and 16S data (Chapt. 4), the presence of numerous well-supported clades containing multiple ecomorph types does allow for a certain degree of confidence with respect to the conclusion that numerous shifts in ecology and morphology have occurred within platymantine radiations in both SE Asia and the SW Pacific.

Gathering morphometric data for a comprehensive analysis of variation that would encompass all platymantine diversity is a major goal for future research. The current study also demonstrates that further investment in the phylogeny is warranted.

The repeated evolution of morphological and associated ecological specializations in platymantine frogs is extraordinary, on par with highly-popularized radiations of Galapagos finches and the lizards of the genus *Anolis* from the Caribbean (Irshick et al., 1997; Bluetell and Losos, 1999) and flying lizards of the genus *Draco* (McGuire and Alcala, 2000; McGuire and Kiew, 2001). Across a series of island archipelagoes of SE Asia and the SW Pacific, a set of ecomorphs has evolved over and over, in a repeated fashion. Some of the larger landmasses (e.g., Luzon Island of the Philippines; Heaney, 1985) contain large, complex communities of platymantines, with as many as 30 species present on a single island and as many as 11 species present at any one locality. Intermediately-sized radiations contain as many as eight to 12 species on a single landmass (e.g., Manus or New Britain Islands) and two to four species found at any one site. On small island groups of the SW Pacific, small oceanic islands contain as few as one (Palau) or two species (e.g., Fiji). In each case, closely-related forms have diverged to occupy disparate ecological niches, and close relatives often have widely differentiated morphology and microhabitat preference. This situation is exemplified at one extreme by the islands of Fiji, which possess two species (Gorham, 1965; Boistel and Sueur, 1997): one Giant ground frog and one Tree/Canopy frog, and the two are sister species.

Platymantine ranids may be viewed as the *Anolis* of the anuran realm; many questions regarding habitat partitioning, bioacoustics of the SW Pacific island forms, the significance of ecological variation in the group, order of ecomorph evolution, and the role of sexual dimorphism in body size evolution remain to be answered.

Chapter 3:

Characterization of advertisement call variation in platymantine ranid frogs of the Philippines

Summary

In this chapter I statistically classify the acoustic diversity of Philippine platymantine forest frogs and define acoustic classes (call types) among Philippine members of the genus *Platymantis*. Philippine platymantines exhibit a startling array of advertisement call diversity: monosyllabic simple calls, pure tone pulse trains, frequency sweeps, strongly amplitude-modulated pulsed calls, and complex calls of two to four syllables.

In a pattern analogous to the ecomorphological variation described in Chapter 2, multivariate analyses of 10 call characters (eight continuous, two categorical) demonstrates that platymantine acoustic diversity falls into four to five major call classes. Although call types generally correspond to the ecomorphs defined in Chapter 2, and are loosely associated with microhabitat preference (perch type and height from ground), this association is not perfect. Repeated evolution of call types across the phylogeny (Chapt. 4) and differential performance of various calls in specific environments (Chapt. 3)

suggests the existence of strong selection for certain temporal and structural characteristics of acoustic signals in this group of frogs.

"As I would gaze into the nighttime canopy, trying to discern the form of one of the treefrogs, there was always a great commotion at my feet. It was the cacophony of the tungara frog chorus…"—Ryan, 1985:26.

Introduction

Upon experiencing for the first time a SE Asian forest on a rainy night, a naive observer would no doubt be impressed by the incredible acoustical diversity exhibited by calling frogs. The cacophony of advertisement calls produced by montane forest frogs on a rainy night is remarkable—and no less so amazing is the fact that most of the conspicuous acoustic diversity and intensity in any given region is produced by frogs of a single genus: *Platymantis*.

Stereotypical , species-specific acoustic signals are nearly ubiquitously employed by anurans communicating over long distances (Blair, 1964, 1972; Wells, 1977; Gerhardt 1994a; Duellman and Trueb, 1994; Stebbins and Cohen, 1995; Bradbury and Vehrencamp, 1988; Littlejohn, 2001). The advertisement calls of frogs serve as the primary species recognition signals (Blair, 1964, 1972; Wells, 1977; Littlejohn, 1977;

Rand, 1988) and are typically assumed to be subject to intense sexual selection (Ryan, 1983, 1985, 1988, 1997; Gerhardt 1994a).

Only a few studies of bioacoustic characteristics of platymantine ranids have been published (Menzies, 1982; W. Brown et al, 1997a, 1997b, 1997c; 1999a, 1999b; Alcala et al., 1998; Gonzales and Dans, 1994; Allison and Kraus, 2001; R. Brown et al., 2003a), and most of these have been associated with species descriptions. There have been no syntheses or even summaries of call variation in platymantines that would allow for definition of the major classes of call types (e.g., Duellman, 1967; Cocroft et al., 1990; Cocroft and Ryan, 1995)

In this chapter I take a descriptive approach to objectively characterizing Philippine *Platymantis* call types. I statistically define classes of advertisement calls to avoid some of the subjective characterizations of earlier authors and arrive at an overview of acoustic diversity in this group. In subsequent chapters I examine phylogenetic distribution of this variation and attempt to ascertain whether it corresponds to the preconceived (Chapt. 2) gestault of ecomorphological evolution and microhabitat preference.

Materials and Methods

I recorded platymantine advertisement calls as described in Chapter 1, digitized calls segments in Soundedit© (Macromedia, 1995), and analyzed oscillograms (waveforms), audiospectrograms (sonograms) and results of the Fast Fourier

Transformation (power spectrum) using Canary© (Charif et al., 1996) software. For the purposes of defining call classes, I concentrated data collection on temporal and spectral characters that could be reliably scored across all platymantine species, subjective call types. Call character selection was based on a subset of characters defined by Cocroft and Ryan (1995) that could be scored and compared among and between species and call types (see also Chapts. 5 and 6 for discussion of call types and call characters).

I attempted to obtain as many high-quality recording segments of individual frogs per species as possible; for some species, I obtained as many as 20 individual recordings (e.g. *Platymantis dorsalis*), but for some, as few as two or three individuals were all that could be obtained (e.g. *P. spelea*). When numerous recordings were available I chose 10 male individuals for which complete data were available and digitized 10 calls per male for a total of 100 calls (Table 3.1).

For each recorded frog, I also measured body temperature (with a fast-reading analog cloacal thermometer) and size (snout-to-vent length, in mm, in life or following preservation). Because temporally-related call characters vary in a predictable way with temperature, and calls were recorded at a variety of body temperatures ranging from 12 to 30°C, I used standard regression analysis to derive species-specific regression equations (e.g. mean individual calling rate regressed on temperature) that allowed me to adjust mean species values for a given species to a common temperature of 18°C when significant slopes were found. Statistical analyses were performed using Statview™ (Abacus concepts, 1992), Statistica™ (StatSoft, 1994), and JMP (SAS institute, 2000) software following confirmations of the assumptions of normality and homoscedasticity (Sokal & Rohlf, 1981) and log-transformation.

I applied principal component analysis of unrotated factors extracted from the correlation matrix, following protocols described in Chapter 2 to assess whether acoustic character variation could form the basis of detectable group structure in the data. In this chapter I ask: can call types be statistically defined on the basis of continuously-varying call characters? Can acoustic types be objectively defined among Philippine platymantines in the same way that morphological and ecological variation defines natural classes?

Results

Using the root curve criterion, I extracted four principal components, together accounting for 88% of the total variation. Four of the five groups are clearly discernable in the ordination of principal components 1 vs. 2 (Fig. 3.1) and 1 vs. 3 (Fig. 3.2). The loadings for PC 1 (Table 3.2) were variable and differed in magnitude and size, indicating that this axis can not be attributed to a single dominant acoustic character. Dominant frequency, call length, and call number per group loaded strongly and positively whereas frequency modulation and call group length loaded strongly and negatively. Principal component 1 distinguishes pulsed calls from the remaining call types and tonal calls from remaining calls types (but with some overlap with pulsed calls). Frequency sweeps, complex calls, or single pulse "tick" calls did not form the basis of group separation along PC 1.

Principal component 2 loads most heavily and positively on calling rate and negatively on dominant frequency, frequency modulation, and call number per call group, indicating high correlations with these variables. Principal component 2 distinguishes single pulse "tick" calls from remaining call types. Principal component 3 loads heavily and positively on calling rate and modulation time and negatively on dominant frequency. This axis nearly forms the basis of discrimination between tonal calls and frequency sweeps and also nearly discriminates between tonal calls and complex calls.

In summary, with one exception, all call types are distinguished or nearly distinguished by use of principal components analysis of acoustic characters. The exception is the case of frequency sweep calls, a class of call types that are encompassed by a wide range of multivariate acoustic variation in complex calls (Figs. 3.1, 3.2).

The correspondence between ecomorphs (Chapt. 2) and call types is not perfect, but some trends are evident. First, simple, unmodulated tonal calls are limited to Shrub/Cloud frogs (the "*Platymantis hazelae*" group of Brown et al., 1997a). Single pulse "tick" calls are limited to the Miniatures ecomorph (*P. pygmaea, P*. n. sp. cf. *pygmaea*) and a single small ground frog of Mindanao island (*P*. n. sp. "clicker"). Pure frequency sweep calls are limited to medium sized ground frogs (*P. dorsalis, P*. n.sp.2 Sibuyan "bank frog," *P. levigata*, *P*. n. sp. Mindanao "sweeper," *P*. n. sp. "softcaller," and *P. pseudodorsalis*) and one member of the Tree/Canopy ecomorph class (*P. guentheri*). The majority of complex call species are also members of the Ground frogs ecomorph class (*P*. sp. cf *"jagori*," *P*. sp. cf *"laticeps*," *P. corrugata,* n. sp. cf corrugata Mindoro, *P. cagayanensis,* n. sp. "yokyok," *P. taylori, P. indeprensa,* n. sp. cf "whee-ahhh," n. sp. seeyok, n. sp. "limestone frog," *P. mimula, P. naomiae,* n. sp. "Redor's frog," *P*. n. sp. cf Redor's frog, *P*. n. sp "Rizal's frog," *P*. n. sp. Subic) previously assigned to the *P. dorsalis* and *P. mimula* species groups (Brown et al., 1997a, 1997c, 1999b, Alcala et al., 1998; Alcala and Brown, 1998, 1999). Finally, the pulsed call class of species consists of frogs of the Tree/Canopy ecomorph class which corresponds to the *P. guentheri* species group (minus *P. guentheri*; Brown et al., 1997a; 1997b): *P. insulata*, *P. banahao, P. cornuta, P. luzonensis,* n. sp. "fastcaller," *P. negrosensis, P. rabori,* n. sp. "species F"), and a few ground frogs with unusual ecological preferences: *P*. n. sp. "Balblan sp. 2," *P*. n. sp. "Katipunan frog," *P*. n. sp."benedict," and *P*. n. sp. "cliff frog."

Discussion

That specific call types can be recognized in multivariate analyses of acoustic characters comes as no surprise. Taxonomists have long known and had made use of call types for comparisons among Philippine *Platymantis* (Brown et al., 1997a, 1997c, 1999b, Alcala et al., 1998; Alcala and Brown, 1998, 1999), but these comparisons to date have been extremely general, and qualitative in nature.

The observed trends in ecomorph and call type evolution are striking when the full range of morphological, ecological, and acoustic variation is considered for this group. Rapidly-pulsed, amplitude-modulated calls are produced by generally arboreal canopy frogs that are found high above the ground and that generally aggregate around forest edges and canopy gaps (pers. obs). But some ground species also produce rapidly-pulsed calls and several of these have interesting microhabitat preferences. For example, *P*. n. sp. "Benedict" is an entirely diurnal frog; *P. insulata* is a limestone crevice and cave frog; *P*. n. sp. "Cliff frog" calls exclusively at the edge of steep cliffs, and *P. taylori* calls from the edges of deep drainage creeks or "arroyos" at high elevation. The convergence of these ground frog species on pulsed calls may, therefore, represent special circumstances in all the known exceptions to the Tree/Canopy ecomorph pulsed-call generalization. Interestingly, all four species of ground frogs with pulsed calls load negatively on PC 2 (Fig. 3.1). Clear separation between these and the true arboreal canopy frog pulsed call species (positive on PC 2) is evident in ordination of PC 1 vs. 2. This appears to be a consequence of relatively short call group duration and fewer calls per call group in these species.

Simple, non-modulated tonal calls are limited to the monophyletic (Chapt. 4) "*P. hazelae*" (Brown et al., 1997a) species group: the Cloud/Shrub frog ecomorph class. As suggested in Chapter 5, pure tones may be favored by environmental selection for signal transmission in dense shrubs and cloud elfin forests. No known cases of convergence on this call type from a clade dominated by another ecomorph class is yet known.

Brief pulse "tick" calls appear to be limited to two closely related species (*P. pygmaea, P*. n. sp. cf *pygmaea*) and a single undescribed ground frog from Mindanao Island (*P*. n. sp. "clicker"). I expect numerous additional species in the Miniature ecomorph class will be discovered with additional field work; preliminary fieldwork in the Sierra Madres of Luzon suggests the “tick” call type maybe be present in other, as of yet unidentified species (*pers. comm.* with A. C. Diesmos).

Philippine ground frogs for the most part call with frequency sweeps and complex calls with one to four distinct syllables. The separation of these call types in acoustic space is nonevident on the basis of call characters examined here (Figs. 3.1, 3.2). Many “complex” calls contain tonal, frequency-modulated elements (e.g., *P. spelea, P.* n. sp. “Redor’s frog”), and a tendency for the analysis to group these species with pure frequency sweep species makes good sense. Accordingly, lack of group structure between these call types is not surprising. In any case, frequency swept calls make up a relatively small portion of the acoustic space encompassed by complex calls, and so for my purposes, referring to these as a distinct call class is a reasonable act of convenience. It is interesting to note that frogs with pure frequency sweep calls come from disparate regions of the phylogeny (including ground frogs of the basal- and distal-most clades in the phylogeny; Chapts. 4, 6) and that one tree frog understory specialist (*P. guentheri*) has converged on this call type, as has one Shrub/Cloud frog ecomorph (*P.* n. sp. cf “rivularis”).

The repeated convergence of unrelated species on this series of five call types lends credence to the hypothesis of strong selection on spectral and temporal aspects of the advertisement calls of these species. Whether these processes have occurred in the context of sexual selection (Ryan, 1980, 1983, 1985), environmental selection (Ryan et al., 1990), as a consequence of radiation and community structure (Losos et al., 1998; Gillespie, 2004), are important questions for future field research.

Chapter 4:

Phylogenetic systematics and biogeography of platymantine ranid frogs of SE Asia and the SW Pacific

Summary

In this chapter I provide a phylogenetic estimate of evolutionary relationships of frogs of the subfamily Platymantinae (genera *Platymantis, Batrachylodes, Palmatorappia, Discodeles, Ceratobatrachus*) and their relatives (genus *Ingerana* and various SE Asian ranids) based on 12S and 16S ribosomal RNA mitochondrial gene sequences. I use Parsimony, Likelihood, and Bayesian methods of phylogenetic inference to reconstruct estimated evolutionary relationships among platymantines and ranid outgroup taxa of SE Asia and the SW Pacific using mitochondrial gene sequence fragments between 900 and 2400 bp of 12S and 16S sequences. In order to address historical relationships with respect to species boundaries (Chapt. 1), I also conducted phylogenetic/phylogeographic analyses of dense and geographically robust taxonomic sampling from within Philippine members of the genus *Platymantis* using approximately 900 bp of 16S.

In general, platymantines consist of two reciprocally monophyletic clades, one composed of Philippine *Platymantis* and the other containing all Papuan-Solomon-

Bismarck archipelago taxa. Non-*Platymantis* genera are nested within *Platymantis* and fall basal to SW Pacific island archipelago species. The genus *Platymantis* is thus paraphyletic with respect to *Batrachylodes, Palmatorappia, Discodeles,* and *Ceratobatrachus*.

I use parametric bootstrapping to test alternative biogeographic and systematic hypotheses for the origins of platymantines. My data reject two published hypotheses for platymantine relationships, namely that the frogs of the SW Pacific are derived from within the Philippine radiation ("Asian Origins Hypothesis"), and, conversely, that the Philippine radiations are nested within the Papuan-Solomon-Bismarck clade ("Reverse Asian Origins Hypothesis"). Instead, the data are consistent with the "Papuan Progenitor" hypothesis of reciprocal monophyly of SW Pacific and SE Asian clades, suggesting that platymantines are an older group than previously thought and that they may have evolved in isolation on ancient landmasses that later accreted to the north coast of the current island of Papua New Guinea, allowing for simultaneous dispersal east and west from this point or origin.

The data also reject taxonomic hypotheses of earlier authors, including the monophyly of *Platymantis* and monophyly of some of the hypothesized species groups within the Philippines (and equivalent classes from throughout platymantine distribution). Instead of species group or "ecomorph" (Chapt. 2) monophyly, the prevailing trend that emerges is one of repeated evolution of ecological and morphological types across a series of replicated radiations of species ranging in size from 50+ (the Philippines) to two (Fiji) species. Due to this pattern of multiple origins of ecomorphs, platymantine ranids appear to be an excellent model system for the study of patterns and processes of evolution of coupled morphological, ecological, behavioral, and acoustic traits.

“There is a large element of chance in successful island colonization”—MacArthur, 1974: 84.

“It is very likely that *Platymantis* arose from *Rana* and has no relationship to *Micrixalus*…*Palmatorappia* of the Solomons seems to be a case of parallel evolution in a different stock, namely *Cornufer* or an allied genus”—Noble, 1931: 522–523.

“The Philippine fauna includes lineages with clear Papuan affinities, *Platymantis* and *Oreophryne*”. The presence of these two genera iin the Philippines (but not in Palawan) may date from either pre-Tertiary or Oligocene…when the eastern Philippines-Halmaherra arc was closest to New Guinea and the Melanesian Islands”.—Inger, 1999:462.

Introduction

The family Ranidae is an enormous taxon (800 + species) of dubious monophyly (Ford and Cannatella, 1993; Duellman and Trueb, 1994; Darst and Cannatella, in press), global distribution (Hutchins et al., 2003), and incredibly diverse content (Duellman and Trueb, 1986; Duellman, 1993; Frost, 2002). Current systematic understanding of this cosmopolitan family has been characterized as "...a state of chaos" (Duellman and Trueb, 1994; Ford and Cannatella, 1993; Inger 1996; Inger and Tan, 1996a, 1996b), and few groups are as poorly understood as the morphologically diverse Asian ranids (Dubois 1981; 1992; Roelants et al., in press).

The platymantine ranids (subfamily *Platymantinae*; genera *Platymantis, Batrachylodes, Discodeles, Ceratobatrachus, Palmatorappia*, and possibly *Ingerana*) are a remarkable assemblage of frogs distributed from the Philippines (Brown et al., 1997a, 1997b, 1997c, 1999a, 1999b; Alcala and Brown, 1998, 1999) to Papua New Guinea and SW Pacific islands (Solomon-Bismarck Archipelago and New Britain; Brown, 1952; Brown and Tyler, 1968; Zweifel, 1969; Allison, 1996; Brown, 1997; Fig. 4.1). In addition to several synapomorphies of osteology and external morphology (Brown, 1952), platymantines are noted for direct larval development (Brown and Alcala, 1982b) and ability to colonize habitats that otherwise conspicuously lack ranid frogs (high elevation, mossy rain forests with no standing water and small oceanic islands). The ability to persist and reproduce in environments lacking standing freshwater may have allowed dispersal events across the SW Pacific that gave rise to the endemic species of *Platymantis* on distant oceanic islands like Palau and the Fijis (Gorham, 1965; Gibbons, 1985; Kuramoto, 1985, 1997; Ota and Matsui, 1985), Platymantine direct development also has been suggested as a “key innovation” that may have contributed to the success of *Platymantis* species at extremely high elevations in cloud forests of volcanic peaks of SE Asia (Inger, 1954) or on oceanic islands lacking standing fresh water (Tyler, 1979).

Whatever the characteristics or set of circumstances that led to the establishment, persistence, and diversification of platymantines in SE Asia and the SW Pacific, we can be certain that the systematic relationships and biogeographical patterns of this group will be of interest to biogeographers and students of island biology. No other group of ranid frogs comes close to exhibiting a distribution pattern found in platymantines (Brown, 1952, 1997; Tyler, 1979; Allison, 1996; Inger, 1999), and no other group has such an appreciable portion of its diversity located in the islands of the SW Pacific (Allison, 1996). Platymantines are, for example, the only ranid frogs found in the isolated islands of Fiji (Gorham, 1965).

Because of the dramatic array of platymantine species diversity (e.g., see Chapt. 1), their particularly curious distribution (Noble, 1931, Brown, 1952, 1997; Tyler, 1979), their high degree of morphological variation (Boulenger, 1884, 1918; Günther, 1859; Brown, 1952; W. C. Brown et al., 1997a, 1997b, 1999a, 1999b), and confused taxonomic history (Boulenger, 1918; Brown, 1952; Dubois, 1981, 1987, 1992), I undertook the present study: a comprehensive phylogenetic analysis of platymantine ranids using partial 12S and 12S ribosomal RNA mitochondrial gene sequences.

My specific goals are to (1) provide a phylogenetic estimate of relationships among the platymantine frogs (species of the genera *Platymantis, Palmatorappia, Ceratobatrachus, Discodeles, Batrachylodes*, and *Ingerana*), (2) to address the monophyly and validity of the genus *Platymantis*, (3) to address competing hypotheses regarding biogeography, dispersal, and systematic origins of the platymantines, and (4) to provide a robust phylogenetic/phylogeographic estimate of relationships among Philippine *Platymantis* for the purpose of providing an historical framework for studies of ecomorphology (Chapt. 2), call variation (Chapt. 3), and a comparative analysis of rates of evolution of different classes of call characters (Chap. 6).

Taxonomic overview

The genus *Platymantis* has one of the most extensive and confusing synonymies of any taxon in the family "Ranidae" (sensu Ford and Cannatella, 1993; Darst and Cannatella, In press). The unusual distribution of the platymantine ranids (Chapt. 1; Fig. 4.1), coupled with uncertainty about their systematic relationships, and a particularly unstable nomenclatural history has led to an unsatisfactory situation in which biologists have referred a century of new species discoveries to the suspected paraphyletic taxon *Platymantis*.

These actions of convenience have largely obscured a possible understanding of the evolutionary and biogeographic relationships of platymantines while undermining an appreciation of their diversity (W. C. Brown, *pers. comm.*). They also have prevented the empirical test of obvious hypotheses regarding the biogeography and phylogenetic origins of platymantines. Furthermore, without a robust phylogenetic estimate of relationships of the species, discussion of the evolution of the most exciting characteristics of the platymantines (direct terrestrial development, complex advertisement calls, unusual ecology, rates of speciation) has been impossible (but see Alcala, 1962; Tyler, 1979; Allison, 1996; Brown and Alcala, 1982b; Alcala and Brown, 1999; Brown et al., 1999a, 1999b).

Cornufer was described by Tschudi (1838) on the basis of single specimen of uncertain locality data (Zweifel, 1967). In later years, approximately 20 species from the Philippines, Papua, the Solomons, New Britain, the Fijis, and New Ireland were described and assigned to *Cornufer* (and its synonyms *Hylodes* and *Halophila*) on the basis of several osteological and external morphological characters (e.g., Peters 1863; Boulenger, 1886, 1918; Taylor, 1920, 1922a, 1922b; Brown, 1949, 1952; Brown and Alcala, 1963b; Gorham, 1965; Parker, 1939, 1940; Schmidt, 1932).

Meanwhile, a number of similar species were assigned to the genus *Platymantis* (Günther, 1859), differing from species of *Cornufer* primarily on the basis of widely expanded terminal toe disks. Advocates of the validity of both *Cornufer* and *Platymantis* included Boulenger (1918), Noble (1931), Brown (1952), and Gorham (1965). Inger (1954) proposed synonymizing *Platymantis* with *Cornufer*, and later, when it was determined that the type species of *Cornufer* was in fact a leptodactylid frog in the genus *Eleutherodactylus* (Zweifel, 1967) and the name *Cornufer* was suppressed (Anonymous, 1978)—all species previously assigned to *Cornufer* were included in *Platymantis*. The lengthy literature debate surrounding this taxonomic confusion caused a number of investigators (notably Zweifel,1967 and Gorham, 1965) not to coin a new generic name in order to accommodate the wide- and narrow-disked platymantines in separate genera.

This appears to have been an admirable attempt to avoid further instability of the literature but, as Dubois wrote, "...this is a case where purely nomenclatural reasons have imposed on systematists a unanimity which purely taxonomic arguments had not allowed them to reach (Dubois, 1981:248; translation from original French by M. Berson, CAS).

Platymantis (sensu lato) lacks an explicit phylogenetic definition (sensu de Queiroz, 1988; de Queiroz and Gauthier, 1990) and is almost certainly paraphyletic with respect to non-*Platymantis* genera. Furthermore, renewed interest in the diversity of Philippine platymantines has just recently resulted in descriptions of eight new species (Brown et al., 1997a, 1997b, 1997c; Brown et al., 1999a, 1999b; Alcala and Brown, 1999), and as many as 26 new species await description (Chapt. 1). Thus, a comprehensive phylogenetic analysis of the platymantine frogs is warranted. The following study includes more than 45 Philippine species of *Platymantis*, representative species of the four other "platymantine" genera (Frost, 2002; Dubois, 1992), a few species of SE Asian *Ingerana* (=*Micrixalus* of earlier authors; Inger, 1954, 1966; Inger and Tan, 1996a, 1996b), and representative potential ranid outgroups from Asia and Papuan faunal regions.

Competing hypotheses of phylogenetic origins of *Platymantis*

In the absence of a phylogenetic estimate for platymantine ranids, a variety of somewhat speculative hypotheses have been offered to explain the evolutionary origins and unusual distribution of *Platymantis* and associated ranids (Fig. 4.1). **Hypothesis 1** (Noble's "Asian Origins" hypothesis; AO), most convincingly argued by Tyler (1979) and Kuramoto (1985, 1997; see also Noble, 1931; Inger, 1954, 1966; Duellman and Trueb, 1986; Mahoney et al., 1996) suggests that platymantine ranids first radiated in the Philippines (derived from some unknown SE Asian ranid stock) and dispersed over water to Palau, Papua New Guinea, the Solomon-Bismarck Archipelagoes, and the Fijis (Fig. 4.2). Evidence for this scenario cited by earlier workers includes the larger number of *Platymantis* species in the Philippines (approximately 12 species at the time; now possibly as many as 51 [Chapt. 1]), prevailing equatorial oceanic currents (Kuramoto , 1985), and the seemingly-derived karyotype of several Pacific island species (Philippine populations were said to possess the typical ancestral SE Asian ranid karyotype; Duellman and Trueb, 1994). Thus, Tyler (1979), Kuramoto (1985, 1997), Ota and Matsui (1985), Brown and Alcala (1970a), Gibbons (1985), and Mahoney et al. (1996) all state or imply that platymantine ranids of the SW Pacific are derived from the Philippine radiation and are the result of long-distance, over-water rafting or waif dispersal events from the oceanic (Philippine) islands just east of the Sunda Shelf (Inger 1954). According to this hypothesis, one would expect Papuan-Solomon-Bismarck archipelago platymantines to be a monophyletic assemblage, nested within a possible grade-like series of paraphyletic Philippine species (Fig. 4.2).

Hypothesis 2, (the "Reverse Asian Origins" hypothesis; RAO) not usually favored, but at various times discussed by some earlier authors (Kuramoto, 1985, 1997; Ota and Matsui, 1985; Mahoney et al., 1996), is essentially the reverse biogeographic scenario suggested above (Fig. 4.3). According to this notion, platymantines might have presumably been derived from Australo-Papuan ranids and, as such, potentially first diversified in Papuan landmasses, eastern Indonesia, and/or the Solomon-Bismarck archipelagoes and later dispersed east, through eastern Indonesia, to eventually give rise to the endemics of Palau and the Philippines. The primary evidence for this interpretation was comparison of calls and karyotypes of only a few species (Kuramoto, 1985, 1997; Mahoney et al., 1996). Although not formally developed, this hypothesis also makes testable predictions in the context of a phylogenetic analysis. According to this interpretation, if the Philippine frogs are a secondary radiation, we might expect Philippine platymantines to be a monophyletic group, nested within a paraphyletic Papuan-Solomon-Bismarck archipelago clade (Fig. 3).

Hypothesis 3 (the “Papuan Progenitor” hypothesis; PP), recently favored by Allison (1996), Brown (1997), and Inger (1999) asserts that *Platymantis* and its relatives are a much older group than previously thought (actual age not specified) and that they evolved in isolation on former landmasses (Torricelli and Finisterre; see Tyler, 1979; Allison, 1996; Hall, 1996) that later accreted to the north coast of what is now Papua New Guinea, thrusting up the Torricelli and Finisterre mountain ranges, and allowing platymantines to disperse simultaneously east and west to give rise to the two major, parallel radiations of the Philippines and the Solomon-Papuan-Bismarck archipelagoes (Fig. 4.4). Evidence to support this scenario includes the call and karyotype for the Palau endemic, which would indicate an affinity to Papuan species, and not the Philippine populations (Ota and Matsui, 1985; Kuramoto, 1997; Allison, 1996). Other support for this hypothesis may be taken from the absence of platymantines on the Asian mainland and Sunda Shelf islands (with the possible exception of Sunda Shelf *Ingerana* and potentially mainland *Micrixalus*; Inger, 1954, 1966, 1999; Zhao and Adler, 1993). Furthermore, a recent reconstruction of Cenozoic SE Asia (Hall, 1996) indicates a potential dispersal pathway for the east-west dispersal hypothesis through an island arc containing the Sarangani bank of S. Philippines, and portions of landmasses that now make up N. Sulawesi and Halmaherra (Inger, 1999). Under the Papuan Progenitor hypothesis, one might expect Papuan and Philippine groups of species to be reciprocally monophyletic (Fig. 4.4) to the exclusion of an Asian, Papuan, or possibly African ranid outgroup.

The fourth and final existing hypothesis for platymantine affinities was that of Dubois (1981), namely that the platymantine ranids are somehow allied to the largely African subgenus *Euphlyctis* (Frost, 2002). No discussion of the biogeographical implications of his taxonomy was offered by Dubois (1981; 1987), and this hypothesis has largely been ignored by biogeographers. Dubois' current taxonomic arrangement allies *Platymantis, Discodeles, Palmatorappia, Ceratobatrachus* and *Ingerana* (=SE Asian *Micrixalus* species formerly assigned to *Platymantis*) in the tribe Ceratobatrachini, while *Batrachylodes* and *Micrixalus* were united with other taxa in the tribe Ranini (Dubois, 1992). Difficulties with Dubois' gestalt approach have been discussed elsewhere (Inger, 1996) and will not be addressed here.

Finally, it is worthwhile to note that there exist numerous problems with all extant hypotheses for the origins and systematic placement of platymantines among other ranid taxa. All current hypotheses are plagued by reliance on a single or few variable characters for which the polarities have not unequivocally been established. Although one might tend to adopt the opinion of prominent SE Asian and SW Pacific anuran authorities (Allison, 1996; Brown, 1997; Inger, 1999) and accept the Papuan Progenitor hypothesis as the best plausible explanation for platymantine origins, the empirical testing of the three (or four) hypotheses listed above requires a phylogenetic framework to test. Additionally, a phylogenetic estimate was required to distinguish between the three major competing hypotheses for the origins of platymantines (Fig. 4.2–4.4) and to establish the polarity/direction of hypothesized dispersal events.

Materials and Methods

Fieldwork and Taxon Sampling

Over the past eight years, I have attempted to sample all known species of Philippine *Platymantis* by conducting fieldwork in the islands of this archipelago; additionally I have conducted limited faunal sampling in eastern Indonesia. By targeting island bank systems separated by water channels deep enough to have persisted through Pleistocene sea level regressions (Heaney, 1985, 1986; Brown and Diesmos, 2002), I attempted to sample all evolutionary lineages (Chapt. 1) with substantial histories of isolation in an attempt to densely approximate true species diversity. On larger islands (e.g., Mindanao and Luzon, Philippines), I attempted to incorporate geographical variation by targeting isolated mountain ranges and by sampling across potential barriers to gene flow.

Colleagues and I conducted fieldwork on the Philippine islands of Luzon, Palaui, Polillo, Leyte, Samar, Palawan, Mindanao, Bohol, Mindoro, Negros, Cebu, and Panay between 1994 and 2002 (Chapt. 1). Additional samples were provided by fieldwork by colleagues working in Papua New Guinea, the Admiralty Islands (e.g., Manus), the Bismarck archipelago (New Britain and New Ireland), and several islands in the Solomon Island archipelago (see Acknowledgements). Frogs were captured by hand, over-anesthetized in chlorobutanol (1, 1, 1-trichloro-2-methyl-2-propanol), and dissected for liver, and muscle; tissues were preserved by immersion in liquid nitrogen, 95% ethanol, or high-salt DMSO tissue preservation buffer. Specimens were fixed in buffered 10% formalin, and later transferred to 70% ethanol (Simmons, 1987). Voucher specimens (Chapt. 1) are deposited in collections at the National Museum of the Philippines (PNM), The Cincinnati Museum of Natural History (CMNH), Louisiana State University (LSUMZ), the Texas Natural History Collections of the University (TNHC), the United States National Museum of Natural History (USNM), The Field Museum of Natural History (FMNH), the South Australian Museum (SAMA), and the Western Australian Museum (WAM). All museum acronyms (with the exception of CMNH) follow Leviton *et al*. (1985).

DNA Extraction, Amplification, Sequencing and Alignment

I extracted total genomic DNA from liver or muscle samples using the Qiagen DNeasy™ kit. I used eight primers in four pairs to amplify segments from within a 2.5 kb region spanning the tRNA-phe, 12S, tRNA-val, and 16S rRNA mitochondrial genes via polymerase chain reaction (PCR). Primers were either designed in the laboratories of David Hillis and David Cannatella at UT Austin or were adopted/modified from Goebel at al. (1998). This region corresponds to positions 2153-4574 in the complete mitochondrial sequence of *Xenopus laevis* (GenBank Accession # NC 001573 derived from M10217; provisional reference sequence).

Primer pairs included (5' to 3'): MVZ 59 (#29; modified from Goebel et al., 1998) ATAGCACTGAAAAYGCTDAGATG and tRNA-val (#73 Goebel et al., 1998) GGTGTAAGCGARAGGCTTTKGTTAAG, 12Sm GGCAAGTCGTAACATGGTAAG and 16Sa ATGTTTTTGGTAAACAGGCG (#87 modified from Goebel et al., 1998); 12L1 AAAAAGCTTCAAACTGGGATTAGATACCCCACTAT (#46 Goebel et al., 1998) and 16Sh GCTAGACCATKATGCAAAAGGTA (#76 Goebel et al., 1998); 16sc GTRGGCCTAAAAGCAGCCAC (#82 modified from Goebel et al., 1998) and 16Sd CTCCGGTCTGAACTCAGATCACGTAG (#95 modified from Goebel et al., 1998).

Amplifications for PCR began with denaturation at 94 °C for 1 min, followed by 30 cycles of denaturation at 92–94°C for 30 s, annealing at 42–48°C for 30 s, and extension at 72°C for 60 s, followed by a final extension at 72°C for 7 min. Negative controls were run for all amplifications to preclude the possibility of contamination. I purified PCR product with QIAquick Gel Extractions, and cycle sequencing was carried out with the following cycling conditions for 25 cycles: 10 s at 96°C; 5 s at 50°C; and 4 min at 60°C, using identical primers, ABI Big Dye terminators, and Sephadex clean-ups on an ABI 3100 PRISM™ sequencer (Applied Biosystems Inc.).

I used Sequencher 4.1 (GeneCodes Corp.) to pair complementary, single-stranded fragments and then (when sequences were available, see Missing Data section, below) assemble the four overlapping double-stranded regions into a single contiguous sequence of approximately 2.4 kb. I aligned sequences initially in Clustal X 1.8 (Thompson et al., 1997) and then manually adjusted sites by eye using the criterion of minimizing informative sites. All autapomorphies were verified against the original electropherograms/chromatograms. I identified and defined ambiguously aligned regions as character sets using MacClade and excluded regions of uncertain positional homologies (Gatesy et al., 1993) from further analyses after determining that doing so yielded no difference in tree topology and unappreciable changes in nonparametric bootstrap values for parsimony searches (see below).

Missing Data

Across all extant frog diversity this far sequenced for 12S and 16S (e.g., Darst and Cannatella, In press; Roelants et al., In press; Bossuyt and Milinkovitch, 2000; Biju and Bossuyt, 2003; Moriarty and Cannatella, 2003; Evans et al., 2003; Santos et al., 2003; Pauly, Evans, Brown, Santos, Moriarty, Holloway, and Cannatella, *unpubl. data*), the primers used in this study (or some close derivations of them) have proven successful for amplifying relatively converged regions of 12S and 16S ribosomal RNA mitochondrial genes. It appears that something unique and unusual among frogs has occurred within Philippine *Platymantis* such that very few converged regions can be identified and utilized for designing primers, especially towards the 5' end of 12S. Whether this situation arose via a relaxation of secondary structure or through an extremely rapid rate of molecular evolution is unknown; what has become clear is that standard PCR-based sequencing techniques have been insufficient for collecting comparable 12S sequence data for Philippine *Platymantis*. I employed FailSafe^{TM} PCR buffer optimization kits and exhaustive iterations of primer re-design in attempting to amplify problematic regions and obtained several additional sequences, but, by and large, problems persisted.

Because I was unable to collect the complete 2.4 kb targeted region, a number of strategies were employed to address the problem of missing data. I constructed a single master dataset and analyzed it in two subsets (by excluding taxa and/or data partitions). The result functionally was two unique datasets, which I will refer to as separate matrices and with which I performed separate analyses. One matrix contained nearly complete 12S and 16S (2400 bp) sequences for as many taxa as possible; this matrix has dense taxon sampling from the frogs of the SW Pacific but had relatively poor sampling within the Philippine grounds frogs. The other matrix had fewer data (900 bp) but extensive taxon sampling from the Philippines; this matrix contained only a subset of the representative diversity of the frogs of the SW Pacific. My goals were to (1) gain as much information regarding overall platymantine relationships based on as many phylogenetically-informative nucleotide positions as possible, and (2) infer species/population level relationships within the Philippines based on the densest geographic sampling possible (even if only a subset of the data were available). In both matrices I excluded identical or redundant haplotypes from the same locality but included closely-related sequences if they were from different localities.

The first subset of the dataset (**Matrix I**) was composed of as many complete or near complete 12S and 16S sequences as possible. This matrix has the unique property of being nearly 75% complete for 12S ands 16S genes (1600-1800 bp), with 600–650 nucleotides missing for the 5' end of 12S in some taxa. This matrix has good representation in SE Asian/SW Pacific ranid outgroup frogs (genera *Rana, Limnonectes,* "*Papurana*," "*Sanguirana*," "*Pulchrana*," "*Odorrana*," "*Chalcorana*," *Amolops, Huia, Ingerana* [quotes indicate taxa of dubious monophyly, sensu Inger, 1996]), species of the platymantine genera *Batrachylodes, Palmatorappia, Batrachylodes, and Ceratobatrachus,* Papuan-Solomon-Bismarck *Platymantis*, and Philippine members of the *Platymantis hazelae* group as well as frogs related to *P. corrugata*. This matrix has relatively poor representation among Philippine members of the *P. dorsalis, P. mimula,* and *P. guentheri* Philippine species groups but has at least a few taxa per species group (sensu Brown et al., 1997a) and near-complete data for all Philippine taxa included.

Because the focus of my comparative analyses of advertisement call variation (Chapt. 5 + 6) is Philippine *Platymantis*, it was imperative that I closely examine all available data for species/population level relationships within the Philippines. Accordingly, I also performed a second set of analyses (**Matrix II**) with representation of all 16S sequences available for Philippine populations (12S data excluded when available). The second has dense sampling from within Philippine populations but is limited to fewer nucleotide positions per sample. This dataset is composed of approximately 900 bp 16S but has far denser taxon sampling within the Philippines and allows for limited discussion of phylogeographic relationships for some widely-distributed taxa (i.e., *P. dorsalis*).

Model Selection and Phylogenetic Analyses

I conducted phylogenetic analyses using Maximum Parsimony (MP), Maximum Likelihood, and Bayesian methods of phylogenetic inference (review: Huelsenbeck et al., 2001). I initially analyzed data in PAUP* 4.0b8 (Swofford, 2000) using heuristic searches under equally-weighted MP, 200 random taxon-addition sequences, and a single tree bisection-reconnection (TBR) branch swapping per replicate (Mulpars = no). I saved the most parsimonious trees from this first round of searches, and then swapped on these trees (Mulpars = yes). Nodal support was evaluated using nonparametric bootstrapping (Felsenstein, 1985; Hillis and Bull, 1993) with heuristic searches of 2,000 replicates and 10 random taxon addition sequences per replicate in PAUP.

There is considerable recent interest in methods of phylogenetic analysis of combined datasets, representing conceivable dataset partitions and heterogeneous data types within a Bayesian framework. Of considerable importance with respect to Bayesian analysis is the process of assigning separate models of sequence evolution to disparate partitions of sequence data while performing mixed-model combined analyses

(Nylander et al., 2004). In order to accommodate distinct processes of sequence evolution in the major partitions of the data (i.e., 12S and 16S; valine t-RNA excluded), I tested the fit of unique models of sequence evolution to each different gene. Subsequent analysis then had the potential to incorporate separate models and parameter estimates per data partition, all within the context of a single analysis (Nylander et al., 2004).

For model-based analyses, I took a mixed approach to the selection of an appropriate evolutionary model of sequence evolution. For ML analyses, I employed successive likelihood ratio tests (Goldman, 1993) using Modeltest 3.06 (Posada and Crandall, 1998, 2001) to determine the best fitting model of evolution, following recommendations of Huelsenbeck and Crandall (1997) and Posada and Crandall (2001). Likelihood ratio test were conducted by attempting to identify the best model of evolution for each data partition (12S/16S where appropriate) and starting with the best MP tree for all (combined) data. Modeltest was then used to identify the best model and parameter estimates per partition, starting with the MP tree for the combined data. Thus, I avoided the potential pitfalls of parameter estimation on different neighbor-joining starting trees that could potentially be calculated as part of the default settings associated with testing model fit to each specified data partition.

ML analyses were conducted through successive iterations with starting parameters input from successive searches. Parameters for the first iteration were estimated from the tree with the best likelihood score from the equally most-parsimonious tree set and then subsequent analyses employed starting topologies and parameter estimates from previous analyses (Huelsenbeck and Crandall, 1997).

The GTR+Γ+I model best-fit my data across all data partitions and was therefore used in subsequent ML and Bayesian analyses. MacIntosh G4 and G5 computers with dual processors, equipped with parallel MrBayes and Pooch multiple-processor enabling software or used MrBayes 3.0 (Huelsenbeck and Ronquist, 2001) installed on a on a NPACI Rocks cluster (http://www.rockscluster.org) comprised of a master node and eight compute nodes, each with dual AMD 1533MHz processors. For each Bayes run, I initiated four independent Metropolis-Coupled, Markov Chain Monte Carlo (MCMCMC) runs starting with random trees for each of four simultaneous chains, using dirichlet priors and a differential heating parameter set to 0.5. I sampled chains every 1000 generations for runs of 10^7 generations. The proportion of tree samples (collected after burn-in) that contained observed bipartitions was taken as the estimate of the posterior probabilities. I ran four MrBayes runs per matrix permutation (Matrix I and II) and checked results of each run for convergence in results; tree visualization was accomplished in PAUP (Swofford, 2000) and TreeView (Page, 1996).

Hypothesis testing

I used a probabilistic topology-based test to address phylogenetic and biogeographical hypotheses. The first approach was the parametric bootstrapping and sequence simulation method described by Hillis et al. (1996; see also Huelsenbeck et al., 1996; Huelsenbeck and Rannala, 1997; Goldman et al., 2000; Wilcox et al., 2002). Referred to as the "SOWH" test (Swofford-Olsen-Waddell-Hillis; Goldman et al., 2000;

Buckley 2002), this parametric approach to hypothesis testing has the advantage (over nonparametric tests) of increased power, decreased probability of Type II statistical error, and is attractive in that it is logically implemented in a straight -forward manner amenable to hypothesis testing (Goldman et al., 2000; Wilcox et al., 2002; Evans et al., 2003; Santos et al., 2003). Parametric bootstrapping techniques involve generating a null distribution of expected tree-length differences or Likelihood score differences (Huelsenbeck et al., 1996; Wilcox et al., 2002), against which one can directly compare an observed test statistic (the quantity of interest to a particular evolutionary hypothesis), the difference between the observed tree from the original data and the best tree consistent with the null hypothesis under consideration.

I simulated (using Seq-Gen1.25; Rambaut and Grassly, 1997) 100 datasets of the same size as the original under the null hypothesis using realistic conditions (dataset size and ML parameter estimates derived from those observed in my original sequence data) and then conducted two heuristic searches on each replicate dataset. The shortest unconstrained tree, the shortest tree consistent with the null hypothesis, and the tree-length difference between these two topologies were found. I then compared this distribution of the simulated tree-length differences to the same difference from the original dataset (e.g., the difference between shortest tree from the observed data and the shortest tree compatible with the null hypothesis imposed on analysis of the original data). In cases where multiple most parsimonious trees were discovered, trees were sorted according to likelihood tree score and used the most likely tree from the subset of equally-parsimonious trees for sequence simulation (see Evans et al., 2003). By asking whether the observed test statistic falls within the 95% limits of the distribution of the expected tree-length differences, the null hypothesis can be assessed with statistical rigor and, potentially, rejected with confidence if it falls outside the statistically defined 95% bounds of the tree-length difference distribution from the simulated datasets (Huelsenbeck et al., 1996; Wilcox et al, 2002). This involves determining a *p*-value for the null hypothesis according to $p = 1 - (N/T)$, where N is the number of simulations with a tree-length difference greater than that observed in the original data and T is the total number of simulations. For this tabulation, I used the LogReader program (D. Zwickl, *unpubl.*).

Methods described here are presumably similar to those described for the parametric bootstrap (SOWH-test) in Goldman et al. (2000), and Buckley (2002) except that I analyzed the datasets under parsimony for the following reasons: as pointed out by Hillis et al. (1996), Huelsenbeck et al. (1996), and more recently, Buckley (2002), parametric tests can suffer from Type I error if the assumed model used to generate sequences deviates too far from the actual model that generated the observed data. Because at present it seems unrealistic to imagine that one might be able to perfectly match the generating model and the natural model that generated the observed data (D. M. Hillis, *pers. comm.*), a trade-off exists in the decision to use more powerful parametric (possibly prone to Type I error if their assumptions are violated) tests versus less powerful nonparametric (requiring fewer assumptions, but possibly prone to Type II error) tests. As a consequence of these issues, Buckley (2002) recently criticized the use of parametric bootstrapping and advocated a more conservative nonparametric approach through the use of the Wilcoxon sign-ranked ML analog, the Shimodaira-Hasegawa (SH) test (Shimodaira and Hasegawa, 1999; Goldman et al., 2000). Another, potentially more profitable approach to this trade-off might be to develop improved parametric techniques, ideally so that they are less limited by their assumptions. In any case, for the present study, the same effect can be achieved by using complex, relatively parameter-rich models to generate simulated datasets and then using a simpler model or parsimony scores to evaluate test statistics. Presumably, this will result in some loss of power, but will also reduce type I error rate and render the test more "conservative" (D. M. Hillis, *pers. comm.*). Additionally, to counter the potential for inflated Type I error rates, I used the sequential Bonferroni alpha-level protection procedure to correct for multiple comparisons (Rice, 1989; see Evans et al., 2003).

Finally, due to the nature of the hypotheses under consideration, I employed novel techniques for the construction and review of constraint trees. In my case, there was no way to "constrain" an island radiation (i.e., Philippines vs. Papuan/Solomon/Bismarck radiations) to be a grade-like series of paraphyletic lineages, so I filtered randomly-generated, near-most parsimonious trees in PAUP, and in this way selected the most parsimonious tree (but not the only possible) with the desired paraphyletic relationship. I evolved sequence data on this tree and tested the subsequent test statistic with the assumption that this was the best tree exhibiting the paraphyly of the desired group. In cases where multiple most-parsimonious paraphyletic hypotheses trees were discovered, I used PAUP to assess each for its Likelihood score, and chose the best tree by this criterion.

Results

Sequence Variation and Alignment

In the final alignment of all contigs, positional homology was ambiguous for 14 regions totaling 202 bases. Comparisons to secondary structure and a large dataset of non-bufonid hyloids (D. C. C. and D. M. H., unpubl. data) were not informative in resolving the alignment of these regions, and they were excluded from the analysis. In the final Matrix I alignment (126 taxa, after 12 redundant sequences were removed), of the 2267 nucleotide positions, 1189 were variable and 880 were parsimony-informative. In the final Matrix II alignment (130 taxa after redundant haplotypes were excluded) of the 922 nucleotide positions, 822 were variable and 469 were parsimony-informative.

I used the single preferred topology for all data combined (256 taxa) for model selection but different parameter estimates were obtained from separate analyses of the 12S and 16S data partitions. In both partitions the GTR+I+Γ model was selected. For 12S, parameters estimated were base frequencies (A: 0.381; C: 0.242; G: 0.146; T: 0.2409), rate matrix (A↔C: 1.8610, A↔G: 5.4122, A↔T: 2.4120, C↔G: 0.8802, C↔T: 10.971, G↔T: 1.0000), shape parameter (0.4987) and proportion of invariant sites (0.04621). For 16S, parameters estimated were base frequencies (A: 0.375; C: 0.2361; G: 0.1545; T: 0.2379), rate matrix (A↔C: 1.8570, A↔G: 5.4223, A↔T: 2.5005, C↔G: 0.8866, C↔T: 10.9681, G↔T: 1.0), shape parameter (0.5993) and proportion of invariant sites (0.0341). These parameter estimates were used in the subsequent partitioned Bayesian analysis.

Phylogenetic relationships

General relationships (Parsimony analysis, Matrix I)

Maximum parsimony analysis with a single round of branch swapping per random addition sequence generated nine most-parsimonious trees of 4026 steps (CI = 0.402; RI = 0.398), and swapping on these trees generated no additional topologies. Differences between the nine most-parsimonious trees involved changes in the positions of basal, poorly-supported nodes (*Discodeles bufoniformes* vs. *Batrachylodes* clades) and a tendency for the *Platymantis browni* + *Palmatorappia solomonis* + *Batrachylodes minutus* clade to move to a more basal position with respect to the entire Papuan radiation.

Among Asian and Papuan ranids, platymantines appear not to be closely related to common to mainland or Papuan species. There is very weak support (bootstraps [bp] of 52) for a relationship between the Asian fanged frogs (genus *Limnonectes*) and platymantines, so this relationship should be viewed with caution, especially in absence of African or other continental species in the analysis. Platymantines do appear to be closely related (bp 96) to high-elevation aquatic Sunda Shelf species of the genus *Ingerana* (Fig. 4.5). There is strong evidence (bp 100) for the monophyly of the remaining platymantines and a reciprocally monophyletic relationship between Philippine (bp 97) and Papuan/Solomon/Bismarck (bp 99) radiations. All analyses conducted as part of this study showed identical results with respect to the monophyly of platymantines and their close relationship to Sunda Shelf *Ingerana* (below).

Within the Papuan/Solomon/Bismarck radiation, basal nodes are weakly supported, but several major well-supported distal clades are evident (Philippine relationships will be discussed below). One such clade (bp 100) consists of several species of *Batrachylodes* and a single undescribed "*Platymantis*." Another well-supported (bp 100) clade consists of the giant leaf-mimic frogs of the Solomon Islands (genus *Ceratobatrachus*) plus *Platymantis aculeodactyla*. One clade with moderate support (bp 79) suggests a sister relationship between aquatic platymantines of the Bismarcks (genus *Discodeles*) and the two Fijian endemics, *Platymantis vitiensis*, and *P. vitiana* (bp 100 in each case). Another moderately-well-supported clade consists of miniaturized platymantines *Palmatorappia solomonis* (tree frog), *Batrachylodes minutus* (scansorial species), and *Platymantis browni* (shrub frog). One well-supported clade (bp 100) consists of the tree canopy specialist *Platymantis neckeri*, an undescribed miniature tree frog, and four giant ground frog species of the Solomons (*P. solomonis, P. myersi, P. magna*). I find strong support for the monophyly of two populations of the giant tree frog *Platymantis guppyi* but only weak support (bp 57) for a relationship between this species and the remaining Papuan species of *Platymantis*. The remaining *Platymantis* consist of five major clades, the most basal of which (bp 76) consisting of *P. weberi* and three undescribed forms from Manus Island and Papuan New Guinea. The next major clade (bp 100) consists of frogs related to *P. papuensis*, including *P. p. occidentalis* from E. Indonesia and the Palau Island group endemic *P. pelewensis*. There is moderate support (bp 84) for a sister relationship between the *P. papuensis* clade and a well-supported clade (bp 100) consisting of *P. gillardi, P. boulengeri*, and possibly *P. rhipiphalca*. Finally, the remaining platymantines fall into a monophyletic group, consisting of three major clades. There is moderate support (bp 76) for a sister relationship between frogs related to *P. schmidti* and the shrub frogs (*P. macrosceles* and undescribed species) of New Britain+Manus (bp 100). There is moderate support (bp 71) for a relationship between this clade and a group of four or five species (bp100), including *P. nexipus* and several undescribed species from New Britain and Manus. Finally, there is moderate support (bp 84) for a monphyletic relationship between these three clades and an undescribed Manus Island species (*P.* n. sp. "clicker"). *Discodeles bufoniformes* can not be placed with confidence in any of the above described clades and falls basal to the entire Papuan radiation.

General relationships (Partitioned Bayesian analysis, Matrix I).—The consensus topology from the partitioned Bayesian analysis is presented in Figures 6a and 6b. Bayesian analysis of 12S and 16S partitioned data with dense taxonomic sampling within the Papuan and SW Pacific island archipelagoes produced a preferred topology with most of the same relationships as found in the parsimony analysis (Fig. 4.8). There is excellent support (posterior probabilities [pp] of 100) for the *Ingerana+Platymantis* basal relationship and the monophyly of the Philippine *Platymantis* is upheld with posterior probability values of 100%. To the extent that more limited Philippine taxonomic sampling is available in these analyses, two of the three same clades found in parsimony analyses were again observed in Bayesian analyses. The corrugated ground frogs and *P. hazelae* group shrub frogs are each well supported (pp 100) and are sister clades. The Bayesian analysis departs from results of the parimony analyses in that the remaining three species (*P. spelea, P.* sp. E, and *P. insulata*) fall out as a moderately supported monophyletic group (pp 80), whereas in the parsimony analysis *P. spelea* was the most basal member of the Philippine clade (with weak support for *P.* sp. E+*P. insulata* plus the remaining Philippine *Platymantis*).

Frogs of the Papuan and SW Pacific island archipelagoes fall into a single monophyletic clade with excellent nodal support (pp 100). The primary division in this clade is between Solomon Islands *Discodeles bufoniformes* and the remaining memberso of this radiation. There is moderate support (pp 70) for a large unresolved group that contains three major (well supported) clades: one clade, with nodal support of 100, contains the shrub frogs *Palmatorappia solomonis, Platymantis browni*, an undescribed small-bodied *Platymantis*, and four species of the genus *Batrachylodes*. Another major clade, its monophyly supported with posterior probability of 98, contains Solomon Islands *P. aculeodactylus*, several populations of the monotypic *Certaobatrachus guentheri*, and a clade depicting a well supported (pp 100) sister relationship between two members of the genus *Discodeles* and the *Platymantis*of Fiji (*P. vitiensis* and *P. vitiana*). Finally, the remaining member of this basal unresolved polytomy contains the remaining *Platymantis*. Thes form seven well supported clades (pps 89–100). The basal most clade (pp 100) contains two tree frogs (*P. neckeri* and *P.* n. sp. arboreal) and three ground species: *P. magnus*. *P. meyersi,* and *P. solomonis*. The next most basal clade contains sequences for the large-bodied tree frog *P. guppyi*, followed distally by a well-supported (pp 100) clade consisting of *P. weberi* (Solomons), two new species from Manus island, and north coast Papua New Guinea samples of *P. papuensis*. Remaing *Platymantis* consist of five major groups divided into three major clades. One clade consists of two subclades (all supported by pp 100), one containing western Papuna New Guinea *P. papuensis*, *P, occidentalis* of Eastern Indonesia and *P. pelewensis* of Palau. The other major subclade consists of New Britain species *P. boulengei, P. gillardi*, and possibly *P. rhipiphalcus*. The remaining three groups fall into a single well supported clade (nodal support of 100) consisting of a new species, *P*. n. sp "clicker" which is sister to two reciprocally monophyletic groups. One of these contains the tree frog *P. nexipus* (New Britain) and four undescribed arboreal or scansorial forms froom New Britain and Manus Island. The other contains *P. schmidti* and its (undescribed) relatives, an undescribed species from Manus Isl., and New Britain species *P. macrosceles* and *P*. n. sp. "bamboo" (Foufofoupolis and Brown, in press).

Ingroup Philippine phylogenetic/phylogeographic relationships (Parsimony analysis; Matrix II)

Maximum parsimony analysis with a single round of branch swapping per random addition sequence generated 16 most-parsimonious trees of 3336 steps (CI = 0.336; RI = 0.624) and swapping on these trees generated an additional eight equally-parsimonious trees. Differences between these 24 most-parsimonious trees involved changes in the positions of species of the *P. hazelae* species group (Cloud/Shrub frogs), intraspecific relationships between some populations of *P. dorsalis*, and the positions of basal, poorly-supported nodes.

Among basal Philippine *Platymantis* relationships (Fig. 4.7a), I find strong support (bp 97) for a basal clade of Philippine *Platymantis*, consisting of ground frog species from the southern Philippines (*P*. n. sp. "Clicker" and *P*. cf. "laticeps"), the miniaturized species *P. pygmaea*, Sibuyan Island ground frog *P*. n. sp. "Bank frog" and miniaturized *P*. n. sp. cf *pygmaea*, and a group of Luzon Island canopy frogs (*P. cornuta, P*. n. sp. E, *P. banahao*), and Gigante island ground frog *P. insulata*. There is moderate support (bp 70) for a sister relationship between masked ground frogs of the *P. corrugata* complex and cloud frogs of the *P. hazelae* complex. Within this couplet, the monophyly of masked frogs and cloud frogs are each well supported (bp of 88 and 100, respectively). Relationships within masked ground frogs are well-resolved, with support for the recognition of at least three distinct species. Relationships within Cloud/Shrub frogs are less supported, with good support for the sister relationship between *P. hazelae* (Negros Isl.) and *P. panayensis* (Panay Isl.), moderate support for a relationship between *P. polillensis* and *P*. "*sierraamadrensis*" (= *P*. n. sp. Enteng's frog), and moderate support for populations of uncertain taxonomic status related to *P. montana* and *P. isarog*. I find good support (bp 86) for a clade consisting of canopy frogs (*P. guntheri, P. rabori, P. negrosensis, P. luzonensis* and four undescribed species related to these forms) + the undescribed Malinao cliff frog (=Ground frog ecomorph) and good support for a relationship (bp 100) between this group and a clade consisting of all remaining Philippine *Platymantis* (bp 96). Within this remaining Philippine *Platymantis* (Fig. 4.7b) the most basal species is high-elevation, miniature *P. naomiae*, and then two large, poorly-supported clades of mixed ground frog and miniaturized species. I find poor support for a relationship between *P. levigatus* (ground frog; Sibuyan Isl.) and the widely-distributed ground frog *P. dorsalis* (monophyly = 100 bp). Within *P. dorsalis,* there is weak support for two clades, one from Luzon and another from the Visayan islands of Panay and Negros. Cebu Island *P. dorsalis* appears to be a unique (undescribed) lineage. The other large clade of N. Philippine frogs consists of a large number of undescribed species. I have moderate support (bp 71) for a clade consisting of ground frogs *P. taylori, P. cagayanensis* (ground frogs) and two miniaturized undescribed species from the Cordilleras of Luzon (*P.* n. sp. "shek-shek," Balbalan*,* and *P.* n. sp. "Benedict frog"). There is poor support for a clade consisting of the undescribed "Limestone frog," *P.* cf. *mimula* from Palanan, and *P.* n. sp "seeyok" of central Luzon. There is also poor support for the Negros cave giant *P. spelea*, the Banahao creek frog *P. pseudodorsalis*, and a miniature undescribed species from S. Luzon (*P.* n. sp. "June's frog"). I find strong support (bp 98) for a clade consisting of frogs similar to *P.* n. sp. cf. "seeyok" from central and western Luzon, and strong support for a clade consisting of ground frog *P.* n. sp. "Wheee-ahh" (Mt. Isarog), *P.* n. sp. "Katipunan" frog (Mt. Banahao), *P. indeprensa* (Mt. Banahao)*, P.*, n. sp. "yok-yok" (Guttaran, N. Luzon), and *P. mimula* (S. Luzon).

Ingroup Philippine phylogenetic/phylogeographic relationships (Bayesian analysis; Matrix II)

Bayesian analysis of the 16S data for dense taxonomic sampling within the Philippines produced a tree with most of the same relationships upheld as found in the parsimony analysis (Fig. 4.8). Disparities included lack of resolution of relationships among species of the *P. hazelae* group, and distal relationships among the various clades of the N. Luzon clade (i.e., relationships among *P. naomiae, P. levigata,* the clade consisting of [Zamables mountains *P.* n. sp. "seeyok," *P.* n. sp. "wheee-ahh," *P.* n. sp. "Katipunan" frog, *P.* n. sp. "yok-yok," and *P. indeprensa* and *P. mimula*], and *P.* n. sp. "limestone," *P.* n. sp. "seeyok," *P. pseudodorsalis, P.* n. sp. "June's frog," *P. taylori, P. cagayanensis, P. spelea, P. dorsalis, P.* n. sp. "shek-shek," and *P.* n. sp. "Benedict"). In general, Bayesian support values (posterior probability values) were high throughout the tree, with the exceptions noted above. There was good agreement between well-supported Parsimony (bootstraps) and Bayesian (posterior probability) nodes. Relationships that were well supported in parsimony analyses (e.g., bp ≥ 70) were well supported in Bayesian analyses (e.g., pp ≥ 95%).

Parametric tests of biogeographic and taxonomic hypotheses

In both the case of the Asian Origins and Reverse Asian Origins hypotheses (Figs. 4.2–4.3), the tree-length difference test statistic falls well outside the distribution of simulated tree length differences (Fig. 4.9), allowing confident rejection of both hypotheses with high significance ($P \leq 0.01$) in favor of the single biogeographical scenario with predictions that are consistent with the observed relationships: the Papuan Progenitor Hypothesis (Fig. 4.4). Although basal relationships within each of the reciprocally-monophyletic clades are poorly resolved, the data are in strong conflict with constraint topologies in which either the Philippine or the Papuan/Solomon/Bismarck archipelagoes are paraphyletic with respect to the other; imposing these alternative constraints resulted in longer topologies and significantly greater differences between expected and observed tree-length differences (Fig. 4.9).

Constraining Matrix II trees to be consistent with the monophyly of Philippine species groups (Brown et al., 1997a) also resulted in significantly longer trees for frogs of the *P. dorsalis, P. guentheri*, and *P. "mimula*" species groups, allowing me to reject three of the four previous morphology-based species groups (Brown et al, 1997a, 1997b, 1997c, 1999a, 1999b; Alcala and Brown, 1998, 1999) for Philippine platymantine diversity. In the cases of the Philippine frogs of the *P. hazelae* species groups, this group was monophyletic in all phylogenetic analyses, suggesting that within the Philippines at least, the Cloud/Shrub frog ecomorph type is monopyletic and has evolved only once. Finally, although no formal hypotheses have been extended for species groups across the Papuan/Solomon/Bismarck archipelagoes, these platymantines exhibit the same kinds of structural specializations (Boulenger 1882, 1918; Brown, 1952), ecological preferences (S. Richards, and W. C. Brown, *pers. comm.*), morphological diversity (Brown, 1952; Gunther, 1852; Peters, 1863; Noble, 1931; Schmidt, 1932; Parker, 1939, 1940; Zweifel, 1967, 1969; Dubois, 1981, 1987 1992; Chapt. 3), and call types (Kuramoto, 1997; Menzies, 1982). Giant canopy frogs such as *P. neckeri* are very similar in all respects to Philippine frogs of the *P. guentheri* species group and shrub frogs such as members of the genus *Palmatorappia* and *Batrachylodes*, as well as several species of *Platymantis* (e.g., *P. macrosceles, P.* n. sp. “Bamboo”) that are analogous to the Philippine *P. hazelae* species group. Throughout the

Papuan/Solomon/Bismarck archipelagoes there are a wide variety of ground forms, similar in morphology and ecology to the Philippine *P. dorsalis* species group. Both radiations also possess giants (*P. spelea* of the Philippines vs. *P. vitiana* of Fiji, *P. magna* of New Ireland, etc.) and miniatures (*P. pygmaeus* of the Philippines vs. *P. parkeri* of the Solomons). So although SW Pacific island species have not formally been organized into the same taxonomic species groups that have been erected in the Philippines, they do exhibit the same range of morphological, ecological and acoustic variation (i.e., the ecomorph classes defined in Chapt. 2), and so it is reasonable to hypothesize the monophyly of each of these cohesive, phenotypically-similar (Chapt. 2) groups as well. In all cases, parametric bootstrapping of Matrix I rejects the hypothesis of monophyly of each of the ecomorph types ($P \leq 0.001$; plots not shown), suggesting multiple origins of the evolution of morphological, ecological, and acoustic forms (Chapts. 2 and 3).

Discussion

The phylogenetic portions of this study revealed numerous surprises that promise to cause a great upheaval in our understanding of systemic relationships and evolutionary biology of platymantines. The reciprocally-monophyletic relationships between the major radiations of SE Asia (the Philippines) and the SW Pacific (Papuan/Solomon/Bismarck archipelagoes) reflect expectations of anuran biologists well-versed in amphibian diversity of the region (reviews: Brown, 1952, 1997; Allison, 1996; Inger, 1999) with respect to the genus *Platymantis*, but are still somewhat surprising in light of the extraordinary range of morphological variation within platymantines as a whole. The generic arrangements corresponding to morphological variation exhibited by the species of *Platymantis, Palmatorappia, Ceratobatrachus, Batrachylodes*, and *Discodeles* is a testament to the extraordinary degree of morphological divergence and specialization in these forms yet is untenable in light of the phylogenetic framework presented here. That *Platymantis* is paraphyletic with respect to these other platymantine genera emphasizes the degree of convergence exhibited across replicated radiations of separate island archipelago radiations of platymantines.

In one sense, the systematic relationships uncovered in this study come as no surprise. Biogeographically, one might expect species from geographically proximate island groups to be more closely related to one another, even in the face of parallel morphological specializations in island group after island group. However, previous studies revealed no precedence for the high degree of repeated evolution of ecomorph patterns suggested by the phylogeny (Chapt. 2). This scenario, of repeated evolution of ecomorph types across repeated radiations of frogs, ranges through each geographic component of platymantine diversity—from the larger radiations of the Philippines and the Solomon Islands, to moderately-sized radiations of the Bismarcks and Admiralty Islands, and finally culminating in the minor radiation of Fiji, with a monophyletic pair of species consisting of a single ground frog and a single tree frog.

In light of the phylogenetic relationships and parametric bootstrapping rejection of previous taxonomic hypotheses, taxonomic arrangements of previous authors clearly require modification. Not only are the species group taxonomies of the Philippines not supported by the data (with the exception of the *P. hazelae* species group), but also *Platymantis* is paraphyletic with respect to *Palmatorappia, Ceratobatrachus, Batrachylodes*, and *Discodeles*. Resolution of these problems will not be straightforward. One option will be to resurrect older names for distinct clades of species referred to *Platymantis*. This might entail resurrection of the genera *Hylodes* and *Halophila* (*Cornufer* cannot be applied; Dubois, 1981) and to name new genera for the additional monophyletic groups. Another, more conservative option might be to subsume all platymantine genera under the name *Platymantis*. A third solution might be to submerge all platymantine genera under the name *Platymantis* and recognize clade names for each monophyletic group contained within, in accordance with principles of phylogenetic nomenclature/classification (de Queiroz and Gauthier, 1990). However, because of the possibility of hybridization and mitochondrial introgression, I hold taxonomic decisions in abeyance until a later date when comparable sequences from a nuclear gene are available.

Because one major goal of the phylogenetic portions of this study was to estimate intra- and interspecific relationships among Philippine species so as to enable a comparative analysis of advertisement call variation (Chapts. 3 and 6), I am particularly interested in relationships elucidated by the Matrix II analysis (high-density Philippine 16S sequences). Although distal relationships among the highly-speciose northern Philippine ground frogs are not satisfactorily resolved (Figs. 4.7 and 4.9) beyond the assertion that far numerous species are present than previously thought (Alcala and Brown, 1998, 1999), it is clear that the estimated phylogeny involves numerous extensive evolutionary transitions between ecomorph types (Chapt. 2) within the Philippines alone. Resolving the relationships within the Philippines will be a priority of future work. Clearly, one immediate goal will be to sequence a less-rapidly evolving (e.g., nuclear) gene as well as a more rapidly-evolving mitochondrial gene (other than 12S) such as ND2 or ND4 in hopes of resolving poorly-supported nodes in basal and distal portions of the phylogeny.

Limited available evidence from molecular phylogenies of widespread Philippine taxa (McGuire and Kiew, 2000; Brown and Guttman, 2002; Evans et al., 2003) suggest that resolving relationships between taxa from separate Pleistocene aggregate island complexes (PAIC) of the Philippines (Heaney, 1985; Brown and Diesmos, 2002) may be a challenge that reflects a genuine evolutionary history of rapid-radiation characterized by short internodes at basal portions of trees and long branch lengths from subsequent histories in isolation (Brown and Diesmos, 2002). The difficulty I experienced reconstructing distal Philippine platymantine relationships (Figs. 7 and 8) may be yet another example of this type of evolutionary history and, if true, is probably caused by rapid changes in sea level (Heaney, 1985, 1986; Voris 2000) or earlier geological events (Hall, 1996).

Despite more than 100 years of taxonomic intrigue, the stunning array of morphological diversity among platymantine ranids has only recently begun to be understood. Future studies will profit from a phylogenetic perspective and, hopefully, the application of numerous unlinked loci for phylogeny estimation. Results garnered from 12S and 16S mitochondrial gene sequences suggest that traditional methods have captured only a portion of the diversity and meaning of platymantine ranid variation. Numerous evolutionary hypotheses remain to be addressed.

Chapter 5:

Transmission performance of advertisement calls of Philippine platymantine frogs in complex forest environments

Summary

If different structural properties of the environment differentially attenuate or degrade acoustic signals, then natural selection acting on acoustic signals and the subsequent evolution of habitat-specific signals may result. One simple prediction is that species should produce acoustic signals in microhabitats where those signals transmit best. This Acoustic Adaptation Hypothesis (AAH) suggests that signals may be maximally or differentially suited to transmit in certain environments, but not others.

I tested the AAH using calls from a large number of species of Asian forest frogs (genus *Platymantis*). I broadcasted the calls of 31 species along distance transects at low (400 m), mid (900m) and high (1500 m) elevations and played calls into a variety of vegetation types from four heights (0, 1.5, 3, and 5 m above the ground). I then re-recorded calls at five stations along distance transects and compared these experimentally attenuated and degraded calls to non-degraded call exemplars to arrive at habitat-specific measures of loss of call structure and fidelity.

Distance and perch height have profound effects on call attenuation and degradation. All species calls perform better (i.e., attenuate and degrade less) over shorter distances and most performed significantly better when calls were broadcasted above the ground.

I find moderate support for the predictions of the AAH. In low elevation forests where diversity is high in ground- and herb-layer plants species, calls of local forms generally perform better than high elevation species. With some exceptions, calls of species that call at or near the ground level (complex calls and frequency sweeps) outperform pulsed midmontane species calls or tonal cloud forest species calls. At midmontane sites where diversity in understory and canopy species (with pulsed calls) is high, pulsed calls perform as well and sometimes better than frequency sweeps and complex calls and always better than tonal calls. At high elevation cloud forests where diversity in species that produce tonal calls is highest, tonal calls outperform other call types at the preferred perch height of these species (just below or at the canopy of the elfin cloud forest). While there are exceptions to the trends described above, and numerous intriguing trends are not statistically significant, this study is the first of its kind to employ a large number of closely related species from widely different microhabitats and one of the first to find limited support for the AAH in frogs.

“The hypothesis that habitat acoustics influence signals and signaling behavior would be supported by showing: (1) that animals within a given habitat signal from places or at times that increase their communication range; (2) that environmental factors influence signal propegation and integrity in ways the affact communication range; and (3) that signal structure, signaling behavior, or both vary within a species…or among closely related species in ways that reflect acoustically relevant differences in the environment.”—Gerhardt and Huber, 2002:370.

Introduction

Conspicuous, stereotyped acoustic signals are frequently utilized by amphibians communicating over large distances (Blair, 1962, 1964, 1972; Gerhardt 1994a; Duellman and Trueb, 1994; Stebbins and Cohen, 1995; Littlejohn, 2001). As acoustic signals travel between sender and receiver, they are affected in various ways depending on distance traveled, atmospheric conditions and physical interference by objects and surfaces (Wiley and Richards, 1978; Bradbury and Vehrencamp, 1988; Forrest, 1994). Depending on the environment through which a signal travels, considerable variation in receiver response can be introduced into a communication system by extrinsic factors (Bradburry and Vehrencamp, 1998).

In anuran amphibians, acoustic signals frequently represent the basis of species mate recognition systems. Advertisement call transmission performance can have a tremendous immediate impact on the fitness of an individual if interference in transmission reduces a signal's ability to elicit a response from a receiver (Gerhardt, 1994b; Bradbury and Vehrencamp, 1988; Parris, 2002; Ryan and Kime, 2003). Thus, in addition to the recognized importance of sexual selection in shaping signal evolution (Ryan, 1980, 1983, 1988, 1990, 1991, 1997; Endler, 1992; Eberhard, 1993; Dawkins and Guillford, 1996), natural selection may play a role in the evolution of acoustic signals if variation in call performance is related to differential reproductive success through female choice (Ryan et al., 1990; Ryan and Kime, 2003). To elicit a meaningful response, a signal must at a minimum be coupled to the environment, travel through it over distance, encounter a receiver, and be effectively detected, decoded, and processed (Ryan and Wilczynski, 1988; Wilczynski et al., 1992; Wilczynski and Ryan, 1999; Ryan and Kime, 2003).

One link in the coevolution of communication systems that has until recently received little attention is the role of the environment in transmission of acoustic signals of frogs and toads (Ryan et al., 1990; Kime et al., 2000; Ryan and Kime, 2003). When frogs vocalize during communication (for review see Rand, 1988), metabolic energy is used to produce muscle contractions that drive mechanical displacement or vibrations of physical structures of the larynx and arytenoid cartilages yielding pressure fluctuations in the environment (McAlister, 1961; De Jong and Gans, 1969; Martin, 1972; Martin and Gans, 1972; Duellman and Trueb, 1994). Frequency modulation may be achieved by control of rates of airflow through the larynx (Dudley and Rand, 1991) and costly energetics of sound production (Ryan, 1985) may be offset through elastic energy storage in the anuran vocal sac (Rand and Dudley, 1993; Jaramillo et al., 1997). If efficient coupling of vibrations of physical structures of the larynx to the environment follows, the signal may travel over long distances through the environment (Gerhardt, 1994a; Brenowitz et al., 1984; Ryan and Kime, 2003). If an acoustic signal then arrives at the receiver with appropriate temporal and structural properties that allow it to be detected, decoded, and processed, a behavioral response may be forthcoming and communication has occurred (Ryan and Kime, 2003). This interaction of a mechanical disturbance in medium pressure (sound) with the sensory and nervous system of the receiver presumably requires a degree of fidelity of the original signal (Wilczynski et al., 1992; Wilczynski and Ryan, 1999).

Thus, another suite of challenges to this kind of a system is a variety of alterations to the temporal and structural properties of a signal that can be introduced by a signal's passage through time, objects, and space. Collectively, these alterations are known as transmission effects (Ryan et al., 1990; Kime et al., 2000; Ryan and Kime, 2003).

Distance alone has a profound effect on acoustic signals. All else being equal, a signal's amplitude decreases 6 dB per doubling of distance from the source due to the spherical geometric spread of sound (Bradbury and Vehrencamp, 1988). Thus, a dramatic decline in a receiver's ability to detect a signal would be expected with increasing distance from the signal's source. Additionally it has been shown that distance alone can have a significant impact on female response to a stimulus if spectral distribution of energy in a call varies with distance (Sun et al., 2000). Height of signaler is also known to have a profound effect on signal transmission in certain contexts (Dabelsteen et al., 1993; Nemeth et al., 2001) and absorption of high frequency components of signals by the ground is often offered as a proximate explanation as to why many ground birds perch to call (Bradbury and Vehrencamp, 1988).

Stationary heterogeneities (objects of different size and densities; atmospheric variation) interfere with sound through a variety of different mechanisms. Air and objects such as vegetation may scatter, absorb, or dampen sound waves (Wiley and Richards, 1978; Richards and Wiley, 1980). Frequency-dependent sound attenuation may occur if passage through large objects differentially attenuates or filters out one component of spectral variation in a signal but not others (Wiley and Richards, 1978). Reverberations and reflections of sound waves is known to disrupt the temporal structure of signals in complex environments such as forests (Wiley and Richards, 1978; Ryan et al., 1990) and boundary layer interference of signals can result from passage of acoustic signals through density heterogeneities such as layers of the atmosphere or surfaces such as forest canopies, the ground, or standing water (Bradbury and Vehrencamp, 1988; Nemeth et al., 2001).

In all of these cases, changes in fidelity and amplitude of signals (degradation) caused by distance or objects can result in loss of signal efficacy (Kime et al., 2000). Changes in temporal or spectral properties of a signal can render it unrecognizable to the receiver or increase the probability of receiver error via a decline in signal-to-noise ratio (Kime et al., 2000). Commonly-identified environmental conditions that influence signal degradation include meteorological conditions, temperature gradients, environmental complexities and object size/density variation, broadcast height, and background noise of the environment and related species (Duellman, 1967; Hodl, 1977; Marten and Marler, 1977; Waser and Waser, 1977; Brenowitz et al, 1984; Waser and Brown, 1986; Ryan and Sullivan, 1989; Ryan et al., 1990; Wollerman and Wiley, 2002a, 2002b; Parris, 2002).

One of the obvious predictions derived from environmental acoustics studies of the last several decades is that species calling in different environments may be expected to have evolved habitat-specific signals that allow for maximum signal efficacy in the specific environments within which a given species vocalizes (Marten and Marler, 1977; Marten et al., 1977; Morton, 1975, Waser and Brown, 1986). One general prediction is simply that natural selection should favor signals that transmit best in the specific environment in which they are produced (Ryan and Brenowitz, 1985; Zimmerman, 1983; Kime et al., 2000). If this is so, we would expect calls of species from local environments to outperform (i.e., suffer less degradation) calls foreign to that environment (Ryan et al., 1990). Yet, several recent studies have failed to show the predicted acoustic adaptation to local environments (Penna and Solis, 1998; Kime et al., 2000).

Still, one study involving closely-related subspecies of cricket frogs occupying markedly different structural habitats in North America found strong evidence for the “Acoustic Adaptation Hypothesis” (AAH; Ryan et al.,1990; Ryan and Kime, 2003) and for the notion that species may be maximally-adapted by natural selection for signal efficiency/performance in different environments (Ryan et al., 1990). The implications of Ryan et al.’s (1990) findings in the face of contrary evidence (Penna and Solis, 1998; Kime et al., 2000) suggest that the best place to look for evidence in support of the AAH is in closely-related lineages that occupy markedly different microhabitats.

Platymantine ranids of the rainforests of SE Asia and the SW Pacific are an ideal system for testing the AAH for the following reasons: (1) platymantines are the dominant frog fauna of the uplands of the mountains of the Philippines; at any one locality we find between 7 and 11 sympatric species occupying a variety of structural forest niches (*pers. obs.*); (2) a phylogenetic estimate of relationships within this group (Chapt. 4) suggests that diversity is extremely high (Chapt. 1) and is partitioned among closely-related species/populations with markedly different ecomorphologies (Chapt. 2), and vocalizations (Chapt. 3); (3) an historical perspective suggests that evolution in this group has been dominated by multiple occurrences of specialized morphological/ecological types, suggesting numerous evolutionary transitions between habitats (and the acoustic challenges each represents); and finally, (4) high levels of species diversity in this group are centered around the volcanic peaks of S. Luzon Isl., in an easily-accessible series of sites, within a day's drive from a major metropolitan area (Manila).

I have undertaken the following experimental study to test the Acoustic Adaptation Hypothesis and the notion that the environment may fuel or constrain the evolution of acoustic signal diversity via natural selection. I used call playback experiments and distance-transect experimental degradation of calls of 31 species from distinct microhabitats to ask the question: do calls transmit best in the environment in which they are naturally produced (Morton, 1975)?

Materials and Methods

Exemplars of calls of 31 species (Table 5.1) of Philippine frogs of the genus *Platymantis* were selected from my own acoustic collections (original recordings deposited in the W. Frank Blair Sound Collection of the Texas Memorial Museum, University of Texas at Austin). A number of calls of each species (recorded at maximum amplitude without clipping) corresponding to naturally-observed call-group patterns (*pers. obs.*) were transferred to a single audio metal cassette tape; output amplitudes were arbitrarily standardized to match that of a typical *P. corrugata* advertisement call recorded on Mt. Isarog, Luzon island, at 1.5 m and 25°C and that of a synthesized pure tone standard of 300 Hz (amplitude of these two signals were standardized to each other before experiments began). The master tape used in all field trials consisted of these 31 calls and a synthesized pure tone.

I conducted transmission experiments at the Mt. Makiling Forest Reserves of the University of the Philippines at Los Baños, Laguna Province, Luzon Island, Philippines from 10 August–22 August, 2000 (preliminary pilot studies) and 28 July–16 August, 2001 (full experiments), at the approximate beginning of the S. Luzon rainy season. All trials were performed between 2200 at night and 0200 hr, the next morning, following rainy afternoons so as to ensure a natural wet forest environment with constant temperature/atmospheric conditions. The master tape was played with a Sony™ WM DC6 Professional Walkman and broadcasted with a 6 inch, full-range dynamic speaker (Mineroff Corp.). At the start of each trial, the sound pressure level (SPL) of the pure tone and *P. corrugata* call output was adjusted to 80 dB SPL at 0.5 m from the source. The 31 exemplar calls were then broadcasted and re-recorded along distance transects with a Sennheiser™ ME80 condenser microphone (equipped with K3U power module) attached to a second Sony WM DC6 recorder. Ambient noise levels (from calling frogs in the area) were minimized immediately prior to these trials by using acoustic disturbance caused by activating canned pressurized airhorns and/or by firing a 32-caliber pistol (loaded with blanks). Calls were broadcasted and recorded horizontally along straight-line transects (microphone and speaker held at same heights; checked with a carpenter's level and a string) from the source at 1, 2, 4, 8, 16 and 32 m. The distance transect was replicated at four heights: 0 m (ground level), 1.5 m, 3 m, and 5 m above the ground.

Because both platymantine habitats and frog communities vary in composition with forest type and elevation (Brown and Alcala, 1961, 1963, 1986, 1994; R. Brown et al., 1996; 2000, 2001; W. Brown et al, 1997a, 1997b, 1997c; Diesmos, 1998; Diesmos et al., 2002; see also Heaney and Rickart, 1990), I attempted to incorporate realistic variables into an elevational transect that encompassed atmospheric and structural variation in observed frog habitats. I replicated the entire transect array at three elevational stations on Mt. Makiling: 400, 900, and 1400 m above sea level. The resulting configuration (Fig. 5.1) constituted a 4 X 5 experimental design (4 heights vs. 5 distances), replicated three times at different elevations, for a total of 60 experimental treatments with five cross-correlations calculated and five amplitude readings taken at each combination of height, distance, and elevation (see below).

For SPL readings, I used a portable digital Radioshack sound pressure level meter, sighted the speaker visually for a straight-line orientation with the source, and recorded SPL of stimuli five times per station. I calculated expected SPL levels from the logarithmic decibel scale using the formula for a sphere in order to incorporate the geometrically-expanding nature of the spherical spread of sound (dB SPL = 20 log [d1 / d2]; Bradbury and Vehrencamp, 1988). With the expectation that SPL measurements should fall 6 dB per doubling distance from the source, I subtracted observed from expected SPL values and subjected this "Excess Attenuation" to Analysis of Variance (ANOVA) techniques following qualitative confirmations of the assumptions of normality.

Five re-recorded calls per species per station per height were digitized with a sampling rate of 44 kHz using SoundEdit (Macromedia, 1995) and Canary (Charif et al., 1996) and were digitally band-pass filtered to decrease ambient noise outside the range of the signal of interest (filter ranges ascertained from visual inspection of sonograms and/or the power spectrum calculated for undegraded calls of ≤ 2 m from source). For species that call in groups (e.g., *P. hazelae* group species), I arbitrarily selected five calls from a variety of call groups and arranged these together.

I measured call degradation across distance as a function of the cross-correlation coefficient (amplitude-normalized covariances of signals as a function of time offset between them; Kime et al., 2000), calculated between non-degraded calls re-recorded at 1 m and each of the subsequent distance transect recording stations (2, 4, 8, 16, 32 m). For each distance transect station and height from the ground, I performed five cross-correlation analyses of the experimentally-degraded sonogram and the re-recording of the non-degraded signal at 1 m, and then saved the highest value for subsequent statistical analyses. I followed Kime et al. (2000) in classifying calls that could not be distinguished from background noise (insects, frogs, or wind) as missing data.

A maximum sonogram cross-correlation coefficient represents the point at which two stimuli are optimally time-aligned (Kime at al., 200), thus obviating the need to subjectively align two signals during the comparison process. Because a cross-correlation of two sonograms (frequency vs. time plots with energy in various frequency components indicated in signal intensity) incorporates amplitude, spectral, and temporal axes information, they are useful proxies for assessing call degradation in terms of both loss of amplitude and disruption of spectral and temporal structure (Ryan et al., 1990; Kime at al., 2000).

I used mean species values of maximum sonogram cross-correlation in analyses of the effects of elevation, call type, and distance on call degradation. I used standard analyses of variance (ANOVA) techniques or their nonparametric equivalent (Kruskal-Wallis tests) when assumptions of normality were violated. If assumptions of normality were violated at a particular station but not others, I took a conservative approach to analysis and analyzed the entire distance transect with nonparametric tests using median cross-correlation values instead of sample means (Sokal and Rholf, 1981).

Study site gradient variation and bioacoustic considerations

Considerable variation in forest type and structure occurs in the moist tropical forests on volcanic mountains of the Philippines (review: Heaney and Regalado, 1998; Fig 5.1). With increasing elevation, mean temperatures drop and precipitation increases dramatically (Whitmore, 1984; Heaney and Regalado, 1998). Forests at higher elevations exhibit steadily thicker leaf litter detritus build up (Saplacao et al., 2001) and all surfaces (tree trunks, branches, fallen logs, etc.) become increasingly festooned with thicker layers of epiphytic moss coverage (Brown, 1919; Richardson, 1973; Whitmore, 1984). Along this same elevational gradient, forest structure changes dramatically (Brown, 1919; Gruezo, 1997). As one climbs higher on the mountain, dominant tree species canopy height and mean trunk diameter at breast height (DBH) decreases, while trunk and stem densities steadily increase (Brown, 1919; Richardson, 1973; Saplacao et al., 2001). This trend towards smaller, denser forest type culminates at Makiling's cloud forest peaks where old growth climax canopy may only reach a few meters from the ground, but the scrub is so thick that one can hardly pass (*pers. obs.*). Cloud forests of the Philippines are some of the wettest terrestrial environments on earth with as many as ten meters of annual rainfall per year (Heaney and Regalado, 1998). All of these atmospheric, temperature, and structural forest gradients could conceivably have significant impacts on the bioacoustics and signal transmission profiles of calling frogs at any given elevation (review: Ryan and Kime, 2003).

For example, sound-absorbing layers of moss and detritus on the ground and vegetation might be expected to attenuate calls at higher elevations where detritus accumulates. Complex forest structure at higher elevations where stem densities are high might be expected to disrupt temporally structured pulsed calls but favor tonal calls (Morton, 1975; Sorjonen, 1986; Richards and Wiley, 1980). At lower elevations where open space abounds in forest gaps, amplitude-modulated calls may be favored (Morton, 1975; Sorjonen, 1983; Handford, 1981; Catchpole and Slater, 1995). At ground levels, lower frequency calls, simple calls, and frequency sweeps may be favored if boundary layer interference differentially filters high frequency calls (Morton, 1975; Marten and Marhler, 1977; Waser and Waser, 1977; Endler, 1992). In contrast, calls emitted above the forest floor might experience less high-frequency dependent attenuation, thus allowing higher frequencies to transmit with relatively less attenuation—or allowing for a greater range of frequencies (Mathevon et al., 1996; Endler, 1992).

Because SE Asian frog communities vary in composition with forest type and elevation (Brown and Alcala, 1961, 1963, 1986, 1994; R. Brown et al., 1996; 2000, 2001; Diesmos, 1998; Diesmos et al., 2002), I conducted signal transmission experiments at three elevational stations on Mt. Makiling: at 400, 900, and 1400 m above sea level. The dominant forest types at these stations correspond to Whitmore's (1984; see also Gruezo, 1997) (1) "Lowland close-canopy dipterocarp forest" (2) transitional mid-montane forest, and (3) upper montane/mossy forest (Whitmore, 1984; Saplacao et al., 2001). Mt. Makiling has the benefit of being one of the best botanically-studied mountains of the Philippines (Brown, 1919; Richardson, 1973; Whitmore 1984; Gruezo, 1997; Saplacao et al., 2001) as well as having some of the best-studied frog communities of the Philippines (Diesmos, 1998; Gonzales and Dans, 1994, 1997). As a result of previous work conducted at this site, I had the advantage of knowing the limits of each species' elevational distribution on the mountain (Gonzales and Dans, 1997; Diesmos, 1998), the preferred microhabitat of each species of frog (Gonzales and Dans, 1994; Diesmos, 1998), and the structural characteristics of vegetation at various elevations (Brown, 1919; Gruezo, 1997). This allowed me to consider aspects of experimental design that might otherwise not have been available if I had been limited to cursory knowledge of the natural history of each species (Kime et al., 2000).

Results

Attenuation of complex calls

Significant distance from source (ANOVA: $P < 0.0001$) and height from ground ($P \leq 0.001$) main term effects were observed at low elevation transects (400 m), midmontane forest transects (900 m), and the cloud forest transect (1500 m). At low elevations, complex calls attenuated nearly as expected (i.e., as predicted by the spherical spread of sound; Fig. 5.2) or exhibited negative excess attenuation (attenuation less than expected) until 4–8 m distance along transects and then exhibited marked excess attenuation at further points along the transect (16–32 m). At these stations, calls broadcast at ground level suffered disproportionately more excess attenuation than did calls played above ground level (Sheffe's F tests; p's ≥ 0.01). At the cloud forest transect (1500 m), complex calls exhibited a near perfect step-wise incremental increase in excess attenuation with distance. Excess attenuation was particularly exhibited at heights lower to the ground, and especially at longer distances from the source. At higher elevations, the effects of height became increasingly more pronounced with increasing distance from the source (Fig. 5.2). A significant distance X height interaction effect was detected at each of the transects (F = 126.63, df = 12, $P < 0.0001$), although differential response to sources of variation clearly are different in the case of the cloud forest. Whereas in the 400 m and 900 m transects, the interaction effect was produced by minimal or negative excess attenuation at lesser distances along the transect, the interaction effect at the 1500 m transect appears to be produced by the increasingly severe effects of calling height with increasing distance from the source. Complex, multi-syllable calls generally performed best (i.e., experienced less excess attenuation) when broadcast in lower- to midmontane forests, and especially at lesser distances from the source.

Attenuation of frequency sweep calls

Attenuation of frequency sweep calls followed a pattern that was generally identical to that exhibited by complex calls (Fig. 5.3). Distance and height each had significant main effects on call attenuation ($P \leq 0.0001$) and at the 400 m and 900 m transects, excess attenuation was minimal or negative for the first (i.e., 2 and 4 m) stations, where as longer distances from the source (8–32 m) produced significant increases in excess attenuation (Scheffe's F-tests; p's ≤ 0.001). At these same elevations and at later stations on the distance transects, wildly marked decreases in excess attenuation were not observed with greater call heights, suggesting that in understory, lower-, and mid-montane forests, differences in ground- vs. elevated call heights are not as pronounced as they are for complex calls and frequency sweeps when these calls are broadcasted in cloud forests at 1500 m. (compare Figs. 5.2 and 5.3). As in complex calls, excess attenuation, at the 1500 m cloud forest transect is pronounced even at the beginning of the distance transect (2–4 m) and the effects of call height become increasingly severe with distance from the source (distance X height interaction, F = 5.84; df = 12, $P = 0.001$). Like complex calls, frequency sweeps generally performed best when broadcasted in lower- to midmontane forests, and especially when traveling shorter distances.

Attenuation of pulsed calls.—Although distance and height both produced significant main effects on attenuation (ANOVA; p's ≤ 0.0001), attenuation of amplitude-modulated pulsed calls followed a pattern somewhat different than that exhibited by complex and frequency swept calls (Fig. 4). At lower (400 m) and higher (1500 m) transects, excess attenuation was increasingly pronounced with distance, and the effects of call height became increasingly intense with increasing distance from the source. However, at mid-montane elevations (900 m), minimal or slightly negative excess attenuation was observed at distances of lesser magnitudes (2–4 m) and differences between call heights were less pronounced with increasing distance (Fig. 5.2). Again, significant interaction effects were observed between distance and height at all elevations ($P \leq 0.001$), although the differential response to the source appeared to be different when comparing the patterns exhibited by 400 m and 1500 m transects to that observed at the mid-montane transect (900 m). Thus, in general, amplitude-modulated pulsed calls experienced less excess attenuation when broadcasted at greater heights in midmontane forests across canopy gaps.

Attenuation of pure tone calls

Distance and height had significant main effects on attenuation (ANOVA; p's ≤ 0.0001) but attenuation of pure tone calls exhibited a pattern markedly different than that exhibited by other call types (Fig. 5.5). Tonal calls suffered incrementally greater excess attenuation with distance (with less severe, but significant [ANOVA; $P \leq 0.001$] effects of calling height) at low- and mid-elevation transects. However substantial levels of excess attenuation, at the 1500 m cloud forest transect were primarily observed when calls were broadcast at the ground level only; only at greater distances do higher perch heights exhibit significant excess attenuation (Scheffe's F-tests; $P \leq 0.01$). Thus transmission of pure, non-modulated tonal calls, when broadcasted above the ground, exhibited almost no excess attenuation or showed negative excess attenuation (Fig. 5.5). A significant interaction effect between height and distance was observed at the 400 m and 1500 m transects ($P \leq 0.001$), but not at the 900 m transect ($P = 0.08$). Of the significant interaction effects, differential response to the sources of variation were different between low elevation 400 m forest transect (increasingly severe attenuation at lesser heights with distance) and the 1500 m cloud forest transect (excess attenuation only apparent at great call heights only towards the end of the transect). In general, non-modulated tonal calls performed best at high elevations, in cloud forests, when broadcasted above the canopy of the dense cloud forest scrub.

Call degradation

Due to the tendency of platymantine call variation to fall into four major classes (Complex, multi-syllable calls, frequency sweeps, amplitude modulated pulsed calls, and non-modulated pure tone calls; Chapt. 3), I grouped maximum cross correlation values by call type and subjected these to statistical analysis. In the following sections, I present and discuss mean maximum cross correlation (XC) coefficients for each call type, calling height, and calling distance, and I used 3-Way ANOVAs to test for group mean differences with height, call type, and distance terms.

Call degradation in low elevation (400 m) closed canopy dipterocarp forest

At low elevations, distance, call type, and call height all had significant main effects on call degradation (as measured by cross correlation coefficient; ANOVA; $P \leq 0.001$). At all heights, signal fidelity generally declined with distance from the source, although the effects of broadcast height are significantly positive (higher XC coefficients at 1.5 and 3 m call heights). At 5 m broadcast heights in low elevation (400 m) forests, the calling transect passed directly through lower portions of the understory, and XC coefficients are again lowered by dense vegetation, similar to herb and shrub layer vegetation that interferes with calls broadcast from the ground (Fig. 5.6; 0m plot). Call type had a significant main effect (ANOVA F = 209.62, df = 3, $P < 0.0001$) and throughout numerous stations of the distance transect, complex calls and frequency sweeps exhibited significantly higher XC coefficients (Sheffe's F-tests, $P \leq 0.01$). Pulsed calls and tonal calls both suffered more severe degradation, but at 3 m call heights (i.e., calling under the understory canopy) pulsed calls performed markedly better than tonal calls, when produced across forest gaps (3 m plot).

Call degradation in midmontane (900 m) transitional forest

At the midmontane transect (900 m; Fig. 5.7), distance, call type, and call height all produced significant main effects (ANOVA; $P \leq 0.001$). Frequency sweeps and complex calls again outperformed tonal and pulsed calls when broadcast through dense herb and shrub vegetation at lower call heights (0–1.5 m), but pulsed calls compete with and occasionally surpass other call types when played at 3–5 m from the ground, although these effects at individual stations were either rarely or marginally statistically significant (Sheffe's F-tests; $P = 0.10$–0.05).

Call degradation in high elevation (1500 m) mossy cloud forest

In the high elevation mossy cloud forest scrub vegetation, distance, call type, and call height all produced significant main effects on attenuation (ANOVA; $P \leq 0.001$). As before, all calls performed best when lifted off the ground (Fig. 5.8) and complex and frequency sweep calls performed noticeably better at ground level (0 m plot). Tonal calls performed as well as sweeps and complex calls and outperformed other calls types (although not significantly at all stations, especially at 5 m broadcast height; Sheffe's F-tests, $P > 0.05$). In the canopy of the elfin cloud forest (approximately 3 m above ground) tonal calls out perform all other calls types (Sheffe's F-tests, p's ≤ 0.001), although, if produced in the open air well above the canopy, all call types suffered minimal degradation with distance (Fig. 5.8; 5 m plot).

Discussion

Upland anuran communities in the Philippines are unique in many respects, not least of which is the diversity of forest species not significantly aggregated in the vicinity of fresh water. Platymantine non-reliance on standing fresh water by virtue of their direct development mode of reproduction (Alcala, 1962; Brown and Alcala, 1982) may be directly related to the presence of high diversity and abundance of non-riparian montane habitats for *Platymantis* (Inger, 1954; Tyler, 1979; Ota and Matsui, 1995). One possible consequence of the relaxation of this semi-aquatic ecological constraint is that platymantine montane forest communities may have been free to assemble the complexity and rich diversity that we see today (Brown et al., 1996, 2000; Diesmos, 1988; Diesmos et al., in press). The presence of complex frog communities throughout the forested slopes of the mountains of Luzon, when coupled with significant variation in forest structure across elevational gradients, suggests that different species may face separate challenges for communication in their respective acoustic environment (Brown, 1919; Richardson, 1973; Gruezo, 1997; Saplacao et al., 2001). As the structure of forest changes with increasing elevation (review: Heaney and Regalado, 1998), different acoustic signals may represent "maximally-adapted" solutions to the challenges posed by each of these environments.

Despite the wide degree of variation in temporal and spectral characteristics of Asian forest frog advertisement calls, Philippine populations can conveniently be classified into several call types, including complex calls, frequency sweeps, pulsed calls, and tonal calls (Chapt. 3). Some species producing these calls are closely-related, whereas others are distantly related (Chapt. 4). Nevertheless, they share call (apparently via niche conservatism in some instances and evolutionary convergence in others) properties, behaviors, and microhabitat preferences that contribute to differential transmission and, in some cases, superior performance in the preferred microhabitats of those species.

For example, most species producing complex calls and frequency sweeps call from the ground, or slightly raised perches on banks, fallen detritus, herb layer vegetation, ferns, or suspended leaf litter. The calls of these species consistently outperform pulsed calls and tonal calls when played at or near the ground level (Figs. 5.2

and 5.6) in low- or mid-elevation forests where species diversity is highest (Brown et al., 2000a, 2000b; Diesmos, 1998; Diesmos et al., in press). One explanation that might account for the superior transmission of complex calls near the ground's surface is the tendency for the second syllable of these calls to be a low-frequency component. In general, most complex calls in Philippine platymantines are composed of two syllables: one of higher, and another of relatively lower frequency (e.g., "ee-yak" or "see-yok"; Chapts. 1, 3). Low frequency components of acoustic signals are known to suffer less boundary-layer interference across dense surfaces (the ground, moss-covered logs, etc) whereas relatively higher frequency signal components often are differentially filtered out of acoustic signals by environmental structural heterogeneities or dense surfaces (Wiley and Richards, 1978; Bradbury and Vehrencamp, 1988). Why the frequency sweeps would perform so well in herb and shrub layer vegetation is somewhat less clear, although these calls possess significant portions of calling energy, at least initially, in low frequencies. In any case, the highest diversity in the ground frog ecomorphs of the Philippines (Chapt. 2) is found at lower- to mid-elevations (Diesmos, 1998) and so the superior performance of these calls in low- to mid-elevation forests suggests acoustic adaptation to these specific environments (Ryan et al., 1990).

At the other end of extremes in variation in transmission performance is the case of high-elevation shrub frogs ("cloud frogs") with tonal calls. These simple, temporally brief, pure unmodulated tone calls consistently performed poorly in the climax dipterocarp forests of low- to mid-elevation (Figs. 5.5–5.7) but outperformed all other calls types when broadcasted at or above the elfin scrub cloud forest canopy of 2–4 m

(Figs. 5.5 and 5.8). These patterns are again suggestive of adaptation to bioacoustic constraints and the boundaries imposed by the physics of sound transmission. High-frequency signals are known to be differentially attenuated and degraded by the ground and it comes as no surprise that large, dense objects (i.e., the wide trunks of climax dipterocarp trees at low elevations) alter these signals in much the same fashion. It also comes as no surprise that the simple, unmodulated structure of these signals performs well in dense cloud forest scrub where environmental complexity is high, but the size of objects (e.g., narrow stems, small leaves, etc) is low (Brown, 1919; Richardson, 1973; Saplacao et al., 2001). Indeed, it is when tonal calls are lifted up into the preferred microhabitats of these species (at or just below the scrub canopy) that they outperform all other call types (Fig. 5.8). The minimal or negative excess attenuation exhibited by tonal calls in cloud forest at perch heights of 1.5–3 m (Fig. 5.5) might be explained by additive "interference" of reflections of sound waves from the top of the dense, relatively uniform surface (pers. obs) cloud forest canopy. Previous studies have identified the benefits of reverberations for optimal propagation of pure tone, (sometimes high frequency) narrow-frequency bandwidth sounds in dense forested habitats (e.g., Slabberkoorn et al., 2002); the narrow frequency range of the tonal calls produced by the cloud/shrub frog ecomorphs (Chapts. 2–3) may also explain a portion of these calls' propegation in cloud forest scrub. The fact that all calls fare equally well above the cloud forest canopy (5 m plot, Fig. 5.8) comes as no surprise as these calls are essentially traveling through open air, well above the canopy at this point.

The case of amplitude-modulated pulsed calls is somewhat less clear though trends are evident and worthy of discussion. Pulsed calls are notoriously inferior in complex environments where reverberations and scattering of complex signals tends to "blur" or "smear" temporal structure of signals (Marten and Marler, 1977; Wiley and Richards, 1978; Richards and Wiley, 1980; Ryan et al., 1990). It has been argued that amplitude-modulated signals may be preferred in open habitats where stationary heterogeneities that would disrupt these signals are lacking (Wiley and Richards, 1978; Richards and Wiley, 1980; Zimmerman, 1983). In this study I conducted transmission experiments in forested habitats, and pulsed calls consistently performed relatively poorly. However, I can ask the following: among all combinations of elevation, forest type, distance, and perch height, where do pulsed calls perform best? Does the area or conditions of maximal transmission performance of pulsed calls correspond to the observed microhabitat preferences of these frogs? Pulsed calls suffer less attenuation at shorter distances in low- to –mid-elevation forests (Fig. 5.4) and the differences between low and high perches were not so pronounced at the 900 m transect (Fig. 5.4; 900 m plot). Additionally, pulsed calls exhibited less or similar levels of call degradation (especially over longer distances) as did frequency sweeps and complex calls at the mid-elevation transect (Fig. 5.7). These trends suggest that the structure of mid-elevation forests (intermediate stem/trunk densities and moderate trunk sizes; Brown, 1919; Richardson, 1973; Saplacao et al., 2001) allows for the maximal transmission efficiencies observed for these calls. At both 3 and 5 m from the ground, pulsed calls did indeed significantly (Sheffe's F-tests; $P \leq 0.01$) outperform all other call types at the end of the

900 m transect (Fig. 5.7; 3 and 5 m plots). It is, in fact, at moderate elevations that the highest diversity (2–4 sympatric species) has been observed in this ecomorph (Diesmos, 1998; Chapt. 2) and one frequently finds these frogs calling from the canopy or from high *Pandanus* fronds, 3–10 m from the ground, clustered around clearings, apparently directing calling effort into the relatively open forest gaps (*pers. obs.*).

In this study I found evidence in support of the predictions of the Acoustic Adaptation Hypothesis using tests of actual call performance, as measured by call attenuation and degradation, in complex structural habitats. This study has the advantage of useing a large number of closely-related species (Chapt. 1), some of which inhabit widely different habitats and produce acoustic signals with divergent temporal and spectral structure (Chapt. 3). This study also made use of natural variation in forest structure along an elevational transect on a well-studied and isolated isolated forested peak.

Disadvantages of the approach taken here include general criticisms of cross-correlation as a measure of call degradation (review: Kime et al., 2000), the absence of a signal recognition or receiver assay component of the study, and the difficulties associated with untangling the complexity of species-rich assemblages like those found in the Philippines.

It would be illustrative to now study in detail less such complex systems as isolated mountains or islands with few platymantine species or known localities with single representatives of each of the ecomorphs (Chapt. 2). If acoustic niche partitioning (Drewry and Rand, 1983; Duellman and Pyles, 1983) does occur in these frogs, comparisons between simple and complex platymantine communities might reveal not only the true axes of acoustic niche space in SE Asian forests but also the assembly rules for niche packing (Losos et al, 1998; Gillespie, 2004) and the order of ecomorph evolution in complex frog assemblages. Additionally, whereas this study has elucidated intriguing patterns in call attenuation and degradation, the adaptive significance of those patterns ultimately depends on female choice among signals. Thus, the use of female choice assays and experimentally degraded signals provides opportunities for future studies.

Chapter 6:

A comparative analysis of mate recognition signals: platymantine ranids, call character diversity, and the tempo of advertisement call evolution

Summary

Platymantine ranids are noted for their complex and unusual advertisement calls (Chapt. 2). Due to their taxonomic, morphological, ecological, and acoustic diversity (Chapts. 1–3), these Asian forest frogs are an ideal system for a comparative study of call evolution. Using mitochondrial DNA sequence data, I estimated phylogenetic relationships, with particular attention to Philippine members of the genus *Platymantis* for which call data are available from my fieldwork. I used the phylogenetic estimate as an historical framework for a study of platymantine call evolution, focusing on variation in rates of acoustic character evolution.

I re-examined the “CR Hypothesis” (Cocroft and Ryan, 1995), namely that call characters related to morphology (e.g., call dominant frequency; inversely proportionate to body size) are more evolutionarily conservative than the presumably more labile characters related to neurophysiology (e.g., call rate; which might vary proportionaly to state of physiological arousal). Marginal evidence for differences in rates of evolutionary character change between “morphological” and “behavioral” call character partitions was found but the differences are opposite from expectations and are not statistically significant. I discuss possible sources of error, bias, and evolutionary change for observed trends.

"Although an anuran mating call is often considered a single, stereotyped unit of behaviour, calls do not evolve in a unitary fashion. Instead, because there are multiple sources of variation in the call-producing system, calls comprise a set of characters and these characters evolve at different rates" (Cocroft and Ryan, 1995: 293)

Introduction

Acoustic communication in anurans facilitates species recognition through stereotypical patterns in spectral and temporal characters of the advertisement call (Blair, 1962, 1964, 1972; Gerhardt 1994a Duellman and Trueb, 1994; Stebbins and Cohen, 1995; Littlejohn, 2001). The advertisement calls of frogs and toads are produced by integration of a wide variety of physiological mechanisms and morphological structures (Littlejohn, 1977; Rand, 1988; Duellman and Trueb, 1994). When frogs call, metabolic energy produced is utilized to contract the muscles associated with forcing air through the larynx; vibration is produced in the vocal folds and arytenoid cartilages; the resulting sound waves are then coupled to the environment (air, water, ground, vegetation); sound travels from the signaler to the receiver (Rand, 1988).

Ryan (1988; Cocroft and Ryan, 1995) suggested a fundamental distinction between spectral properties of the advertisement call (characteristics related to call frequency) and temporal properties (those associated with rates of call deliverance). He argued that spectral characters were constrained by morphology (McAlister, 1961; McLelland et al., 1996, 1998; Martin 1972; Martin and Gans, 1972) whereas temporal characters were associated with variation in neurophysiology and behavior (Ryan, 1985, 1988; Littlejohn, 2001). Thus, call characters such as dominant frequency would be expected to be correlated with aspects of morphology such as body size, larynx size and shape, and vocal fold length. In contrast, characters such as call duration and rate of call note production should be highly correlated with the physiological, hormonal, or physical state of the animal. An obvious and important prediction of these findings is that frequency-related spectral characters should exhibit significantly less phylogenetic variation (once the effects of body size are removed), whereas temporal call characters should be evolutionary more labile (once the effects of temperature are removed). Cocroft and Ryan (1995) further developed and articulated the this hypotheses (termed here the “CR Hypothesis”) and tested these predictions with calls of bufonid and hylid frogs. They found call characters associated with morphology to be more conservative (evolving at slower rates) than those associated with neurophysiology and behavior in chorus frogs (*Pseudacris*), but not in toads (*Bufo*).

Thus, available evidence regarding this hypothesis conflicts to some degree but fits well within the generalized historical debate concerning the phylogenetic utility of behavioral characters. Earlier authors have often assumed that behavioral characters "exhibit too much homoplasy" or are "too variable" to be useful in phylogeny estimation (Brooks and McLennan, 1991; de Queiroz and Wimberger, 1993; Wimberger and de Queiroz, 1996; Price and Lanyon, 2002). That is, aside from the practical problem of scoring or measuring behavior and assigning homology to plastic behavioral characters (McLennan and Brooks, 1993; Brooks, 1996), there has been an assumption inherent in the dismissal of behavioral characters or the suggestion that behavioral characters were not appropriate for use in phylogeny estimation (Brooks and McLennan, 1991; see also Brooks, 1996). Nevertheless, quantitative assessments of large numbers of behavioral characters in the context of phylogenies have continued to provide evidence to the contrary. In numerous recent studies, behavioral characters (even those under sexual selection; Irwin, 2000) map consistently onto phylogenies with little homoplasy (Payne, 1986; Irwin, 1988, 1996; Prum, 1990; Patterson et al., 1995; Foster et al., 1996; Kennedy et al., 1996; Van Buskirk, 1997; Cannatella et al., 1998; Slikas 1998; Slabbekoorn et al., 1999; Podos, 2001; Johnson et al., 2002; Price and Lanyon, 2002), providing vindication for classic studies of the value of ethology in the context of evolutionary history (Lorenz, 1941; Timbergen, 1959; Atz, 1970).

The underlying assumption has been that behavior is too variable, too homoplastic, too unreliable for use in phylogenetic studies—or that labile behavioral traits are rapidly erased by selection. Although this latter assumption may be equally untested, it does allow for specific predictions to be made with respect to the evolution of behavior. For example, Ryan (1980, 1985, 1991,1997) has shown certain properties of advertisement calls of *Physalaemus pustulosus* are under intense sexual selection via female choice of acoustic male traits. And although species have evolved reliable significant interspecific differences in acoustic traits (Ryan, 1991, 1997), thereby suggesting that these traits may bear the historical stamp of phylogenetic signal, a recent phylogenetic analysis of call characters (Cannatella et al., 1998) found little congruence between the phylogenetic estimates generated by call characters and all other (e.g., morphological, molecular) character partitions. This result suggested that the phylogenetic signal in behavioral traits may have been obliterated by intense sexual selection on these presumably labile and non-neutral characters.

Nevertheless, a growing body of studies using robust phylogenies and analyses of multi-species assemblages has found strong evidence for the persistence of phylogenetic signal in call characters in birds and insects (Shaw, 1996; McCracken and Sheldon, 1997; Martens et al., 1998; Henry et al., 1999; Price and Lanyon, 2002 Packert et al., 2003), suggesting that not all behavioral traits are excessively labile when measured with the common yardstick of a robust phylogenetic estimate. Given the degree of conflict in the literature and a lack of a consensus regarding the evolutionary lability of behavioral characters, a more profitable approach might be to expand studies beyond focal clades of a few closely related species and to incorporate a phylogenetic analysis of a large number of species with a wide range of call diversity. In this chapter I take such an approach.

I made use a model anuran system for a test of Cocroft and Ryan's (1995) hypothesis. I used a large group of frogs (genus *Platymantis*) with a remarkable degree of call variation that fits conveniently into four or five call types (Chapt. 3): frequency sweeps, complex (multi-syllable) calls, amplitude-modulated, pulsed calls, and pure tone calls with multiple origins of call types in association with preferred microhabitat of species (Chapt. 4). Use of these call types allowed for quantitative descriptions of call evolution and increased statistical power for robust tests for differences in rates of call character classes. Additionally, because calls differed in a fundamental manner among call classes (Chapt. 3), the analysis of *Platymantis* call variation enables me to focus not only on minor differences between closely related species, but also on nodes in the phylogeny where call type changes and presumably rapid evolutionary shifts occur between clades possessing different call types. Thus, I can ask at several levels, both at relatively shallow divergence and also at more basal nodes, deep within the phylogeny, if there is evidence for the hypothesis that morphology-related call characters evolve at more conservative pace?. Conversely, might behavior-related call characters be more evolutionary labile and exhibit increased rates of evolution across an independent historical estimate of evolution in the group.

Materials and Methods

Collecting call recordings.—Colleagues and I recorded advertisement calls of Philippine *Platymantis* species using two Sony™ WM DC6 Professional Walkman recorders, equipped with a Sennheiser™ ME80 condenser microphone and a K3U power module. Calls were recorded on individual 90 m high-fidelity TDK metal cassettes and only one side of each tape was used to ensure minimal signal degradation from use or distortion from tape stretching. Calls were recorded at the maximum amplitude possible without clipping and calls from frogs judged to be calling irregularly or erratically were discarded. Only advertisement calls were saved (though in many cases alarm or disturbance calls also were recorded and archived).

I attempted to obtain as many separate recordings or individual males per species as possible. As many as 20 individual recordings (e.g. *Platymantis dorsalis*) were obtained for some species, but for others only two or three individuals could be recorded (e.g. *P. spelea, P. negrosensis*). When numerous recordings were available I chose 10 males for which complete data were available and digitized 10 calls per male for up to 100 calls in some species (Chapt. 3). Because taxonomy of Philippine *Platymantis* is in a state of upheaval (Chapt. 1), I familiarizing myself with all the known calls of *Platymantis* species, by traveling to sites to record each and then acoustically diagnosing putative undescribed forms on the basis of the advertisement call. When differences between putative taxa were slight to the human ear, suspected new species call recordings were preliminarily analyzed immediately in the field on a laptop computer and compared against exemplars of known species. With this approach, my field colleagues and I were able to target each putative call type or species and to efficiently collect as many high quality recordings as possible in a relatively short period of time. Calls were recorded at 1–2 m from the subject and calls for which temperature data (below) were unavailable (e.g., when the calling frog escaped subsequent capture) were examined but discarded from the final analysis. Although only call recordings with complete data were included in statistical analyses, many more segments were examined per species to ensure accurate representation of call charactes. Accompanying data (frog identification, recording number, ambient, and substrate temperature, frog snout-to-vent length, and wet mass of frog) were collected during or immediately following the collecting of call recordings; recorded subjects were preserved the day following collection of call data (Chapt. 1) and field catalogs clearly specified from which individual frog each call was collected.

Scoring call data

Call exemplars were selected from my own recordings, deposited in the W. Frank Blair sound collections of the Texas Memorial Museum of the University of Texas at Austin. Calls were digitized using Soundedit© (Macromedia, 1995) and analyzed in Soundedit© and Canary© (Charif et al., 1996). Amplitude spectra oscillograms (waveforms), audiospectrograms (sonograms) and results of the Fast Fourier Transformation (power spectrum) were examined and most data were collected from on-screen displays on ≥ 15 inch computer monitors. Measurements requiring relatively long recording segments (e.g. call group rate) were collected in Soundedit©. A number of factors could have affected the accuracy of these measurements. I attempted to control for potential sources of bias by (1) including only recordings collected by myself or my close colleague who used the same field protocol (A. C. Diesmos), thus minimizing potential inter-observer bias, (2) always using one of only two ≤ 2 yr old Sony WM DC6 recorders, microphones, and power module combinations (minimizing possible differences between machines and performance degradation with age), (3) collecting most call segments within a three-year period (minimizing other unidentified sources of temporal bias), (4) using fresh batteries at all times (minimizing variation in recording speed introduced by battery wear), (5) recording call segments with exactly the same field protocol (minimizing potential for confusing individual frogs with their call recordings and maximizing precision of data collection), (7) recording frog, ambient, and substrate temperature, frog snout-to-vent length, and wet mass of frog immediately following every recording (ensuring high data quality and accuracy, and decreasing likelihood of mistakes), (8) including a large number of recordings from individual frogs (3–27 males recorded per species; mean = 8.97 ± 1.09 SD for 51 species), and (9) performing all data measurements from on-screen audiospectrograms, oscillograms, and results of Fast-Fourier Transformations by myself (minimizing inter-observer bias) using the Canary measurement and data log features whenever possible.

For the purposes of defining call characters, I concentrated on call characters that could be reliably scored across all platymantine species and subjective call types. Call-character selection was based on a subset of characters defined by Cocroft and Ryan (1995) that could be scored and compared among and between species and call types (see also Chapts 3 and 5 for further discussion of call types). Call characters included: (1) number of discrete syllables per call (No.Syl.), (2) dominant frequency (calculated across the entire call; DF), (3) fundamental frequency (calculated across the entire call; FF), (4) absolute magnitude of frequency modulation across the call (Abs.Mod.), (5) direction of frequency modulation (Mod.Dir.), (6) time duration of frequency-modulated segment of the call (in ms; Mod.Time), (7) call duration (in ms; CD), (8) calling rate (calls/s; CR), (9) call group length (in s; Grp.Len.), (10) call group rate (in s; Call.Grp.Rat.), (11) number of pulses per call / calls per call group (Pulse.No.), and (12) call type (Chapts 3; Complex, sweeps, pulsed, tonal, “tink”). For illustrative purposes, I also examined patterns of evolution in the following ratios of characters: (13) DF/Snout-to-Vent length, and (14) the number of calls per call group/call group length. Numerous other spectral and temporal aspects of the advertisement calls of particular call types or clades (Chapts 3) could be reliably scored across a particular call type or portion of the phylogeny, but because of problems associated with reliably assigning or assuming homology of call properties between widely divergent call types, these data were not examined in the context of the complete phylogeny and so are not included.

Data and analysis

Because temporally-related call characters vary in a predictable way with temperature and because calls were recorded at a variety of temperatures (12–30°C), I used standard regression analysis to derive species-specific regression equations (e.g. mean individual calling rate regressed on temperature) that permitted adjustment of mean values for a given species to a common temperature of 18°C when significant slopes were found. Similarly, some spectral properties of the advertisement call are known to vary predictably with body size. To ensure that interspecific comparisons were not confounded by body size differences between individuals or species, a simple method of attempting to incorporate body size information into the analysis was used. However, rather than adjust call frequencies to a common body size using regression techniques, I focused on the relationship between these variables by instead analyzing the ratio between each species' mean calling frequency and its mean body size. Although this approach does not include intraspecific range of variation in these variables in the same way that regression techniques do, I consider it a fairly reasonable proxy for the same idea: the frequency/body size ratio incorporates body size and frequency information, it accomplishes this on a per species basis, and it avoids the problematic adjustment of species body size. As a final check to ensure that DF/SVL ratio was not correlated wwith body size (and thus body size had been controlled in the analysis), I examined simple correlatios between DF/SVL and SVL and DF/SVL and body mass. Univariate statistical analyses were performed using Statview^{TM} (Abacus concepts, 1992), Statistica^{TM} (StatSoft, 1994), and JMP (SAS institute, 2000) software following confirmation of the assumptions of normality and homoscedasticity (Sokal & Rohlf, 1981) and log-transformation to homogenize variances.

Mapping call characters and tree visualization

I used MacClade (Maddison and Maddison, 1993; Cunningham et al., 1998) to map discrete call characters onto preferred molecular trees (Chapt. 4) and to generate basic tree statistics. I used TreeView v1.5 (Page, 2002) and TreeEdit v1.0 alpha10 (Rambault and Charleston, 2002), and PAUP* v4.0b10 (Swofford, 2002) to manipulate, edit, visualize, and compare tree topologies. Before proceeding with comparative test of phylogenetic hypotheses I examined univariate distributions of individual call characters across an ultrametric molecular clock tree derived from the 16S data partition after a likelihood-ratio test failed to reject a molecular clock. This approach allows for a straightforward and convenient appraisal of the relationships of taxa, relative degree of divergence between lineages, and a direct comparison with character evolution patterns (Blomberg et al., 2003).

Comparative methods

Because species values for mean phenotypic variables are not independent but are, in fact, related via their evolutionary history, conventional statistical methods are inappropriate for comparative analyses (Felsenstein, 1985; Harvey and Pagel, 1991; Garland, 1992; Garland et al., 1993, 1999). This realization has led to the development of numerous methods for analyzing comparative data in the context of a phylogeny, all to some degree attempting to account for phylogeny and the tendency for inflation of Type I error rates due to the simple fact that related species tend to resemble one another whereas non-related forms do not (Martins and Garland, 1991; Purvis et a., 1994; Harvey and Rambaut, 1998; Blomberg et al, 2003). Accounting for this fact, while retaining statistical power in comparative analyses, has been the major challenge and focus of numerous recent empirical tests and simulation studies aimed at verifying the properties of the methods and determining the degree to which various methods are robust to violations of their assumptions (Martins and Garland, 1991; Diaz-Uriarte and Garland, 1996; Harvey and Rambaut, 1998; Martins et al., 2002).

One major challenge to the proposition that all comparative data be analyzed in the context of a phylogeny has been the realization that not all closely-related species resemble one another. Numerous real and theoretical circumstances in which distantly-related species might be expected to resemble each other (or at least, more so than by chance alone) have been identified. For example, selection (natural or sexual) on certain traits may drive phenotypes away from the pattern expected by hierarchical relationships of the underlying tree topology (Cannatella et al., 1998). Convergent evolution on traits of interest can cause apparent similarity in phenotypes not due to common ancestry (Wake, 1991, 1996; Henry et al., 1999), and character displacement in sympatry has long been suggested to drive phenotypic norms of sister species apart (Losos, 2000; Littlejohn, 2001), resulting in closely-related species that differ more than expected on the basis of the phylogeny. These and other methodogical and theoretical issues have suggested to some workers that the best solution in certain circumstances might not be to incorporate phylogenetic information into comparative analyses (Price, 1997; Irshick et al., 1997; Losos, 1999). Still others have reasoned that one should first test the data for phylogenetic effect or phylogenetic signal and then make informed decisions about whether to incorporate phylogeny into the analysis once the effect of the underlying topology is known (Abouheif, 1999; see also Pagel, 1999; Freckleton et al., 2002).

Blomberg et al. (2003) dismissed as illusionary these concerns and drew attention to the well-known fact that analyses that do not incorporate phylogenetic information essentially still make the implicit phylogenetic assumptions—assumptions of species independence that are embodied in a "star" phylogeny (Felsenstein, 1985; Blomberg et al., 2003 and citations therein), equal branch lengths, absence of hierarchical relationships between data points, and equal variances expected among terminals.

Hypothesis testing

I tested the "CR hypothesis" and analyzed call data from 51 species of Philippine *Platymantis*. To address potential variation in rate of character divergence, major trends in Philippine *Platymantis* call evolution (Fig. 6.1) were assessed; my goal was to identify major trends and key transitions between call types in order to arrive at expectations before quantifying evolutionary change of different classes of call characters. Call characters were mapped onto the preferred tree using MacClade (Maddison and Maddison, 1992) and ancestral call character states were estimated following the procedures of Garland et al. (1997; see also Garland, et al., 1999; Losos, 1999). Correlations between various call characters and morphology were conducted using independent contrasts (Felsenstein, 1981; Harvey and Pagel, 1991; Garland et al., 1992).

My goal was to test each character for non-random variance in evolutionary change and to compare the relative rates of evolution in different classes of call characters to one another. For convenience, simplicity, and reliability (accuracy and precision), some call characters as were scored as continuous and others were scored as discrete or meristic. No attempt was made to gap-code or otherwise categorize continuously-varying characters into discrete states (e.g., Cocroft and Ryan, 1995; Price and Lanyon, 2003) because such states are artificial. For simplicity and ease-of-interpretation, I focused instead on methods that were developed for the analysis of continuous characters. Two main approaches were used to the study of call character rate variation: (1) examination of independent contrasts (Felsenstein, 1985; as described by Garland, 1992; implemented in CAIC v 2.3 [Purvis and Rambaut, 1995] and Phylogenetic Diversity Analysis Program [Garland, 2003: http://www.biology.ucr.edu/faculty/Garland/PDAP.htm]) and (2) a randomization test for phylogenetic signal as described by Blomberg et al. (2003; implemented in PHYSIG.M and/or PDAP) for quantitative/continuous data. For discrete, meristic, and categorical call characters, I used the retention index as a measure of fit of data to a tree (Archie, 1996; de Queiroz and Wimberger, 1993; Wimberger and de Queiroz, 1996; Price and Lanyon, 2002), again to examine for variance in the evolutionary lability of discrete call characters.

Use of independent contrasts for studying character evolution

Independent contrasts were proposed by Felsenstein (1985) for studies of correlated evolution. However, as discussed by Garland (1992), they are also useful for studying evolutionary rates. Because each contrast provides an independent estimate of the amount of phenotypic evolution that has occurred since the hypothetical ancestor diverged into two daughter species (i.e., from a clade of N species, one can extract $N - 1$ independent indices of the minimum rate of evolution between two species values for a given trait). Garland's (1992) approach compares the amount of phenotypic evolution, standardized by branch lengths, in two or more clades. Use of branch lengths based on sequence divergence is a sufficient scalar for this technique because the variance of each contrast is proportional to the branch lengths separating each species pair (Garland, 1992). Hypothesis testing then is easily accomplished using t-tests for normally distributed independent contrasts or nonparametric alternatives (Mann-Whitney U or Kruskal-Wallis tests). I used this technique to test for differences in evolutionary rates of morphologically-based and behavioral/physiologically-based call characters. The randomization test for phylogenetic signal (Blomberg et al., 2003) uses the variance for standard independent contrasts (Felsenstein, 1985; Garland, 1992; Garland et al., 1992) as an index of how well real data fit the preferred tree. If phylogenetic signal is detected (i.e., character distribution patterns in which related species are similar for a given trait), then contrasts variances are low; conversely, contrast variances are expected to be high if related species are not similar with respect to the trait under study (Blomberg et al., 2003). The test statistic K is derived from comparison of the real contrast variances to variances obtained following a random permutation of the variances across the tree irrespective of topological relationships. A simple comparison between the real and randomized tip variances is then applied, and the hypothesis of no phylogenetic signal can be rejected at an alpha level of 0.05 (and K is relatively closer to one) if 95% of the permuted datasets contain variances that are greater than those found when contrasts/variances are in their correct topological position. If relatives are not significantly more similar than if placed randomly on a tree, *K* will be relatively low (closer to zero) and the hypothesis of no signals cannot be rejected (Garland, 1999; Garland and Ives, 2000; Blomberg et al., 2003). In simple terms, *K* is the ratio of the amount of phylogenetic signal observed in the data set divided by the expected random Brownian motion of character evolution along the specific (=observed) tree topology and branch lengths.

Discrete call character data: homoplasy as an indication of phylogenetic lability

Traditional measures of homoplasy include the consistency index (Farris, 1969) and the retention index (Farris, 1989). Originally conceived as measures of homoplasy, these indices can be useful measures of the fit of data to a tree. Additionally, they can be viewed as indicators of the evolutionary lability of a characters (Archie, 1996, 1989; de Queiroz and Wimberger, 1993; Wimberger and de Queiroz, 1996; Wake, 1991; see also Wake, 1996). The retention index (equivalent to the "Homoplasy Excess Ratio Maximum, HERM"; Archie, 1989) is the measure of fit of discrete characters to a tree; it is insensitive to data set size, is generally correlated with bootstrap values, and is insensitive to uninformative states (Archie, 1989; Sanderson and Donoghue, 1996). The Retention index is calculated as (M – obs.) / (M – m) where M is the maximum number of steps possible over a phylogenetic tree, m the minimum numbers of steps possible, and obs is the observed number of steps for the character of interest (Archie, 1989, 1996). In this sense, the RI can be viewed as the percentage or proportion of initial synapomorphies that remain synapomorphic that stay together across a tree topology. It is directly comparable between different characters within a dataset and can be compared among datasets because of the manner in which it is scaled (Archie, 1989).

Results

General patterns of call structure evolution

Tracing the evolution of call structure across the preferred phylogenetic estimate (Chapt. 4) reveals major trends in call evolution within the monophyletic Philippine *Platymantis* clade. The preferred phylogenetic estimate (Figs. 6.1, 6.2) depicts the presence of five major clades that I divide into informal groups for convenience and reference. These include the Basal Clade (Figs. 6.1, 6.2a, 6.3a), the Corrugated & Cloud Frogs Clade (Figs. 6.1, 6.2b, 6.3b), the Canopy Clade (Figs 6.1, 6.2c, 6.3c), Ground Frogs, groups 1 (Figs. 6.1, 6.2d, 6.3d) and 2 (Figs 6.1, 6.2e, 6.3e).

Basal Clade members include mostly species with single pulse “tink” calls and amplitude-modulated pulsed calls; a single exception is one frequency sweep call of an undescribed species from the southern Philippines (Figs. 6.2a, 6.3a). Corrugated Ground Frogs (*P. corrugata* and related species) form the sister group to Shrub/Cloud Frogs related to *P. hazelae* (Brown et al., 1997). Corrugated Frogs have noisy, harsh, vibrational calls and Cloud Frogs have pure tone calls of various durations. A few species have low-frequency introductory notes, and one possesses a frequency sweep call (Figs. 6.2b, 6.3b). The Canopy Frog Clade consists of species with calls resembling the amplitude-modulated calls of the distal Basal Clade members; most species in this group have pulsed calls, some of which consist of a rapid production of a series of short frequency sweeps (Figs. 6.2c, 6.3c). The remaining clade is divided for convenience into Groups 1 and 2 and consists of Ground Frogs with complex calls, frequency sweeps, and a few pulsed calls (Figs 6.2d–6.2e, 6.3d–6.3e). Several call types have evolved numerous times within the Philippines alone (call types followed by numbers of trait occurrence, estimated by parsimony): “tink” (1); frequency sweeps (5–6); pure tone calls (1); pulsed calls (5–7); complex calls (3).

Phylogenetic patterns of individual call character evolution

Individual inspections of the univariate distributions of call characters with respect to an ultrametric tree allowed qualitative assessment of the presence/absence of phylogenetic signal in tandem with the randomization test for phylogenetic signal in continuous traits and calculation of homoplasy levels of discrete characters. For example, Character 1 – No.Syl. (number of discrete syllables per call) exhibited a phylogenetically-dependent increase in number of syllables in the ground frog taxa and has a relatively low RI (RI = 0.412; Fig. 6.4). Character 2 – DF (Dominant Frequency) exhibited no phylogenetic signal ($K = 0.113$; $P > 0.05$; Fig. 6.5) and neither did Character

3 – FF (Fundamental Frequency) ($K = 0.172$; $P > 0.05$; Fig. 6.6). Character 4 - Abs.Mod (absolute magnitude of frequency modulation) exhibited no phylogenetic signal ($K = 0.202$; $P > 0.05$; Fig. 6.7) but direction of frequency modulation and/or frequency shifts (Character 5 – Mod.Dir.) exhibited positive shifts (RI = 0.704; Fig. 6.8) associated with the Corrugated and Canopy Frog Clade (Figs. 6.1, 6.8). The pattern of character variation in Character 6 - Mod.Time (time duration of frequency-modulated segment of the call) failed to reject the hypothesis of no phylogenetic signal ($K = 0.092$; $P > 0.05$; Fig. 6.9) but Character 7 – CD (Call Duration) exhibited significant phylogenetic signal ($K. = 0.372$; $P = \leq 0.01$), with longer individual calls concentrated in members of the Basal and Ground Frog Clades (Fig. 6.10). Character 8 – CR (Calling Rate) contained significant phylogenetic signal (higher rates concentrated in Basal and Canopy Frog species; $K = 0.329$; $P < 0.01$; Fig. 6.11) as did Character 9 – Grp.Len (Call Group Length) whereby the majority of Ground Frogs and Corrugated Frogs have relatively short call group durations, Cloud Frogs exhibit intermediate call group lengths, and Basal Frogs and Canopy Frogs for the most part have much longer call group lengths ($K = 0.407$; $P < 0.05$; Fig. 6.12). Call group rate (Character 10 - Call.Grp.Rat.) was marginal with respect to significant phylogenetic signal ($K = 0.221$; $P = 0.07$; Fig. 6.12) but Character 11 – Pulse.No. (pulse/call number per group) did contain significant signal ($K = 0.611$; $P = < 0.001$; Fig. 6.13). In this last character, large numbers of calls per group were concentrated in some species from the Basal Clade, low call numbers/group were concentrated in the Corrugated+Cloud Clade, and intermediate numbers of calls/group were exhibited by members of the Ground Frog Clade (Fig. 6.14). Trends were apparent

in clade specific evolution of call types (Character 12), with “tink” calls limited to several species in the Basal Clade, frequency sweeps found in some members of each clade, tonal calls limited to the Cloud Frog Clade, and complex calls concentrated in Corrugated Frogs and Ground Frogs (RI = 0.688; Fig. 6.15). Number of discrete frequency components of the call (exclusive of harmonics) exhibited low levels of character change/homoplasy (RI = 0.381).

There was no relationship between the size-adjusted dominant frequency ratio (DF/SVL) and body size as measured by SVL or mass (SVL: $y = 2.93 - 0.02x$; $R^2 = -0.184$; mass: $y = 2.12 + 0.17x$; $R^2 = 0.21$) suggesting that the use of this ratio is an acceptable measure of size-corrected frequency. Character ratios (Character 13) DF/SVL, and (Character 14) the number of calls per call group showed opposite patterns. No significant signal was detected in DF/SVL ($K = 0.170$; $P > 0.05$; Fig. 6.16) but significant signal was uncovered in the number of calls per call group/call group length ($K = 0.276$; $P < 0.05$; Fig. 6.17). In the latter case, higher numbers of calls adjusted by call group length were observed in Basal and Ground Frog clades (Figs. 6.1, 6.17).

With the exception of duration of the frequency-modulated segment of calls (Mod.Time), behavior-related call characters scored higher signal scores when phylogeny was taken into account (Fig. 6.18). Although samples sizes of call characters were too small to allow power in a direct statistical test of *K* or RI values, there is a clear trend for behavior- or neurophysiologically related call characters to exhibit markedly more change across (and are influenced more by) the phylogeny. Discrete call characters examined here (number of call syllables, number of basic frequency components, call type, and direction of frequency modulation) are all difficult to defensibly categorize into behavior-related or "morphology-related" call types. Nevertheless, Call Type and direction of frequency modulation exhibited nearly twice the retention index seen in numbers of syllables and frequency components.

Discussion

De Queiroz and Wimberger (1993) and Wimberger and de Queiroz (1996) found no significant differences between behavioral and morphological traits as measured with consistency indices and retention indices. However, as emphasized by these authors the behavioral traits they examined were specifically chosen by systematists for their potential use in phylogeny estimation, and thus may have been biased towards non-labile traits or character-state characterizations. In another study, Cocroft and Ryan (1995) found evidence for accelerated rates of evolution in characters related to the behavioral and physiological aspects of call production (vs. relative stasis in morphology-related characters) in hylid frogs, whereas these two character partitions did not differ in bufonids. In an additional study, McCracken and Sheldon (1997) interpreted the conservative nature of frequency-related song characters of birds to be the result of environmentally imposed constraint, whereas behavioral characters related to song production rate where considered more labile and reflective of phylogeny.

Several different factors could contribute to apparent differences in evolutionary lability of behavioral vs. morphological traits. Measurement error, problems associated with assigning homology to behavior, seasonal variation in behavior, thermal dependency or acclimation effects, individual variation, and sample size issues all could conceivably contribute to the general conclusion that behavior evolves faster or that it is more prone to evolutionary change than body size or morphology (Bush, 1986; Gittleman et al., 1996).

Blomberg et al. (2003) provided a large comparative analysis of a variety of different classes of characters, using randomization approaches to hypothesis testing described above and concluded that behavioral traits were more evolutionary labile than morphological, ecological, life-history, or physiological traits. Their study used direct comparisons of more than 100 comparative datasets and a wide variety of classes of continuous data. Blomberg et al.'s (2003) contention that behavioral traits are more evolutionary labile may be the most convincing argument so far in favor of this interesting evolutionary phenomenon.

Pagel (1999) and Freckleton (2002) presented a similar alternative method for examining data for phylogenetic signal and higher-than-expected evolutionary rates of character change. These authors describe the use of Pagel's (1999) Lambda (derived from the covariance matrix, V), which scales from 0 (a polytomy) to 1 (the original tree recovered), and tests the null hypothesis of no association with phylogeny (e.g., Lamda = 0) in a likelihood framework. Blomberg et al. (2003) draw parallels between the use of Lamda and the *K* statistic but criticize the approach taken by Pagel (1999) on several grounds: (1) Lamda is not associated with an explicit model of evolution; (2) log-likelihood tests are only asymptotically valid in the comparative framework used to develop the test; (3) given small sample sizes (like the data set studied here), log-likelihood ratio tests can produce noticeably imprecise *P*-values, and (4) branch length transformation approaches advocated by Pagel (1999) and Freckleton et al. (2002) were non-biologically motivated (in contrast to the accelerated- decelerated ["ACDC"] evolutionary rate change method devised by Blomberg et al., 2003). Given the limitations of my own dataset, I concur with Blomberg et al. (2003) that perhaps the best way to characterize the phylogenetic comparative approach to a small number of call characters is through the use of randomization procedures (see also Maddison and Slatkin, 1991).

In this study, the use of retention indices appeared to be the appropriate measure for discrete character fit (and evolutionary lability) but this approach is limited to analysis of discrete call characters, of which I scored relatively few (n=4) across all Philippine *Platymantis*. Call type and direction of frequency modulation (behavioral call characters) have RIs nearly twice the magnitude seen in the numbers of syllables per call (a behavioral character) and number of frequency components per call (a morphological character), suggesting that number of call syllables and frequency components change more frequently across the phylogeny than do call type and direction of frequency modulation. Thus, the overall trend is opposite of expectations based on Ryan (1988) and Cocroft and Ryan (1995).

The fact that morphology-related frequency characters DF, FF, DF/SVL exhibit lower *K* values than "behavioral", rate-related call characters was surprising. Following Blomberg et al.'s (2003) reasoning, one might argue that morphological call characters are thus more evolutionary malleable (and thus “fit” the phylogeny poorly). Although a simple *t*-test found no significant differences in *K* between morphological vs. behavioral call characters ($t = 2.17$; $P > 0.05$), this may be more reflective of a lack of statistical power rather than a lack of a true difference between the means. Two characters were difficult to assign to morphological or behavioral call character classes. These included the absolute value of frequency modulation across the entire call (Abs.Mod) and the time duration of the frequency-modulated segment of the call (Mod.Time). I considered them both tentatively “behavioral” call characters but the close association of frequency modulation with purely frequency-dependent characters (and body size) makes this assignment somewhat uncertain. Thus, it may be reasonable to include these characters in the morphological character class or exclude them all together from the analysis. If Abs.Mod and Mod.Time are excluded, then *K* statistic values for behavioral and morphological call classes no longer overlap.

In any case, differences between the two classes of call characters as measured here are either non-significant, or (if the apparent trend is to be believed) exhibit a reverse of the previous expectations (Ryan, 1988; Cocroft and Ryan, 1995). If these observed trends reflect true patterns in platymantine call data, some possibilities are worthy of consideration. I would argue that numerous instances exist in which related species would be expected to be dissimilar (i.e., not reflecting phylogeny). Numerous situations are known whereby closely-related species might be expected to be significantly dissimilar to one another and so their trait values for certain characters might be less similar than expected by chance or phylogeny alone. Additionally, numerous instances of distantly related taxa being more similar to one another than expected on the basis of phylogeny or chance are well known.

First, character displacement between closely related species, especially in areas of sympatry, is known to disrupt similarity-by-descent expectations (Losos, 1990, Losos, 2000; Gerhardt, 1994b; Hobel and Gerhardt, 2003). In this case, if the "morphological" call characters examined in this study are under disruptive selection due to character displacement in sympatry, one might expect sister-species pairs to be less similar on average than predicted by the phylogeny (e.g., branch lengths and Brownian motion evolution of characters). However, in the available studies, it has often been temporal rather than spectral call characters that have shown clear patterns of character displacement (Littlejohn, 2001; Gerhardt, 1994c; Hobel and Gerhardt, 2003). Additionally, only a few cases of sister-species sympatry have clearly been identified in Philippine *Platymantis* (Brown and Diesmos, unpublished data).

Evolutionary convergence (Wake, 1991, 1996) is another phenomenon in which a phylogeny's tip data might be expected to vary widely from expectations imposed by ancestry. It is well known that similar environments often produce similarity in biological structures and function in unrelated species by convergent evolution. A well-studied example is the case of evolution of morphologically, ecologically, and behaviorally similar "ecomorphs" that are produced in replicated radiations of *Anolis* lizards (Losos et al., 1998; Bluetell and Losos, 1999; see also Chapt. 2). I have shown evidence for remarkable prevalence of convergence in morphology (Chapt. 2) and advertisement call (Chapt. 3) in *Platymantis*, suggesting that this phenomenon m ay be a viable explanation for explaining the observed absence of a phylogenetic effect in size-related frequency characters.

If sexual selection drives frequency-related call characters towards extremes preferred by females, or if environmental transmission affects (Ryan et al., 1990; Chapt. 5) the ranges of variability observed in frequency-related characters, one might expect low *K* values, the absence of phylogenetic signal in the data, elevated levels of homoplasy, and/or the appearance of accelerated rates of evolution in these traits. In fact, the morphological call characters I examined (call frequency and related characters) are known to be under intense sexual selection in at least one well-studied anuran (Ryan, 1985), further suggesting that call frequency-related trait phenotype values might be heavily influenced by selection, and thus subject to processes that drive species values away from the expectations posed by the specified phylogeny (and lower observed *K* values).

In any case, it is clear that not all characters related to the anuran advertisement call are equivalent and do not evolve in a unitary fashion. The acoustic communication system of frogs and toads is complex and subject to a variety of morphological, behavioral, and environmental influences in any given context. Future studies would benefit from the study of a larger number of call characters, with particular attention paid to both transitions between major call types as well as close comparisons between members of clades that have relatively homogeneous call types (e.g., trilled calls of chorus frogs and toads) but markedly different microhabitats (e.g., Ryan et al., 1990). It may be fruitful to extend the current study from the relatively complex anuran communities of upland Philippine habitats to the somewhat simpler communities found on islands of the SW Pacific. Hopefully, by studying large-scale phylogenies and smaller focal clades, all within the context of additional call characters, general trends in frog call character evolution can be brought to light.

Tables

Table 1.1.— Enumeration of 51 putative evolutionary lineages (species) of Philippine *Platymantis* and onomatopoeic characterization of the advertisement calls of each. PAIC = Pleistocene Aggregate Island Complex (*sensu* Heaney, 1985; Hall, 1996; Brown and Diesmos, 2001).

Species group	Species or Nickname	Onomatopoeic call description	Island
P. hazelae	*P. hazelae*	"Ting…ting…ting"	Negros
"	*P. isarog*	"Ting…ting…ting"	Luzon
"	*P. lawtoni*	"Cherenk-cherenk"	Sibuyan,
"	*P. montana*	"Twenk…twenk…twenk"	Luzon
"	*P. panayensis*	"Pinnggg… pinnggg … pinnggg"	Panay
"	*P. polillensis*	"Plink…plink…plink"	Polillo
"	n. sp. cf polillensis Imugan	"Ting…ting…ting"	Luzon
"	*P. subterrestris*	"Wheep…wheep…wheep"	Luzon
"	n. sp. "Enteng's frog"	"Cheerp…cheerp…cheerp"	Luzon
"	n. sp. "plaintive montanus"	"Tu-ting…tu-ting…tu-ting"	Luzon
"	*P.* sp. cf "rivularis" Magdalao	"Sweeet…sweeeet"	Luzon
"	cf "rivularis" (real rivularis)	"Pi-ing…pi-ing…pi-ing…"	Luzon
P. guenthei	*P. guentheri*	"Sweeet…sweeet…sweet"	Mindanao
"	*P. banahao*	"Tut-tut-tut-tut-tut…"	Luzon
"	*P. luzonensis*	"Kwenk…kwenk…kwenk"	Luzon
"	n. sp. "fastcaller"	"Klu-klu-klu-klu-klu…"	Luzon
"	*P. negrosensis*	"Kwek-kwek-kwek"	Negros
"	*P. cornuta*	"Tutututututututu…"	Luzon
"	*P. insulatua*	"Tik…tik...tik..tik-tik-tik"	Gigante
"	*P. rabori*	"Chur-enk…chur-enk…"	Bohol
"	n. sp. "species F"	"tuuu..tu-tu…tu-tu…tu-tu…"	Luzon
P. mimula	*P. mimula*	"Osek…osek…osek"	Luzon
"	*P. naomiae*	"Psik…psik"	Luzon
"	n. sp. "Redor's frog"-Banahao	"Choo-rink, choo-rink"	Luzon
"	n. sp. (cf Redor's frog)	"Kee-oo-lee…kee-oo-lee"	Luzon
"	n. sp. "Katipunan frog"	"Zzzz-zzz-zzz"	Luzon
"	n. sp."benedict"	"Benidict! Benidict!	Luzon
"	n. sp. "Balblan sp. 2"	"Shek-shek-shek-shek"	Luzon
"	n. sp "Rizal's frog"	"Psu-rot…psu-rot"	Luzon

“	n. sp. Subic “Thompson’s”	“Psk…psk…psk…”	Luzon
miniatures	*P. pygmaea*	“Tik…tik…tik…tik”	Luzon
“	n. sp. cf *pygmea* Sibuyan	“Syk-syk…syk-syk…”	Sibuyan
P. dorsalis	*P. dorsalis*	“Sweet…sweet…sweet”	Luzon
“	*P*. sp. cf *“jagori / plicifera*”?	“Weeah-weeah- weeah”	Minanao
“	*P*. sp., cf *“laticeps*”?	“Soo-it…soo-it…soo-it…”	Mindanao
“	n. sp. “clicker”	“Click-click-click…”	Mindanao
“	*P. corrugata*	“Whaah…whaah…whaah”	Luzon
“	n. sp. cf corrugata Mindoro	“Whak-whak…whak-whak”	Mindoro
“	*P. levigata*	“Shree-er-ee…shree-er-ee…”	Sibuyan
“	n. sp.“bank frog”	“Sweet-sweet…sweet-sweet”	Sibuyan
“	*P. spelaea*	“Pee-coh, pee-coh”	Negros
“	*P. cagayanensis*	“Cree-eek…cree-eek”	Luzon
“	n. sp. “yokyok”	“Yok…yok…yok”	Luzon
“	*P. taylori*	“Tiktiktiktiktikrtik…”	Luzon
“	*P. pseudodorsalis*	“Tseeo-lek …Tseeo-lek”	Luzon
“	*P. indeprensus*	“eeyak-eeyak”	Luzon
“	n. sp. cf indeprensus	“Wheeee-ahhhhhh….”	Luzon
“	n. sp. seeyok	“See-yok…seeyok	Luzon
“	n. sp “softcaller”	“Whoo…whoo…whoo”	Luzon
“	n. sp. “limestone frog”	“Eahhh….eahhh”	Luzon
“	n. sp. “cliff frog”	“Yeer-yeer…yer-yer-yer”	Luzon

Table 2.1.— Multivariate analyses of 16 continuous morphological characters. Loadings for the first four unrotataed principal components (PCs I–IV), extracted from the correlation matrix. Heavily loading variables with relatively greater discriminating power are in bold for emphasis (see text for discussion). All data were log transformed.

	PC I	PC II	PC III	PC IV
SVL	**0.989**	-0.067	0.002	0.079
HL	**0.971**	-0.136	0.096	0.053
SNL	**0.981**	**-0.304**	0.045	0.036
IOD	**0.957**	0.037	0.022	0.232
HW	**0.973**	-0.116	0.073	0.065
FA	**0.982**	-0.040	-0.050	0.100
TBL	**0.939**	-0.227	-0.012	-0.098
TSL	**0.976**	-0.186	0.014	-0.022
PL	**0.932**	-0.279	0.005	-0.090
ML	**0.975**	0.058	-0.113	0.022
Toe4L	**0.951**	-0.245	0.036	-0.084
Fin1L	**0.914**	-0.296	-0.035	-0.187
Fin3L	**0.964**	0.156	-0.187	-0.013
Fin3DW	0.580	**0.758**	-0.278	-0.003
Toe4DW	0.650	**0.687**	0.306	-0.014

Table 3.1.— Sample sizes for species, individuals, and calls. See Chapts. 5 and 6 for representative audiospectrograms and waveforms of the calls of these and other species.

Species	No. Males recorded	No. Calls
P. hazelae	10	100
P. isarog	8	80
P. montana	10	100
P. polillensis	3	37
n. sp. cf polillensis Imugan	2	24
P. subterrestris	6	60
n. sp. “Enteng’s frog”	2	25
n. sp. “plaintive montanus”	2	18
P. sp. cf “rivularis”	10	100
cf “rivularis” (real rivularis)	4	49
P. guentheri	7	70
P. banahao	4	12
P. luzonensis	10	100
n. sp. “fastcaller”	6	27
P. negrosensis	2	6
P. cornuta	2	4
P. insulatua	2	13
P. rabori	4	22
n. sp. “species E”	2	8
n. sp. “species F”	4	11
P. mimula	8	85
P. naomiae	6	52
n. sp. “Redor’s frog”-Banahao	10	100
n. sp. (cf Redor’s frog) Malinao	8	80
n. sp. “Katipunan frog”	10	100
n. sp.“benedict”	6	48
n. sp. “Balblan sp. 2”	2	9
n. sp “Rizal’s frog”	8	55
n. sp. Subic “Thompson’s frog”	6	60
P. pygmaea	5	40
n. sp. cf *pygmea* Sibuyan	7	70
P. dorsalis	10	100
P. sp. cf *“jagori / plicifera*”?	8	80
P. sp., cf *“laticeps*”?	4	40
n. sp. “clicker”	6	75
P. corrugata	8	80
P. levigata	3	30

n. sp.“bank frog”	3	30
P. spelaea	2	25
P. cagayanensis	7	70
n. sp. “yokyok”	8	80
P. taylori	1	11
P. pseudodorsalis	2	25
P. indeprensus	8	80
n. sp. seeyok	6	60
n. sp “softcaller”	3	27
n. sp. “limestone frog”	4	55
n. sp. “cliff frog”	3	11

Table 3.2.— Multivariate analyses of eight continuous acoustic characters. Loadings for the first four unrotataed principal components (PCs I–IV), extracted from the correlation matrix. Heavily loading variables with relatively greater discriminating power are in bold for emphasis (see text for discussion). All data were log transformed.

	PC I	PC II	PC III	PC IV
Dominant Frequency	**0.540**	**-0.401**	**-0.539**	-0.013
Frequency Modulation	**-0.566**	**-0.447**	0.108	-0.325
Modulation Time	-0.189	-0.304	**0.414**	**0.769**
Call Length	**0.787**	0.133	0.391	0.056
Call Group Length	**-0.940**	0.119	-0137	-0.103
Call Rate	0.258	**0.695**	-0.378	0.217
Call Group Rate	0.275	0.264	**0.568**	**-0.450**
Pulse/Call no. Per Group	**0.790**	**-0.428**	-0.081	-0.133
Eigenvalue	2.917	1.222	1.117	0.978
% Variance	0.465	0.153	0.140	0.122

Table 5.1.—Summary of species, call type, and general preferred microhabitat for 31 species of Philippine *Platymantis* used in call transmission experiments. See Chapt. 3 for illustrations of each call type.

Recording No.	Species	Call type	Preferred microhabitat
1	P. dorsalis	sweep	herb layer
2	P. guentheri	sweep	shrub-understory
3	P. “softcaller”	sweep	herb layer
4	P. pseudorsalis	sweep	banks
5	P. sp.1 Malagos	sweep	herb layer
6	P. cf. dorsalis	sweep	herb layer
7	P. sp. Sibuyan	sweep	banks
8	P. “seeyok”	complex	herb layer
9	P. indeprensus	complex	herb layer
10	P. cagayanensis	complex-pulsed	herb layer
11	P. “yokyok”	complex	herb layer
12	P. mimula	complex	herb layer
13	P. sp. Palay	complex	herb layer
14	P. sp. Subic	complex	herb layer
15	P. levigata	complex	herb layer
16	P. corrugata	complex	herb layer
17	P. “redor’s”	complex	herb layer
18	P. hazelae	tonal	shrub layer
19	P. polilloensis	tonal	shrub layer
20	P. sp. Imugan	tonal	shrub layer
21	P. montana	tonal	shrub layer
22	P. subterrestris	tonal	shrub layer
23	P. “enteng’s”	tonal	shrub layer
24	P. sp“plaintive”	tonal	shrub layer
25	P. luzonensis	pulsed	understory
26	P. cf luz.Bicol	pulsed	understory
27	P. fastcaller	pulsed	canopy
27	P. cornuta	pulsed	canopy
29	P. sp. F	pulsed	canopy

30	P. rabori	pulsed	canopy
31	P. “cliff frog”	pulsed	canyon

Table 6.1.—Character diagnostics for four discrete categorical call characters.

Character	Range	Min steps	Tree steps	Max steps	CI	RI
1 (call type)	4	4	14	36	0.286	0.688
2 (mod dir)	2	2	10	29	0.200	0.704
3 (no syllabs)	3	3	13	20	0.231	0.412
4 (no freq comps)	1	1	14	22	0.071	0.381

Figures

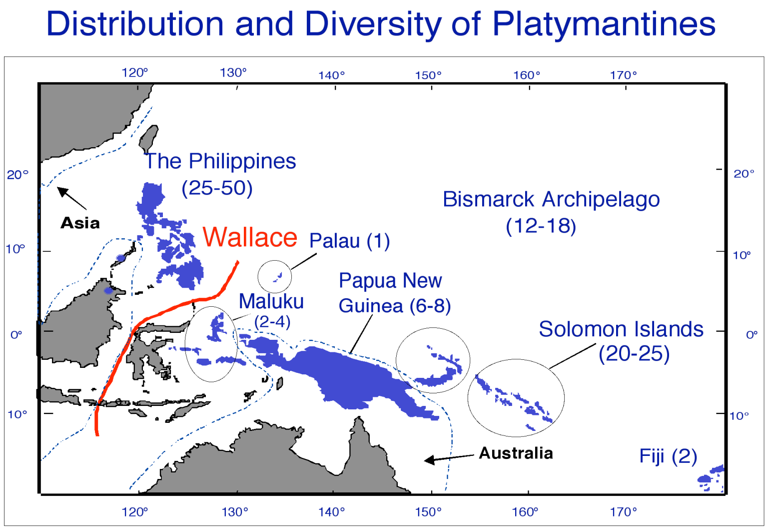

Fig. 1.1—The geographic distribution of platymantine ranids frogs.

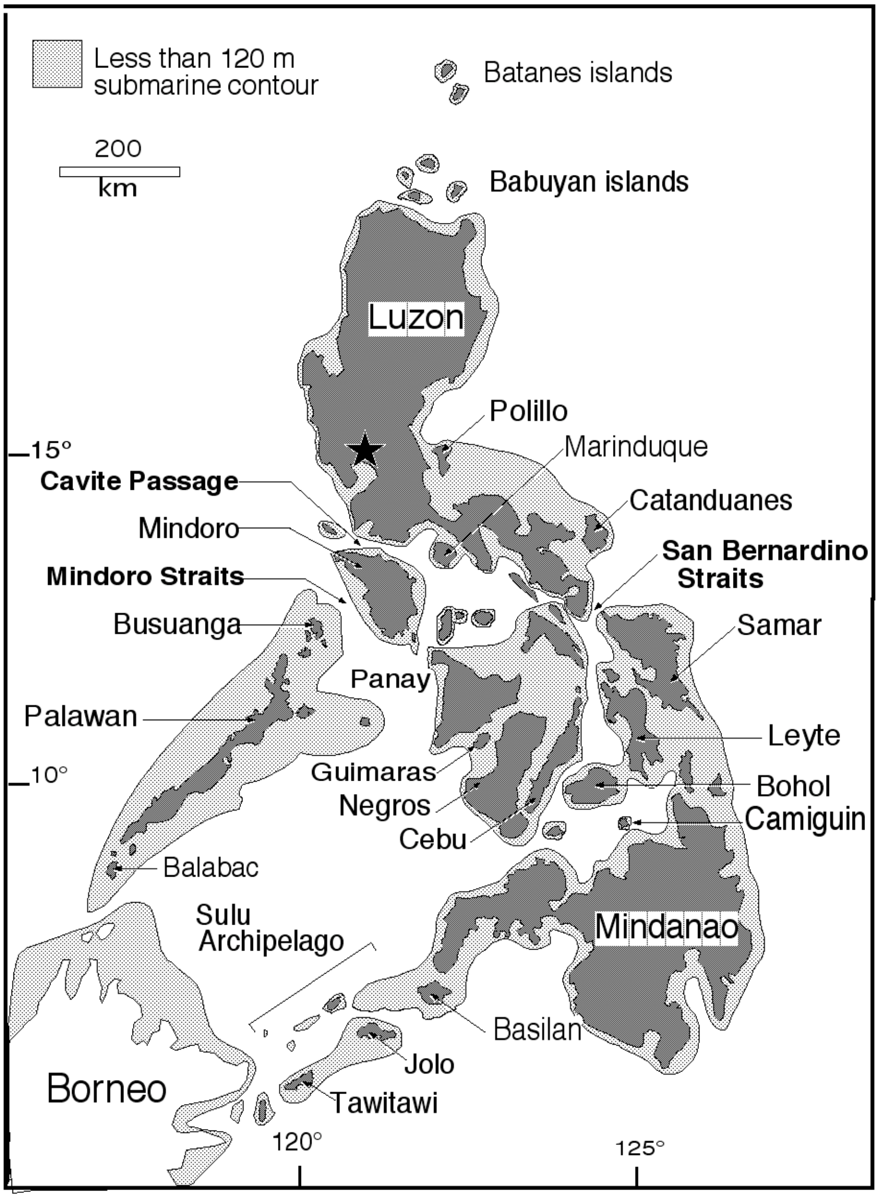

Fig. 1.2—The Philippines, with 120 m underwater bathymetric contours traced around island groups to reveal mid- late-Pleistocene exposure of Pleistocene Aggregate Island Complexes (Heaney, 1985, 1986; Brown and Diesmos, 2002).

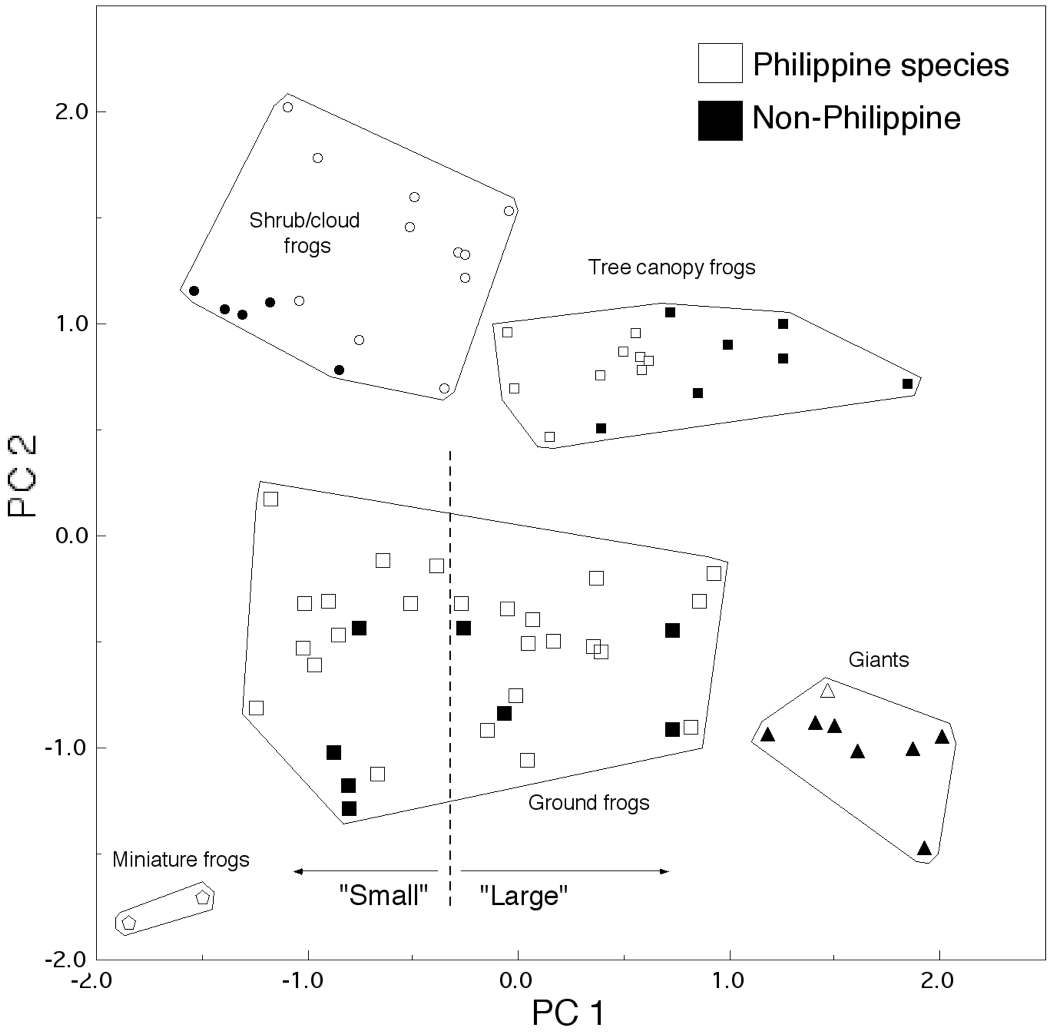

Fig. 2.1.—Orthogonal bivariate orientation of species means in 17 morphometric characters reduced in dimensionality to the first two principal components. See Table 1 for loadings and text for explanation of characters. Circles = Shrub/cloud frogs; small squares = Tree canopy species; large squares = Ground frogs; triangles = Giants; Pentagons = Philippine Miniatures. The dashed line corresponds to the boundary of small-bodied (e.g.,"P. mimula" species group) vs. large-bodies (e.g., P. dorsalis species group) and corresponds roughly to an average snout-to-vent length cut-off of 22–25 mm.

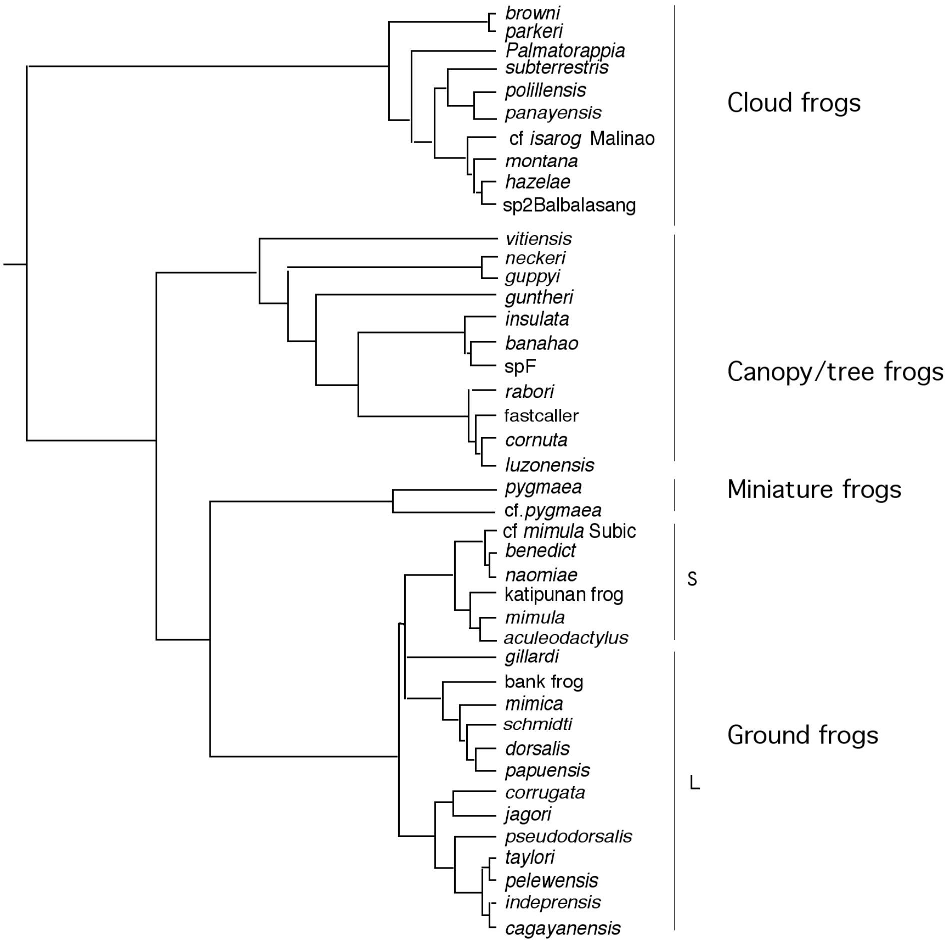

Fig. 2.2—Positions of platymantine species in morphological space as determined by a UPGMA phenogram based on Euclidean distances. Branch lengths are relative, and proportional to distances separating species in morphological space. "S"and "L" indicate small-bodied and large-bodied Ground frogs, respectively.

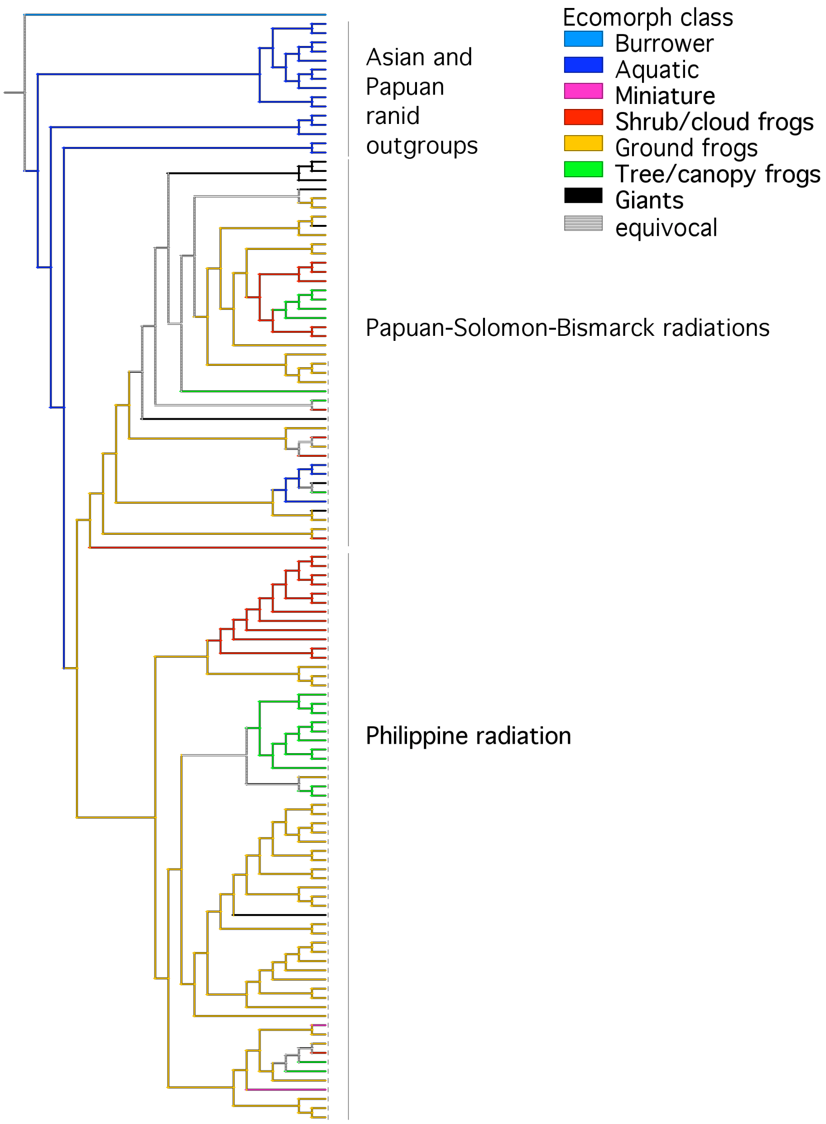

Fig. 2.3.—The distribution of ecomorph types mapped on the most parsimonious tree with all platymantine frog species included (taxon sampling limited to a single terminal per species). See Chapt. 4 for details of phylogenetic analysis.

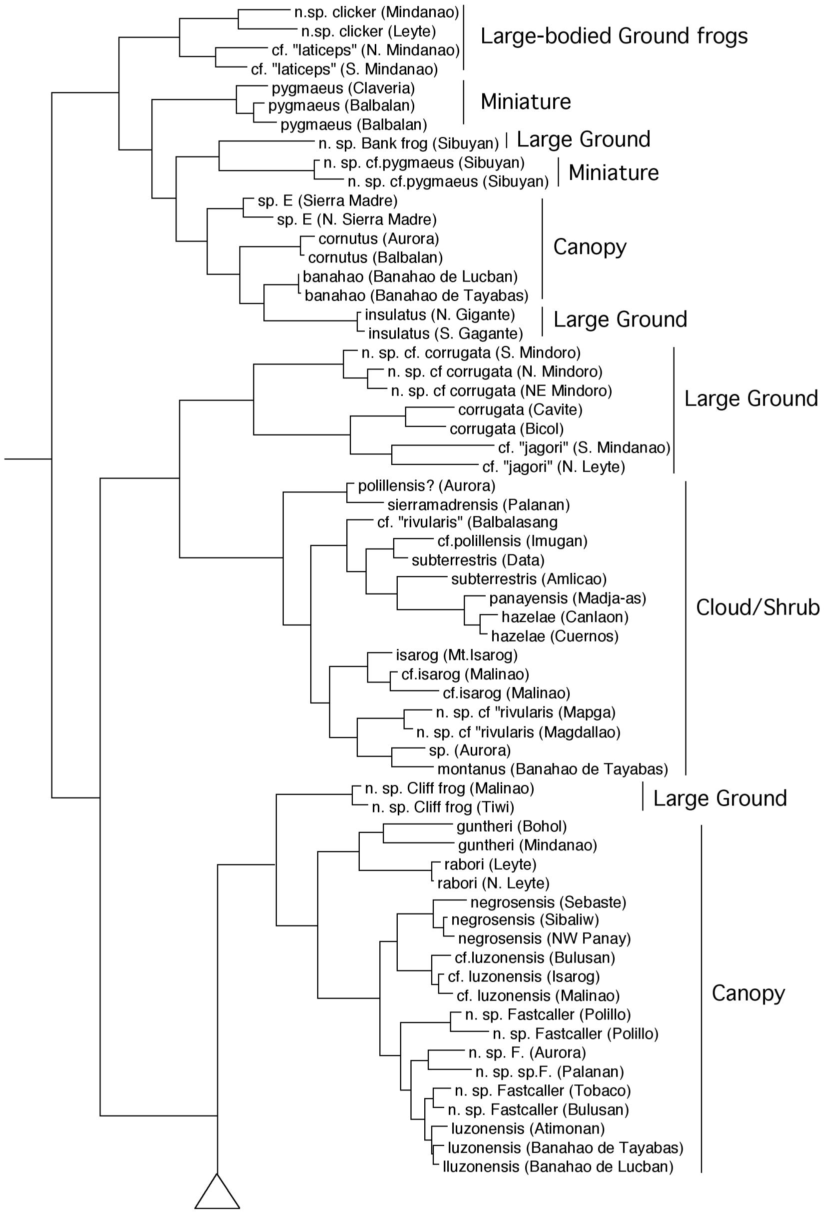

Fig. 2.4A.— Basal relationships of Philippine species from one of 24 equally-parsimonious trees (Chapt. 4) with ecomorph class indicated to the right. See Chapt. 4 for details of phylogenetic analysis.

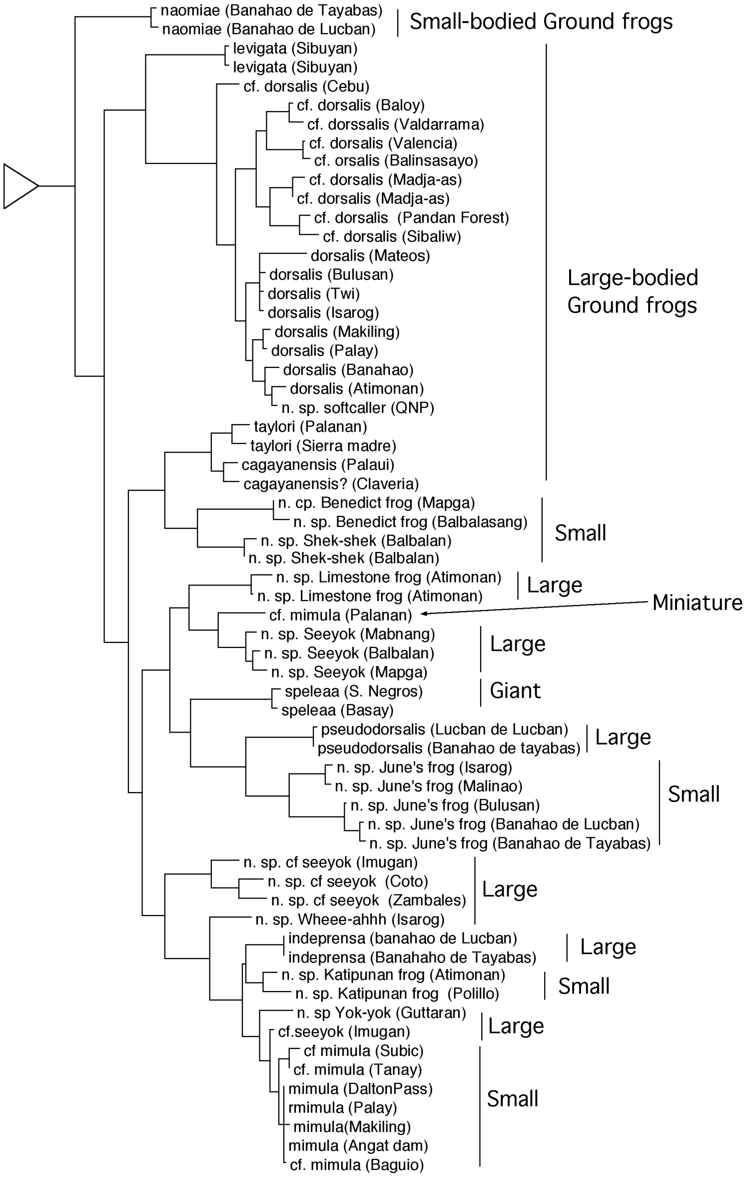

Fig. 2.4B.— Distal relationships of Philippine species from one of 24 equally-parsimonious trees (Chapt. 4) with ecomorph class indicated to the right. See Chapt. 4 for details of phylogenetic analysis.

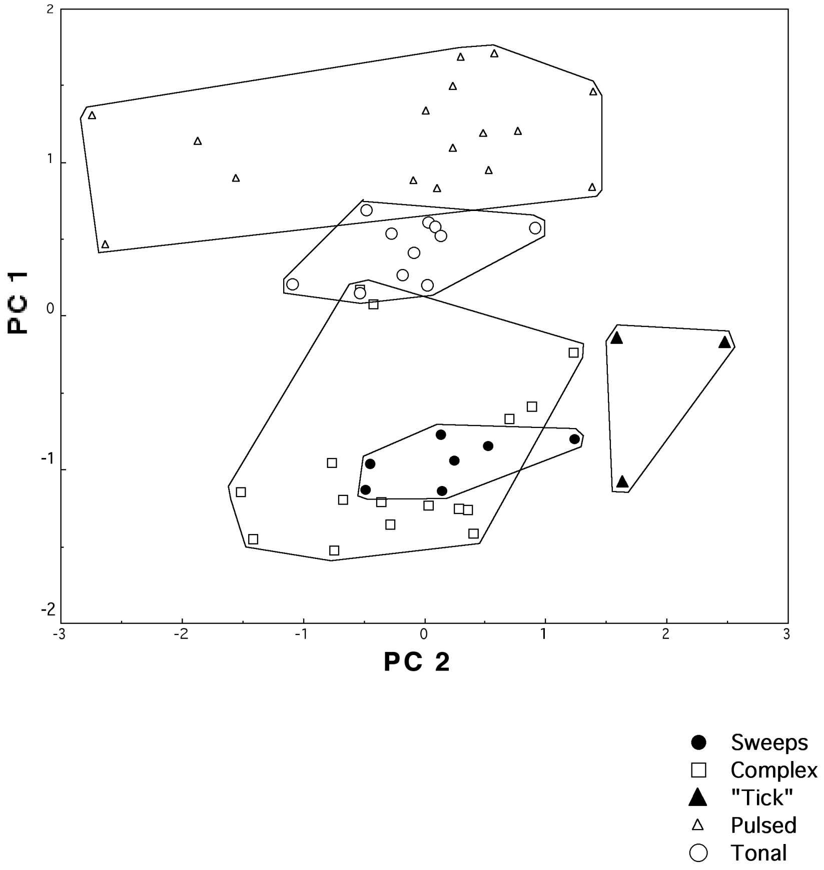

Fig. 3.1.—Orthogonal bivariate orientation of among principal components 1 and 2 for species means in 8 acoustic characters. See text for details of analysis and Table 2.2 for character loadings.

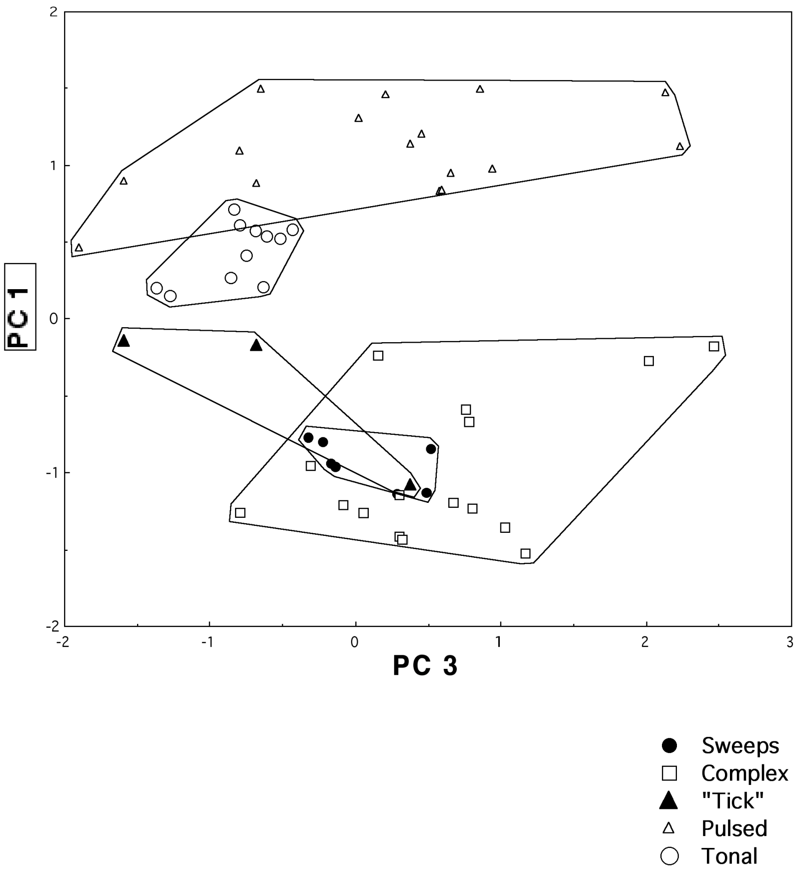

Fig. 3.2.— Orthogonal bivariate orientation of among principal components 2 and 3 for species means in 8 acoustic characters. See text for details of analysis and Table 2.2 for character loadings.

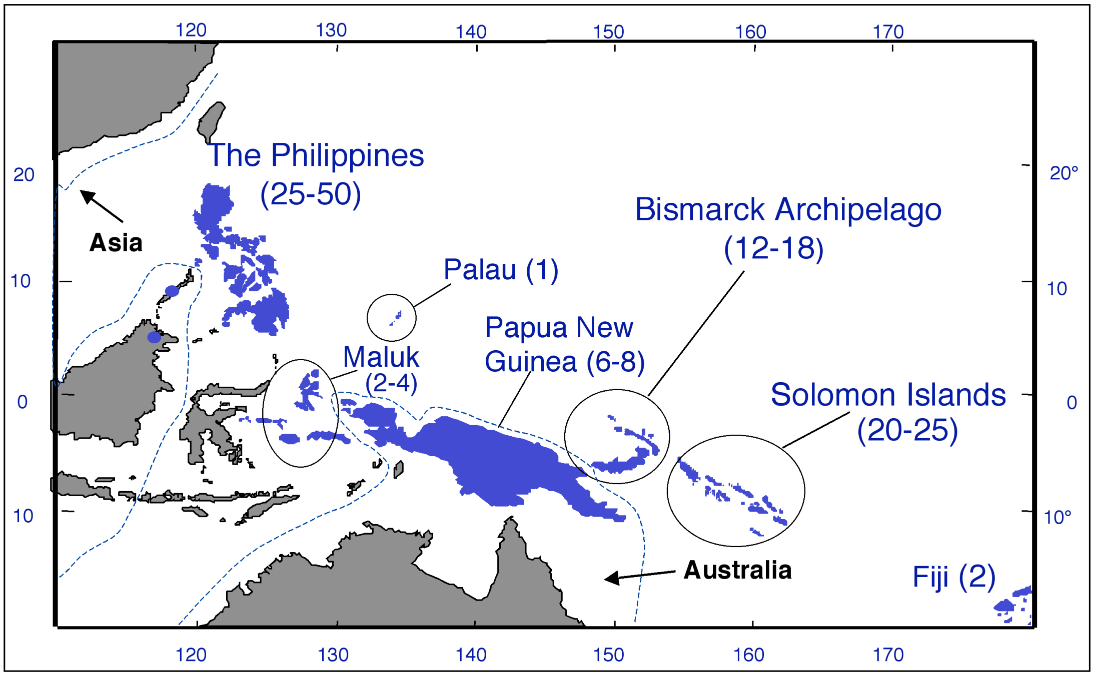

Fig. 4.1.—The distribution of platymantine ranids in the islands of SE Asia and the SW Pacific. Numbers in parentheses indicate approximate numbers of species per island group.

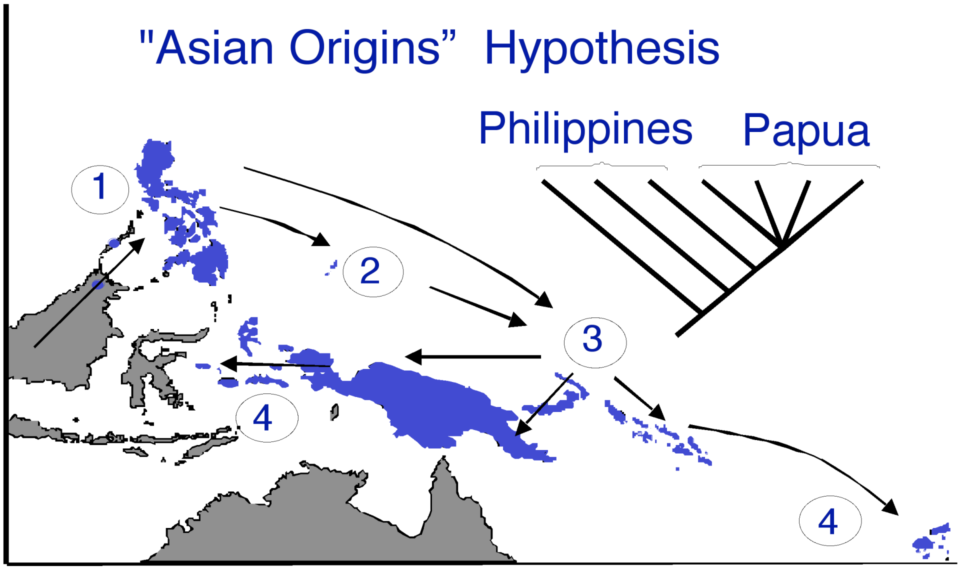

Fig. 4.2.—The “Asian Origins” hypothesis of platymantine origins (see text for details): Philippine radiation nested within a paraphyletic Papuan/Solomon/Bismarck archipelago radiation. Circled numbers indicate hypothesized steps in the history of the radiation.

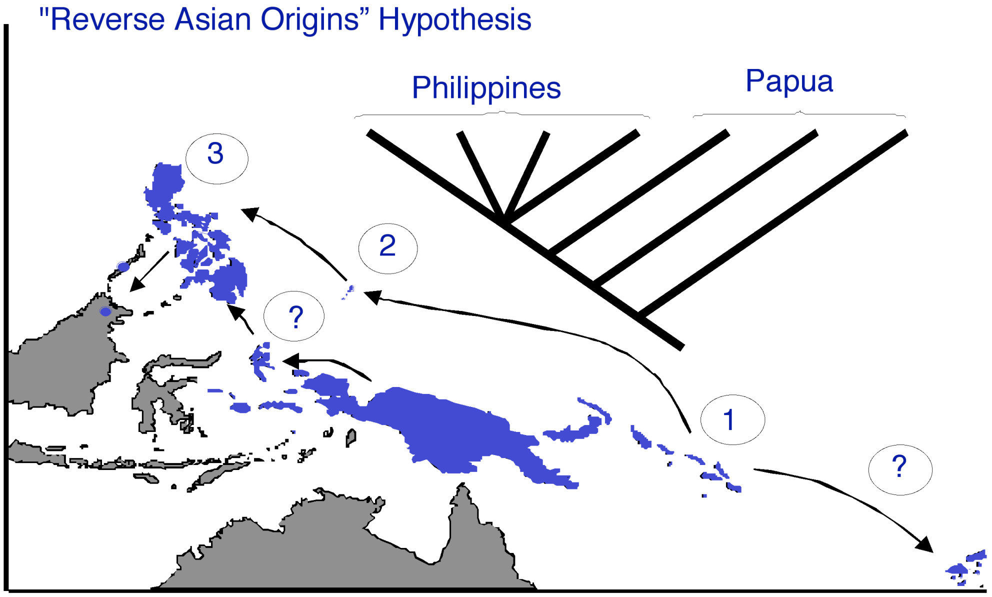

Fig. 4.3.—The “Reverse Asian Origins” hypothesis: Papuan/Solomon/Bismarck radiation nested within a paraphyletic Philippine radiation. Circled numbers indicate hypothesized steps in the history of the radiation.

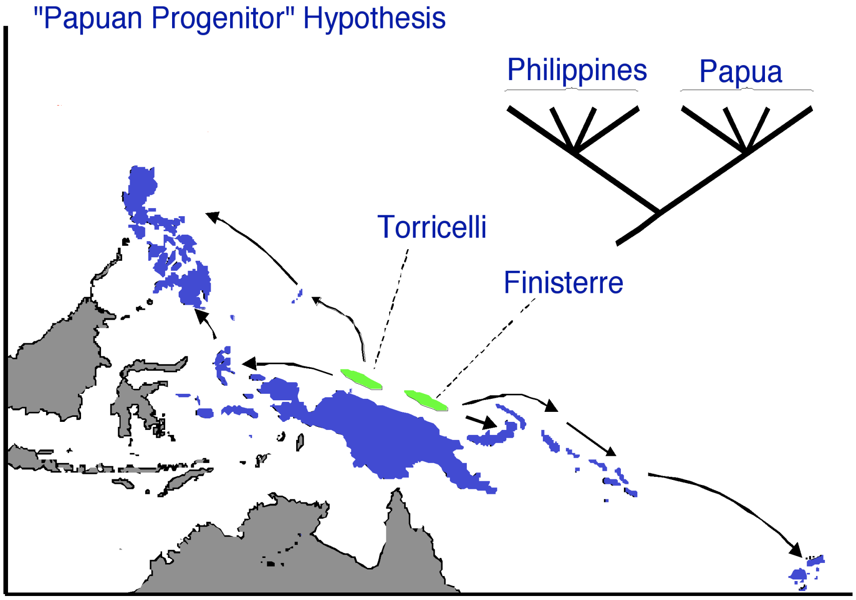

Fig. 4.4.—The "Papuan Progenitor" hypothesis: reciprocal monophyly of Philippines and Papuan/Solomon/Bismarck radiations.

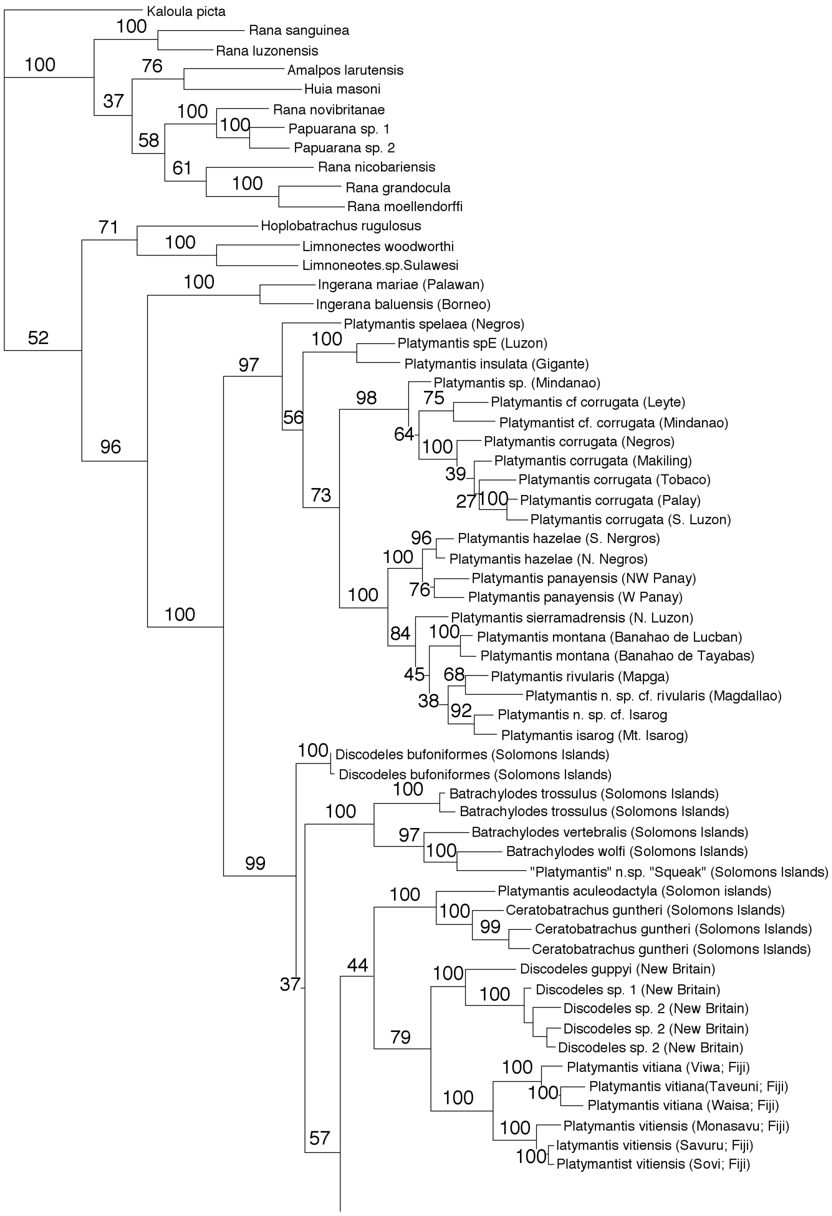

Fig. 4.5A.—Basal relationships in one of nine most-parsimonious trees generated from Maximum Parsimony analysis of near-complete 12S and 16S data and diverse taxon sampling; numbers above internodes indicate non-parametric bootstrap proportions from 2000 iterations.

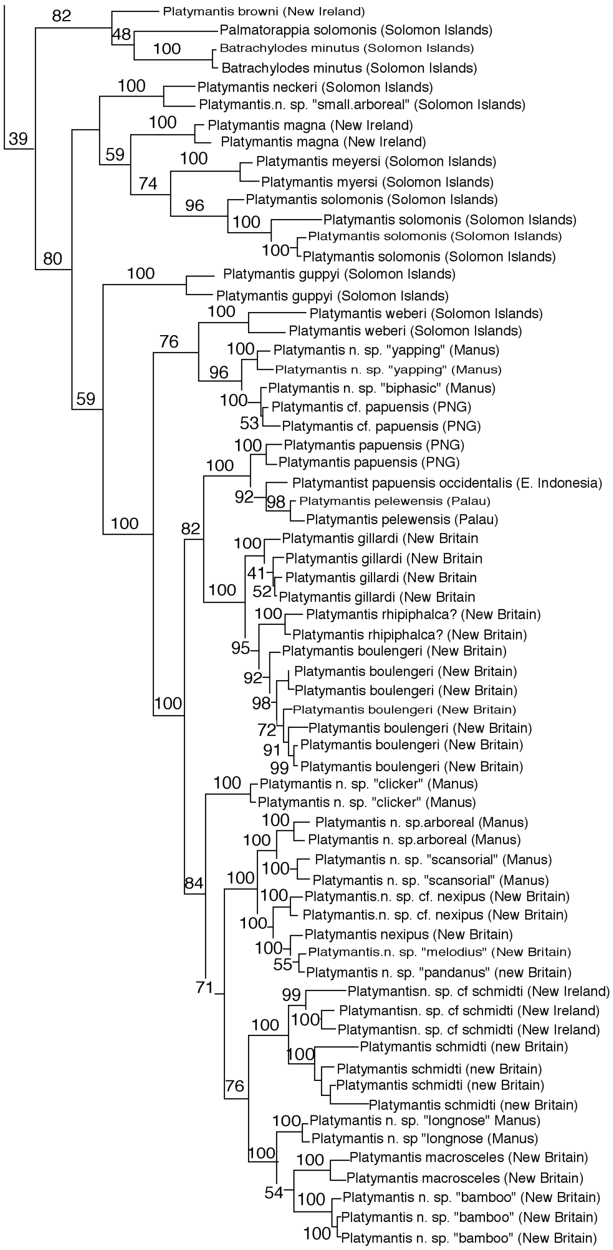

Fig. 4.5B.—Distal relationships in one of nine most-parsimonious trees generated from Maximum Parsimony analysis of near-complete 12S and 16S data and diverse taxon sampling; numbers above internodes indicate non-parametric bootstrap proportions from 2000 iterations.

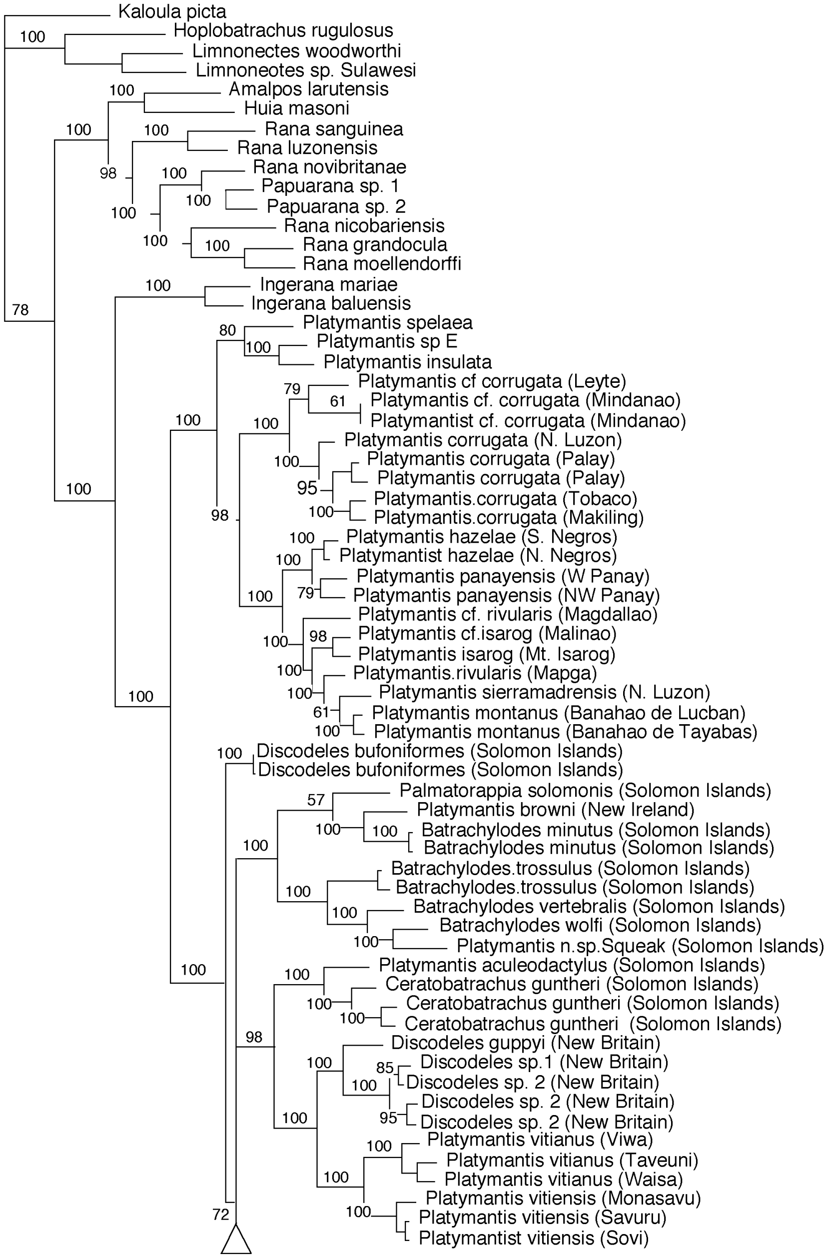

Fig. 4.6A.—Basal relationships within the preferred Bayesian estimate of phylogeny from analysis of near-complete 12S and 16S data and diverse taxon sampling; numbers above internodes are posterior probabilities.

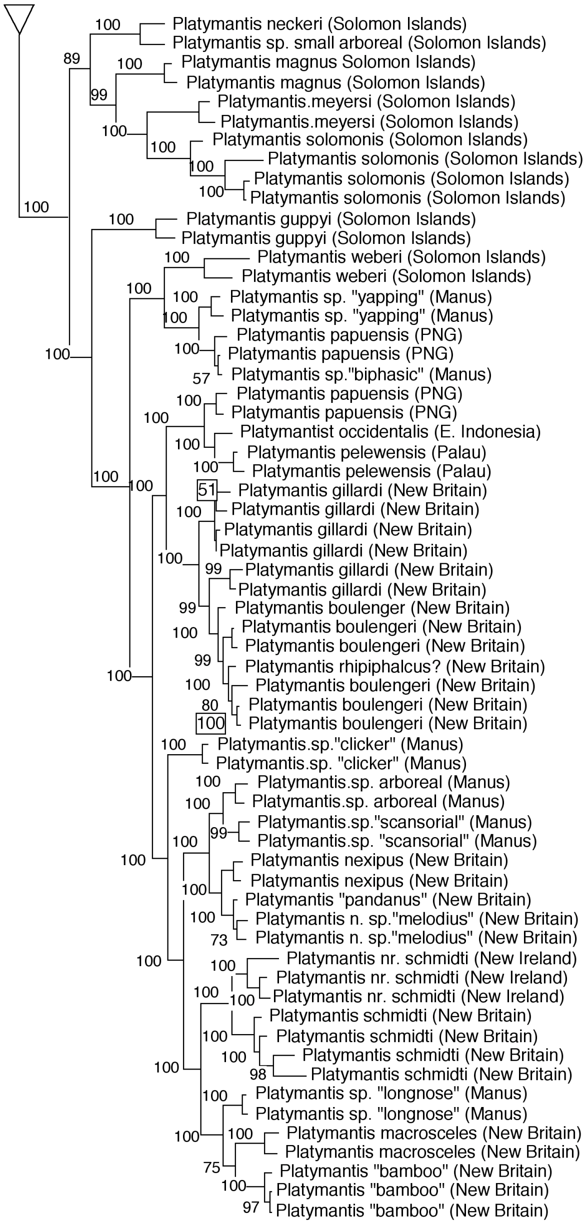

Fig. 4.6B.—Distal relationships within the preferred Bayesian estimate of phylogeny from analysis of near-complete 12S and 16S data and diverse taxon sampling; numbers above internodes are posterior probabilities.

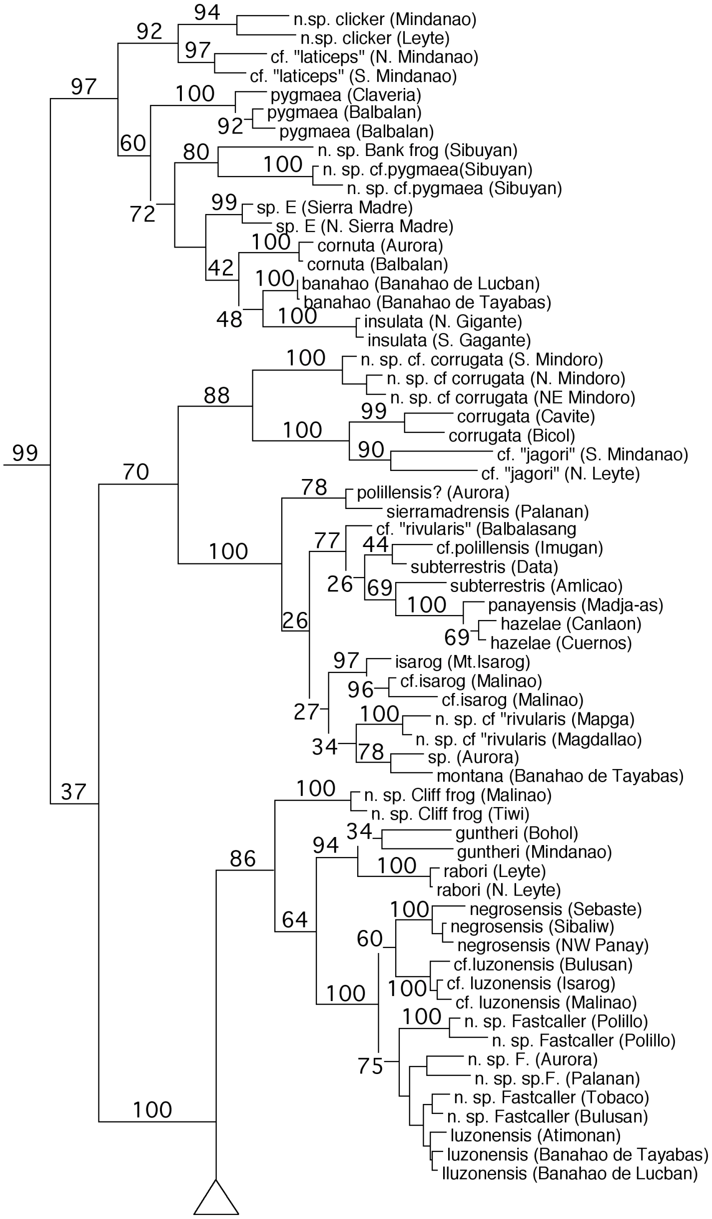

Fig. 4.7A.— Basal relatuionships within one of 24 most-parsimonious trees generated from Maximum Parsimony analysis of 900 bp of 16S data and dense taxonomic sampling within the Philippines; numbers above internodes indicate parametric bootstrap proportions from 2000 iterations.

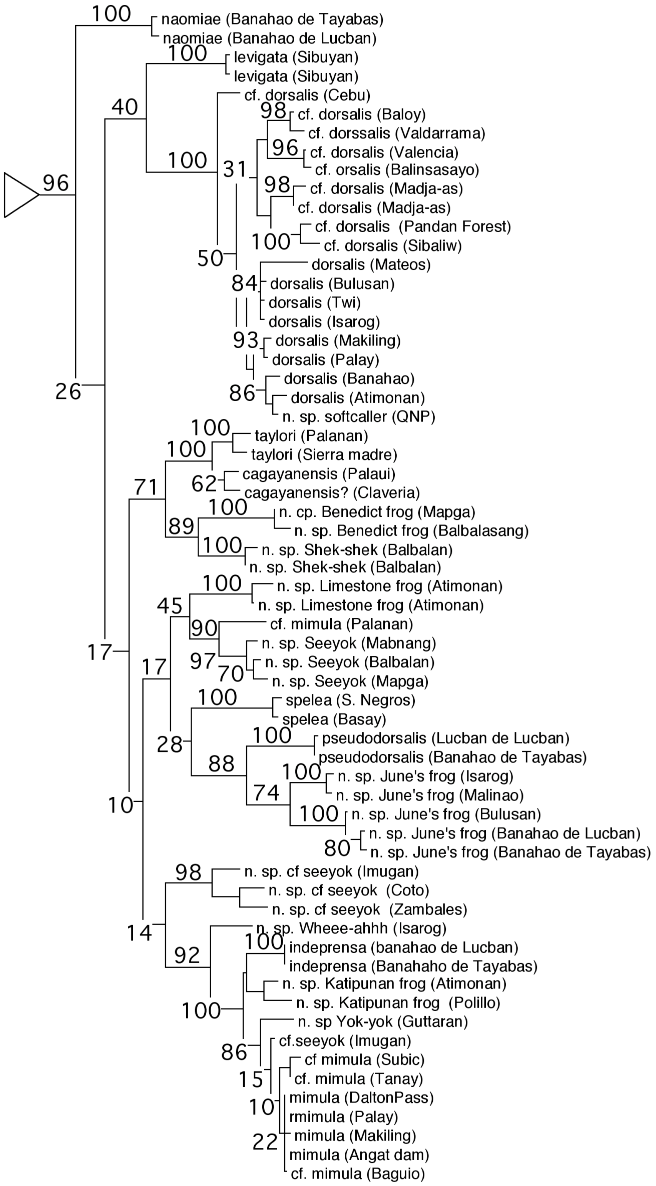

Fig. 4.7B.— Distal relatuionships within one of 24 most-parsimonious trees generated from Maximum Parsimony analysis of 900 bp of 16S data and dense taxonomic sampling within the Philippines; numbers above internodes indicate parametric bootstrap proportions from 2000 iterations.

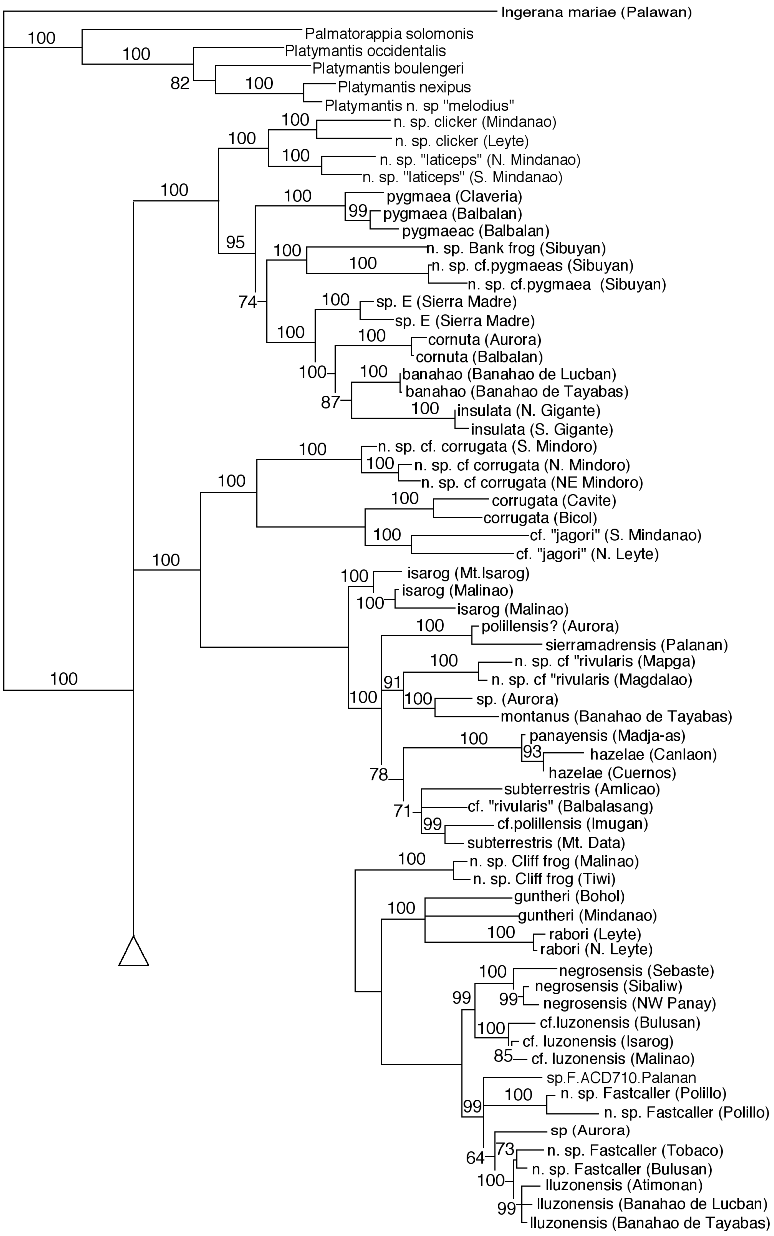

Fig. 4.8A.— Basal relationships within one of the preferred Bayesian topology from analysis of 900 bp of 16S data and dense taxonomic sampling within the Philippines; numbers above internodes are posterior probabilities.

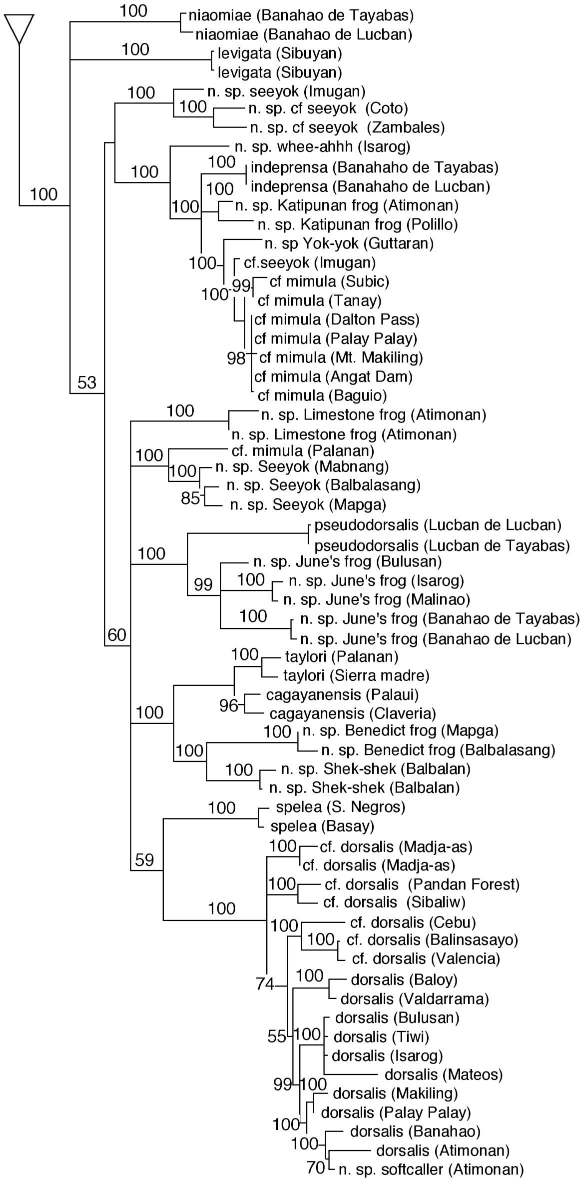

Fig. 4.8B.— Distal relationships within one of the preferred Bayesian topology from analysis of 900 bp of 16S data and dense taxonomic sampling within the Philippines; numbers above internodes are posterior probabilities.

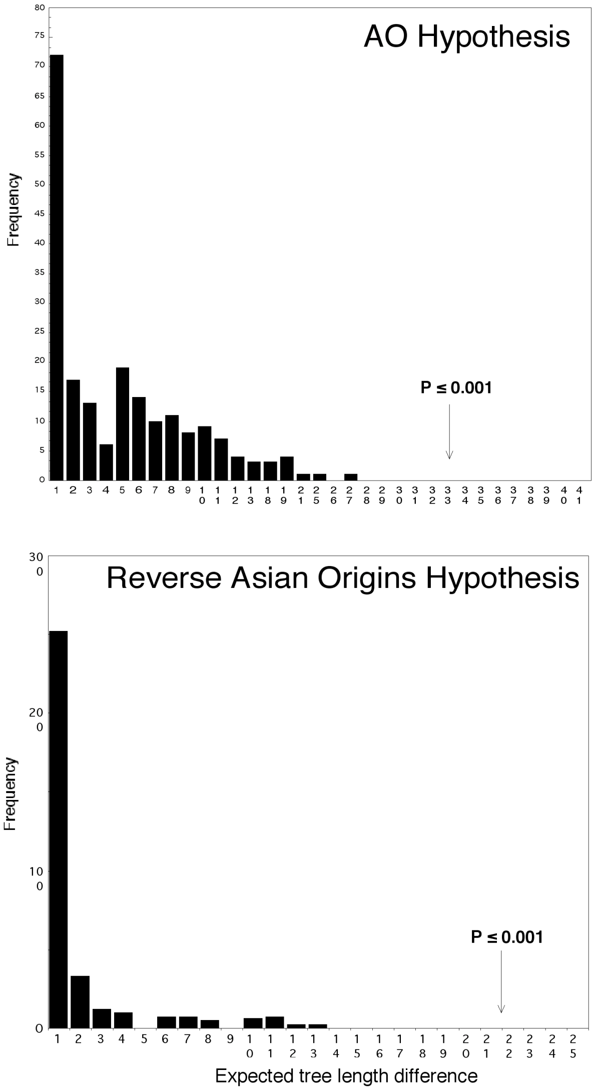

Fig. 4.9.—Null distributions of expected tree length differences from parametric bootstrapping tests of topological hypotheses. The arrow in each figure indicates the position of the observed tree length difference (test statistic).

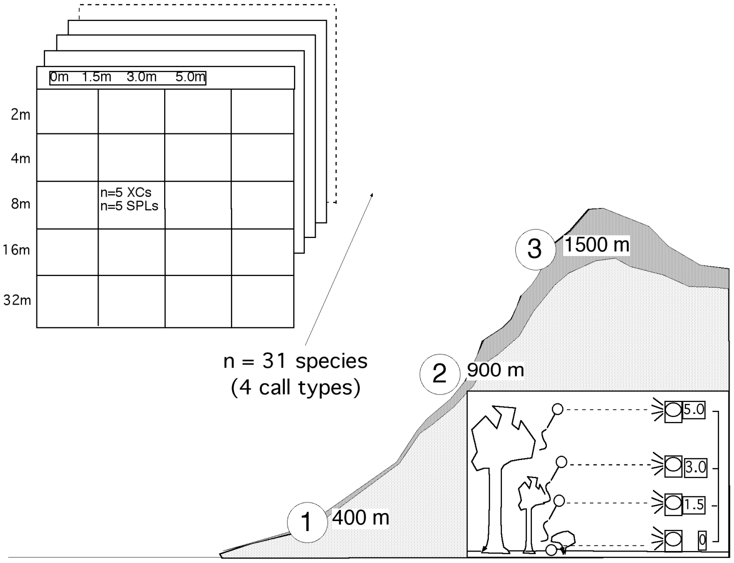

Fig. 5.1.—Experimental design for transmission trials, conducted at the Mt. Makiling forest reserve, Luzon Island, Philippines. The protocol included a 3-by-5 experimental design (with perch height and distance treatments), and was replicated at three different elevations (400, 900, 1500) for 31 species of four distinct call types (complex calls, frequency sweeps, pulsed calls, and tonal calls). At each station (cell), data collected included five sound pressure level measurements, and five cross correlations of non-degraded to degraded signals.

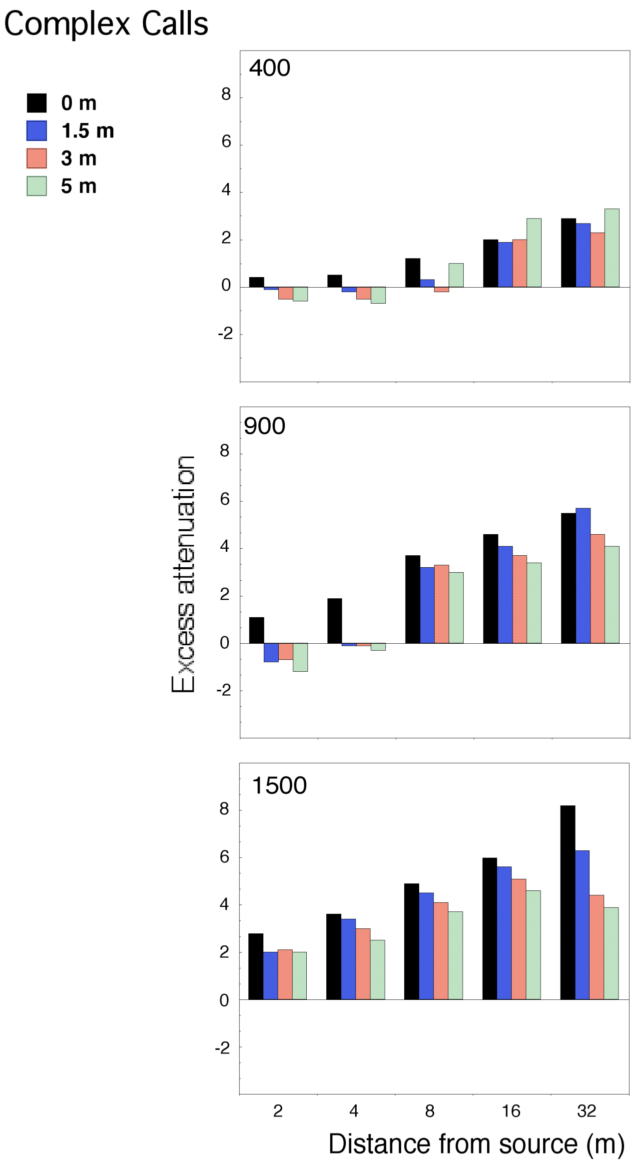

Fig. 5.2.—Excess attenuation (predicted–observed amplitude levels) profiles for ten (table 1) complex, two-, three-, or four-syllable calls. Transmission experiments were conducted at low- (400m dipterocarp forests), mid- (900 m transitional montane forest) and high-elevation (1500 m mossy and/or elfin upper montane or cloud forest) transects. Calls were broadcasted along distance transects from 2 to 32 m from the source and from five "perch" heights (0, 1.5, 3, and 5 m) above the ground. At each station (cell) five sound pressure level (SPLs) measurements were taken and five cross-correlations (XCs) of non-degraded to degraded signals were performed.

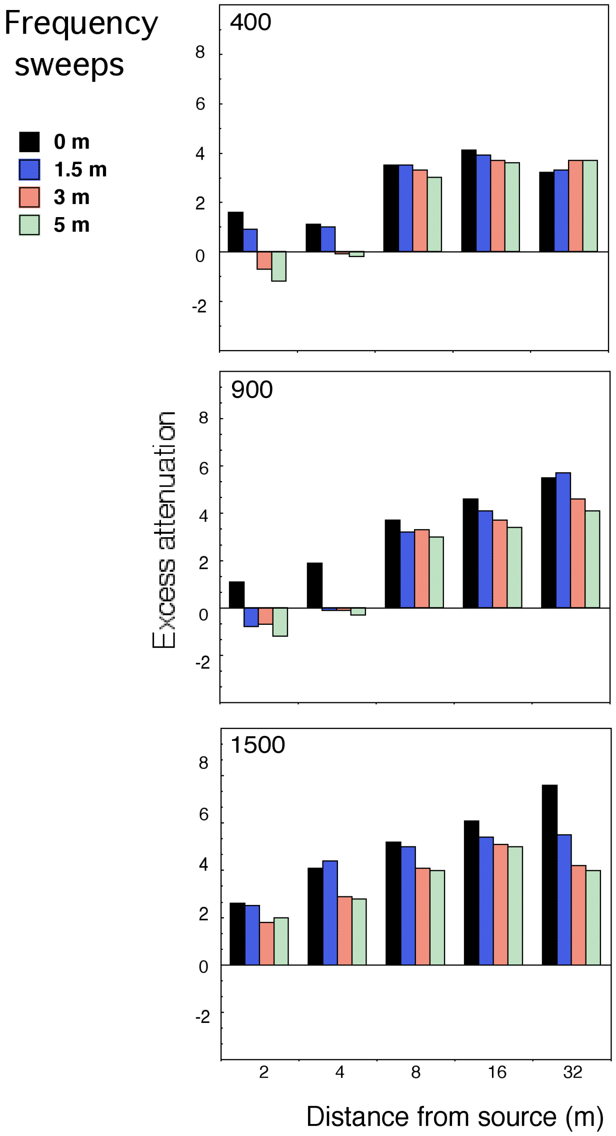

Fig. 5.3.— Excess attenuation profiles for seven (Table 1) frequency sweep calls. See Figures 1 and 2 and text for details of experimental design and discussion of statistical significance of trends.

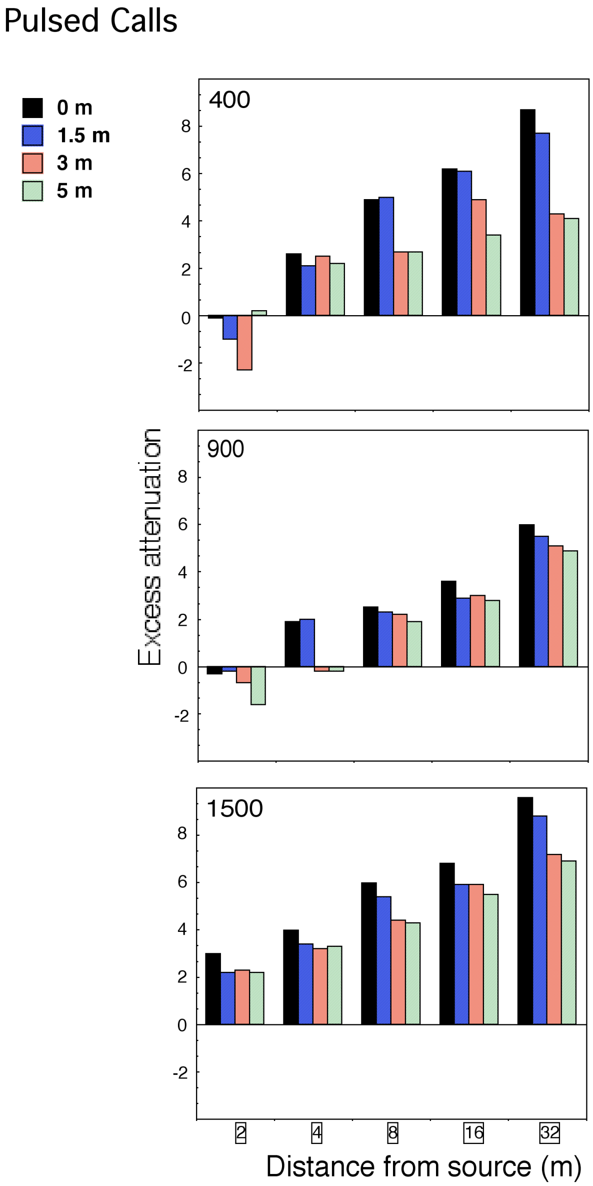

Fig. 5.4.— Excess attenuation profiles for seven (Table 1) pulsed calls. See Figures 1 and 2 and text for details of experimental design and discussion of statistical significance of trends.

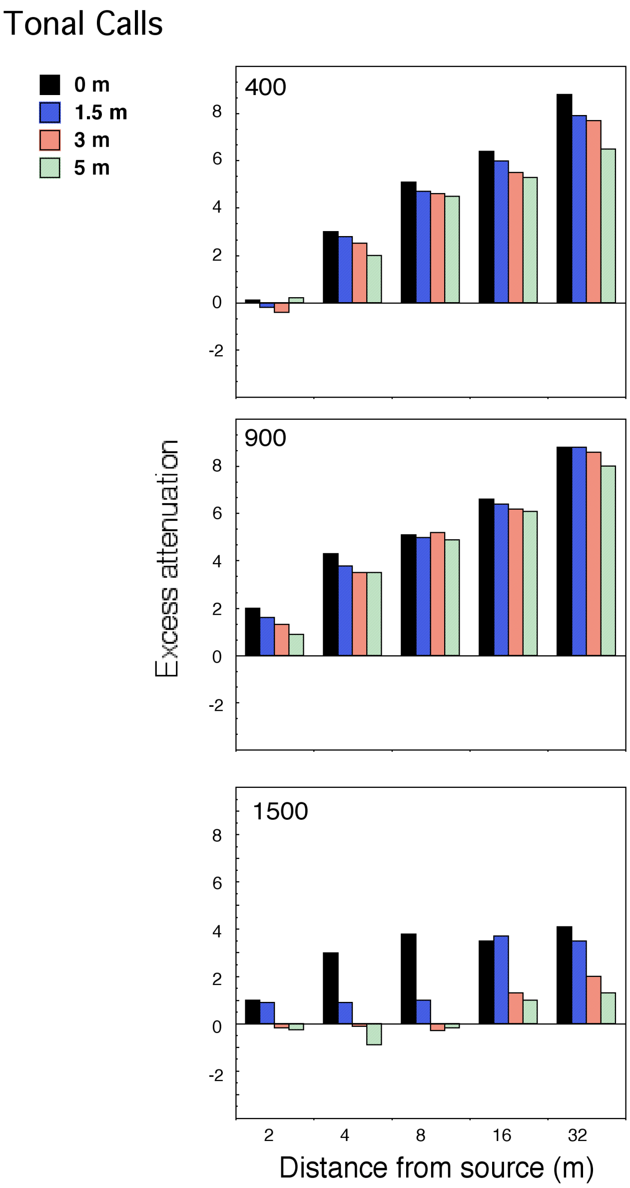

Fig. 5.5.— Excess attenuation profiles for seven (Table 1) tonal sweep calls. See Figures 1 and 2 and text for details of experimental design and discussion of statistical significance of trends.

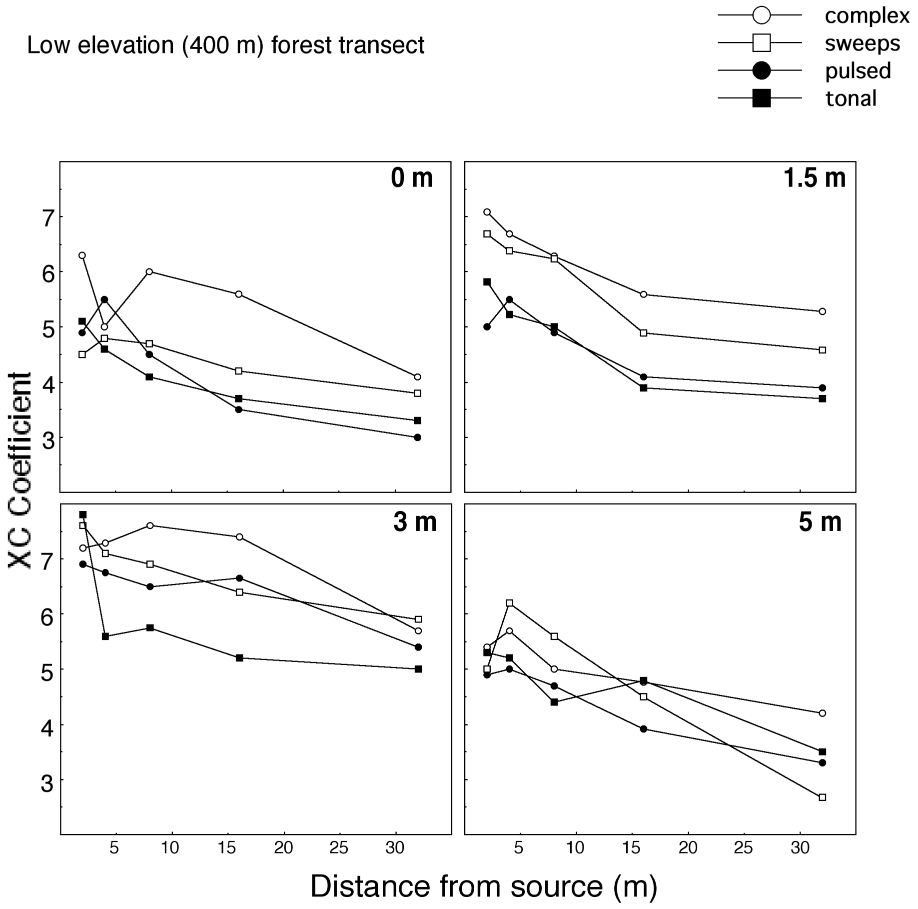

Fig. 5.6.—Patterns of call degradation in lowland (400 m) climax dipterocarp forests as measured by cross-correlation coefficients (XC). Treatments included distance (2–32 m) and perch height (0–5 m) for four call types (complex calls, frequency sweeps, pulsed calls, and tonal calls).

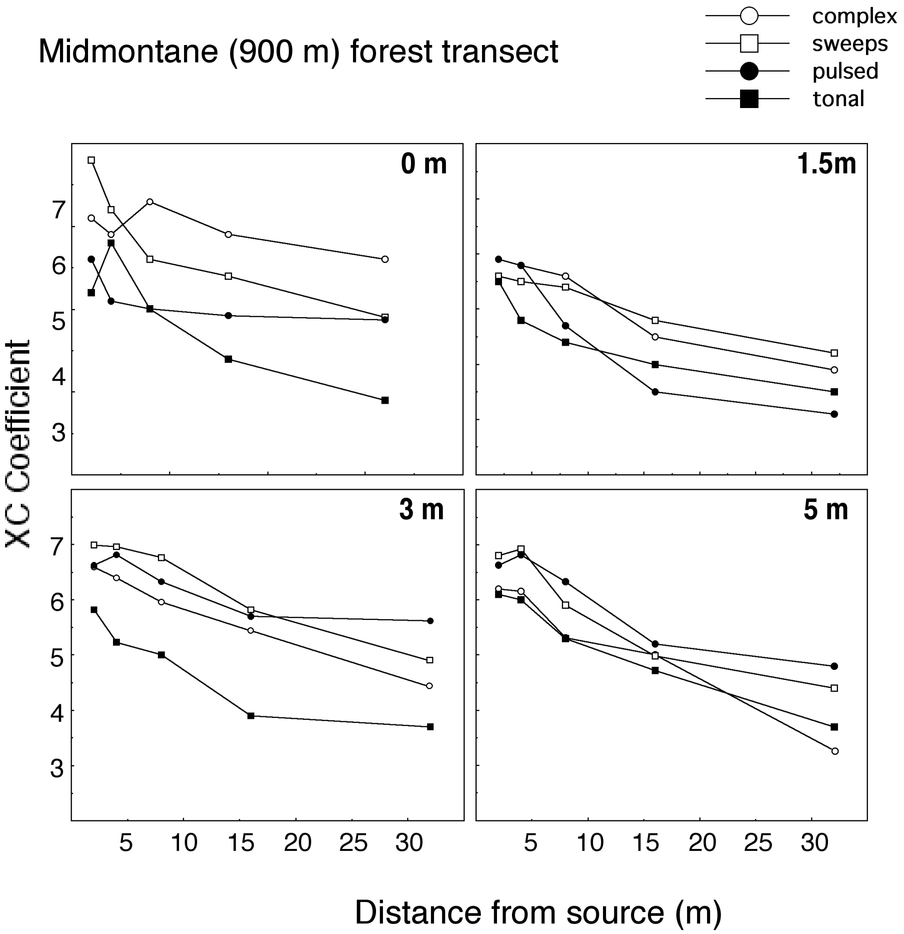

Fig. 5.7.— Patterns of call degradation in mid-elevation (900 m) transitional montane forest, as measured by cross-correlation coefficients (XC). Treatments included distance (2–32 m) and perch height (0–5 m) for four call types (complex calls, frequency sweeps, pulsed calls, and tonal calls).

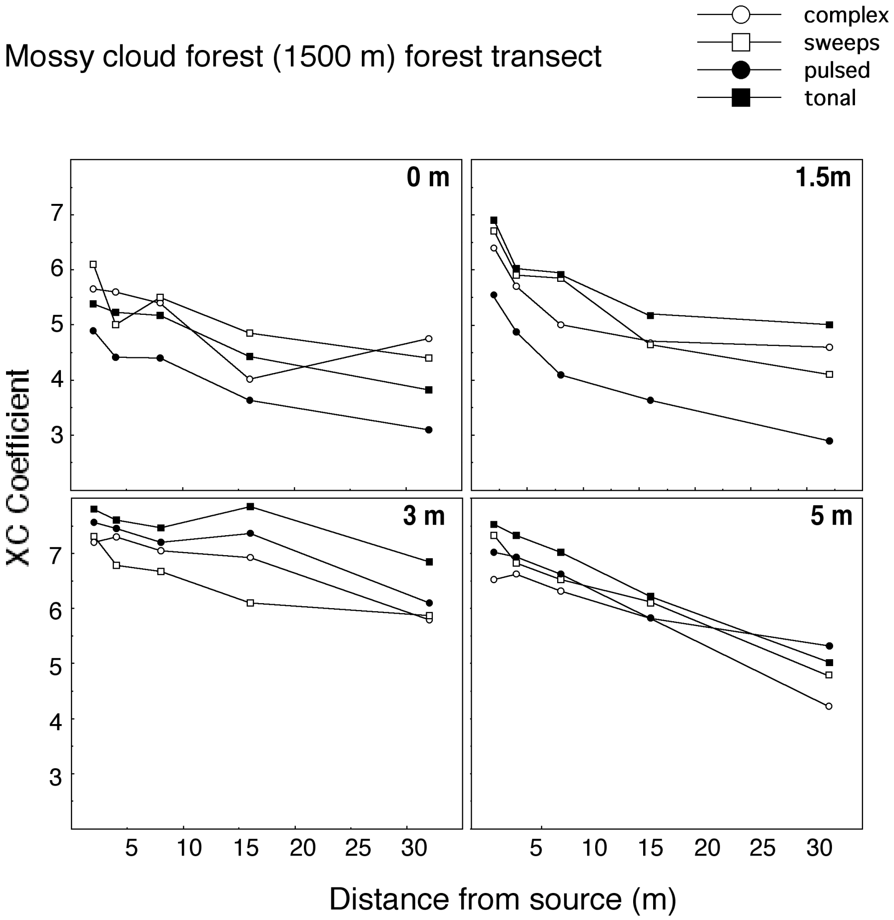

Fig. 5.8.— Patterns of call degradation in high-elevation (1500 m) upper montane mossy/ cloud forest, as measured by cross-correlation coefficients (XC). Treatments included distance (2–32 m) and perch height (0–5 m) for four call types (complex calls, frequency sweeps, pulsed calls, and tonal calls).

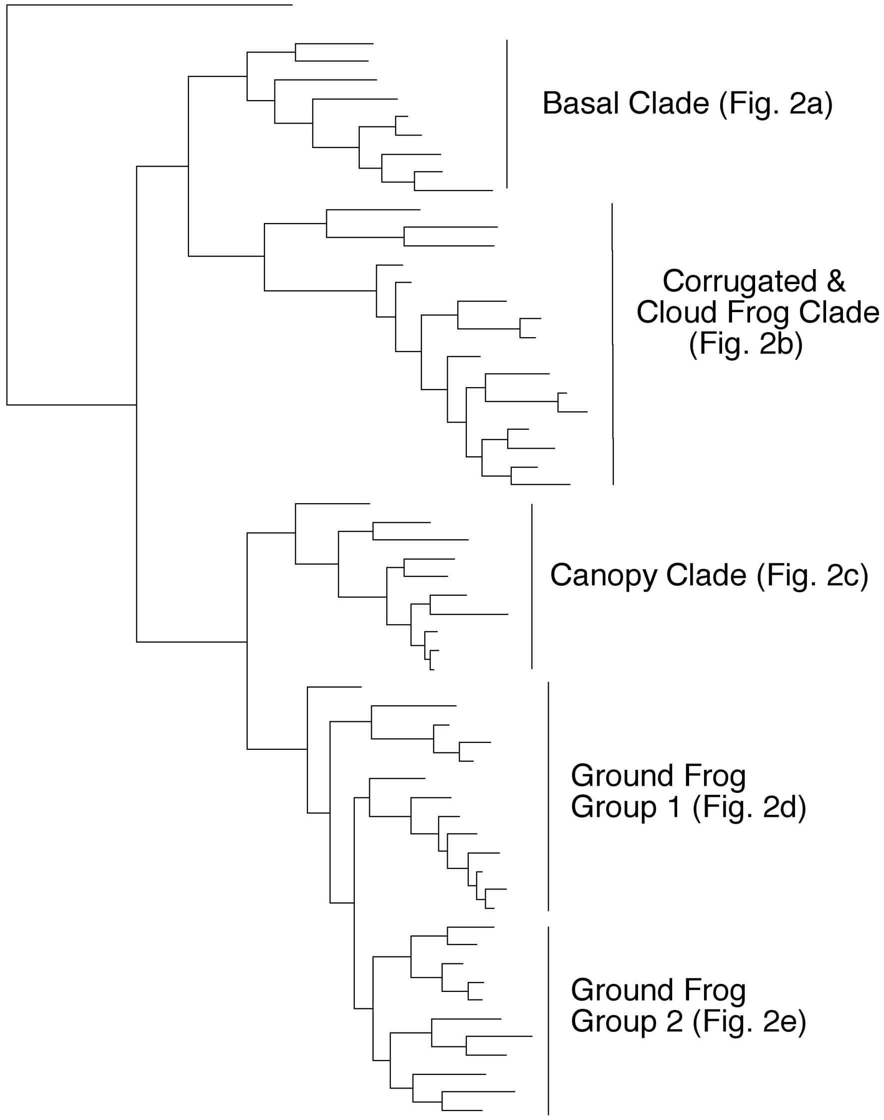

Fig. 6.1.—Preferred phylogenetic estimate (Chapt. 4) from Parsimony and Bayesian analyses of molecular sequence data with a single terminal per species and clade/group names indicated for reference to Figs 2 and 3.

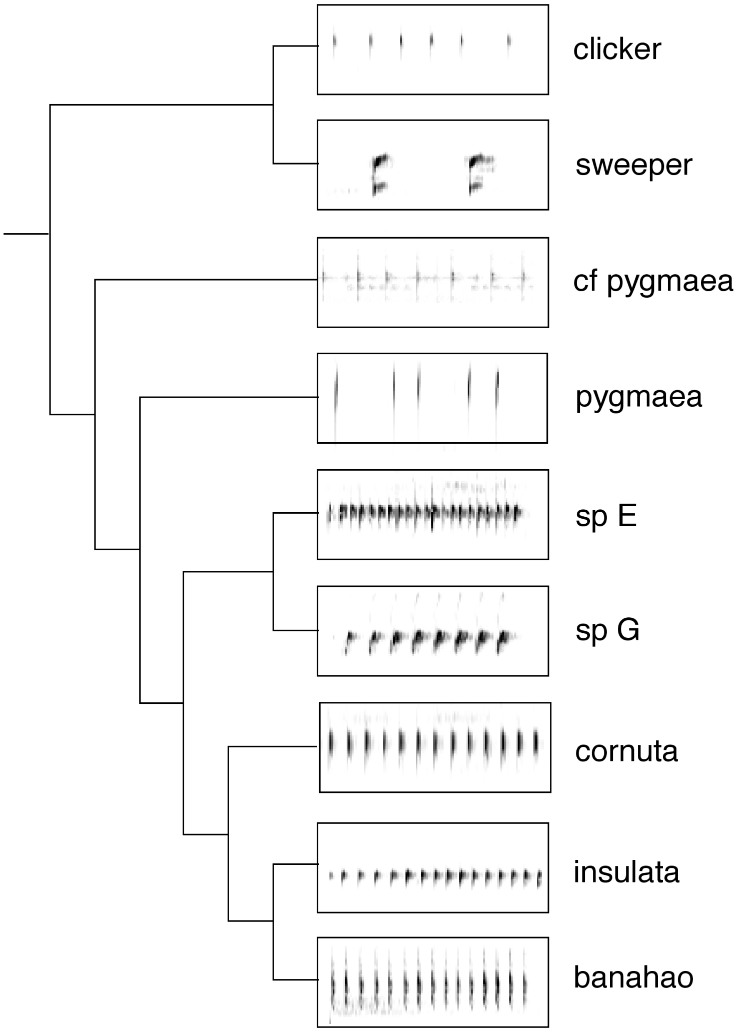

Fig. 6.2A.—Patterns of call evolution in Basal Clade of Philippine Platymantis. Audiospectrograms scaled to same dimensions (frequency vs time with relative energy different portions of call indicated by intensity of shading; axes = 5 kHz x 2 s) and mapped onto the preferred phylogenetic hypothesis.

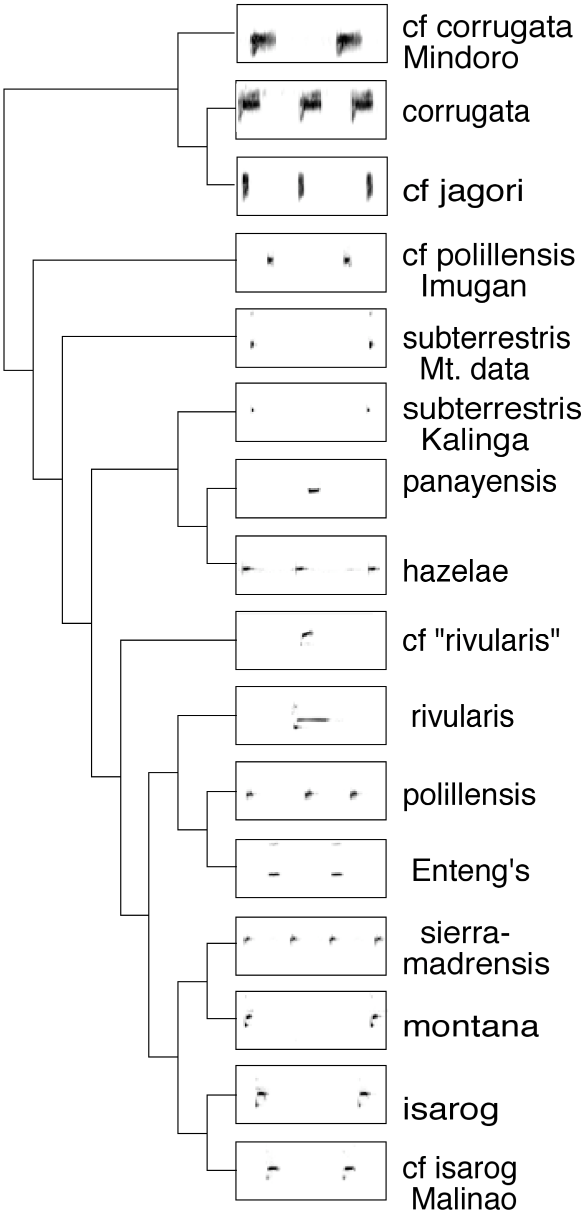

Fig. 6.2B.—Patterns of call evolution in Corrugated Frogs and Cloud Frogs Clade of Philippine *Platymantis*. Audiospectrograms scaled to same dimensions (frequency vs time with relative energy different portions of call indicated by intensity of shading; axes = 5 kHz x 2 s) and mapped onto the preferred phylogenetic hypothesis.

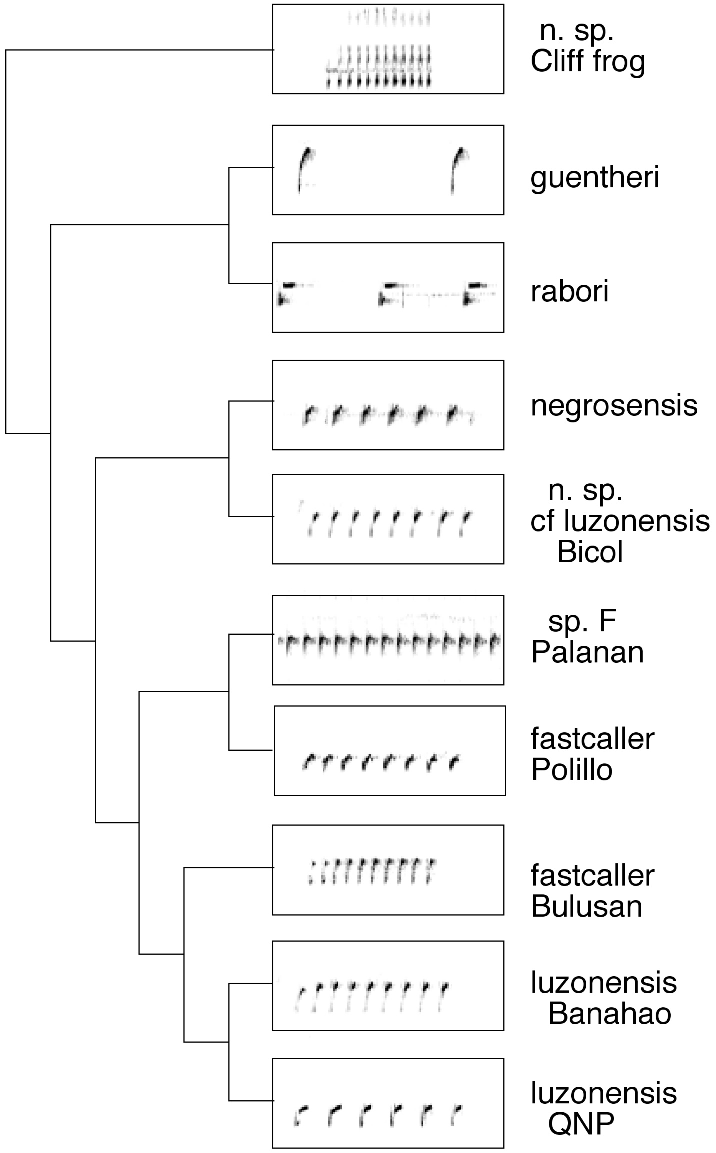

Fig. 6.2C.—Patterns of call evolution in Canopy Frogs of Philippine *Platymantis*. Audiospectrograms scaled to same dimensions (frequency vs time with relative energy different portions of call indicated by intensity of shading; axes = 5 kHz x 2 s) and mapped onto the preferred phylogenetic hypothesis.

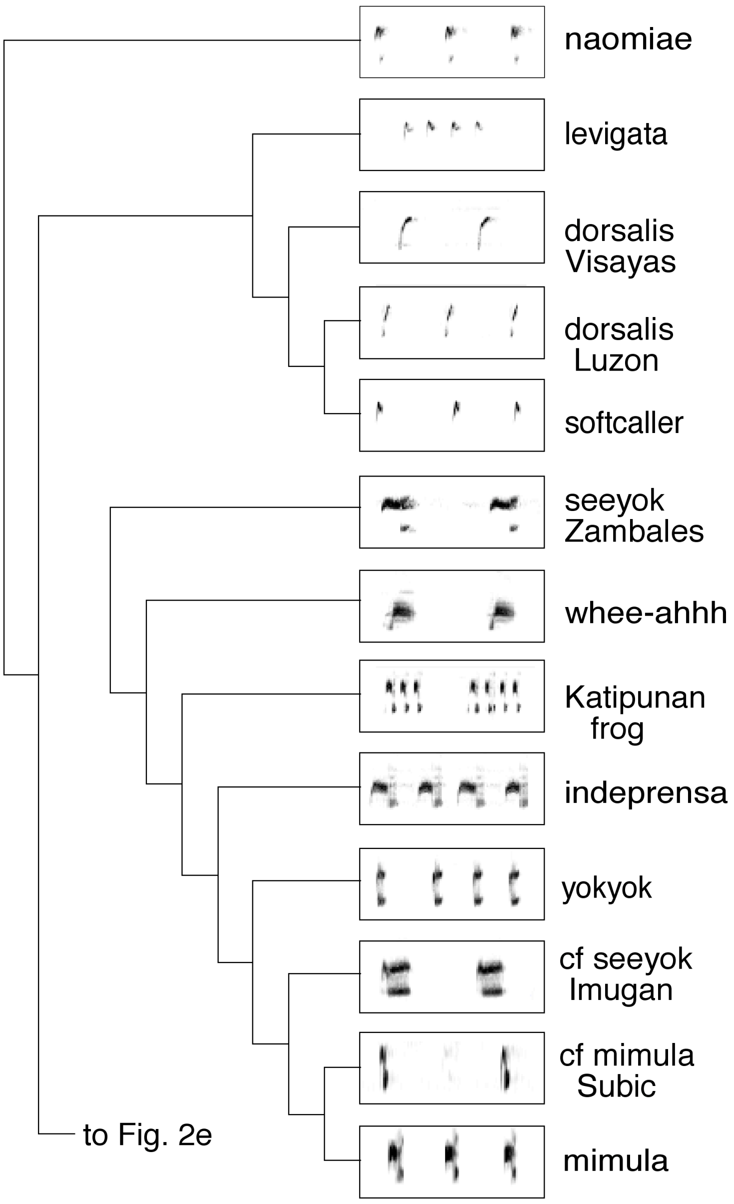

Fig. 6.2D.—Patterns of call evolution in Philippine Ground Frogs Group1. Audiospectrograms scaled to same dimensions (frequency vs time with relative energy different portions of call indicated by intensity of shading; axes = 5 kHz x 2 s) and mapped onto the preferred phylogenetic hypothesis.

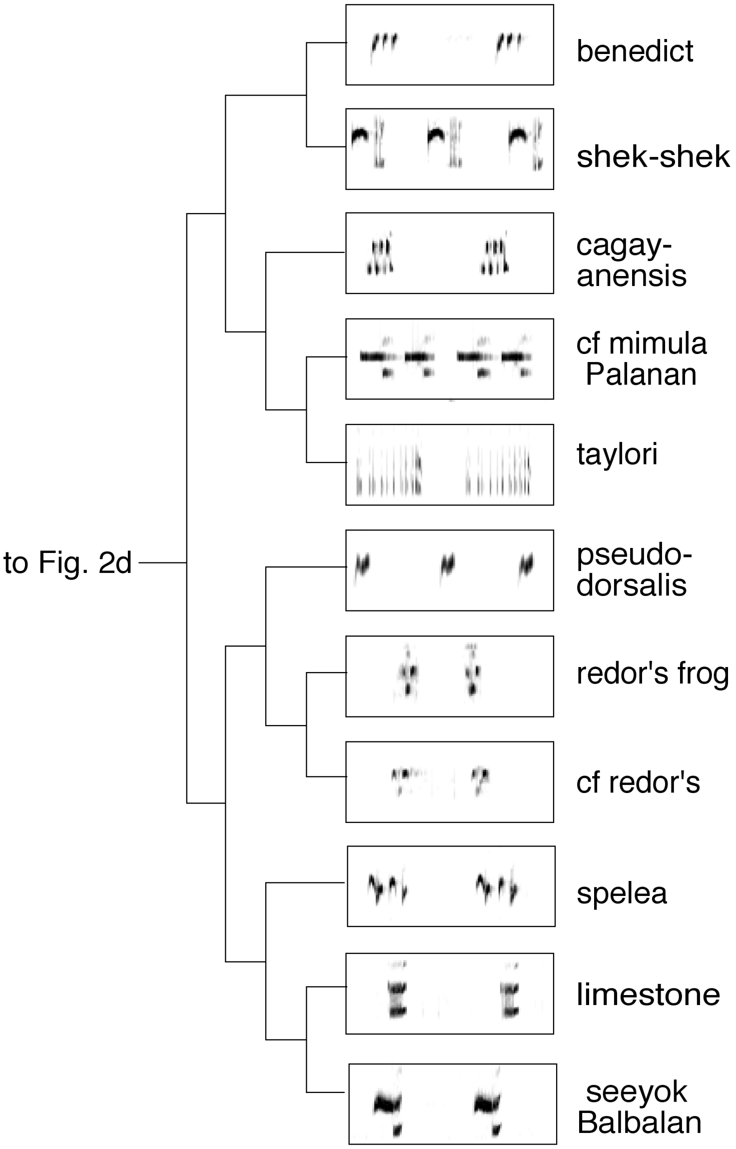

Fig. 6.2E.—Patterns of call evolution in Philippine Ground Frogs Group 2. Audiospectrograms scaled to same dimensions (frequency vs time with relative energy different portions of call indicated by intensity of shading; axes = 5 kHz x 2 s) and mapped onto the preferred phylogenetic hypothesis.

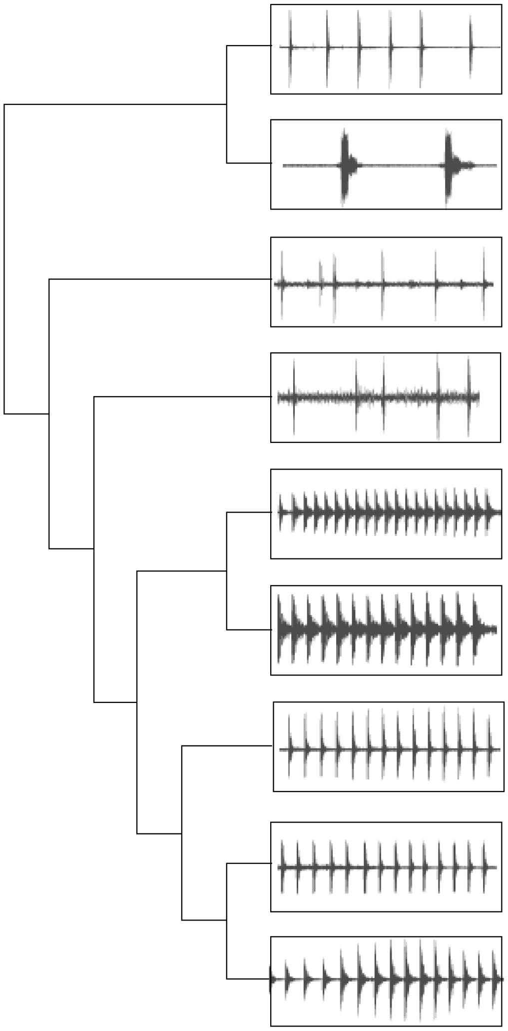

Fig. 6.3A.—Patterns of call evolution in Basal Clade of Philippine *Platymantis*. Oscillograms scaled to same dimensions (relative amplitude vs time with relative energy different portions of call indicated by intensity of shading; axes = 20 uPa x 2 s) and mapped onto the preferred phylogenetic hypothesis.

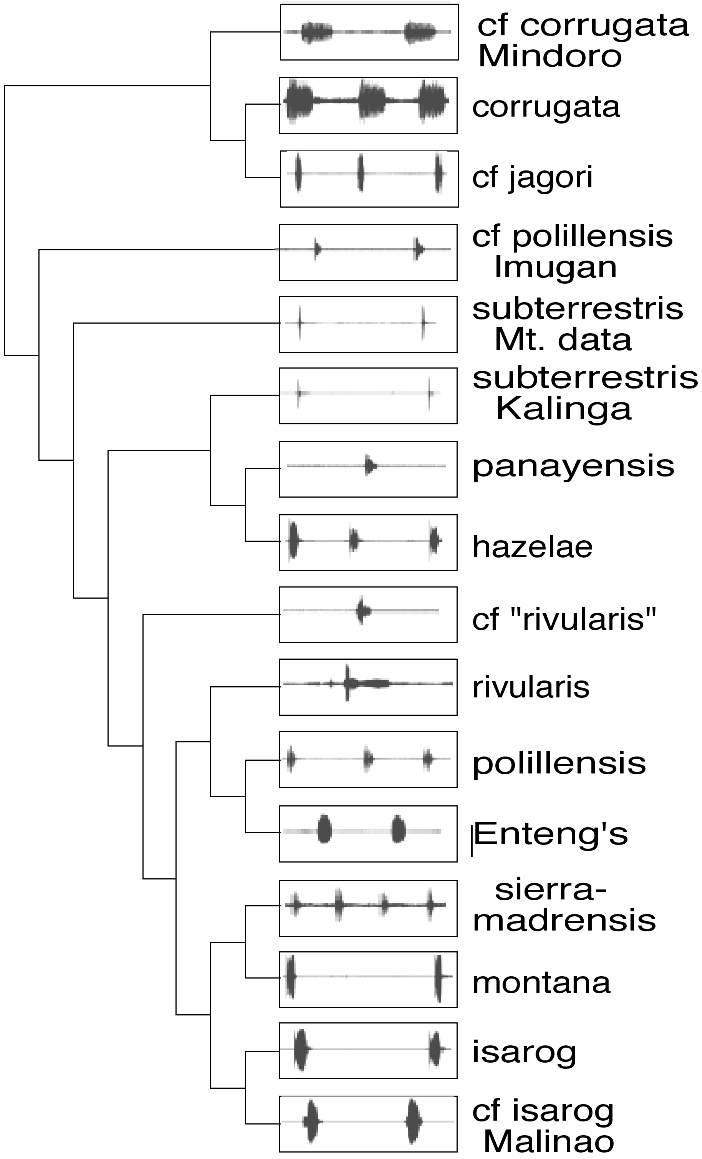

Fig. 6.3B.—Patterns of call evolution in Corrugated Frogs and Cloud Frogs Clade of Philippine Platymantis. Oscillograms scaled to same dimensions (relative amplitude vs time with relative energy different portions of call indicated by intensity of shading; axes = 20 uPa x 2 s) and mapped onto the preferred phylogenetic hypothesis.

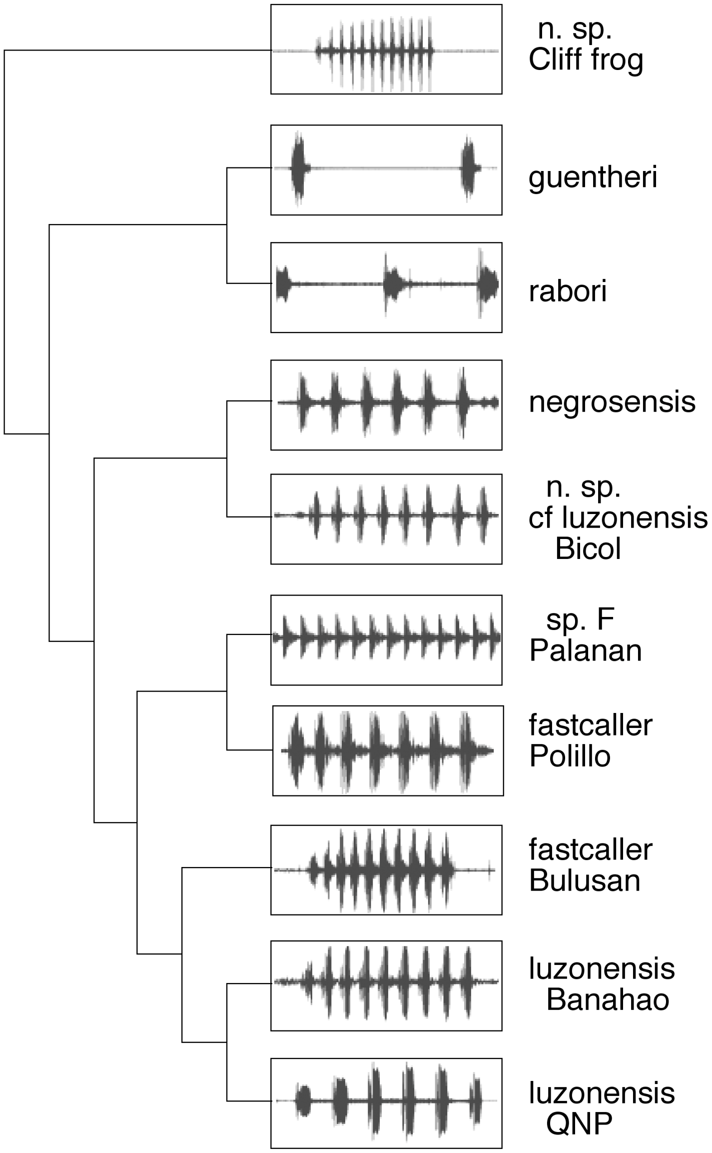

Fig. 6.3C.—Patterns of call evolution in Canopy Frogs of Philippine *Platymantis*. Oscillograms scaled to same dimensions (relative amplitude vs time with relative energy different portions of call indicated by intensity of shading; axes = 20 uPa x 2 s) and mapped onto the preferred phylogenetic hypothesis.

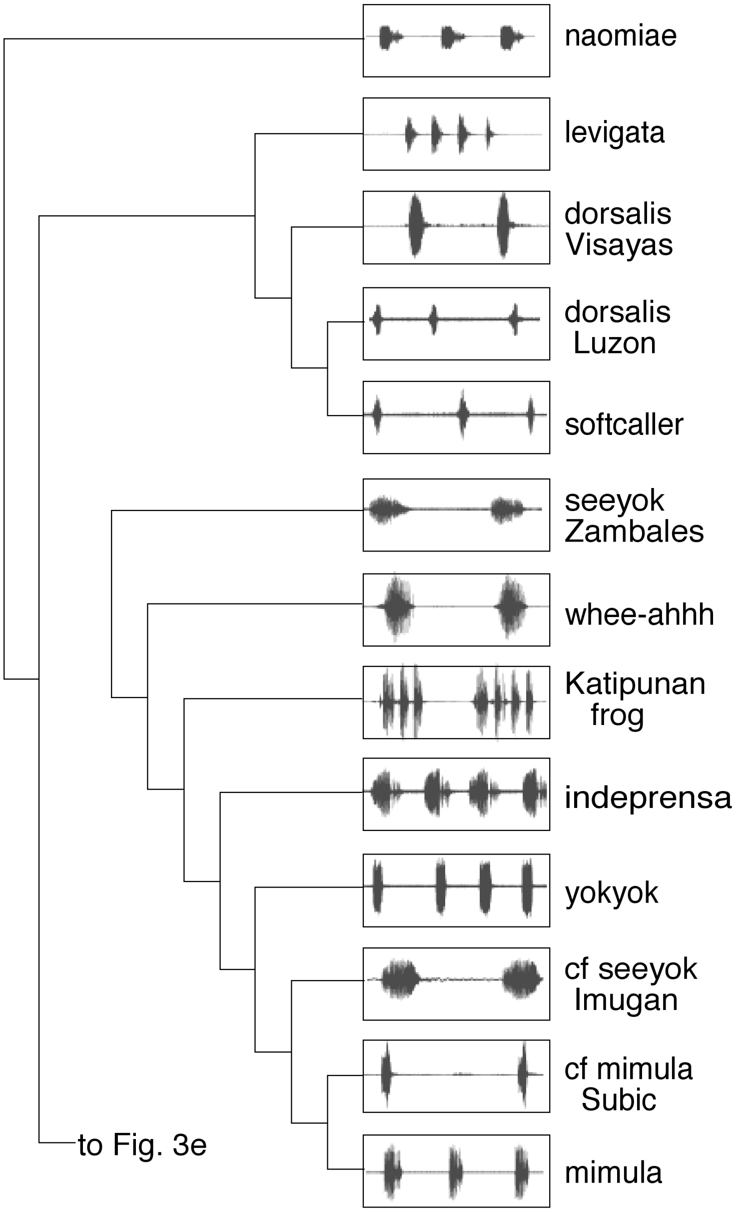

Fig. 6.3D.—Patterns of call evolution in Philippine Ground Frogs Group 1. Oscillograms scaled to same dimensions (relative amplitude vs time with relative energy different portions of call indicated by intensity of shading; axes = 20 uPa x 2 s) and mapped onto the preferred phylogenetic hypothesis.

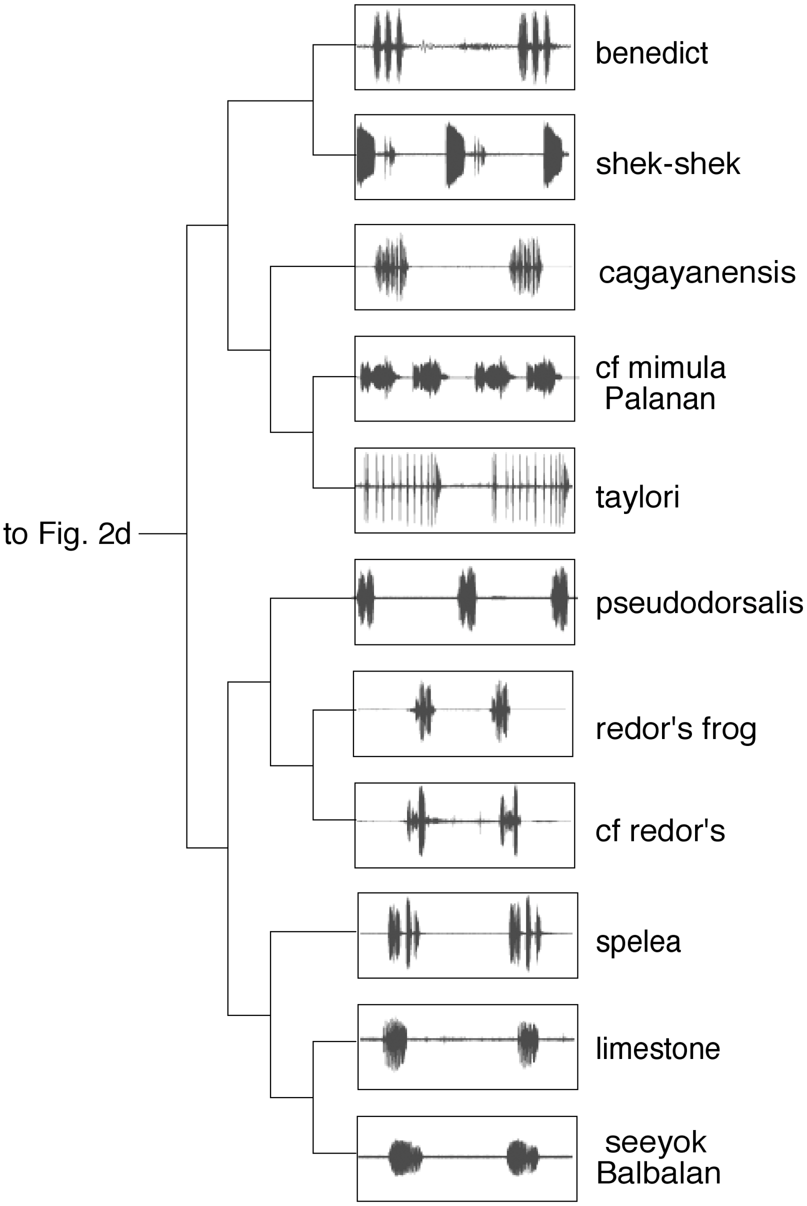

Fig. 6.3E.—Patterns of call evolution in Philippine Ground Frogs Group 2. Oscillograms scaled to same dimensions (relative amplitude vs time with relative energy different portions of call indicated by intensity of shading; axes = 20 uPa x 2 s) and mapped onto the preferred phylogenetic hypothesis.

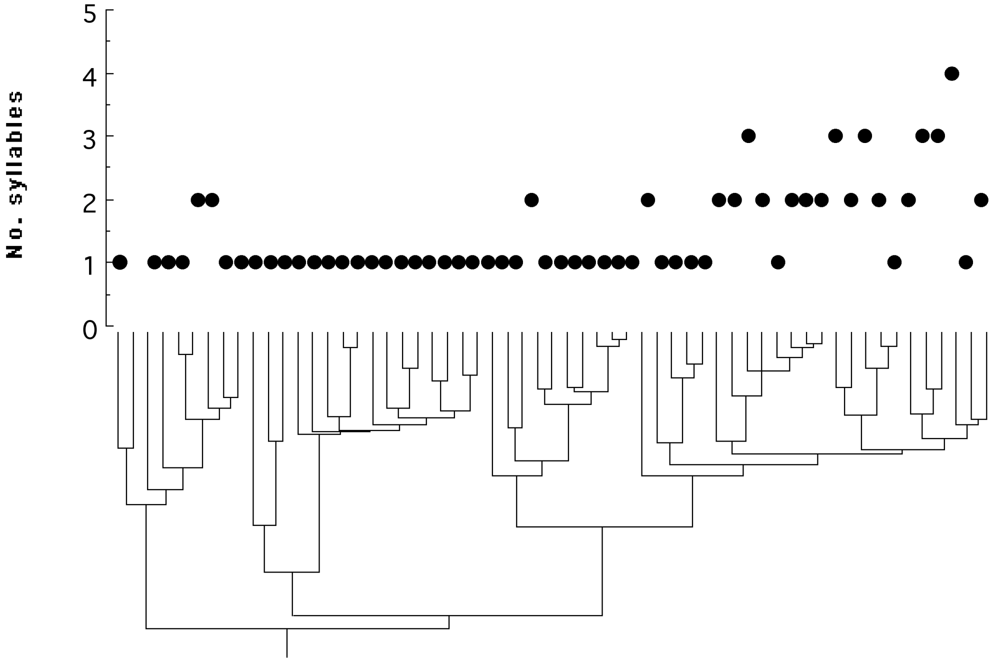

Fig. 6.4.—Patterns of univariate character variation in number of syllables per call across the preferred phylogenetic hypothesis (ultrametric tree) following the rejection of a molecular clock. See Figures 1 and 2 for species group/clade identities and text for discussion of character measurement.

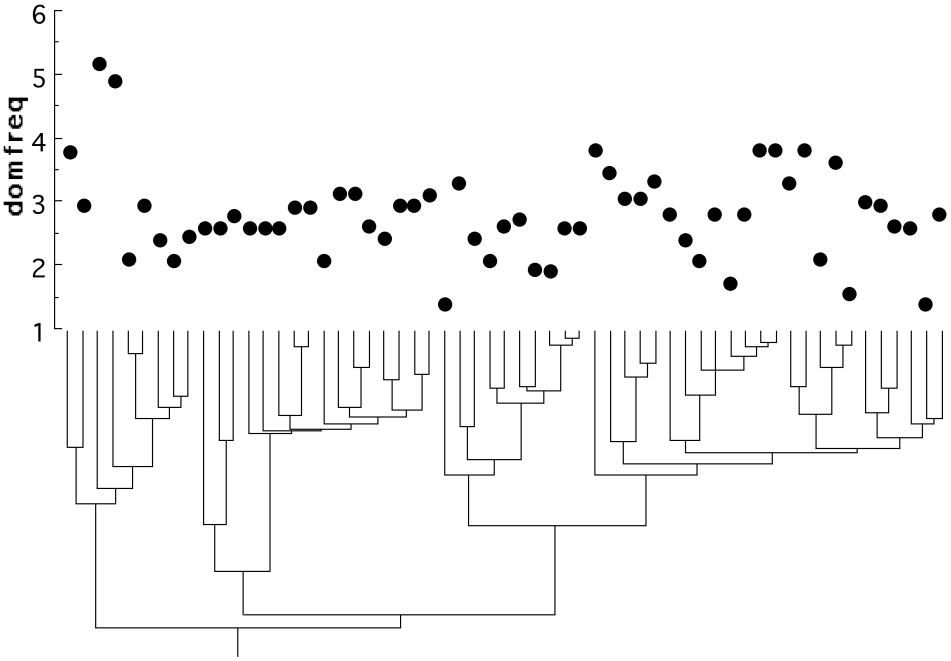

Fig. 6.5.—Patterns of univariate character variation in dominant frequency across the preferred phylogenetic hypothesis (ultrametric tree) following the rejection of a molecular clock. See Figures 1 and 2 for species group/clade identities and text for discussion of character measurement.

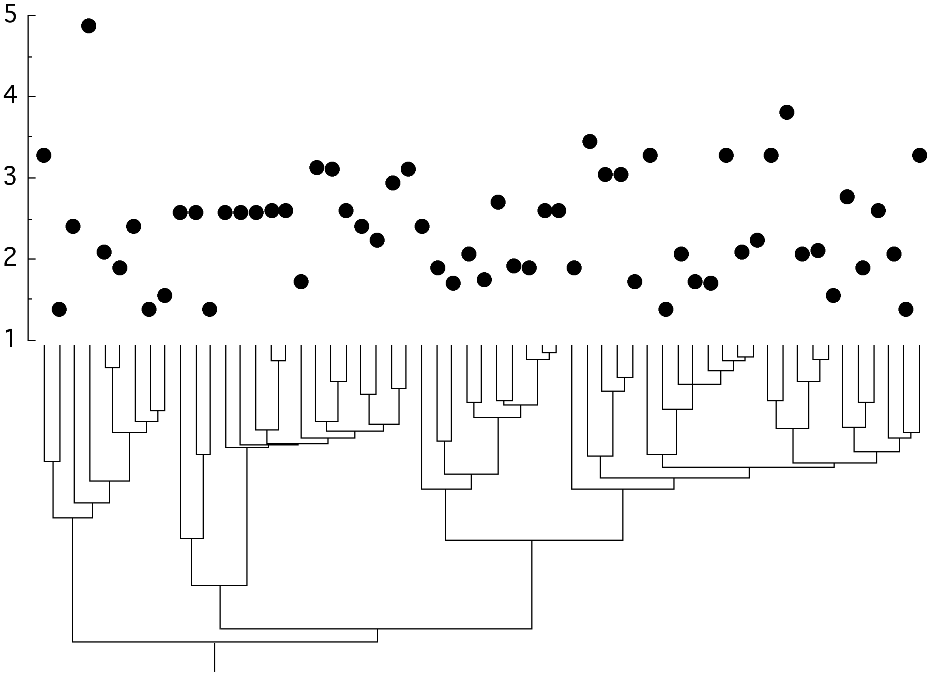

Fig. 6.6.—Patterns of univariate character variation in fundamental frequency across the preferred phylogenetic hypothesis (ultrametric tree) following the rejection of a molecular clock. See Figures 1 and 2 for species group/clade identities and text for discussion of character measurement.

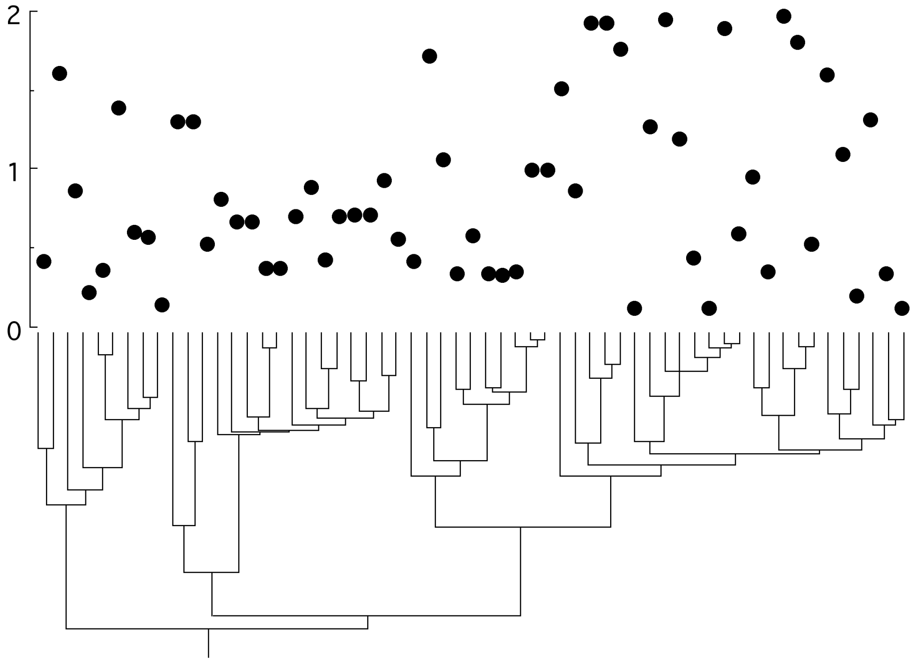

Fig. 6.7.—Patterns of univariate character variation in absolute magnitude of frequency modulation across the preferred phylogenetic hypothesis (ultrametric tree) following the rejection of a molecular clock. See Figures 1 and 2 for species group/clade identities and text for discussion of character measurement.

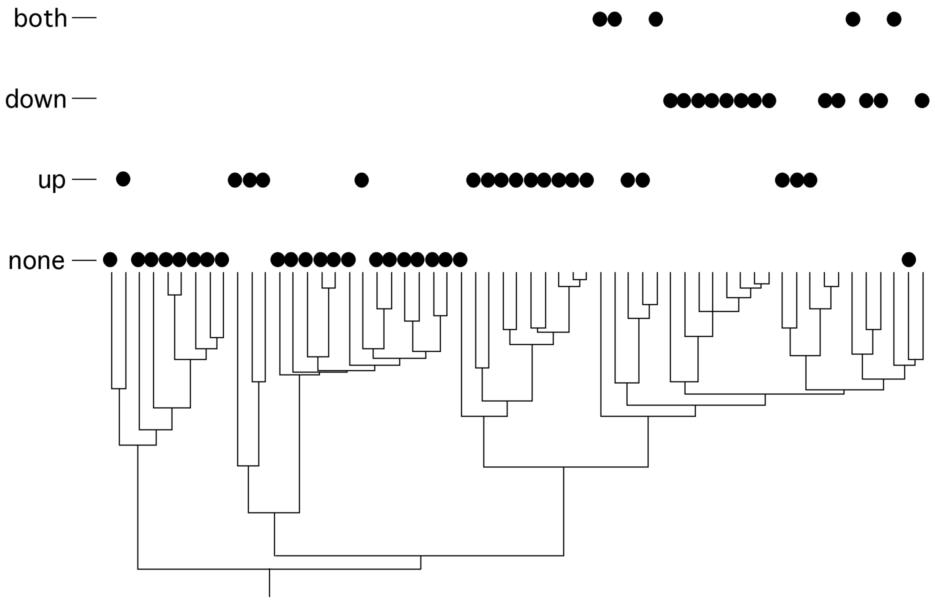

Fig. 6.8.—Patterns of univariate character variation in direction of frequency modulation across the preferred phylogenetic hypothesis (ultrametric tree) following the rejection of a molecular clock. See Figures 1 and 2 for species group/clade identities and text for discussion of character measurement.

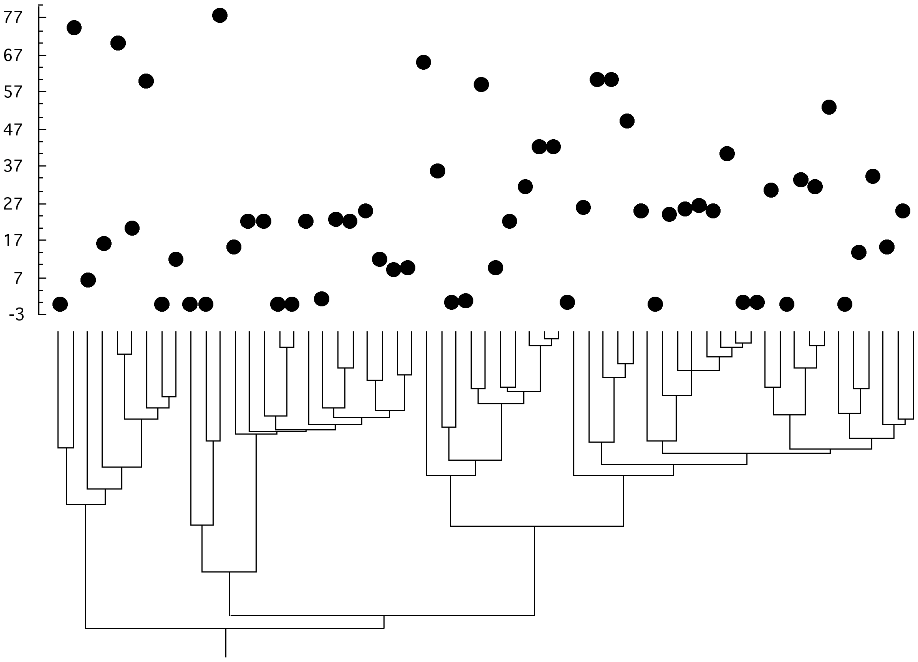

Fig. 6.9.—Patterns of univariate character variation in the time duration of frequency-modulated call segments across the preferred phylogenetic hypothesis (ultrametric tree) following the rejection of a molecular clock. See Figures 1 and 2 for species group/clade identities and text for discussion of character measurement.

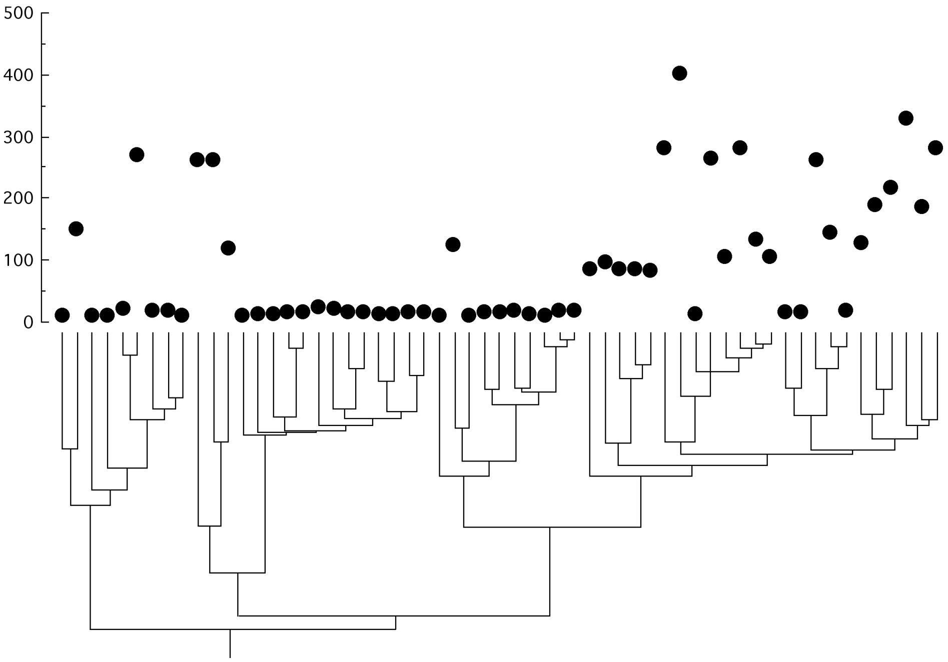

Fig. 6.10.—Patterns of univariate character variation in call duration across the preferred phylogenetic hypothesis (ultrametric tree) following the rejection of a molecular clock. See Figures 1 and 2 for species group/clade identities and text for discussion of character measurement.

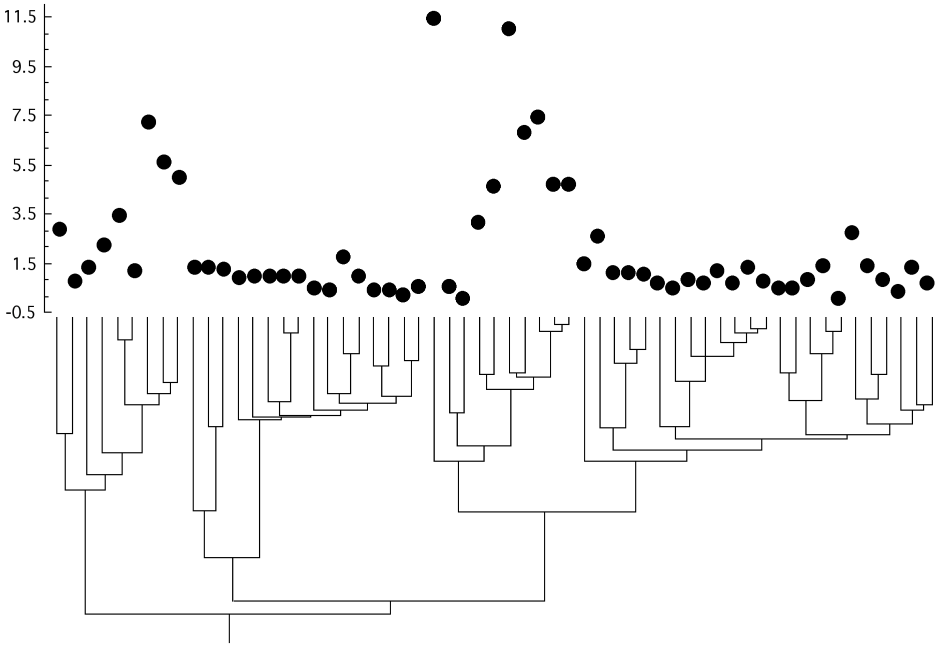

Fig. 6.11.—Patterns of univariate character variation in calling rate across the preferred phylogenetic hypothesis (ultrametric tree) following the rejection of a molecular clock. See Figures 1 and 2 for species group/clade identities and text for discussion of character measurement.

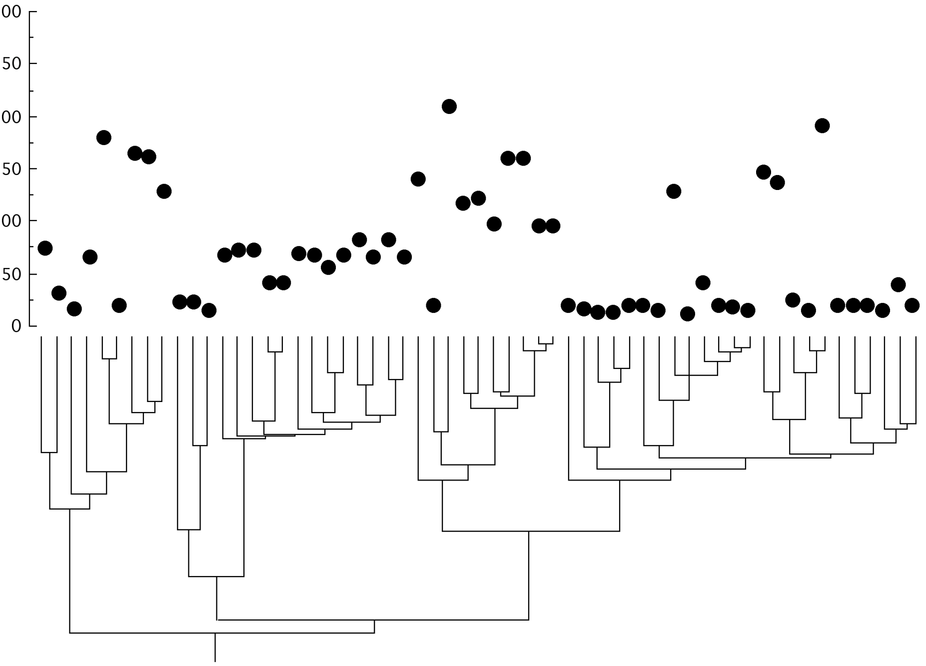

Fig. 6.12.—Patterns of univariate character variation in call group duration across the preferred phylogenetic hypothesis (ultrametric tree) following the rejection of a molecular clock. See Figures 1 and 2 for species group/clade identities and text for discussion of character measurement.

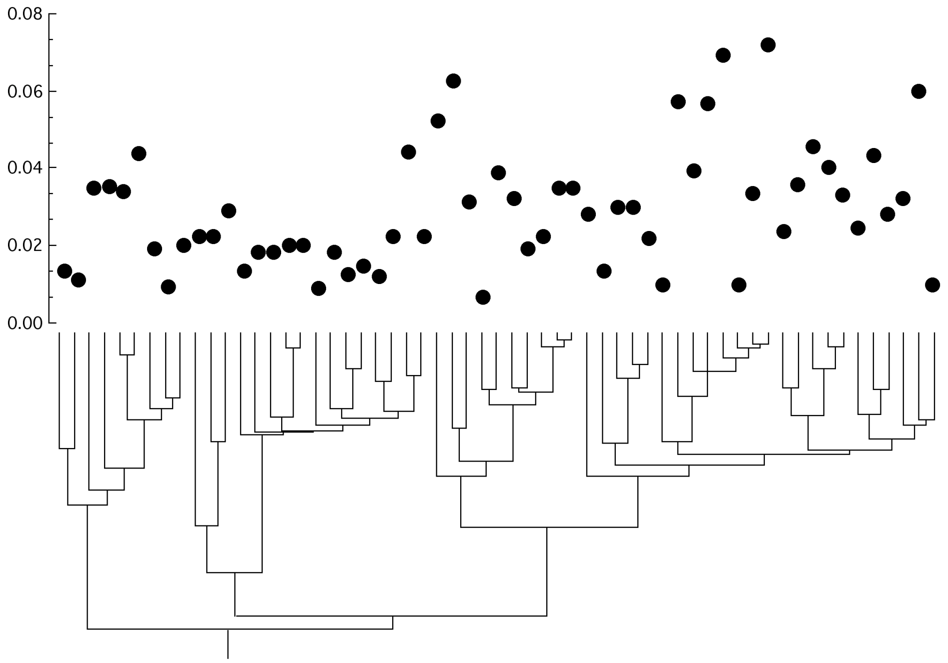

Fig. 6.13.—Patterns of univariate character variation in call group rate across the preferred phylogenetic hypothesis (ultrametric tree) following the rejection of a molecular clock. See Figures 1 and 2 for species group/clade identities and text for discussion of character measurement.

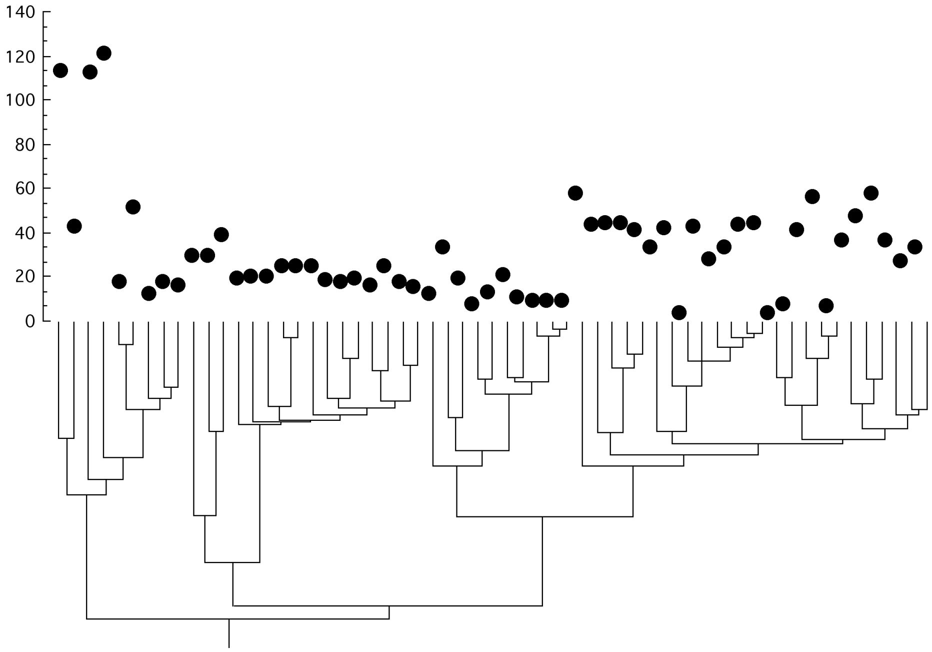

Fig. 6.14.—Patterns of univariate character variation in call (or pulse) number per call group across the preferred phylogenetic hypothesis (ultrametric tree) following the rejection of a molecular clock. See Figures 1 and 2 for species group/clade identities and text for discussion of character measurement.

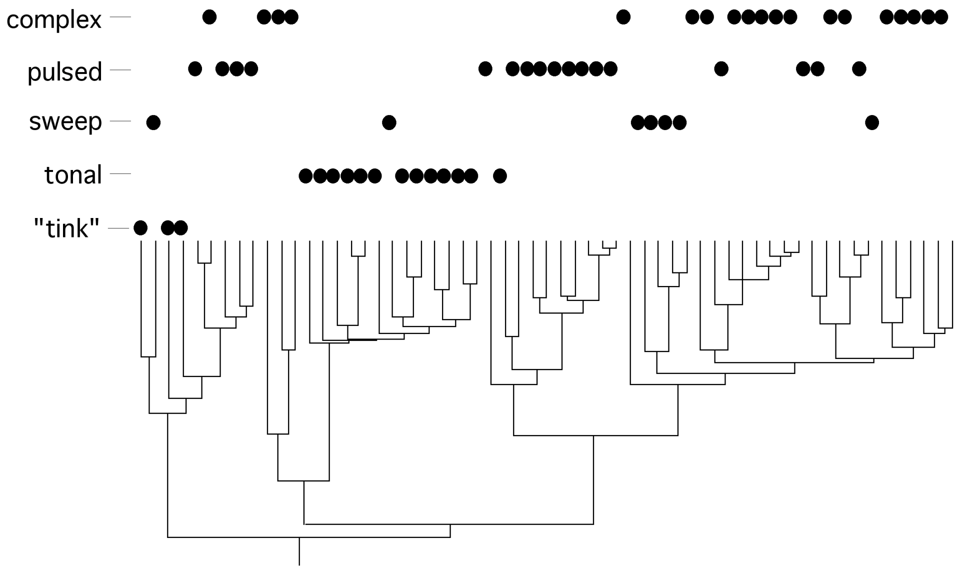

Fig. 6.15.—Patterns of univariate character variation in call type (call complexity) across the preferred phylogenetic hypothesis (ultrametric tree) following the rejection of a molecular clock. See Figures 1 and 2 for species group/clade identities and text for discussion of character measurement.

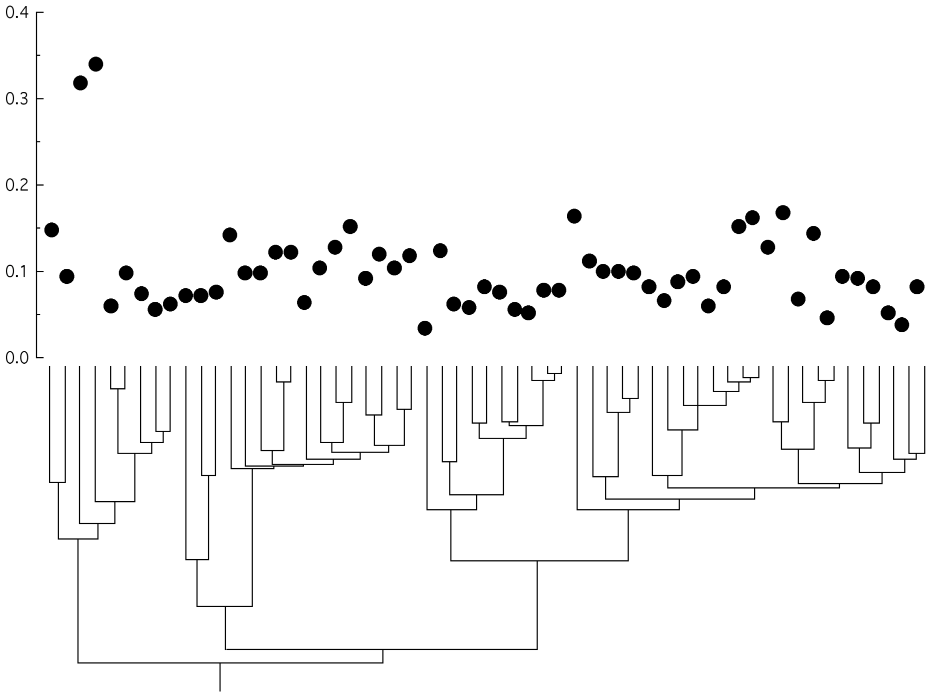

Fig. 6.16.—Patterns of univariate character variation in size-corrected dominant frequency (DF/SVL) across the preferred phylogenetic hypothesis (ultrametric tree) following the rejection of a molecular clock. See Figures 1 and 2 for species group/clade identities and text for discussion of character measurement.

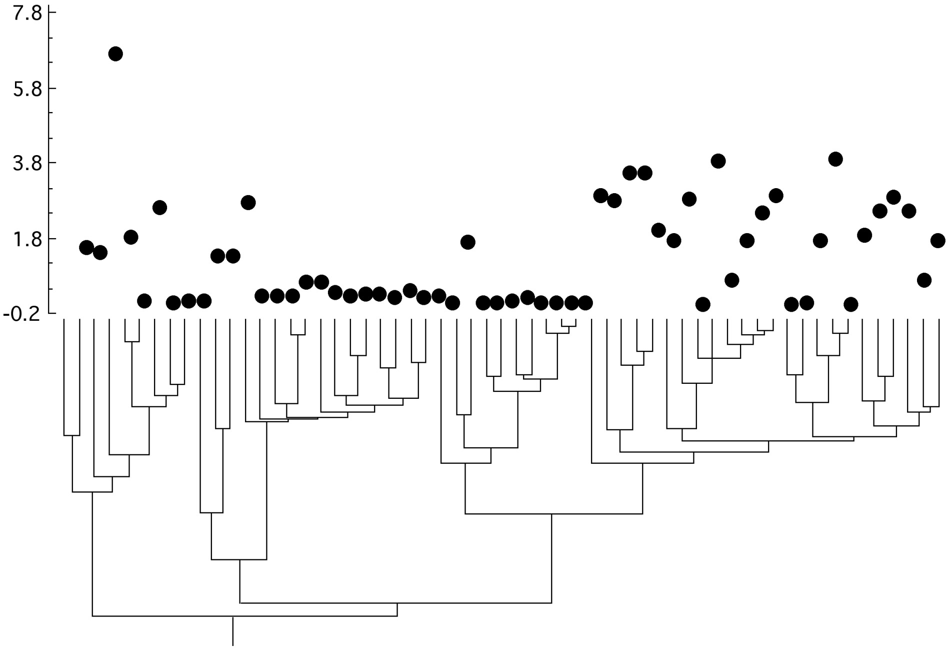

Fig. 6.17.—Patterns of univariate character variation in Call or pulse number/call group length across the preferred phylogenetic hypothesis (ultrametric tree) following the rejection of a molecular clock. See Figures 1 and 2 for species group/clade identities and text for discussion of character measurement.

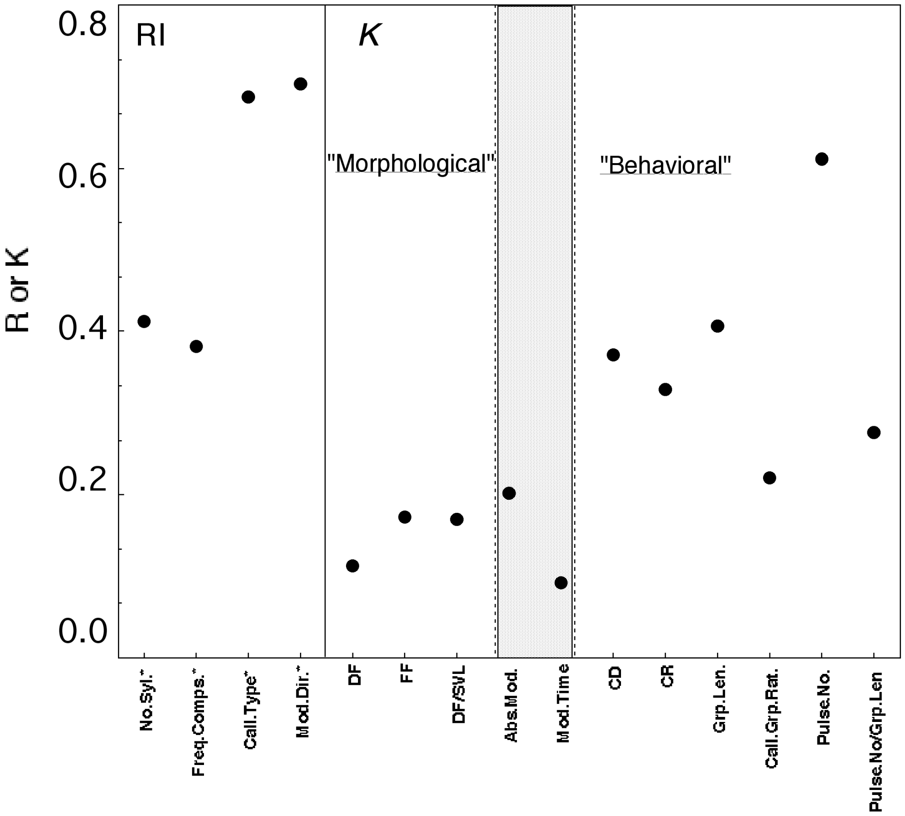

Fig. 6.18.—Retention Index and K scores for four discrete characters and 11 continuous characters. Continuous characters are divided into morphology-related and behavior-related bins and gray panel contains two characters (Abs.Mod. and Mod.Time) of uncertain assignment. See text for discussion.

Appendix: Non-Philippine Specimens Examined

In addition to representatives of all Philippine species (see individual species accounts, Chapter 1), the following non-Philippine taxa were examined and/or measured for morphometric portions of this study.

Shrub frog ecomorphs

P. parkeri.—(10) Solomon Islands, North Solomons, Bougainville Isl., Bougainville Province, Kunua: MCZ-A 36914—22 (Paratypes), 36923 (Holotype).
Platymantis browni.—- (10) New Ireland Island, Weitin River Valley, 8 km N, 7 km W of river mouth, "River Camp" (04.544°S 152.964°E), 150 m above sea level: BPBM 12090, 12099, 12102, 12104, 12106l, 12109, 12113, 12115, 12188, 12191 (Paratypes).

Platymantis browni.—(10) New Ireland Island, Weitin River Valley, 8 km N, 7 km W of river mouth, "River Camp" (04.544°S 152.964°E), 150 m above sea level: BPBM 12090, 12099, 12102, 12104, 12106l, 12109, 12113, 12115, 12188, 12191 (Paratypes).

P. n. sp. "bamboo".—UWZM 23720 (field no. JF 0134; **Holotype**), UWZM 23719 (JF 0133),UWZM 23722 (JF 0131), and UPNG 9992(JF 0132; **Paratypes**), 1503 m above sea level on a ridge between the Ivule and Sigole rivers on the northern edge of the

Nakanai Plateau, (05° 33.112'S, 151° 04.269'E), northern Nakanai Mountains, West New Britain Province, Papua New Guinea, by Johannes Foufopoulos.

Platymantis macrosceles.—(3) Papua New Guinea, New Britain Isl., West New Britain Province, Nakanai Mountains, “Ti”: BPBM 1005 (Holotype); New Britain Isl., Western New Britain Province, Nakanai Mountains, 1500 m above sea level on the ridge between the Ivule and Sigole rivers: UWZM 23721 (Field no. JF 052) and UPNG 10007 (JF 095) collected 14 April, 1999, at 900 m above sea level on the ridge between the Ivule and Sigole Rivers (05°32.3'S, 151°03.1'E), Nakanai Mountains, West New Britain Province.

Small ground frog ecomorphs

P. akarithyma.—(2) Papua New Guinea, Bismarck Archipelago, New Britain Island, West New Britain Province, S coast, ca 14 km NW Pomugu, Kandrian: CAS-SU 22875 (Paratype); Moramora, 3 km N, 7 km E Hoskins: MCZ-A 88823

P. acrochorda.—(15) Solomon Islands, North Solomons, Bougainville Isl., Bougainville Province, Kunua: MCZ-A 38196 (Paratype); Asesi, S. of Kunua MCZ-A 41871–72, 44256–67 (Paratypes).

P. aculeodactyla.—(4) Solomon Islands, Bougainville Isl., Bougainville Province, Kunua: MCZ-A 36961–64.

Medium ground frog ecomorphs

P. mimica.—(3) Papua New Guinea, Bismarck Archipelago, New Britain Island, West New Britain Province, ca 18 mi S of Talasea, Numundo Plantation on Willaumez Peninsula: CAS-SU 22874 (Paratype); Moramora, 3 km N, 7 km E Hoskins: MCZ-A 88826, 89053.

P. rhipiphalca.— (1) Papua New Guinea, Bismarck Archipelago, New Britain Island, West New Britain Province,ca 40 km S of Talasea, San Remo Plantation on Willaumez Peninsula: CAS-SU 22873 (Paratype).

P. macrops.—(4) Solomon Islands, North Solomons, Bougainville Isl., Bougainville Province, Kunua: MCZ-A 38195—96 (Paratypes); Aresi, S. of Kunua: MCZ-A 41864 (Holotype); Matsiogu: MCZ-A 78820.

P. schmidti.—(7) Papua New Guinea, Bismarck Archipelago, New Britain Island, East New Britain Province, Karat, Cherub Plantation: CAS 139651–52; New Ireland, Kanam: TNHC 51392—95; New Ireland, ca. 80 km N of Namatani logging camp: TNHC 51403.

P. papuensis.—(12) Indonesia, Irian Jaya Province, Hollandia: CAS-SU: 8790–91; Lake Sentani: CAS-SU 9709—12; Indonesia, Irian Jaya Province, Madang, Naru Village: TNHC 51544-46; Indonesia, Irian Jaya Province, Madang, Baiteta cave: TNHC 51541, 51978, 51980.

P. weberi.—(19) Solomon Islands, North Solomons, Bougainville Isl., Bougainville Province, Mutahi: CAS 106567–72, 108313–19, 110918–19; MCZ-A 64586–87, 64589–90.

P. gillardi.—(2) Papua New Guinea, Bismarck Archipelago, New Britain Island, West New Britain Province, S coast, ca 7 mi NW Pomugu, Kandrian: CAS-SU 22877–78; Nakanai Mountains: UWZH XXXX-XX (23 uncataloged specimens collected by J. Fofopoulis)

Giant ecomorphs

P. boulengeri.—(4) Papua New Guinea, Bismarck Archipelago, New Britain Island, West New Britain Province, ca 40 km S of Talasea, San Remo Plantation on Willaumez Peninsula: CAS-SU 22876; "New Britain Archipelago": MCZ-A 1729, 9372; Moramora, 3 km N, 7 km E Hoskins: MCZ-A 92711.

P. vitiana.—(8) Fiji, Viti Levu Isls., Viwa Isl., Viwa Village, SW side of island: CAS 172510—-12; Ovalau Isl., 0.5 mi N of Navuloa Village: CAS 172525–29.

P. magna.—(3) Papua New Guinea, New Ireland Isl., New Ireland Province, W. Coast, approx. 88 km S Kavieng: CAS 143639 (Paratype); Utu, 1 km S, 5 km E Kavieng: MCZ-A 92671–72 (Paratypes).

P. solomonis.—(6) Solomon Islands, North Solomons, Bougainville Isl., Bougainville Province, Topanas: CAS 109817; Mutahi: CAS 109825–26; 109829–30, 109840.

P. myersi.—(5) Solomon Islands, Guadalcanal Isl., river E Popomaneseu track: MCZ-A 79068–72.

Wide disked Tree/canopy ecomorphs

P. nexipus.—(1) Central New Britain Isl., West New Britain Province, Baining Mountains, St. Paul's: BPBM 1009 (Holotype).

P. vitiensis.—(13) Fiji, Viti Levu Isls., Viti Levu Isl., Savura Creek Rd., ca 1 km W of Savura Creek: CAS 172437, 172439–40, 172447, 172449–50, 172452–55, 172457; Ovalau Isl., 10 km S, of Levuka, St. John's: CAS 172531–32.

P. neckeri.—(43) Solomon Islands, Bougainville Isl., Bougainville Province: MCZ-A 30145–46 (Paratypes); Bougainville Isl., Kunua: USNM 217441; Melilup: MCZ-A 66853–56, 66849, 66849, 66851–53; Mutahi: MCZ-A 66877–78, 66881–82, 66885–90, 66893; 66926–38; CAS 106451–106458.

P. guppyi.—(38) Solomon Islands, Bougainville Isl., Bougainville Province, Camp Torokina: USNM 120852–53; Kunua: MCZ-A 38628, 38632–33, 38635, 38638–39, 38664–666, 38668, 38674; Melilup: MCZ-A 38629, 38659–60, 38667, 38669–72, 59498–501; Mutahi: CAS 106553–106565.

P. nexipus.—(1) Central New Britain Isl., West New Britain Province, Baining Mountains, St. Paul's: BPBM 1009 (Holotype). Papua New Guinea, New Britain Island, West New Britain Province, Nakanai Mountains: UWZH XXXX-XX (6 uncataloged specimens, collected by J. Fofopoulis.

P. "little nexipus".— Papua New Guinea, New Britain Island, West New Britain Province, Nakanai Mountains: UWZH XXXX-XX (6 uncataloged specimens, collected by J. Fofopoulis.

P. "melodius".— Papua New Guinea, New Britain Island, West New Britain Province, Nakanai Mountains: UWZH XXXX (1 uncataloged specimen, collected by J. Fofopoulis.

Other species for which morphometric data were not available; published literature suggests the following putative ecomorph classifications.

Batrachylodes trossulus (SVL=18.1–20.8 mm)	small ground frog, non-expanded toes
Batrachylodes minutus (16.7–19.3)	small ground frog, non-expanded toes
Batrachylodes mediodiscus (21.7–27.0)	small ground frog, non-expanded toes
Batrachylodes wolfi (25.2–30.6)	shrub frog, widely expanded toes
Batrachylodes vertebralis (24.5–29.5)	shrub frog, widely expanded toes
Batrachylodes gigas (38.6–34.1)	shrub frog, widely expanded toes
Batrachylodes elegans (25.0–32.0)	shrub frog, widely expanded toes
Batrachylodes montanus (27.0–35.0)	shrub frog, widely expanded toes
Discodeles malukuna (48.0–58.3)	aquatic, non-expanded toes with webbing
Discodeles bufoniformes (78.5)	aquatic, non-expanded toes with webbing
Discodeles guppyi (128)	aquatic, non-expanded toes with webbing
Discodeles opisthrodon (103)	aquatic, non-expanded toes with webbing
Discodeles vogti	aquatic, non-expanded toes with webbing
Ceratobatrachus guntheri (65.0)	Giant leaf litter mimic, non-expanded toes

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