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Multilocus phylogeny and a new classification for Southeast Asian and Melanesian forest frogs (family Ceratobatrachidae)

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We present a near comprehensive, densely sampled, multilocus phylogenetic estimate of species relationships within the anuran family Ceratobatrachidae, a morphologically and ecologically diverse group of frogs from the island archipelagos of Southeast Asia and the South-West Pacific. Ceratobatrachid frogs consist of three clades: a small clade of enigmatic, primarily high-elevation, semi-aquatic Sundaland species currently assigned to *Ingerana* (for which we erect a new genus), which is the sister taxon of two large, monophyletic radiations, each situated on islands on either side of Wallace's Line. One radiation is composed of Philippine species of *Platymantis* and the other contains all taxa from the eastern Indonesian, New Guinean, Solomon, Bismarck, and Fijian archipelagos. Several additional genera (*Batrachylodes*, *Discodeles*, *Ceratobatrachus*, and *Palmatorappia*) are nested within *Platymantis*, and of these *Batrachylodes* and *Discodeles* are nonmonophyletic. To address the widespread paraphyly of the genus *Platymantis* and several additional nomenclatural issues, we undertook a wholesale nomenclatural reorganization of the family. Given our partially unresolved phylogeny, and in order to impart a conservative, stable taxonomy, involving a minimal number of genus-species couplet changes, we propose a conservative classification representing a few compromises. These changes are designed to preserve maximally the presumed original intent of taxonomy (widely used group names associated with morphological and ecological diversity of particular species or groups of species) while implementing a hierarchical system that is consistent with the estimate of phylogeny based on new molecular data.

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ADDITIONAL KEYWORDS: admiralty webbed frogs – evolutionary radiation – new genus – New Guinean wrinkled frogs – Philippine forest frogs – phylogenetic taxonomy – Solomon horned frogs – Solomon palm frogs – Solomon sticky-toed frogs – Sundaland mountain frogs – subgenera – taxonomy.

The Cornuferinae have arisen from *Rana* in different parts of its range. They represent a very uniform group. Some of the genera apparently grade into others, making the limits of these groups almost impossible to define. (Noble, 1931: 521).

Platymantis probably evolved within the Philippines in the late Tertiary and subsequently dispersed southwards into New Britain, the Solomon Islands, and Fiji by rafting. The direction of the secondary radiation is a reflection of the demonstrable phylogenetic affinities of the extant species. (Tyler, 1979: 78–79).

The Philippine fauna includes lineages with clear Papuan affinities, *Platymantis* and *Oreophryne*. The presence of these

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two genera in the Philippines (but not in Palawan) may date from either pre-Tertiary or Oligocene. . .when the eastern Philippines-Halmahera arc was closest to New Guinea and the Melanesian Islands. (Inger, 1999: 462).

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).

Rather than think of *Platymantis* as territory that you need to 'divide up' why not just see how much you can achieve together in collaboration? [W. C. Brown (deceased), 1998, personal communication with R. M. B.].

INTRODUCTION

The frog family Ceratobatrachidae (currently *Platymantis*, *Batrachylodes*, *Discodeles*, *Ceratobatrachus*, *Palmatorappia*, and portions of the genus *Ingerana*) is a remarkable assemblage of amphibians distributed throughout the Philippines, Palau, eastern Indonesia, New Guinea, the Solomon–Bismarck–Admiralty archipelagos, and the islands of Fiji (Brown, 1952; Zweifel, 1960, 1969; Brown & Tyler, 1968; Edgar & Lilley, 1993; Allison, 1996; Brown, 1997; Günther, 1999; Alcala & Brown, 1999; Inger, 1999; Tyler, 1999). Ceratobatrachids are noted for conspicuous characteristics of morphology (Boulenger, 1886, 1887; Brown, 1952; Norris, 2002), larval direct development (Alcala, 1962; Brown & Alcala, 1982), including unique structures and patterns of embryonic growth (Thibaudeau & Altig, 1999; Narayan *et al*., 2011), and the ability to colonize habitats that otherwise conspicuously lack ranoid frogs (small, arid islands, dry limestone habitats, and high-elevation mossy rain forests with no standing water; Menzies, 2006; Pikacha, Morrison & Richards, 2008). This ability to persist and reproduce in environments lacking standing fresh water has been hypothesized to represent a key innovation that has facilitated dispersal and colonization across the South-West Pacific, and in the literature this life-history trait is associated with the presence of *Platymantis* on distant oceanic islands such as Palau (Crombie & Pregill, 1999) and Fiji (Gorham, 1965, 1968; Tyler, 1979; Ryan, 1984; Gibbons, 1985; Kuramoto, 1985, 1997; Ota & Matsui, 1995; Narayan, Christi & Morley, 2008; Zug, 2013).

Whatever the combination of developmental, life history, ecological characteristics or history, and circumstances of colonization that led to the diversification of ceratobatrachid frogs in Southeast Asia and the South-West Pacific, the systematic relationships and patterns of insular distributions of this group are of interest to biogeographers (Noble, 1931; Tyler, 1979; Inger, 1999). No other group of amphibians comes close to exhibiting a similar distribution pattern with near-equivalent species diversity on either side of Wallace's Line (Brown, 1952, 1997; Tyler, 1979, 1999; Inger, 1999; Fig. 1). Furthermore, this radiation is unique in having such an appreciable portion of its diversity on distant islands of the South-West Pacific (Allison, 1996; Brown, 1997; Inger, 1999).

Recent interest in species diversity of Philippine ceratobatrachids has resulted in a sharp increase in descriptions of new species (Brown, Brown & Alcala, 1997a; Brown *et al*., 1997b, 1999a; Brown, Alcala & Diesmos, 1997c, 1999b; Alcala & Brown, 1998, 1999; Brown, 2007; Brown & Gonzalez, 2007; Siler *et al*., 2007, 2009, 2010)

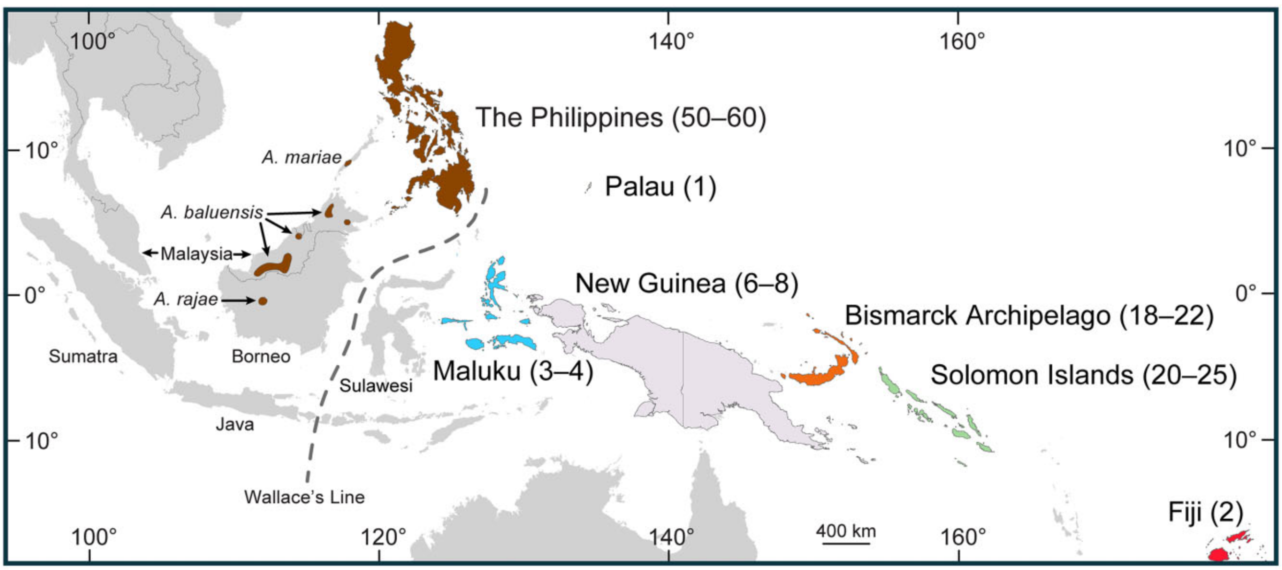


Figure 1. Distribution of the frog family Ceratobatrachidae. Numbers of species per major region are included in parentheses.

and 35–40 new species await description (Brown, 2004, 2009; Brown, Diesmos & Alcala, 2008; Brown *et al*., 2013a). Known Melanesian ceratobatrachid diversity has increased as well, with new species described from mainland New Guinea (Günther, 1999, 2006), New Ireland (Brown & Menzies, 1979; Allison & Kraus, 2001), Manus (Richards, Mack & Austin, 2007; Kraus & Allison, 2009; Richards, Oliver & Brown, 2014), New Britain (Foufopoulos & Brown, 2004; Brown, Foufopoulos & Richards, 2006; Brown *et al*., 2006; Kraus & Allison, 2007, 2009; Brown, Richards & Broadhead, 2013), and the Solomon Islands (Brown & Richards, 2008).

To date, *Platymantis* (*sensu lato*) lacks an explicit phylogenetic definition (*sensu* de Queiroz & Gauthier, 1990). Based on limited taxon sampling, *Platymantis* is clearly paraphyletic with respect to the morphologically derived non-*Platymantis* genera (Bossuyt *et al*., 2006; Wiens *et al*., 2009). Because of their considerable species diversity (approximately 90 species; AmphibiaWeb, 2014), their curious distribution (Noble, 1931; Brown, 1952, 1997; Tyler, 1979, 1999), their striking array of morphological variation (Boulenger, 1884, 1918a; Günther, 1859; Brown, 1952; Gorham, 1965; Brown *et al*., 1997a; Norris, 2002), and complex taxonomic history (Boulenger, 1918b; Brown, 1952; Dubois, 1981, 1987, 1992; Inger, 1996; Frost, 2014), we undertook a phylogenetic analysis of the family, which has only been represented in previous systematic studies by few species and sequences.

This study includes most *Platymantis* species diversity from both sides of Wallace's Line (i.e. the Philippines vs. Solomon–Bismarck–Admiralty archipelagos; Fig. 1), representatives of the other four ceratobatrachid genera (*Ceratobatrachus*, *Palmatorappia*, *Batrachylodes*, and *Discodeles*; AmphibiaWeb, 2014; Frost, 2014), a few species of Southeast Asian *Ingerana* (= *Micrixalus* of earlier authors; Inger, 1954, 1966; Inger & Tan, 1996a, b; now known to be allied to Ceratobatrachidae: Bossuyt *et al*., 2006), and representative ranid outgroups from Asia and Papuan faunal regions (Wiens *et al*., 2009; Blackburn & Wake, 2011). Here we provide a phylogenetic estimate of relationships amongst the frogs of the family Ceratobatrachidae (species of the genera *Platymantis*, *Palmatorappia*, *Ceratobatrachus*, *Discodeles*, *Batrachylodes*, and some members of the genus *Ingerana*) with particular attention to the monophyly and validity of the genera *Platymantis* and *Cornufer*. We also address long-standing nomenclatural problems with respect to generic taxonomy, and provide a new comprehensive classification scheme to facilitate future studies.

TAXONOMIC HISTORY OF CERATOBATRACHIDAE

The genus *Platymantis* has one of the most confusing histories and lengthy synonymy of any group of ranoid frogs (Dubois, 1981, 1987, 1992; Ford & Cannatella, 1993; Frost, 2014). The unusual distribution of the Ceratobatrachidae (Fig. 1), coupled with uncertainty about their systematic affinities (Noble, 1931) and a particularly unstable nomenclatural history, has led to the current state in which relationships in the family are poorly understood (Norris, 2002; Brown, 2004; Frost *et al*., 2006; Köhler *et al*., 2008; Pyron & Wiens, 2011). Biologists have indiscriminately referred a century of new species discoveries to the paraphyletic taxon *Platymantis* and, to date, no comprehensive efforts to understand the group's diversity or utilize phylogeny to inform classification have been undertaken. These actions of convenience have compromised attempts to understand the evolutionary relationships of the group (W. C. Brown, pers. comm.) and have prevented the empirical test of hypotheses regarding the biogeography and phylogenetic affinities of this evolutionary radiation (Allison, 1996; W. Brown, 1997; Inger, 1999; R. Brown, 2004; Bossuyt *et al*., 2006). Below, we summarize the taxonomic history of the family to elucidate the nomenclatural issues that need to be addressed in order to implement a new classification (Dubois, 1981, 1987, 1992; Inger, 1996; ICZN, 1999).

The genus *Cornufer* was named by Tschudi (1838) based on a single specimen from an uncertain locality (Zweifel, 1966). In subsequent years approximately 20 species from the Philippines, New Guinea, New Britain, New Ireland, the Solomons, and the Fijis were described and assigned to *Cornufer*, *Halophila*, and *Hylodes* on the basis of osteological and external morphological characters (Peters, 1863; Boulenger, 1886, 1918a; Taylor, 1920, 1922a, b, 1923, 1925; Schmidt, 1932; Parker, 1939, 1940; Brown, 1949, 1952; Gorham, 1965). Meanwhile, several similar species were assigned to the genus *Platymantis* (Günther, 1859), differing from species of the genus *Cornufer* primarily on the basis of narrowly or non-expanded terminal toe discs. Advocates of the validity of both *Cornufer* (wide discs) and *Platymantis* (narrow discs) included Boulenger (1918b), Barbour (1923), Van Kampen (1923; who recognized *Cornufer* and *Rana*, with the subgenus *Platymantis*), Noble (1931), Mertens (1934), Brown & Myers (1949), Brown (1952), and Gorham (1965). Inger (1954) considered the range of morphological variation in the two genera to be a natural continuum of variation between the two extreme states of wide vs. narrowly expanded finger and toe discs. He proposed synonymizing *Platymantis* with *Cornufer*, and thus rendering species with both wide and narrow terminal finger and toe discs members of a single genus, *Platymantis*, a change followed by Alcala (1962) and most others (but see Gorham, 1965).

Later, when it was determined that the type species of *Cornufer* was in fact a Neotropical frog in the genus *Eleutherodactylus*, Zweifel (1966) proposed to the ICZN that the name *Cornufer* be suppressed (Anonymous, 1978); Zweifel (1967) summarized his reasoning and used *Platymantis* in subsequent publications (Zweifel, 1969, 1975). However, the ICZN committee failed to rule on Zweifel's proposal for nearly ten years (Anonymous, 1978), and when it did, ruled against Zweifel's proposition, which left *Cornufer* an available name, unknown to the systematics community (Anonymous, 1978; ICZN, 1999). For the following 35 years, systematists have referred all Southeast Asian and Melanesian forest frogs to *Platymantis*, of which *Cornufer* was considered a subjective synonym of *Platymantis* (Dubois, 1981; Frost, 1985, 2014).

The lengthy literature debate surrounding this taxonomic confusion discouraged investigators (notably Zweifel, 1967; Gorham, 1965; both assumed *Cornufer* was unavailable) from coining a new generic name for species with wide discs to distinguish them from the species with narrow discs. This appears to have been an admirable attempt to avoid further taxonomic instability but, as noted by Dubois (1981: 248): '. . .this is a case where purely nomenclatural reasons have imposed upon systematists a unanimity which purely taxonomic arguments had not allowed them to reach' (translation from original French by M. Berson, California Academy of Sciences).

MATERIAL AND METHODS

Taxon sampling

We conducted fieldwork in the Philippines, eastern Indonesia, the Admiralty Islands and Bismarck Archipelago of Papua New Guinea, and the Solomon Islands. This sampling was augmented by contributions of tissues from these same areas, plus Palau, Borneo, and Fiji (see Specimens examined and Acknowledgements). Frogs were captured by hand, over-anaesthetized in chlorobutanol (KU IACUC no. 158-01), and dissected for liver and muscle; tissues were preserved by immersion in liquid nitrogen, 95% ethanol, high-salt dimethyl sulphoxide tissue preservation buffer, or RNA*later* (Life Technologies). Specimens were fixed in buffered 10% formalin and stored in 70% ethanol. Voucher specimens are deposited in collections at the National Museum of the Philippines (PNM), The Cincinnati Museum of Natural History (CMNH), Louisiana State University Museum of Natural Science (LSUMZ), the Texas Natural History Collections of the University of Texas at Austin (TNHC), the United States National Museum of Natural History (USNM), The Field Museum of Natural History (FMNH), the South Australian Museum (SAMA) the Western Australian Museum (WAM), the Bishop Museum (BPBM), and the University of Kansas Biodiversity Institute (KU).

Data collection

We extracted total genomic DNA from liver or muscle samples with a Qiagen DNeasy kit or Fujita's Guanidine Thyocyanate protocol (Esselstyn *et al*., 2008). Ingroup sampling included 120 individuals representing the diversity of the family Ceratobatrachidae, including members of all six currently recognized genera (*Batrachylodes*, *Ceratobatrachus*, *Discodeles*, *Ingerana*, *Palmatorappia*, and *Platymantis*). Fifteen species were included as outgroup taxa, representing a broad spectrum of anuran diversity amongst the families Dicroglossidae (*Ingerana*, *Limnonectes*, and *Hoplobatrachus*), Microhylidae (*Kaloula*), and Ranidae (*Amolops*, *Huia*, *Hylarana*, and *Rana*) (Fig. 2; Appendix 1). Data for *Ingerana tenasserimensis* were downloaded from GenBank (accession nos: DQ347030, AY322308). Each extraction was amplified for the genes of interest (Table 1) through standard PCR protocols (Palumbi, 1996).

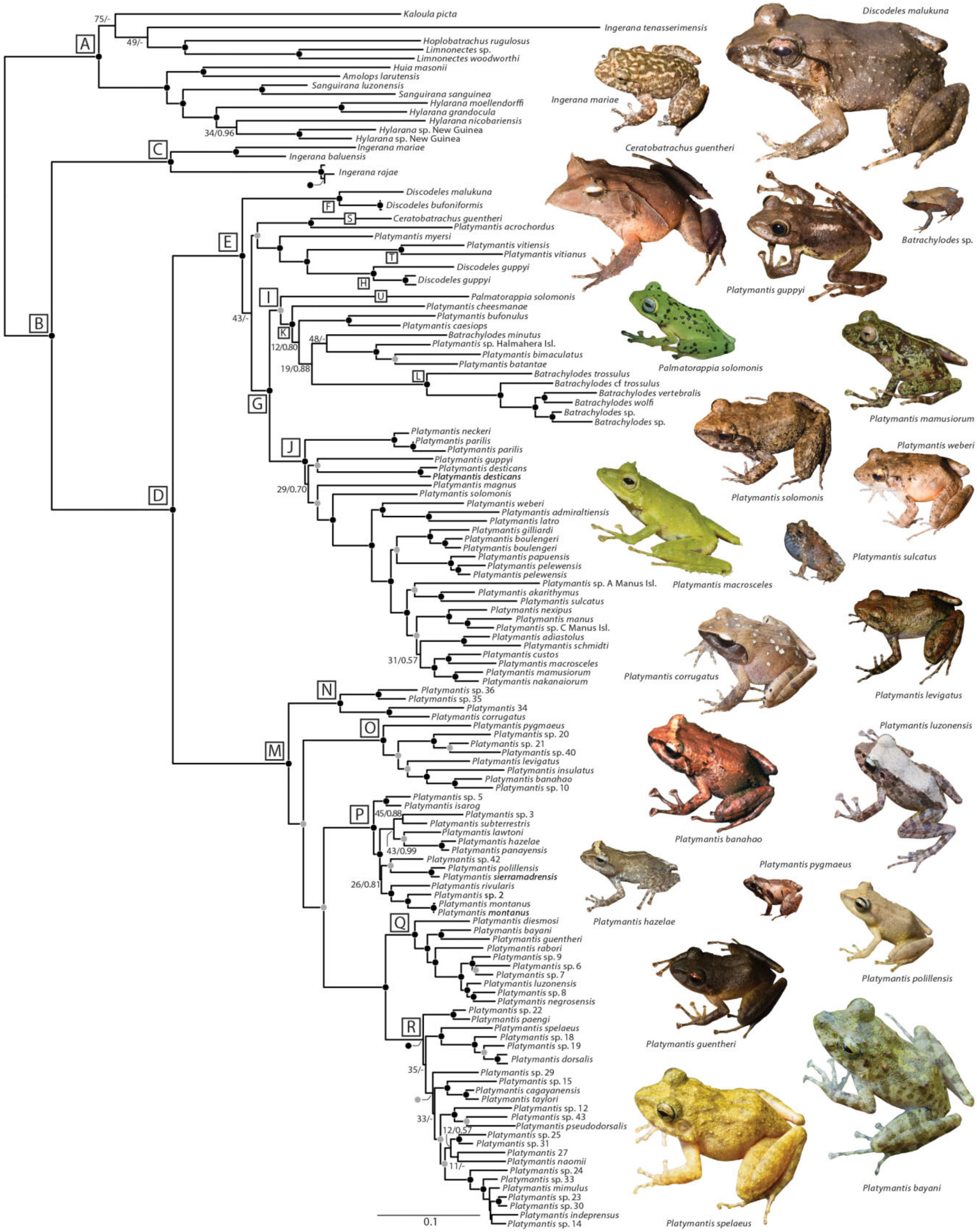
We targeted a ~2500-bp region of the 12S + $tRNA^{Val}$ and 16S rRNA mitochondrial gene fragments using various primers adopted or modified from published studies (Goebel, Donnelly & Atz, 1999; Evans *et al*., 2003; Darst & Cannatella, 2004; Hillis & Wilcox, 2005; Table 1) in eight pairs to amplify segments via PCR; however, not all amplifications were successful. Additionally, we sequenced portions of three nuclear loci: recombinase activating gene 1 (RAG1; ~750 bp), tyrosinase (Tyr; ~535-bp portion of exon 1), and proopiomelanocortin (POMC; ~580 bp), using the primers and protocols of Wiens *et al*. (2005) and Bossuyt *et al*. (2006) (Appendix 2). The nuclear genes were sampled for a subset of taxa for which mtDNA sequence was obtained.

We purified PCR product with QIAquick Gel Extractions or used ExoSAPit (USB Corp.) with a 20% dilution of stock ExoSAPit, incubated for 30 min at 37 °C and then 80 °C for 15 min. 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.

Cleaned PCR products were dye-labelled using BigDye terminator 3.1 (Applied Biosystems), purified using Sephadex (NC9406038, Amersham Biosciences, Piscataway, NJ), and sequenced on an ABI 3100 or 3730*xl* automated capillary sequencer (Applied Biosystems Inc.). Raw sequence data were processed using SEQUENCING ANALYSIS software (Applied Biosystems). Individual sequence chromatograms were examined in SEQUENCHER v. 4.3 (GeneCodes) and individual single-stranded fragments were assembled into contiguous consensus reads, after checking for sequencing error, for subsequent analysis.

Alignment and phylogenetic analysis

Initial alignments were produced in MUSCLE (Edgar, 2004) and minor manual adjustments were made in



75/-
49/-
A
B
C
D
E
F
G
H
I
J
K
L
M
N
O
P
Q
R
S
T
U
Kaloula picta
Ingerana tenasserimensis
Hoplobatrachus rugulosus
Limnonectes sp.
Limnonectes woodworthi
Huia masonii
Amolops larutensis
Sanguirana luzonensis
Sanguirana sanguinea
Hylarana moellendorffi
Hylarana grandocula
Hylarana nicobariensis
34/0.96
Hylarana sp. New Guinea
Hylarana sp. New Guinea
Ingerana mariae
Ingerana baluensis
Ingerana rajae
Discodeles malukuna
Discodeles bufoniformis
Ceratobatrachus guentheri
Platymantis acrochordus
Platymantis myersi
Platymantis vitiensis
Platymantis vitianus
Discodeles guppyi
Discodeles guppyi
43/-
Palmatorappia solomonis
Platymantis cheesmanae
Platymantis bufonulus
Platymantis caesiops
48/-
Batrachylodes minutus
12/0.80
Platymantis sp. Halmahera Isl.
Platymantis bimaculatus
19/0.88
Platymantis batantae
Batrachylodes trossulus
Batrachylodes cf trossulus
Batrachylodes vertebralis
Batrachylodes wolfi
Batrachylodes sp.
Batrachylodes sp.
Platymantis neckeri
Platymantis parilis
Platymantis parilis
Platymantis guppyi
Platymantis desticans
Platymantis desticans
29/0.70
Platymantis magnus
Platymantis solomonis
Platymantis weberi
Platymantis admiraltiensis
Platymantis latro
Platymantis gilliardi
Platymantis boulengeri
Platymantis boulengeri
Platymantis papuensis
Platymantis pelewensis
Platymantis pelewensis
Platymantis sp. A Manus Isl.
Platymantis akarithymus
Platymantis sulcatus
Platymantis nexipus
Platymantis manus
Platymantis sp. C Manus Isl.
Platymantis adiastolus
Platymantis schmidti
31/0.57
Platymantis custos
Platymantis macrosceles
Platymantis mamusiorum
Platymantis nakanaiorum
Platymantis sp. 36
Platymantis sp. 35
Platymantis 34
Platymantis corrugatus
Platymantis pygmaeus
Platymantis sp. 20
Platymantis sp. 21
Platymantis sp. 40
Platymantis levigatus
Platymantis insulatus
Platymantis banahao
Platymantis sp. 10
Platymantis sp. 5
Platymantis isarog
45/0.88
Platymantis sp. 3
Platymantis subterrestris
Platymantis lawtoni
Platymantis hazelae
43/0.99
Platymantis panayensis
Platymantis sp. 42
Platymantis polillensis
Platymantis sierramadrensis
26/0.81
Platymantis rivularis
Platymantis sp. 2
Platymantis montanus
Platymantis montanus
Platymantis diesmosi
Platymantis bayani
Platymantis guentheri
Platymantis rabori
Platymantis sp. 9
Platymantis sp. 6
Platymantis sp. 7
Platymantis luzonensis
Platymantis sp. 8
Platymantis negrosensis
Platymantis sp. 22
Platymantis paengi
Platymantis spelaeus
Platymantis sp. 18
Platymantis sp. 19
Platymantis dorsalis
35/-
Platymantis sp. 29
Platymantis sp. 15
Platymantis cagayanensis
Platymantis taylori
33/-
Platymantis sp. 12
Platymantis sp. 43
Platymantis pseudodorsalis
12/0.57
Platymantis sp. 25
Platymantis sp. 31
Platymantis 27
Platymantis naomii
11/-
Platymantis sp. 24
Platymantis sp. 33
Platymantis mimulus
Platymantis sp. 23
Platymantis sp. 30
Platymantis indeprensus
Platymantis sp. 14
0.1
Discodeles malukuna
Ingerana mariae
Ceratobatrachus guentheri
Batrachylodes sp.
Platymantis guppyi
Palmatorappia solomonis
Platymantis mamusiorum
Platymantis weberi
Platymantis solomonis
Platymantis sulcatus
Platymantis macrosceles
Platymantis corrugatus
Platymantis levigatus
Platymantis luzonensis
Platymantis banahao
Platymantis pygmaeus
Platymantis hazelae
Platymantis polillensis
Platymantis guentheri
Platymantis bayani
Platymantis spelaeus

Figure 2. Molecular phylogenetic estimate of major ceratobatrachid relationships based on maximum likelihood analysis of two mitochondrial gene partitions (12S–16S) and three nuclear genes (proopiomelanocortin, recombinase activating gene 1, and tyrosinase; 11-partition model: Table 2). Maximum likelihood bootstrap and Bayesian posterior probability values are included. Boxed letters denoting selected nodes of interest are discussed in the text. Node B is Ceratobatrachidae. As illustrated, the tree is unrooted, and to save space the outgroups (Node A) are shown as if they form a clade, which they do not. The root of the tree lies on the branch between *Kaloula* and all other taxa. Photographs of selected species are included (approximately to scale), with current taxonomy summarized at tree tips (compare with revised taxonomy, summarized in Fig. 3). Nodal support: black dots ≥ 0.95 and ≥ 70 maximum likelihood bootstrap support (MLBS); grey dots ≥ 0.75, posterior probabilities (PP) ≤ 0.95, and ≥ 50 MLBS ≤ 70. Support values provided (as MLBS/PP) for weakly supported nodes and nodes with disparate levels of support between analyses.

Table 1. Oligonucleotide primer sequences used in this study

Locus	Primer name	Sequence: 5′–3′	Citation
tRNA^{Val}–16S	MVZ59	ATAGCACTGAAAAYGCTDAGATG	Goebel *et al*. (1999)
	tRNA^{Val}	GGTGTAAGCGAGAGGCTT	Darst & Cannatella (2004)
	12L1	AAAAAGCTTCAAACTGGGATTAGATACCCCACTAT	Hillis & Wilcox (2005)
	16Sa	ATGTTTTTGGTAAACAGGCG	Hillis & Wilcox (2005)
	12Sm	GGCAAGTCGTAACATGGTAAG	Hillis & Wilcox (2005)
	16Sh	GCTAGACCATKATGCAAAAGGTA	Hillis & Wilcox (2005)
	16Sc	GTRGGCCTAAAAGCAGCCAC	Darst & Cannatella (2004); Hillis & Wilcox (2005)
	16Sd	CTCCGGTCTGAACTCAGATCACGTAG	Darst & Cannatella (2004)
POMC	POMC-1	GAATGTATYAAAGMMTGCAAGATGGWCCT	Wiens *et al*. (2005, 2009)
	POMC-2	TAYTGRCCCTTYTTGTGGGCRTT	Wiens *et al*. 2005, 2009)
	POMC-3	TCTGCMGARTCWCCYGTGTTTCC	Wiens *et al*. (2005, 2009
	POMC-4	TGGCATTYTTGAAAAGAGTCAT	Wiens *et al*. (2005, 2009)
RAG1	Amp-RAG1 F	AGCTGCAGYCARTACCAYAARATGTA	Mauro *et al*. (2004)
	RAG1-R	GCAAAGTTTCCGTTCATTCTCAT	Fu, Weadick & Bi (2007)
Tyr	Tyr1A	AGGTCCTCTTRAGCAAGGAATG	Bossuyt & Milinkovitch (2000); Bossuyt *et al*. (2006)
	Tyr1B	AGGTCCTCYTRAGGAAGGAATG	Bossuyt & Milinkovitch (2000); Bossuyt *et al*. (2006)
	Tyr1C	GGCAGAGGAWCRTGCCAAGATGT	Bossuyt & Milinkovitch (2000); Bossuyt *et al*. (2006)
	Tyr1D	TCCTCCGTGGGCACCCARTTCCC	Bossuyt & Milinkovitch (2000); Bossuyt *et al*. (2006)

POMC, proopiomelanocortin; RAG1, recombinase activating gene 1.

MacClade v. 4.08 (Maddison & Maddison, 2000). For mitochondrial gene regions, we defined ambiguously aligned regions as character sets using MacClade and excluded regions of uncertain positional homologies from further analyses after determining that doing so yielded no difference in tree topology and unappreciable changes in nonparametric bootstrap values for parsimony searches (not shown).

Preliminary analyses exploring the impact of missing data on inferred outgroup relationships resulted in similar relationships inferred with and without the inclusion of individual nuclear data partitions. To assess effects of missing data, preliminary analyses of individual genes and combinations of gene partitions were conducted. We found that relationships recovered amongst clades N, O, P, and Q (Fig. 2) varied between the nuclear genes and mtDNA only. MrBayes analysis of the nuclear genes yielded only the topology (O,(N,P),(Q,R)). The nodes supporting these relationships had posterior probabilities (PP) = 1, except for the clade O + N + P, which was 0.98. By contrast, analysis of the mtDNA resulted in (O,((N,P),(Q,R))); for all nodes the PP = 1.0. Thus, the nuclear and mtDNA trees are strongly incongruent (Supporting Information Fig. S1). Because of this incongruence the combined tree (Fig. 2) lacks support for the relationships amongst N, O, P, and Q + R; essentially these four clades form a polytomy. However, this does not affect our taxonomy because we did not name any nodes with PP < 0.98. The individual clades M, N, O, P, Q, and R are also each supported by PP > 0.98.

Therefore, we chose to include all data in a concatenated data set. However, we urge careful consideration of incongruence between these partitions before the phylogeny is used for biogeographical inference or comparative analyses. Our final concatenated matrix (deposited in Dryad at: doi:10.5061/dryad.4fd0k) consisted of 4416 nucleotide positions with variable numbers of taxa sequenced for 12S (*N* = 52), 16S (128), RAG1 (102), Tyr (98), and POMC (76).

Partitioned Bayesian analyses were conducted in MrBayes v. 3.2.1 (Huelsenbeck & Ronquist, 2001; Ronquist & Huelsenbeck, 2003). All nuclear gene data sets were partitioned by codon position for protein-coding regions, and the mitochondrial genes 12S-tRNA^{Val} and 16S were each treated as individual partitions, for a total of 11 sequence partitions (Table 2). The Akaike information criterion (AIC), as implemented in jModeltest v. 2.1.4 (Guindon & Gascuel, 2003; Darriba *et al*., 2012), was used to select the best model of nucleotide substitution for each partition (Table 2). We set the *ratepr* (rate multiplier) parameter to 'variable' to allow substitution rates to vary amongst subsets, and set a dirichlet process prior (1,1,1,1) on the state frequency parameter. Default priors were used for all other model parameters. We ran four independent Markov chain Monte Carlo analyses, each with four Metropolis-coupled chains, an incremental heating temperature of 0.02, and an exponential distribution with a rate parameter of 25 as the prior on branch lengths. All analyses were run for 15 000 000 generations, with parameters and topologies sampled every 3000 generations. We assessed stationarity with TRACER v. 1.4 (Rambaut & Drummond, 2007) and confirmed convergence with AWTY (Wilgenbusch, Warren & Swofford, 2004; Nylander *et al*., 2007). We conservatively discarded the first 20% of samples as burn-in, resulting in a total of 4000 topologies from the posterior distribution for each of four runs.

Partitioned maximum likelihood (ML) analyses were conducted in RAxMLHPC v. 7.0 (Stamatakis, 2006) on the concatenated data set using the same partitioning strategy and sets of deleted characters as the Bayesian analysis. The General Time Reversible model with variable sites modeled according to the Gamma distribution was selected via AIC and used for all subsets (Table 2), with ML analyses performed using the rapid hill-climbing algorithm (Stamatakis *et al*., 2007). Each inference was initiated with a random starting tree and nodal support was assessed with 1000 bootstrap pseudoreplicates employing the rapid hill-climbing algorithm (Stamatakis, Hoover & Rougemont, 2008). All new sequences were deposited in GenBank (Appendix 1).

Table 2. Models of evolution selected by Akaike information criterion (AIC; as implemented in jModeltest) and those applied in partitioned, model-based, analyses of mitochondrial (12S, 16S, tRNA^{Val}) and nuclear [proopiomelanocortin (POMC), recombinase activating gene 1 (RAG1), tyrosinase (Tyr)] data

Partition	AIC model	Number of characters
12S + tRNA^{Val}	GTR + Γ*	1624
16S	GTR + Γ	909
POMC, first codon position	GTR + Γ	196
POMC, second codon position	GTR + Γ	196
POMC, third codon position	HKY + Γ	196
RAG1, first codon position	HKY + Γ	251
RAG1, second codon position	GTR + Γ	251
RAG1, third codon position	GTR + Γ	251
Tyr, first codon position	GTR + Γ	178
Tyr, second codon position	GTR + Γ	178
Tyr, third codon position	JC	178

*GTR + Γ, General Time Reversible Model with variable sites modeled according to the Gamma distribution; JC, Jukes-Cantor.

RESULTS

Taxon sampling and phylogenetic analyses

The aligned matrix contains 135 samples (Appendix 1). Similar to other high-level phylogenetic studies (Wiens *et al*., 2009; Pyron & Wiens, 2011) Ceratobatrachidae was found to be monophyletic, except for some species of *Ingerrana* (see below). To economize on space we present the tree (Fig. 2) as if it were rooted between the outgroup and ingroup. The numbers of variable characters are: 996 of 1632 (12S); 627 of 909 (16S); 246 of 588 (POMC); 233 of 534 (Tyr); 187 of 753 (RAG1).

With a few exceptions, all analyses result in topologies with moderate to high ML bootstrap support (MLBS) and PP amongst species and major clades within the family Ceratobatrachidae (Fig. 2). General topological patterns amongst the major clades of outgroup species are congruent with published studies (Bossuyt *et al*., 2006; Frost *et al*., 2006; Wiens *et al*., 2009; Pyron & Wiens, 2011) and are not discussed further. Inferred relationships from Bayesian and ML analyses were broadly similar; however, a few differences were observed. The sample of *Ingerana tenasserimensis*, the type species of *Ingerana*, was recovered by all analyses as part of a clade of outgroup samples (Clade A) with strong support (MLBS = 100; PP = 0.98; Supporting Information Fig. S1). No analyses support the monophyly of *Ingerana* as currently defined (Fig. 2), and *Ingerana mariae*, *Ingerana baluensis*, and *Ingerana rajae* were recovered as a well-supported clade that is the sister group of all remaining ceratobatrachid taxa (Clade C). Amongst ingroup samples (Clade B), all analyses recovered three primary clades with high support (Clades C, E, M). Apart from *Ingerana* (Clade C), the remaining ceratobatrachids were recovered as part of two clades (Clades E, M). The first is composed of members of *Discodeles*, *Ceratobatrachus*, *Palmatorappia*, *Batrachylodes*, and Melanesian species of *Platymantis* (Clade E). A large, well-supported clade of Philippine *Platymantis* (Clade M) is the sister group of Clade E.

Focusing solely on strongly supported clades within the Philippine and non-Philippine ceratobatrachids (excluding *Ingerana*), several relationships are noteworthy: (1) species of *Discodeles* are not recovered as a clade; *Discodeles malukuna* and *Discodeles bufoniformis* are supported as the sister group of all other non-Philippine taxa in Clade E, whereas *Discodeles guppyi* is nested within a group of Pacific species of *Platymantis* (Clades F and H); (2) Bayesian analyses support the monophyly of the genus *Batrachylodes*, albeit with weak support for the inclusion of *Batrachylodes minutus* as the sister taxon of all other sampled members of the genus (PP = 0.69; Supporting Information Fig. S1), whereas ML analyses recover a clade of *Batrachylodes* to the exclusion of *B. minutus* (Clade L), with the placement of *B. minutus* weakly supported (MLBS = 48); (3) the majority of Pacific species of the genus *Platymantis* are inferred to be members of a single clade (Clade J); and (4) within the well-supported Philippine radiation (Clade M), all analyses support five major clades (Clades N–R).

A NEW CLASSIFICATION OF THE FAMILY CERATOBATRACHIDAE

Overview

Our phylogenetic analyses and those of others (Bossuyt *et al*., 2006; Frost *et al*., 2006; Wiens *et al*., 2009; Pyron & Wiens, 2011) unequivocally support two large clades (Clades E and M) that are together the sister group of the new genus described below (including Sundaland and Palawan Island species formerly assigned to *Ingerana*). Given that these two clades are phylogenetically and biogeographically well circumscribed (one is endemic to the Philippines, west of Wallace's Line; and the other is widely distributed east of Wallace's Line throughout eastern Indonesia, New Guinea, Palau, the Bismarcks, Admiralty archipelagos, Solomon Islands, and Fiji), we assign to them the available generic names *Platymantis* (with restricted content, see below), and *Cornufer* (with expanded content, see below), together within a new unranked clade, which we define and name below. Our recognition of three genera, *Alcalus*, *Cornufer*, and *Platymantis*, rather than an extensive splitting of Ceratobatrachidae into numerous genera, also maintains a desirable degree of stability of content of *Platymantis*.

New taxa and allocation of species to existing supraspecific names

We present parallel ranked and phylogenetic taxonomies. Whereas traditional ranked taxonomy is agnostic with respect to phylogenetic relationships and focuses on the content or the concept of the taxon, phylogenetic taxonomies associate a name with a clade and are based on phylogenetic trees (de Queiroz & Gauthier, 1990, 1992, 1994). The phylogenetic definitions of taxon names follow the general recommendations of the draft PhyloCode versions 4c and 5a1 (Cantino & de Queiroz, 2014); we provide traditional diagnoses for most of the same names following the requirements of the ICZN so that these will be available in the sense of the ICZN (1999).

Some explanation of terms is needed; these are taken from Cantino & de Queiroz (2014, particularly Article 9.3 and the Glossary). A specifier is a species, specimen, or apomorphy that serves as a reference point to specify a clade of interest; here we use type species as specifiers. A crown clade is a node-based clade that originates with the last common ancestor of two or more extant species (or organisms); crown clades are delimited by extant and not extinct taxa, although a crown clade may include extinct taxa. A node-based clade originates with a particular node on a tree, rather than a branch (stem). By contrast, a branch-based (stem-based) clade originates with a specific branch. A branch-based clade might include fossils as the most basal branches.

Maximum crown-clade definitions are formed as 'the largest crown clade containing A but not Z' or the crown clade originating in the most recent common ancestor of A and all extant organisms or species that share a more recent common ancestor with A than with Z (or X, or Y, as needed), where A is an extant internal specifier and Z is an external specifier (Article 9.9, Cantino & de Queiroz, 2014). In other words, it is the most inclusive crown clade including A but not Z (and other specifiers as needed). Maximum crown-clade definitions are particularly useful when basal relationships are not well resolved and when it is desirable to include newly discovered species under the existing taxon name, rather than proposing a new clade name or redefining the clade name to include the new species that lie outside of the clade. By contrast, if one wishes to stabilize the content of a taxon (say Ceratobatrachidae) such that the concept of Ceratobatrachidae is not expanded to include a newly discovered sister group, then a node-based definition of Ceratobatrachidae is preferable.

Converted clade names (CCNs) are also defined using phylogenetic conventions. New clade names (NCNs) are newly coined names. All unranked phylogenetic names are italicized. We have generally used type species as specifiers in phylogenetic definitions. The taxonomic authority (author and date) for ranked taxon names is included in Table 3. The authors and date for all NCNs are considered to be Brown, Siler, Richards, Diesmos, and Cannatella 2014.

In some cases we have coined NCNs to refer to the same group denoted by existing ranked names, rather than convert (in the sense of the PhyloCode) the ranked name to a clade name. We have done this to avoid converting names that imply a rank because under the PhyloCode suffixes such as -idae or -ini do not indicate rank. Note that the Phylocode neither encourages nor discourages the use of ranks.

For example, Ceratobatrachidae has been variously ranked as a subfamily (Bossuyt *et al*., 2006), a family (Boulenger, 1884), or a tribe (Dubois, 1992). If Ceratobatrachidae were converted to a clade name, and if in the future Ceratobatrachidae were treated as the subfamily Ceratobatrachinae, then the clade name *Ceratobatrachidae* and the ranked subfamily name Ceratobatrachinae would refer to the same clade, causing confusion.

For phylogenetic definitions of *Alcalus*, *Cornufer*, and *Platymantis* we use maximum crown-clade definitions because the relationships of these taxa to each other are well supported. Similarly we have used maximum crown-clade definitions for those subclades of *Platymantis* that are strongly supported. However, relationships amongst the subclades within *Cornufer* are weakly supported in places, and several species are not assigned to a named subclade of *Cornufer*. For genera that typically have been named based on apomorphies we use apomorphy-based names to restrict the content of these clades to species that possess these apomorphies. An example is *Discodeles*, which is unique amongst ceratobatrachids in having extensively webbed feet.

CERATOBATRACHIDAE BOULENGER, 1884

Type genus
Ceratobatrachus Boulenger, 1884.

Diagnosis
Frogs of the family Ceratobatrachidae differ from their close relatives by the possession of (1) direct development; and (2) T-shaped terminal phalanges with associated expanded finger and toe discs.

Phylogenetic definition
Ceratobatrachia (NCN) is a node-based name that refers to the clade arising from the most recent common ancestor of *Alcalus mariae* (type species of *Alcalus*), *Cornufer vitiensis* (type species of *Cornufer*), and *Platymantis pliciferus* (type species of *Platymantis*; currently a junior synonym of *Platymantis corrugatus*).

Content
The genera *Alcalus* (three or four species), *Cornufer* (58 species), and *Platymantis* (31 described species).

Comment
We define *Ceratobatrachia* using a node-based definition, rather than a maximum crown-clade definition, because the closest relative of *Ceratobatrachia* (= Ceratobatrachidae) from amongst the ranoids is not clear (e.g. Bossuyt *et al*., 2006; Pyron & Wiens, 2011). The node-based name ensures that future use of the *Ceratobatrachia* refers to the same node, regardless of whether that node name is Ceratobatrachidae or Ceratobatrachinae; i.e. its use is independent of any particular ranked taxonomy. We have not converted the ranked name Ceratobatrachidae to a phylogenetic name, but rather we have named *Ceratobatrachia* to avoid confusion between the homonymous ranked name and converted clade name.

We apply the ranked name Ceratobatrachidae (Fig. 2, Clade B) to the node usually identified as Ceratobatrachidae or Ceratobatrachinae. Several family-group names are available for clades within the Ceratobatrachidae, including Cornuferinae Noble 1931, Ceratobatrachinae Boulenger, 1884, and Platymantinae Laurent, 1986. Ceratobatrachidae Boulenger, 1884, is not nomenclaturally problematic. Cornuferinae was named by Noble (1931) to include the genera *Batrachylodes*, *Ceratobatrachus*, *Cornufer*, *Discodeles*, *Hylarana*, *Micrixalus*, *Palmatorappia*, *Platymantis*, and *Staurois* (including *Simomantis*). Savage (1973: 354) later coined Platymantinae as a subfamily of Ranidae. However, he did not explicitly provide a list of characters that diagnose the taxon as required by the International Code of Zoological Nomenclature (ICZN 1999; hereafter, the Code). Thus, the name Platymantinae Savage, 1973, is not available (Article 13.1; ICZN, 1999) and is a *nomen nudum*. Laurent (1986) diagnosed the same taxon and made the name available as Platymantinae Laurent, 1986. Dubois (1992) listed Cornuferinae Noble, 1931 and Platymantini Laurent, 1986, as junior synonyms of Ceratobatrachidae Boulenger, 1884.

By contrast, Frost (2014) listed Cornuferinae Noble, 1931, as a synonym of Eleutherodactylidae Lutz, 1954, stating 'synonymy by implication of synonymy of *Cornufer* with *Eleutherodactylus* by Zweifel (1966).' The nomenclatural history of *Cornufer* is discussed in detail under the *Cornufer* account, but relevant to the issue is that the International Commission on Zoological

Table 3. Classification of the family Ceratobatrachidae based on phylogenetic estimate from two mitochondrial gene fragments (12S + $tRNA^{Val}$, 16S) and three nuclear genes (proopiomelanocortin, recombinase activating gene 1, and tyrosinase). Taxa marked with an asterisk (*) were not included in the phylogenetic analysis; some of these were assigned to clades on the basis of phenotypic similarity and presumed close phylogenetic affinity; taxa marked with a dagger (†) are extinct.

Node	Original designation (author, date)	Previous generic placement	Current generic placement	Subgenus	Clade name	Species	Notes
C		*Ingerana*	*Alcalus* gen. nov.		*Alcalus*		
	Ingerana mariae Inger, 1954	*Ingerana*	*Alcalus*	none	none	*mariae*	
	Cornufer baluensis Boulenger, 1896	*Ingerana*	*Alcalus*	none	none	*baluensis*	
	Rana sariba Shelford, 1905	*Ingerana*	*Alcalus*	none	none	*sariba**	
	Ingerana rajae Iskandar, Bickford & Arifin	*Ingerana*	*Alcalus*	none	none	*rajae*	
E			*Cornufer*		*Cornufer*		
F	*Rana bufoniformis* Boulenger, 1884	*Discodeles*	*Cornufer*	*Potamorana* subgen. nov.	*Potamorana* new clade name	*bufoniformis* comb. nov.	New combination
	Discodeles malukuna Brown & Webster, 1969	*Discodeles*	*Cornufer*	*Potamorana*	*Potamorana*	*malukuna* comb. nov.	New combination
	Rana opisthodon Boulenger, 1884	*Discodeles*	*Cornufer*	*Potamorana*	*Potamorana*	*opisthodon* comb. nov.*	New combination
	Rana vogti Hediger, 1934 (replacement name for *Rana ventricosus* Vogt, 1912)	*Discodeles*	*Cornufer*	*Potamorana*	*Potamorana*	*vogti* comb. nov.*	New combination
T	*Halophila vitiensis* Girard, 1853	*Platymantis*	*Cornufer*	*Cornufer*	*Yanuboto* new clade name	*vitiensis*	Transferred to *Cornufer*, type species for genus *Cornufer*
	Hylodes vitianus Duméril, 1853	*Platymantis*	*Cornufer*	*Cornufer*	*Cornufer*	*vitianus*	Transferred to *Cornufer*
	Platymantis megabotoniviti† Worthy, 2001	*Platymantis*	*Cornufer*	*Cornufer*	*Cornufer*	*megabotoniviti*†*	Transferred to *Cornufer*
S	*Ceratobatrachus guentheri* Boulenger, 1884	*Ceratobatrachus*	*Cornufer*	*Ceratobatrachus*	*Ceratobatrachus*	*guentheri* comb. nov.	New combination
H	*Cornufer guppyi* Boulenger, 1884	*Discodeles*	*Cornufer*	*Discodeles*	*Discodeles*	*guppyi* comb. nov.	New combination
U	*Hylella solomonis* Sternfeld, 1920 (syn. *Hypsirana heffernani* Kinghorn, 1928)	*Palmatorappia*	*Cornufer*	*Palmatorappia*	*Palmatorappia*	*heffernani* comb. nov.	New combination, resurrection of *Co. heffernani* as a substitute name for *solomonis* (see text)
L	*Batrachylodes elegans* Brown & Parker, 1970	*Batrachylodes*	*Cornufer*	*Batrachylodes*	*Batrachylodes*	*elegans* comb. nov.*	New combination
	Batrachylodes gigas Brown & Parker, 1970	*Batrachylodes*	*Cornufer*	*Batrachylodes*	*Batrachylodes*	*gigas* comb. nov.*	New combination
	Batrachylodes mediodiscus Brown & Parker, 1970	*Batrachylodes*	*Cornufer*	*Batrachylodes*	*Batrachylodes*	*mediodiscus* comb. nov.	New combination
	Batrachylodes montanus Brown & Parker, 1970	*Batrachylodes*	*Cornufer*	*Batrachylodes*	*Batrachylodes*	*montanus* comb. nov.*	New combination
	Batrachylodes montanus Brown & Myers, 1949	*Batrachylodes*	*Cornufer*	*Batrachylodes*	*Batrachylodes*	*trossulus* comb. nov.	New combination
	Batrachylodes vertebralis Boulenger, 1887	*Batrachylodes*	*Cornufer*	*Batrachylodes*	*Batrachylodes*	*vertebralis* comb. nov.	New combination
	Sphenophryne wolfi Sternfeld, 1920	*Batrachylodes*	*Cornufer*	*Batrachylodes*	*Batrachylodes*	*wolfi* comb. nov.	New combination
J	*Platymantis adiastolus* Brown, Richards, Sukumaran & Foufopoulos, 2006	*Platymantis*	*Cornufer*	*Aenigmanura* subgen. nov.	*Aenigmanura* new clade name	*adiastolus* comb. nov.	New combination
	Platymantis admiraltiensis Richards, Mack & Austin, 2007	*Platymantis*	*Cornufer*	*Aenigmanura*	*Aenigmanura*	*admiraltiensis* comb. nov.*	New combination
	Platymantis akarithymus Brown & Tyler, 1968	*Platymantis*	*Cornufer*	*Aenigmanura*	*Aenigmanura*	*akarithymus* comb. nov.	New combination
	Platymantis boulengeri	*Platymantis*	*Cornufer*	*Aenigmanura*	*Aenigmanura*	*boulengeri*	Transferred to *Cornufer*
	Platymantis citrinospilus Brown, Richards & Broadhead, 2013	*Platymantis*	*Cornufer*	*Aenigmanura*	*Aenigmanura*	*citrinospilus* comb. nov.	New combination
	Platymantis custos Richards, Oliver & Brown, 2014	*Platymantis*	*Cornufer*	*Aenigmanura*	*Aenigmanura*	*custos* comb. nov.	New combination
	Platymantis desticans Brown & Richards, 2008	*Platymantis*	*Cornufer*	*Aenigmanura*	*Aenigmanura*	*desticans* comb. nov..	New combination
	Platymantis gilliardi Zweifel, 1960	*Platymantis*	*Cornufer*	*Aenigmanura*	*Aenigmanura*	*gilliardi*	Transferred to *Cornufer*
	Platymantis guppyi Boulenger, 1884	*Platymantis*	*Cornufer*	*Aenigmanura*	*Aenigmanura*	*hedigeri*	Transferred to *Cornufer, nomen novum* for *Co. guppyi* (see text)
	Platymantis latro Richards, Mack & Austin, 2007	*Platymantis*	*Cornufer*	*Aenigmanura*	*Aenigmanura*	*latro* comb. nov.	New combination
	Cornufer macrops Brown, 1965	*Platymantis*	*Cornufer*	*Aenigmanura*	*Aenigmanura*	*macrops*	Transferred to *Cornufer*

Table 3. *Continued*

Node	Original designation (author, date)	Previous generic placement	Current generic placement	Subgenus	Clade name	Species	Notes
	Platymantis macrosceles Zweifel, 1975	*Platymantis*	*Cornufer*	*Aenigmanura*	*Aenigmanura*	*macrosceles* comb. nov.	New combination
	Platymantis magnus Brown & Menzies, 1979	*Platymantis*	*Cornufer*	*Aenigmanura*	*Aenigmanura*	*magnus* comb. nov.	New combination
	Platymantis mamusiorum Brown & Foufopoulos, 2004	*Platymantis*	*Cornufer*	*Aenigmanura*	*Aenigmanura*	*mamusiorum* comb. nov.	New combination
	Platymantis nakanaiorum Brown, Foufopoulos & Richards, 2006	*Platymantis*	*Cornufer*	*Aenigmanura*	*Aenigmanura*	*nakanaiorum* comb. nov.	New combination
	Platymantis neckeri Brown & Myers, 1949	*Platymantis*	*Cornufer*	*Aenigmanura*	*Aenigmanura*	*neckeri*	Transferred to *Cornufer*
	Platymantis nexipus Zweifel, 1975	*Platymantis*	*Cornufer*	*Aenigmanura*	*Aenigmanura*	*nexipus*	Transferred to *Cornufer*
	Platymantis corrugatus var. *papuensis* Myer, 1875 ('1874')	*Platymantis*	*Cornufer*	*Aenigmanura*	*Aenigmanura*	*papuensis*	Transferred to *Cornufer*
	Platymantis parilis Brown & Richards, 2008	*Platymantis*	*Cornufer*	*Aenigmanura*	*Aenigmanura*	*parilis* comb. nov.	New combination
	Platymantis pelewensis Peters, 1867	*Platymantis*	*Cornufer*	*Aenigmanura*	*Aenigmanura*	*pelewensis*	Transferred to *Cornufer*
	Platymantis papuensis schmidti Brown & Tyler, 1968	*Platymantis*	*Cornufer*	*Aenigmanura*	*Aenigmanura*	*schmidti* comb. nov.	New combination
	Cornufer solomonis Boulenger, 1884	*Platymantis*	*Cornufer*	*Aenigmanura*	*Aenigmanura*	*solomonis*	Transferred to *Cornufer*
	Platymantis sulcatus Kraus & Allison, 2007	*Platymantis*	*Cornufer*	*Aenigmanura*	*Aenigmanura*	*sulcatus* comb. nov.	New combination
	Platymantis weberi Schmidt, 1932	*Platymantis*	*Cornufer*	*Aenigmanura*	*Aenigmanura*	*weberi*	Transferred to *Cornufer*
	Platymantis acrochordus Brown, 1965	*Platymantis*	*Cornufer*	Not assigned to subgenus	*Cornufer*	*acrochordus*	Transferred to *Cornufer*
	Platymantis aculeodactylus Brown, 1952	*Platymantis*	*Cornufer*	Not assigned to subgenus	*Cornufer*	*aculeodactylus**	Transferred to *Cornufer*
	Platymantis batantae Brown & Zweifel, 1969	*Platymantis*	*Cornufer*	Not assigned to subgenus	*Cornufer*	*batantae* comb. nov.	New combination
	Platymantis bimaculatus Günther, 1999	*Platymantis*	*Cornufer*	Not assigned to subgenus	*Cornufer*	*bimaculatus* comb. nov.	New combination
	Platymantis browni Allison & Kraus, 2001	*Platymantis*	*Cornufer*	Not assigned to subgenus	*Cornufer*	*browni* comb. nov.*	New combination
	Platymantis bufonulus Kraus & Allison, 2007	*Platymantis*	*Cornufer*	Not assigned to subgenus	*Cornufer*	*bufonulus* comb. nov..	New combination
	Platymantis caesiops Kraus & Allison, 2009	*Platymantis*	*Cornufer*	Not assigned to subgenus	*Cornufer*	*caesiops* comb. nov.	New combination
	Platymantis cheesmanae Parker, 1940	*Platymantis*	*Cornufer*	Not assigned to subgenus	*Cornufer*	*cheesmanae*	Transferred to *Cornufer*
	Platymantis cryptotis Günther, 1999	*Platymantis*	*Cornufer*	Not assigned to subgenus	*Cornufer*	*cryptotis* comb. nov.*	New combination
	Platymantis manus Kraus & Allison, 2009	*Platymantis*	*Cornufer*	Not assigned to subgenus	*Cornufer*	*manus* comb. nov.	New combination
	Platymantis mimicus Brown & Tyler, 1968	*Platymantis*	*Cornufer*	Not assigned to subgenus	*Cornufer*	*mimicus* comb. nov.	New combination
	Batrachylodes minutus Brown & Parker, 1970	*Platymantis*	*Cornufer*	Not assigned to subgenus	*Cornufer*	*minutus* comb. nov.	Removed from *Batrachylodes*, new combination
	Platymantis myersi Brown, 1949	*Platymantis*	*Cornufer*	Not assigned to subgenus	*Cornufer*	*myersi*	Transferred to *Cornufer*
	Cornufer parkeri Brown, 1965	*Platymantis*	*Cornufer*	Not assigned to subgenus	*Cornufer*	*parkeri*	Transferred to *Cornufer*
	Platymantis punctatus Peters & Doria, 1878	*Platymantis*	*Cornufer*	Not assigned to subgenus	*Cornufer*	*punctatus*	Transferred to *Cornufer*
	Platymantis wuenscheorum Günther, 2006	*Platymantis*	*Cornufer*	Not assigned to subgenus	*Cornufer*	*wuenscheorum* comb. nov.	New combination
M		*Platymantis*	*Platymantis*		*Platymantis*		

Table 3. *Continued*

Node	Original designation (author, date)	Previous generic placement	Current generic placement	Subgenus	Clade name	Species	Notes
N	*Platymantis corrugatus* Duméril, 1853	*Platymantis*	*Platymantis*	*Platymantis*	*Tagomukhus* new clade name	*corrugatus* (syn. *Pl. plicifera* Guenther, 1854)	*P. plicifera* (syn *P. corrugatus*) is the type species for genus *Platymantis*
O	*Platymantis banahao* Brown, Alcala, Diesmos & Alcala, 1975b	*Platymantis*	*Platymantis*	*Lahatnanguri* subgen. nov.	*Lahatnanguri* new clade name	*banahao*	
	Platymantis biak Siler, Diemsos, Linkem, Diesmos & Brown, 2010	*Platymantis*	*Platymantis*	*Lahatnanguri* subgen. nov.	*Lahatnanguri* new clade name	*biak**	
	Cornufer cornutus Taylor, 1922	*Platymantis*	*Platymantis*	*Lahatnanguri*	*Lahatnanguri*	*cornutus*	
	Platymantis insulates Brown & Alcala, 1970	*Platymantis*	*Platymantis*	*Lahatnanguri*	*Lahatnanguri*	*insulatus*	
	Platymantis levigatus Brown & Alcala, 1974	*Platymantis*	*Platymantis*	*Lahatnanguri*	*Lahatnanguri*	*levigatus*	
	Platymantis pygmaeus Brown, Alcala & Diesmos, 1988	*Platymantis*	*Platymantis*	*Lahatnanguri*	*Lahatnanguri*	*pygmaeus*	
P	*Philautus hazelae* Taylor, 1920	*Platymantis*	*Platymantis*	*Tirahanulap* subgen. nov.	*Tirahanulap* new clade name	*hazelae*	
	Platymantis isarog Brown, Brown, Alcala & Frost (replacement name for *Platymantis reticulatus* Brown, Brown & Alcala, 1997a)	*Platymantis*	*Platymantis*	*Tirahanulap*	*Tirahanulap*	*isarog*	
	Platymantis lawtoni Brown & Alcala, 1974	*Platymantis*	*Platymantis*	*Tirahanulap*	*Tirahanulap*	*lawtoni*	
	Cornufer montanus Taylor, 1922	*Platymantis*	*Platymantis*	*Tirahanulap*	*Tirahanulap*	*montanus*	
	Platymantis panayensis Brown, Brown & Alcala, 1997	*Platymantis*	*Platymantis*	*Tirahanulap*	*Tirahanulap*	*panayensis*	
	Philautus polillensis Taylor, 1922	*Platymantis*	*Platymantis*	*Tirahanulap*	*Tirahanulap*	*polillensis*	
	Platymantis sierramadrensis Brown, Alcala, Ong, & Diesmos, 1999	*Platymantis*	*Platymantis*	*Tirahanulap*	*Tirahanulap*	*sierramadrensis*	
	Cornufer subterrestris Taylor, 1922	*Platymantis*	*Platymantis*	*Tirahanulap*	*Tirahanulap*	*subterrestris*	
Q	*Platymantis bayani* Siler, Alcala, Diesmos & Brown, 2008	*Platymantis*	*Platymantis*	*Tahananpuno* subgen. nov.	*Tahananpuno* new clade name	*bayani*	
	Platymantis diesmosi Brown & Gonzalez, 2007	*Platymantis*	*Platymantis*	*Tahananpuno*	*Tahananpuno*	*diesmosi*	
	Cornufer guentheri Boulenger, 1882	*Platymantis*	*Platymantis*	*Tahananpuno*	*Tahananpuno*	*guentheri*	
	Platymantis luzonensis Brown, Alcala, Diesmos & Alcala, 1997	*Platymantis*	*Platymantis*	*Tahananpuno*	*Tahananpuno*	*luzonensis*	
	Platymantis negrosensis Brown, Alcala, Diesmos & Alcala, 1997	*Platymantis*	*Platymantis*	*Tahananpuno*	*Tahananpuno*	*negrosensis*	
	Platymantis rabori Brown, Alcala, Diesmos & Alcala, 1997	*Platymantis*	*Platymantis*	*Tahananpuno*	*Tahananpuno*	*rabori*	
R	*Platymantis cagayanensis* Brown, Alcala & Diemsos, 1999	*Platymantis*	*Platymantis*	*Lupacolus* subgen. nov.	*Lupacolus* new clade name	*cagayanensis*	
	Cornufer dorsalis Duméril, 1853	*Platymantis*	*Platymantis*	*Lupacolus*	*Lupacolus*	*dorsalis*	
	Platymantis indeprensus cagayanensis Brown, Alcala & Diemsos, 1999	*Platymantis*	*Platymantis*	*Lupacolus*	*Lupacolus*	*indeprensus*	
	Platymantis mimulus Brown, Alcala & Diemsos, 1997	*Platymantis*	*Platymantis*	*Lupacolus*	*Lupacolus*	*mimulus*	
	Platymantis naomiae Alcala, Brown & Diesmos, 1988	*Platymantis*	*Platymantis*	*Lupacolus*	*Lupacolus*	*naomiae*	
	Platymantis paengi Siler, Linkem, Diesmos & Alcala, 2007	*Platymantis*	*Platymantis*	*Lupacolus*	*Lupacolus*	*paengi*	
	Platymantis pseudodorsalis Brown, Alcala & Diemsos, 1999	*Platymantis*	*Platymantis*	*Lupacolus*	*Lupacolus*	*pseudodorsalis*	
	Platymantis spelaeus Brown & Alcala, 1982	*Platymantis*	*Platymantis*	*Lupacolus*	*Lupacolus*	*spelaeus*	
	Platymantis taylori Brown, Alcala & Diemsos, 1999	*Platymantis*	*Platymantis*	*Lupacolus*	*Lupacolus*	*taylori*	

Nomenclature designated *Halophila vitiensis* Girard, 1853, as the type species of *Cornufer*. As *H. vitiensis* has been placed consistently in either *Platymantis* or *Cornufer* within the Ceratobatrachidae, *Cornufer* and Cornuferinae would not be considered part of Eleutherodactylidae.

ALCALINAE **SUBFAM. NOV.**

Type genus
Alcalus (see account below).

Diagnosis
The diagnosis for Alcalinae is the same as for the genus *Alcalus*, below.

Phylogenetic definition
We have not defined Alcalinae as a phylogenetic name because it would be redundant with *Alcalus*; it adds no new information about phylogenetic relationships. However, we name the ranked subfamily Alcalinae, even though it is also redundant in content with *Alcalus*, to provide a coordinate name for its sister-taxon Ceratobatrachinae.

Content
One genus, *Alcalus*, which includes the species *Al. mariae*, *Al. baluensis*, and *Al. rajae*. We anticipate that *Ingerana sariba* eventually will be transferred to the new genus as well.

Etymology
See Etymology section for the genus *Alcalus* below.

ALCALUS **GEN. NOV.**

Type species
Micrixalus mariae Inger 1954.

Diagnosis
Members of the genus *Alcalus* can be distinguished from many members of the clade *Anurajen* (species of the genera *Cornufer* and *Platymantis*) by having (1) an intermediate body size (*Al. baluensis*: males 20–25 mm Snout-Vent Length (SVL), females 26–31; *Al. mariae*: males 32–37 mm SVL, females 35–43); (2) a broad head (vs. slender to moderately broad); (3) a coarsely textured, shagreened, or 'wrinkled' skin appearance in all species (vs. smooth, tuberculate, or with longitudinal dorsolateral dermal ridges); (4) widely expanded, terminally squared, spatulate toe discs (vs. non- or minimally expanded, terminally rounded); (5) semi-aquatic microhabitat preferences (vs. preferences for terrestrial or arboreal microhabitats in most species); and by the (6) presence of nuptial pads in males (vs. absence); (7) absence of vocal sacs (vs. presence of median subgular vocal sacs); (8) absence of supernumerary tubercles on hand (vs. presence in most species); (9) presence of elongate subarticular tubercles (vs. presence, round); (10) absence of outer metatarsal tubercles on plantar surface of feet (vs. presence in most species); and (11) presence of extensive, usually full, interdigital webbing of the feet (vs. absence).

Phylogenetic definition
Alcalus (NCN) is a maximum crown-clade name that refers to the crown clade (C) originating in the last common ancestor of *Al. mariae* and all extant species that share a more recent common ancestor with *Al. mariae* than with *Cornufer vitiensis* or *Platymantis corrugatus*. It can also be conceived of as the largest crown clade containing *Al. mariae*, but not *Co. vitiensis* or *Pl. corrugatus*.

Content
Southeast Asian (Sunda Shelf and Palawan Island) species formerly placed in *Ingerana* (Table 3): *Al. mariae*, *Al. baluensis*, *Al. rajae*, and presumably *Al. sariba* (Shelford, 1905), which was not sampled (Table 3).

Comment
It is not surprising that the montane, semi-aquatic, Southeast Asian island archipelago species formerly referred to *Ingerana* comprise a monophyletic group, unrelated to the ecologically dissimilar and biogeographically disjunct mainland species of *Ingerana* (as presently understood, from Andaman Islands, Bhutan, China, north eastern India, Myanmar, and Nepal). Erection of a new genus to accommodate these taxa is undertaken here with reference to the phylogenetic placement of the type species of 'true' *Ingerana* (*I. tenasserimensis*), which in our phylogeny is more closely related (but with weak support) to the Dicroglossidae than to the Ceratobatrachidae (Fig. 2). The placement of *Alcalus* as the sister group of the clade *Anurajen* (containing genera *Platymantis* and *Cornufer*) has been confirmed elsewhere (Bossuyt *et al*., 2006; Frost *et al*., 2006; Wiens *et al*., 2009; Pyron & Wiens, 2011), although taxon sampling was not as extensive. The phylogenetic relationships and possible additional generic subdivision of the non-ceratobatrachid (perhaps dicroglossid) species referred to *Ingerana* remain unstudied.

Etymology
A masculine noun honouring our long-term collaborator, friend, and mentor Angel C. Alcala for his numerous contributions to the systematics, ecology, conservation, and developmental biology of Southeast Asian amphibians. Suggested common name: Alcala's dwarf mountain frogs.

CERATOBATRACHINAE BOULENGER, 1884

Diagnosis

Other species of Ceratobatrachinae differ from *Alcalus* by having (1) a relatively narrow head (vs. wide); and (2) smooth skin, with or without dermal tubercles and/or dermal ridges (vs. coarsely textured, shagreened, or 'wrinkled' in appearance); (3) rounded terminal toe discs (vs. spatulate toe discs with squarish terminal shape); (4) absence of nuptial pads in males (vs. presence); (5) presence of a medial subgular vocal sac in most species (vs. absence); (6) presence of palmar supernumerary tubercles (vs. absence); and (7) presence of rounded subarticular tubercles and outer metatarsal tubercles on plantar surface (vs. presence, elongate). Finally, most species of Ceratobatrachinae (except *Cornufer guppyi*, species of the subgenus *Potamorana*, and *Platymantis levigatus*) differ from *Alcalus* by the absence of interdigital webbing on the feet (vs. presence); and by having terrestrial or arboreal microhabitat preferences (vs. semi-aquatic). Morphological synapomorphies for Ceratobatrachinae have not been identified.

Content

The genera *Cornufer* and *Platymantis* (see below).

Comment

We have not converted Ceratobatrachinae (Clade D) to a clade name, but have instead coined a new unranked clade name, *Anurajen*. If Ceratobatrachinae were converted to a clade name, and if the family Ceratobatrachidae (Node B) were re-ranked as Ceratobatrachinae in the future, then the phylogenetic name Ceratobatrachinae and the ranked name Ceratobatrachinae would refer to different clades, which would cause confusion. Therefore, we define a new clade name below denoting the same clade as the subfamily Ceratobatrachinae.

ANURAJEN NEW CLADE NAME

Phylogenetic definition

A maximum crown-clade name referring to the crown clade (D) originating with the most recent common ancestor of *Co. vitiensis* and all extant species that share a more recent common ancestor with *Co. vitiensis* than with *Alcalus mariae*.

Content

Species of *Platymantis* and *Cornufer* (as for Ceratobatrachinae).

Comment

This clade is supported by high bootstrap proportions and posterior probabilities (Fig. 2), and consists of two large subclades (*Platymantis* and *Cornufer*) situated on either side of Wallace's Line (Fig. 1). Ceratobatrachinae is the ranked name equivalent in content to *Anurajen* (Table 4).

Table 4. Comparison of ranked and phylogenetic taxonomies for Ceratobatrachidae

Ranked taxonomy	Phylogenetic taxonomy
Ceratobatrachidae	*Ceratobatrachia* NCN
Alcalinae subfam. nov.	No name needed*
Alcalus new genus	*Alcalus* NCN
Ceratobatrachinae	*Anurajen* NCN
Cornufer	*Cornufer* CCN
Cornufer (subgenus)	*Yanuboto* NCN†
Potamorana new subgenus	*Potamorana* NCN
Ceratobatrachus (subgenus)	*Ceratobatrachus* CCN
Discodeles (subgenus)	*Discodeles* CCN
Palmatorappia (subgenus)	*Palmatorappia* CCN
Batrachylodes (subgenus)	*Batrachylodes* CCN
Aenigmanura new subgenus	*Aenigmanura* NCN
Platymantis	*Platymantis* CCN
Platymantis (subgenus)	*Tagomukhus* NCN†
Lahatnanguri new subgenus	*Lahatnanguri* NCN
Tirahanulap new subgenus	*Tirahanulap* NCN
Tahananpuno new subgenus	*Tahananpuno* NCN
Lupacolus new subgenus	*Lupacolus* NCN

CCN, converted clade name; NCN, new clade name.

*A new phylogenetic name equivalent to the Linnean name Ceratobatrachinae is not necessary as this name would have the same content as the clade (genus) *Alcalus*.

†A NCN is provided to avoid having the same name apply to two different clades, as is the case with the genus and subgenus rank.

Etymology

We are pleased to name the new clade after Jennifer Anne Weghorst in appreciation of the many times that she has arduously proofread our manuscripts and for the devoted support and encouragement that she has provided to R. M. B. for many years. *Anurajen* is derived from the Latin noun *Anura* and the abbreviated appellation *Jen*.

GENUS *PLATYMANTIS* GÜNTHER, 1858

Type species

Platymantis pliciferus Günther, 1858, currently considered a junior subjective synonym of *Pl. corrugatus* (Duméril, 1853); subsequent designation by Zweifel (1967).

Diagnosis

Members of the exclusively Philippine genus *Platymantis* can be distinguished from the three or four known species of *Alcalus* (with the exception of *Al. mariae*, all *Alcalus* occur outside the Philippines) by the (1) absence of interdigital webbing or the presence of highly reduced webbing (vs. presence); (2) presence of median subgular vocal sacs (vs. absence); (3) absence of nuptial pads (vs. presence); (4) presence of supernumerary tubercles on the hands (vs. absence); and (5) presence of metatarsal tubercles on the foot (vs. absence).

Although all Philippine *Platymantis* are readily diagnosed from members of the genus *Alcalus*, and selected species of the genus *Cornufer*, subgenera *Cornufer* (= *Yanuboto*), *Potamorana*, *Discodeles*, *Ceratobatrachus*, *Palmatorappia*, and *Batrachylodes* (see diagnoses of those clades), characters universally distinguishing Philippine *Platymantis* from all members of the genus *Cornufer* (in particular, the subgenus *Aenigmanura* and species formerly referred to '*Platymantis*' from the Solomon–Bismarck–Admiralty Archipelago, Palau, New Guinea, and eastern Indonesia, Table 3; see species not assigned to subgenus) have not been identified. We are unaware of any morphological synapomorphies for *Platymantis*, although our phylogenetic analysis provides very strong support (PP = 1.0) for this clade (Fig. 2, Clade M).

Phylogenetic definition
Platymantis (CCN) is a maximum crown-clade name referring to the crown clade (M) originating with the most recent common ancestor of *Pl. corrugatus* (synonym *Pl. plificerus*, the type species of *Platymantis*) and all extant species that share a more recent common ancestor with *Pl. corrugatus* than with *Al. mariae* or *Co. vitiensis*.

Content
Philippine taxa (currently 31 species) of the subgenera *Platymantis* (*Tagomukhus*, NCN), *Lahatnanguri*, *Tirahanulap*, *Tahananpuno*, and *Lupacolus* (Table 3). Numerous Philippine species await description, suggesting that the content of this genus will expand rapidly in the near future (Siler *et al*., 2007, 2009, 2010, 2011, 2012; Brown *et al*., 2008, 2012, 2013a, 2013b; Brown & Stuart, 2012).

Comment
The content of the genus *Platymantis* Günther, 1858, is hereby restricted to the primary Philippine clade (M) and we apply *Cornufer* Tschudi 1838 to its sister group (Clade E), which includes the type species of the genus *Cornufer*, *Halophila vitiensis* Girard, 1853. Given that the relationships amongst clades O, N, P, Q, and R show some degree of uncertainty, we have used one specifier from each clade to assure that the phylogenetic definition of the name of Clade M will remain stable.

Etymology
From the Greek adjective 'platy', meaning flat and 'mantis'. The meaning of 'mantis' here is confusing; often it is stated that generic names ending in 'mantis' are derived from the Greek noun 'mantis', a term commonly meaning prophet or soothsayer (Liddell & Scott, 1996). However, Günther (1858) specifically stated in his etymology of *Platymantis* that the Greek noun 'mantis' referred to 'tree-frog' rather than soothsayer. 'Mantis' was applied by ancient Greeks to the species *Hyla arborea* (a species perceived to be akin to prophets because it produces advertisement calls prior to the arrival of rain; Liddell & Scott, 1996). Kraus & Allison (2007) resolved previous confusion concerning the gender of *Platymantis*, stemming from Günther's (1858) mistaken use of both masculine and feminine epithets for the two species included in the original definition of the genus, and R. Günther's (1999) assertion that *Platymantis* should be treated as a feminine noun. Günther (1999) stated that 'According to Günther (1858) . . . mantis is Greek, of feminine gender, and means tree frog.' (pp. 327–328), but did not explain his opinion. We follow Kraus & Allison (2007) in considering the gender of *Platymantis* as masculine.

SUBGENUS *PLATYMANTIS* GÜNTHER, 1858

Diagnosis
The subgenus *Platymantis* (currently a single recognized species, *Pl. corrugatus*) differs from other species of *Platymantis* by having (1) elongate longitudinal dermal ridges along the dorsal body surfaces (vs. dorsum smooth or tuberculate); (2) distinctive 'quaaack' advertisement calls (vs. frequency sweeps, pure tones, or complex calls); and (3) distinctive dark lateral head coloration (of varying shades; vs. lateral head pigment undifferentiated from surrounding coloration). The diagnostic dark lateral head coloration forms a dark 'face-mask' that we consider a synapomorphy of this clade. Additionally, members of this subgenus can be diagnosed from species of arboreal variable Philippine forest frogs of the genera *Lahatnanguri* (*Platymantis banahao*, *Pl. cornutus*, and *Pl. insulatus*), and all members of the subgenera *Tahananpuno* and *Tirahanulap*, by the absence of expanded digital tips of fingers and toes (vs. presence of some degree of terminal digital expansion of fingers and toes), and by having a terrestrial microhabitat preference (normally calling beneath leaf litter) and a crepuscular (vs. nocturnal) calling activity pattern (Table 3).

Content
The allopatric populations of (1) the Luzon and West Visayan faunal regions, (2) the Camiguin Norte lineage, (3) the populations from the Mindanao faunal region islands, and (4) the Mindoro Island populations, all currently referred to *Pl. corrugatus* (Table 3). The subgenus *Platymantis* is equivalent in content to the unranked taxon *Tagomukhus*.

Conversion of the name *Platymantis* would result in two different clades, ranked as genus and subgenus, with the same name, *Platymantis*. Therefore we define a NCN, denoting the same clade as subgenus *Platymantis*.

TAGOMUKHUS NEW CLADE NAME

Phylogenetic definition
Tagomukhus (NCN) is a maximum crown-clade name referring to the crown clade (Clade N) originating with the most recent common ancestor of *Pl. corrugatus* and all extant species and populations that share a more recent common ancestor with *Pl. corrugatus* than with *Pl. levigatus*, *Pl. hazelae*, *Pl. guentheri*, or *Pl. dorsalis*.

Content
Platymantis (*Tagomukhus*) *corrugatus* (syn. *P. plicifera*, type species of the genus Platymantis).

Comment
At a minimum, we anticipate that the Luzon (+ W. Visayan) Pleistocene Aggregate Island Complex (PAIC; Brown & Diesmos, 2009; Brown *et al*., 2013a), the Mindanao PAIC, the Mindoro PAIC, and Camiguin Norte Island populations will all eventually be recognized as distinct species (K. Cobb, R.M.B., A.C.D., C.D.S., & A.C. Alcala, unpubl. data). *Platymantis pliciferus*, the type species of the genus, is an available name that applies to the Mindanao PAIC population (Günther, 1859; Peters, 1873), should it be demonstrated to be a diagnosable evolutionary lineage worthy of taxonomic recognition.

Etymology
From the Tagalog adjective *tago*, meaning 'concealed' or 'unseen' and the Tagalog noun *mukha*, meaning 'countenance', in reference to the darkly pigmented facemask present in varying degrees of distinctiveness in most populations. The name is masculine in gender. Suggested common name: Philippine masked frogs.

LAHATNANGURI **SUBGEN. NOV.**

Type species
Platymantis levigatus Brown & Alcala, 1974.

Diagnosis
Individual species of the subgenus *Lahatnanguri* differ from other members of *Platymantis* by characters related to their general classification as arboreal tree frogs (*Pl. banahao*, *Pl. cornutus*, readily distinguished from all Philippine *Platymantis* except members of the subgenus *Tahananpuno*), distinctive mottled-coloured limestone specialist species (*Pl. insulatus*, readily diagnosed from all Philippine *Platymantis* except *Platymantis bayani*, *Platymantis biak*, and *Platymantis speleaus*), miniaturized species (*Platymantis pygmaeus*, SVL 13–15 mm, readily distinguished from all Philippine *Platymantis* except possibly *Platymantis naomiae*), and a unique Romblon Province semi-aquatic species *Pl. levigatus* (vs. all remaining Philippine species terrestrial, scansorial, or arboreal). The wide range of morphological and ecological variation in this clade renders an unambiguously exclusive diagnosis of *Lahatnanguri* impossible. We are unaware of morphological synapomorphies for this group, although our phylogenetic analysis provides very strong support for this clade (Clade O, Fig. 2).

Phylogenetic definition
Lahatnanguri (NCN) is a maximum crown-clade name referring to the crown clade (O) originating with the most recent common ancestor of *Platymantis* (*Lahatnanguri*) *levigatus* and all extant species that share a more recent common ancestor with *Pl. levigatus* than with *Pl. corrugatus*, *Pl. hazelae*, *Pl. guentheri*, or *Pl. dorsalis*.

Content
Platymantis banahao, *Pl. biak*, *Pl. cornutus*, *Pl. insulatus*, *Pl. levigatus*, and *Pl. pygmaeus* (Table 3).

Comment
Several unrecognized terrestrial species eventually will be assigned to the subgenus *Lahatnanguri*, including at least three from Mindanao Island (species 20, 21, and 40), a miniature ground frog from the Romblon Province islands of Sibuyan and Tablas (R. M. Brown, A. C. Diesmos & C. D. Siler, unpubl. data), and at least one arboreal species from Luzon Island (species 10) (Fig. 2). Although some species (*Pl. banahao*, *Pl. insulatus*) of the subgenus *Lahatnanguri* (Clade O) are phenotypically very similar to some species (*Platymantis diesmosi*, *Pl. bayani*, *Pl. guentheri*, *Pl. rabori*, *Pl. negrosensis*) of the subgenus *Tahananpuno* (Fig. 2, Clade Q) and were, in fact, grouped in a nonphylogenetic taxonomy as the *Pl. guentheri* group (Brown *et al*., 1997a, b; Alcala & Brown, 1999), this phenotypic similarity appears to be a case of ecomorphological convergence.

Etymology
From the Tagalog (Filipino) phrase *lahat ng uri*, meaning 'all kinds' or 'every type' in reference to the full range of morphological and ecological variation within this clade, including miniature semifossorial species, large terrestrial ground frogs, semiaquatic species, limestone cave specialists, and high-elevation tree canopy frogs. The name is masculine in gender. Suggested common name: variable Philippine forest frogs.

TIRAHANULAP SUBGEN. NOV.

Type species
Philautus hazelae (Taylor, 1920).

Diagnosis
The morphologically, ecologically, and acoustically similar species of *Tirahanulap* differ from all other subgenera of *Platymantis* by having: (1) widely expanded terminal discs of fingers and toes (vs. non- or minimally expanded): (2) subdigital surfaces relatively flat with low subarticular tubercles (vs. subarticular tubercles prominently rounded to pointed); (3) greatly reduced Finger I (vs. Finger I as long or nearly as long as Finger II); (4) tonal advertisement calls of constant frequency (vs. possession of frequency sweep calls or calls with multiple syllables of different frequencies); (5) small clutch sizes (four to eight eggs vs. clutches typically of 20 or more eggs); and (6) a mid- to upper montane shrub-layer vegetation microhabitat preference (vs. terrestrial, semiaquatic, forest canopy, limestone, or semifossorial). We consider the reduced length of Finger I, and the low, flat subarticular tubercles to be unique synapomorphies for the clade, which is strongly supported in phylogenetic analyses (Fig. 2, Clade P).

Phylogenetic definition
Tirahanulap (NCN) is a maximum crown-clade name referring to the crown clade (Fig. 2, Clade P) originating with the most recent common ancestor of *Platymantis* (*Tirahanulap*) *hazelae* and all extant species that share a more recent common ancestor with *Pl. hazelae* than with *Pl. corrugatus*, *Pl. levigatus*, *Pl. guentheri*, or *Pl. dorsalis*.

Content
Platymantis hazelae, *Pl. isarog*, *Pl. lawtoni*, *Pl. montanus*, *Pl. panayensis*, *Pl. polillensis*, *Pl. sierramadrensis*, and *Pl. subterrestris* (Table 3).

Comment
Species of *Tirahanulap* form a morphologically and ecologically cohesive group that corresponds to the *Pl. hazelae* group of Brown *et al*. (1997a; 1999a) and Alcala & Brown (1999). The members of this clade are ecologically and phenotypically most similar to *Cornufer* (*Palmatorappia*) *heffernani* (formerly *Palmatorappia solomonis*) and the high-elevation shrub frogs of New Britain (*Cornufer macrosceles*, *Cornufer citrinospilus*, and *Cornufer mamusiorum*) and Manus Island (*Cornufer custos*). We are aware of at least four currently unrecognized species in this clade (species 2, 3, 5, and 42; Fig. 2).

Etymology
From the Tagalog verb *tumira*, meaning, when conjugated (‘*tirahan*’), to ‘inhabit’ or ‘reside within’, and the Tagalog noun *ulap*, meaning cloud; together meaning ‘cloud-dwellers’ or ‘they come from the clouds’. The name is masculine in gender. Suggested common name: Philippine cloud frogs.

TAHANANPUNO SUBGEN. NOV.

Type species
Cornufer guentheri Boulenger, 1882.

Diagnosis
Members of this tree canopy specialist clade or Philippine rain frogs, subgenus *Tahananpuno*, differ from other all species of *Platymantis* (except *Pl. banahao*, *Pl. cornutus*, and *Pl. insulatus*, see below) by having (1) widely expanded terminal discs of fingers and toes (vs. non- or minimally expanded in terrestrial species of *Tagomukus* and *Lupacolus*); (2) prominent, rounded to pointed subarticular tubercles (vs. flattened on ventral surfaces in cloud frog species of the subgenus *Tirahanulap*); (3) pulsed advertisement calls (vs. tonal, constant frequency calls of cloud frogs, subgenus *Tirahanulap*; vibrational, stridulated, or complex multisyllable calls of species of terrestrial frogs of the subgenera *Tagomukus* and *Lupacolus*); and (4) understory (*Pl. guentheri*), limestone (*Pl. bayani*), cliff-edge (*Pl. diesmosi*), or canopy vegetation microhabitat preferences (all other *Tahananpuno* species). Although widely expanded terminal discs of fingers and toes appear to be a synapomorphy for this clade, they have evolved independently and diagnose a small subclade of variable Philippine forest frogs only, subgenus *Lahatnanguri* (*Pl. banahao*, *Pl. cornutus*, and *Pl. insulatus*). We are unaware of any unique characters that distinguish species of this new subgenus from other species of *Platymantis*. Nevertheless, our phylogenetic analyses provide strong support for this clade (Fig. 2, Clade Q).

Phylogenetic definition
Tahananpuno (NCN) is a maximum crown-clade name referring to the crown clade (Fig. 2, Clade Q) originating with the most recent common ancestor of *Platymantis* (*Tahananpuno*) *guentheri* and all extant species that share a more recent common ancestor with *Pl. guentheri* than with *Pl. corrugatus*, *Pl. dorsalis*, *Pl. hazelae*, or *Pl. levigatus*.

Content
Platymantis bayani, *Pl. diesmosi*, *Pl. guentheri*, *Pl. luzonensis*, *Pl. negrosensis*, and *Pl. rabori* (Table 3).

Comment
The subgenus *Tahananpuno* corresponds to the readily distinguished *Pl. guentheri* group as defined by Brown *et al*. (1997a, b) and Alcala & Brown (1999).

Interestingly, and in contrast to expectations based on morphology and understory/canopy microhabitat preferences (Brown *et al*., 1997a), *Pl. banahao*, *Pl. cornutus*, and *Pl. insulatus* are not part of this clade (or of the former *Pl. guentheri* group; Brown *et al*., 1997a, b; Alcala & Brown, 1999), but rather fall in Clade O (*Lahatnanguri*). We are aware of at least four additional unrecognized species in this clade (species 6, 7, 8, and 9; Fig. 2).

Etymology
Tahananpuno is a masculine noun, derived from the Tagalog verb *tahanan* meaning 'to dwell upon', or 'to occupy' and noun *puno*, 'tree', in reference to the prevailing microhabitat preference of species in this clade: understory and canopy treefrogs. The name is masculine in gender. Suggested common name: Philippine rain frogs.

LUPACOLUS SUBGEN. NOV.

Type species
Cornufer dorsalis Duméril, 1853.

Diagnosis
Philippine forest ground frogs of the subgenus *Lupacolus* are distinguished from other species of *Platymantis* (except a few species of subgenus *Lahatnanguri*, see below) by having (1) non- to minimally expanded terminal discs of fingers and toes [vs. finger and toe discs expanded in cloud frogs of the subgenus *Tirahanulap*, rain frogs of the genus *Tahananpuno*, and three species of variable forest frogs of the subgenus *Lahatnanguri* (*Pl. banahao*, *Pl. cornutus*, and *Pl. insulatus*)]; (2) prominently rounded to pointed subarticular tubercles (vs. ventrally flattened in cloud frogs of the subgenus *Tirahanulap*); (3) highly variable and often complex multisyllable advertisement calls [vs. tonal, constant frequency calls in cloud frogs of the subgenus *Tirahanulap*, or repeatedly pulsed calls in rain frogs of the subgenus *Tahananpuno* and a few species of variable Philippine forest frogs, subgenus *Lahatnanguri* (*Pl. banahao*, *Pl. cornutus*, and *Pl. insulatus*)]; and (4) a predominantly terrestrial, forest-floor microhabitat preference, with a tendency to call from slightly elevated perches of 0.2–0.5 m [vs. perching in shrub and understory vegetation in cloud frogs, subgenus *Tirahanulap*, and rain frogs, subgenus *Tahananpuno*, and a few species of variable Philippine forest frogs, subgenus *Lahatnanguri* (*Pl. banahao*, *Pl. cornutus*, and *Pl. insulatus*)]. We are unaware of any morphological synapomorphies for this group, but our phylogenetic analysis provides very strong support for this clade (Fig. 2, Clade R).

Phylogenetic definition
Lupacolus (NCN) is a maximum crown-clade name referring to the crown clade (Fig. 2, Clade R) originating with the most recent common ancestor of *Pl. dorsalis* and all extant species that share a more recent common ancestor with *Pl. dorsalis* than with *Pl. corrugatus*, *Pl. hazelae*, *Pl. guentheri*, or *Pl. levigatus*.

Content
Platymantis cagayanensis, *Pl. dorsalis*, *Pl. indeprensus*, *Pl. mimulus*, *Pl. naomiae*, *Pl. paengi*, *Pl. pseudodorsalis*, *Pl. spelaeus*, and *Pl. taylori* (Table 3).

Comment
For the most part, *Lupacolus* corresponds to the *Pl. dorsalis* group of W. Brown *et al*. (1997a, 1999a, b) and Alcala & Brown (1999). This clade of generalized terrestrial ground frogs contains a large percentage of currently unrecognized species (at least 15 small- to medium-sized ground frogs from the northern and central islands of the archipelago, including species 12, 14, 15, 18, 19, 22–25, 27, 29, 30, 31, 33, and 43; Fig. 2), but contrary to predictions from taxonomy (Brown *et al*., 1997a; Alcala & Brown, 1999), does not include the *Pl. corrugatus* clade (*Tagomukhus*) or the morphologically similar terrestrial, species *Pl. pygmaeus* and *Pl. levigatus* (*Lahatnanguri*) (Brown, Brown & Alcala, 1997a; Brown *et al*., 1997b, 1999a; Alcala & Brown, 1999).

Etymology
Lupacolus is derived from the combination of the Tagalog noun *Lupa*, meaning 'ground' or 'terrestrial' and the Greek *colos*, meaning 'inhabitants' or 'dwellers' in reference to the largely terrestrial microhabitat of the included species. It is masculine in gender. Suggested common name: Philippine forest ground frogs.

GENUS *CORNUFER* TSCHUDI, 1838

Type species
Halophila vitiensis Girard, 1853 by subsequent designation, following Opinion 1104 of the Commission (Anonymous, 1978).

Diagnosis
Members of the genus *Cornufer* can be distinguished from species of the genus *Alcalus* by the presence of (1) median subgular vocal sacs (vs. absence); (2) absence of nuptial pads (vs. presence); (3) presence of supernumerary tubercles on hands (vs. absence); (4) presence of metatarsal tubercles beneath feet (vs. absence); and (4) absence or presence but highly reduced of interdigital webbing (vs. presence in species of *Alcalus* and members of *Cornufer*, subgenera *Discodeles* and *Potamorana*).

Although species of *Cornufer*, subgenera *Cornufer*, *Potamorana*, *Ceratobatrachus*, *Discodeles*, *Palmatorappia*, and *Batrachylodes* are phenotypically diagnosable from species of the genera *Alcalus* and *Platymantis* (see diagnoses of those clades), species of *Cornufer* (subgenus *Aenigmanura*) and former members of Solomon–Bismarck–Admiralty, Palau, Papuan, and eastern Indonesian '*Platymantis*' (Table 3; see species not assigned to subgenus) cannot be readily distinguished from species of the genus *Platymantis* on the basis of any one morphological character. We are unaware of any morphological synapomorphies for this clade, although it is strongly supported (Fig. 2, Clade E).

Phylogenetic definition

Cornufer (CCN) is a maximum crown-clade name referring to the crown clade (Fig. 2, Clade E) originating with the most recent common ancestor of *Co. vitiensis* and all extant species that share a more recent common ancestor with *Co. vitiensis* than with *Al. mariae* or *Pl. corrugatus*.

Content

Species of the subgenera (clades) *Potamorana*, *Cornufer*, *Ceratobatrachus*, *Palmatorappia*, *Discodeles*, *Batrachylodes*, *Aenigmanura*, and species of the Pacific (non-Philippine) clade, genus *Cornufer*, formerly referred to '*Platymantis*' and not assigned to subgenus or subclade within *Cornufer* (Fig. 2; Table 3).

Comment

Upon discovering that the overlooked type of *Cornufer* (*Cornufer unicolor* Tschudi, 1838) was in fact a species of the Neotropical taxon *Eleutherodactylus*, Zweifel (1966) petitioned the Commission to suppress the names *Cornufer* and its type species *Cornufer unicolor* Zweifel, 1967, to avoid synonymy of *Eleutherodactylus* within *Cornufer*. His argument was that this discovery would require the assignment of the > 200 species of *Eleutherodactylus* to *Cornufer*. Suppression of *Cornufer* would mean that the next available name for that group of ranoids would, at the time, have been *Platymantis* Günther, 1858.

Darlington *et al*. (1967) countered that *Cornufer* should not be suppressed and that both names, *Cornufer* and *Platymantis*, should be retained as available because *Cornufer* had been widely used for some ranoid species. Additionally, the non-overlapping geographical distributions of *Cornufer* (east of Wallace's Line) and *Platymantis* (west of Wallace's Line) strengthened the argument that both genera should be retained as valid (Darlington *et al*., 1967).

Prior to Zweifel (1966, 1967), *Cornufer* and *Platymantis* were commonly used (Boulenger, 1918b; Taylor, 1920; Noble, 1931; Gorham, 1965; but see Inger, 1954). Although Zweifel (1967: 117) stated that 'the name *Cornufer* is unavailable' (and he was largely followed by working taxonomists), the Commission had not yet ruled on his request (Zweifel, 1966) to suppress this name. A decade later, the Committee ruled against his proposal (Anonymous, 1978) and eventually held that *Halophila vitiensis* Girard, 1853, be designated as the type species of *Cornufer* and that this genus should be considered a junior subjective synonym of *Platymantis*, which '. . .is to be given precedence over *Cornufer* Tschudi, 1838, *by any zoologist who considers the type-species of those nominal genera to belong to the same taxonomic genus* (Anonymous, 1978; italics added).' The Committee also suppressed all previous designations of the type species of *Cornufer*. Importantly, *Cornufer* was not suppressed; both names remain available and may be used either as genera or subgenera.

Given our choice not to place these two type species (*Co. vitiensis* and *Pl. pliciferus*, the latter currently a synonym of *Pl. corrugatus*) in the same genus, and that the name *Cornufer* Tschudi, 1838, remains available (Anonymous, 1978), we recognize both *Platymantis* (west of Wallace's Line, i.e. Philippine species, excluding *Al. mariae*) and *Cornufer* (all species east of Wallace's Line, i.e. taxa from eastern Indonesia, New Guinea, Palau, the Solomon Islands, the Bismarck–Admiralty archipelagos, and Fiji). These names correspond to our newly defined clades (Fig. 2, Clades M and E, respectively).

Because relationships amongst some species of the genus *Cornufer* have low support (Fig. 2), we have used the type species of subgenera as specifiers to ensure that the content of *Cornufer* will remain stable.

Etymology

Although Tschudi (1838) provided no etymology for *Cornufer*, we assume that the name is derived from the Latin 'cornu' meaning horn, and the Latin verb 'ferre' (present infinitive), meaning to carry or bear, in reference to the presence of supraocular dermal tubercles in *Co. vitiensis* (the type species). Suggested common names: Fijian ground frog (*Cornufer vitianus*), Fijian tree frog (*Co. vitiensis*).

SUBGENUS *CORNUFER* TSCHUDI, 1838

Diagnosis

Members of the subgenus *Cornufer* differ from other members of the genus *Cornufer* by having (1) a large male body size (65–150+ mm SVL, vs. male body size usually ~25–40 mm); (2) terminal discs of fingers and toes non- to minimally expanded in *Co. vitianus* (vs. widely expanded in some arboreal riddle frogs of subgenus *Aenigmanura*, palm frogs of subgenus *Palmatorappia*, giant water frogs of subgenus *Discodeles*, and a few sticky-toed frogs of subgenus *Batrachylodes*), or widely expanded in *Co. vitiensis* (vs. non- to minimally expanded in some terrestrial riddle frogs of subgenus *Aenigmanura*, horned frogs of subgenus *Ceratobatrachus*, river frogs of subgenus *Potamorana*, and a few sticky-toed frogs of subgenus *Batrachylodes*). Additionally, both species are restricted to the islands of Fiji, where they are the only native ranoid frogs; they do not possess overlapping distributions with any other known ceratobatrachids. We are unaware of any morphological synapomorphies for this group, although our molecular data clearly provides strong support for Fijian frogs as a monophyletic group.

Conversion of the name *Cornufer* (referring to the subgenus) to a phylogenetic name would result in two different clades bearing the name *Cornufer*. Therefore, we define a new clade name denoting the same clade (Fig. 2, Clade E) as the subgenus *Cornufer*.

Content
Cornufer vitiensis, *Co. vitianus*, and (provisionally) the extinct taxon *Cornufer megabotoniviti* (Worthy, 2001; Table 3). The subgenus *Cornufer* is equivalent in content to the unranked taxon *Yanuboto*.

Yanuboto new clade name

Phylogenetic definition
Yanuboto (NCN) is a node-based name referring to the clade (Fig. 2, Clade T) originating with the most recent common ancestor of *Co. vitiensis* and *Co. vitianus* (both species formerly in *Platymantis*).

Comment
The two living species of Fijian ceratobatrachids (*Yanuboto*) possess nearly a full complement of the ecomorphological variation in the genus *Cornufer* (Brown, 2004). *Cornufer vitiensis* is a fully arboreal tree frog characterized by widely expanded terminal discs of the fingers and toes and an arboreal microhabitat preference and *Co. vitianus* is a large-bodied, fully terrestrial ground frog (with narrowly to non-expanded terminal finger and toe discs). Surprisingly, these morphologically and ecologically disparate forms (Gorham, 1965, 1968; Morrison, 2003; Zug, 2013) are sister species (Fig. 2).

The fossil *Co. megabotoniviti* is known only from Fijian Quaternary deposits. Worthy (2001) allied it to *Co. vitianus* and *Co. vitiensis*. Because of the lack of synapomorphies that ally it to the other Fijian species, we place it tentatively in *Yanuboto* (subgenus *Cornufer*) because of its provenance, but it would not be unreasonable to consider it unassigned to subgenus.

Etymology
Yanuboto is derived from the Fijian terms *yanuyanu*, meaning 'island', and *boto* meaning 'frog', in reference to the status of the included species status as the only native anurans of Fiji. The name is masculine in gender. Suggested common names: Fijian ground frog (*Co. vitianus*), Fijian tree frog (*Co. vitiensis*).

Potamorana subgen. nov.

Type species
Rana bufoniformis Boulenger, 1884.

Diagnosis
River frog species of the subgenus *Potamorana* differ from other subgenera of *Cornufer*, except giant water frogs of the subgenus *Discodeles*, and Fijian frogs subgenus *Cornufer* (= *Tanuboto*) by having (1) a large body size (males 50–75 mm SVL; females 65–140; vs. most species male SVL ~25–40 mm; (2) moderately extensive, but reduced compared with *Co.* (*Discodeles*) *guppyi*, interdigital webbing of feet (vs. highly reduced to vestiges (*Cornufer nexipus*) or absent (all other species); (3) extensive rugosity of dorsal body skin (vs. smooth, weakly rugose, or slightly shagreened body skin); (4) non-expanded terminal discs of fingers and toes (vs. widely expanded in some arboreal riddle frogs of subgenus *Aenigmanura*, palm frogs of subgenus *Palmatorappia*, giant water frogs of subgenus *Discodeles*, and a few sticky-toed frogs of subgenus *Batrachylodes*); and (5) semiaquatic microhabitat preferences (vs. terrestrial). Based on the phylogeny, we consider their large body size, interdigital webbing of the feet, and semiaquatic microhabitat preferences to be shared, derived characters that unambiguously distinguish the species of *Potamorana* from all other species of *Cornufer* except *Discodeles guppyi*, in which these characters most likely have independently evolved (Fig. 2).

Phylogenetic definition
Potamorana (NCN) is an apomorphy-based name for the clade (Fig. 2, Clade F) originating in the ancestor of *Cornufer bufoniformis* and *Cornufer malukuna* in which the following apomorphy, synapomorphic with that in the various populations of *Co. bufoniformis*, originated: moderately extensive webbing between the digits of the feet.

Content
Cornufer malukuna and *Co. bufoniformis* (Table 3). We did not sample *Cornufer* (*Discodeles*) *opisthodon* or *Cornufer* (*Discodeles*) *vogti* but we tentatively place them in *Potamorana* because these species share the synapomorphy (moderately extensive webbing between the digits of the feet) of the clade *Potamorana*.

Comment
The newly discovered relationships of the former '*Discodeles*' *malukuna* and '*Discodeles*' *bufoniformis* reveal that *Discodeles* was polyphyletic in its former sense. These species are unrelated to the clade (Fig. 2, Clade H) containing the type species *D. guppyi*. In retrospect, it is not surprising that these four morphologically similar (moderate body size, moderate interdigital

webbing, terminal digital discs non-expanded) species are now recognized as distinct from *Co.* (*Discodeles*) *guppyi*, a much larger species with full interdigital webbing between the toes and moderately expanded terminal digital discs.

Etymology
Derived from the Greek term *potamo*, meaning 'river or stream', and the Latin *rana*, meaning 'frog', in reference to the semiaquatic habitat preferences of the new clade. The name is feminine in gender. Suggested common name: Solomon–Bismarck river frogs.

SUBGENUS *CERATOBATRACHUS* BOULENGER, 1884

Type species
Ceratobatrachus guentheri Boulenger, 1884, by monotypy.

Diagnosis
The sole species of the subgenus *Ceratobatrachus*, *Cornufer* (*Ceratobatrachus*) *guentheri*, is one of the most charismatic and distinctive species in the Ceratobatrachidae and is readily diagnosed from all members of the genus *Cornufer* by having (1) elaborated ossification of the squamosal (vs. absence of ornamental ossification); and by the (2) presence of mandible odontoids (vs. absence); and (3) presence of ornate dermal protuberances above the eyes ('horns'), at the tip of the snout, and along the posterior edges of fore- and hindlimbs (vs. absence). These characters are uniquely derived in this lineage (Fig. 2, Clade S).

Phylogenetic definition
Ceratobatrachus is an apomorphy-based name for the clade (Fig. 2, Clade S) originating in the ancestor in which the following apomorphy, synapomorphic with those in the known populations of *Co.* (*Ce.*) *guentheri*, originated: ornate dermal protuberances above the eyes ('horns'), at the tip of the snout, and in the form of serrated flaps along the outer edges of the limbs.

Content: Cornufer (*Ce.*) *guentheri* (Table 3).

Comment
Cornufer (*Ce.*) *guentheri* is most closely related to the extremely phenotypically dissimilar miniaturized species *Cornufer acrochordus* (Fig. 2). This bizarre and completely unexpected relationship stands as a testament to the highly variable and at times bewildering patterns of morphological variability and phylogenetic relationships in the family Ceratobatrachidae.

Etymology
Although Boulenger (1884) provided no etymology for *Ceratobatrachus*, the name is probably derived from the Greek 'kerato', meaning 'horned' and the Greek 'batrachos', meaning 'frog'. Suggested common name: Solomon Islands horned frogs.

SUBGENUS *DISCODELES* BOULENGER, 1918

Type species
Rana guppyi Boulenger, 1884.

Diagnosis
The sole species of the subgenus *Discodeles* is easily diagnosed from species of the genus *Cornufer* by having (1) an extremely large body size [females up to 250 mm SVL (mass of up to 1 kg) vs. most species with female SVL ≤ 65 mm]; (2) moderately expanded terminal discs of fingers and toes (vs. widely or non-expanded); (3) fully webbed feet (vs. interdigital webbing absent, limited to basal vestige, or present but with one or two terminal phalanges free of web); and (4) aquatic microhabitat preference (vs. terrestrial or arboreal). We consider its body size and full interdigital foot webbing to be synapomorphies of this distinct lineage (Fig. 2, Clade H).

Phylogenetic definition
Discodeles is the apomorphy-based name for the clade (Fig. 2, Clade H) originating in the ancestor in which the following apomorphies, synapomorphic with that in the known populations of *D. guppyi*, originated: extremely large body size and fully webbed feet.

Content
Composed of highly divergent isolated allopatric and insular lineages of the nominal species, *Co.* (*D.*) *guppyi* is most likely a complex of evolutionary lineages (species) from New Britain, Bougainville, and various Solomon Islands populations (Table 3).

Comment
Two species of Ceratobatrachidae have the specific epithet *guppyi*: *Rana guppyi* Boulenger, 1884 (the type species of the aquatic genus *Discodeles*) and *Cornufer guppyi* Boulenger, 1884 (a tree frog native to the Solomon Islands). Our inclusion of the two species in the resurrected genus *Cornufer* creates homonymy between the names. Under the principle of priority (ICZN, 1999) we normally would retain the senior homonym, the older available name. However, both species were named in the same year, in the same work and on the same page (Boulenger, 1884: 211), an extremely unusual situation.

Under the Code, the preferred and most conservative action would be the substitution of a valid junior synonym of one of these species. *Rana guppyi* Boulenger, 1884, purportedly has a junior synonym; Zweifel (1960) treated *Rana bufoniformis cognata* Hediger, 1933 (NHMB 4605, holotype; Forcart, 1946) as a synonym of *R. guppyi* Boulenger, 1884. However, we reject *cognata* as a junior synonym of *R. guppyi* because its type locality, 'Iriu', Admiralty Islands, falls within the known geographical range of '*D.*' *vogti* and not within that of *D. guppyi*. Hediger's (1933) description additionally lists morphological character states (narrowly expanded toe discs, relatively small body size) that lead us to believe that this species is not referable to *Co.* (*D.*) *guppyi*. We therefore consider *R. bufoniformis cognata* Hediger, 1933, as a junior subjective synonym of *D. vogti* (Hediger, 1934). Thus, there is no junior synonym that can be substituted for *R. guppyi* Boulenger, 1884.

The second species in this conundrum is *Co. guppyi* Boulenger, 1884, which also lacks any junior synonyms. However, the Code provides for a resolution in such cases. Article 24.2 of the Code states that the principle of first reviser (ICZN, 1999:30) is to be used in situations in which the precedence between names cannot be determined and an available junior synonym does not exist. Acting as first reviser, we fix precedence of *R. guppyi* Boulenger, 1884, over *Co. guppyi* Boulenger, 1884. This action maintains the name of the well-known species *D. guppyi* (= *Rana guppyi* Boulenger, 1884), which is also the type species of *Discodeles*. We provide a new replacement name for *Co. guppyi* Boulenger, 1884, below (see under subgenus *Aenigmanura*).

Etymology
Although Boulenger (1918b) provided no etymology for *Discodeles*, he distinguished it from other Papuan and Melanesian forms on the basis of the 'horseshoe-shaped groove' (Boulenger, 1918b:238) evident on the tips of fingers and toes. Thus, we assume that the name is derived from the Latin 'discus', meaning a flat and round shape, and the Greek 'delos', meaning visible or evident, in reference to presence of the digital discs. Suggested common name: giant Pacific water frogs.

SUBGENUS *PALMATORAPPIA* AHL, 1927

Type species
Hylella solomonis Sternfeld, 1920.

Diagnosis
The single species *Cornufer* (*Palmatorappia*) *heffernani* (formerly *Palmatorappia solomonis*; see below) can be readily diagnosed from other members of the genus *Cornufer* by having (1) a small, delicate, slender body and limbs (vs. more robust body form and limbs); (2) widely expanded terminal discs of fingers and toes (vs. non- to minimally expanded in some terrestrial riddle frogs of subgenus *Aenigmanura*, horned frogs of subgenus *Ceratobatrachus*, river frogs of subgenus *Potamorana*, and a few sticky-toed frogs of subgenus *Batrachylodes*); (3) flattened subarticular tubercles of hands and feet (vs. subarticular tubercles rounded to pointed); (4) moderate interdigital webbing of fingers (unique amongst species of the genus *Cornufer*) and toes (present as vestiges in *Co.* (*Aenigmanura*) *nexipus* (vs. absent or much more extensive); and (5) interdigital webbing extensive in *Co.* (*D.*) *guppyi* but moderate (one or two terminal phalanges free) in species of the subgenus *Potamorana*. We consider this suite of characters to be uniquely derived within *Cornufer*. Based on our phylogeny (Fig. 2), moderate interdigital webbing of the manus appears to be a unique apomorphy distinguishing *Palmatorappia* from all other ceratobatrachids.

Phylogenetic definition
Palmatorappia is an apomorphy-based name for the clade (Fig. 2, Clade U) originating in the ancestor in which the following apomorphy, synapomorphic with that in the various populations of *Palmatorappia heffernani*, originated: moderate interdigital webbing of the fingers.

Content
Cornufer (*Pa.*) *heffernani* (Kinghorn, 1928); formerly a junior synonym of *Pa. solomonis* (Sternfeld, 1920); here designated a *nomen substitutum*; see below (Table 3).

Comment
In general phenotypic characteristics and microhabitat preferences, the sole species of the subgenus *Palmatorappia* is unlike any other Solomon member of the genus *Cornufer* and, in fact, phenotypically and ecologically much more closely resembles the unrelated members of the clade *Platymantis* (*Tirahanulap*) of the Philippines (formerly referred to as the *Platymantis hazelae* Group, *sensu* Brown *et al*., 1997a) and species of *Cornufer* (*Aenigmanura*) from the mountains of New Britain Island (*Co. macrosceles*, *Co. citrinospilus*, *Co. mamusiorum*) and Manus Island (*Co. custos*).

The allocation of the Solomon Islands palm frog, *Pa. solomonis,* originally *Hylella solomonis*, and *Platymantis solomonis* (Boulenger, 1884) (a widespread Solomon Islands ground frog), originally *Cornufer solomonis*, to the genus *Cornufer* creates homonymy. That the identical species names belong to different subgenera within *Cornufer* is not relevant to the issue of homonymy (Article 57.4). Following the principle of priority we retain the senior homonym *Co. solomonis* Boulenger, 1884; in our classification the new combination is *Cornufer* (*Aenigmanura*) *solomonis*.

Hylella solomonis Sternfeld, 1920, is the type and only species of *Palmatorappia* Ahl, 1927; the principle of homonymy requires that this junior homonym be replaced even though it would be desirable to maintain the name of the type species in the interest of stability. The only available junior synonym of *Pa. solomonis* is *Hypsirana heffernani* Kinghorn, 1928, which was synonymized under *Pa. solomonis* by Brown (1952). Therefore, we designate *Hyps. heffernani* Kinghorn, 1928, as a substitute name for *Hyl. solomonis* Sternfeld, 1920. The species commonly known as *Pa. solomonis* will be *Cornufer* (*Palmatorappia*) *heffernani* comb. nov.

Etymology

Most likely from the Latin 'palmat-', meaning the condition in which the spaces between the digits are filled in (as by webbing), and *Rappia*, a patronym for Rapp, who named the genus *Hyperolius*. Günther (1865) unjustifiably proposed *Rappia* as a substitute name for *Hyperolius* Rapp, 1842, so *Rappia* is a patronym and thus *Palmatorappia* is to be treated as masculine. Common name: Solomon Islands palmate frogs.

SUBGENUS *BATRACHYLODES* BOULENGER, 1887

Type species

Batrachylodes vertebralis Boulenger, 1887.

Diagnosis

Species of the subgenus *Batrachylodes* form a phenotypically and ecologically cohesive group, differing from other members of the genus *Cornufer* by having (1) a small body size (males 17–24 mm SVL; vs. ≥ 25 mm); (2) stout, triangular bodies (vs. body shape slender, not triangular); (3) pointed snouts (vs. rounded); and (4) slightly expanded to widely expanded terminal discs of fingers and toes (vs. terminal discs non-expanded); and by the (5) presence of darkened loreal stripes continuing diagonally across the flank to form a distinctly stratified lateral body marking (i.e. clearly demarcated darker dorsal and lighter ventral colours) in most species (vs. absence); and (6) absence of interdigital webbing (vs. presence in *Potamorana* and *Discodeles*). We consider body shape (microhylid-like; generally triangular bodies with very small heads and strongly pointed snouts) and stratified coloration (light above, dark on lateral surfaces) to be synapomorphies for the subgenus (Boulenger, 1887; Sternfeld, 1920; Brown & Parker, 1970), which is strongly supported in our phylogeny (Fig. 2, Clade L).

Phylogenetic definition

Batrachylodes is an apomorphy-based name for the clade (Fig. 2, Clade L) originating in the ancestor of *Cornufer* (*Batrachylodes*) *vertebralis* and *Cornufer* (*Batrachylodes*) *trossulus*, in which the following apomorphy, synapomorphic with that in *Batrachylodes vertebralis*, originated: very small, triangular bodies with small heads and strongly pointed snouts (Fig. 2).

Content

Seven species formerly referred to the genus *Batrachylodes* (i.e. excluding *Cornufer minutus*; Fig. 2, and below), exclusively from the Solomon Islands (Brown & Parker, 1970: *Cornufer elegans*, *Co. gigas*, *Co. mediodiscus*, *Co. montanus*, *Co. trossulus*, *Co. vertebralis*, and *Co. wolfi*; Table 3). Brown *et al*. (2013) discussed an undescribed species from New Britain Island, Bismarck Archipelago (the first report of a species of this genus outside the Solomon Island Archipelago; Foufopoulos & Richards, 2007).

Comment

The species not sampled by us (*B. elegans*, *B. gigas*, *B. mediodiscus*, and *B. montanus*) from the morphologically cohesive and biogeographically circumscribed *Batrachylodes* are also placed in *Batrachylodes* because they share the synapomorphy on which the phylogenetic name is based. We exclude *Co. minutus* from this group on the basis of its unstable phylogenetic affinities (Fig. 2), which, in the combined data set suggest a closer relationship to Melanesian (*Cornufer* sp. Halmahera, *Cornufer batantae*, and *Cornufer bimaculatus*) species than to members of the subgenus *Batrachylodes*, with the caveat that support for this relationship is low (Fig. 2).

Etymology

Although Boulenger (1887) provided no etymology for *Batrachylodes*, the name is most likely derived from the Greek 'batrachus', meaning frog, and possibly 'hylodes', in reference to the genus *Hylodes*. Boulenger's (1882) concept of *Hylodes* included 45 species that are today allocated to *Pristimantis*, *Eleutherodactylus*, *Lithodytes*, *Batrachyla*, and other genera. One of Boulenger's diagnostic characters for *Hylodes* was expanded digital discs, such as are present in some *Batrachylodes* species. *Hylodes* is almost certainly derived from *Hyla*- + '-odes' (Greek), meaning like or similar to *Hyla*, implicitly with expanded discs. Common name: Solomon Islands sticky-toed frogs.

AENIGMANURA SUBGEN. NOV.

Type species

Platymantis papuensis schmidti Brown & Tyler, 1968.

Diagnosis

Individual species of the subgenus *Aenigmanura* differ from other members of *Cornufer* by characters related to their general classification as either generalized terrestrial species with narrow finger and toe discs or arboreal forms with widely expanded finger and toe discs. The arboreal tree frogs of *Aenigmanura* (*Cornufer citrinospilus*, *Co. custos*, *Co. hedigeri* [formerly *Platymantis guppyi*; see below], *Co. macrosceles*, *Co.*

mamusiorum, *Co. nakanaiorum*, *Co. neckeri*, *Co. nexipus*, *Co. parilis*, *Co.* sp. B. Manus and *Co.* sp. C. Manus) can be readily distinguished from ground frogs (selected members of subgenus *Aenigmanura* and all *Cornufer* species not assigned to subgenera, all with non-expanded discs of fingers and toes), aquatic species (subgenera *Potamorana* and *Discodeles,* characterized by the presence of interdigital webbing), sticky-toed frogs (subgenus *Batrachylodes*, small, triangular-shaped bodies with strongly pointed snouts), the Fijian ground frog (*Co. vitianus*, with non-expanded discs of fingers and toes), palm frogs (subgenus *Palmatorappia*, with interdigital webbing present on hands), and horned frogs (subgenus *Ceratobatrachus*, with elaborately casqued skull morphology and dermal horns above the eyelids). The terrestrial species of *Aenigmanura* (*Cornufer adiastolus*, *Cornufer admiraltiensis*, *Cornufer akarithymus*, *Cornufer boulengeri*, *Cornufer bufonulus*, *Cornufer desticans*, *Cornufer gilliardi*, *Cornufer latro*, *Cornufer magnus*, *Cornufer papuensis*, *Cornufer pelewensis*, *Cornufer schmidti*, *Cornufer solomonis*, *Cornufer sulcatus*, and *Cornufer weberi*) can be distinguished from river frogs and giant frogs (subgenera *Potamorana* and *Discodeles*, characterized by the presence of interdigital webbing), sticky-toed frogs (subgenus *Batrachylodes*, small, triangular-shaped bodies with strongly pointed snouts), the Fijian tree frog (*Co. vitiensis*, with widely expanded discs of fingers and toes), palm frogs (subgenus *Palmatorappia*, an arboreal species with expanded finger and toe discs, and interdigital webbing present on hands and feet), and horned frogs (subgenus *Ceratobatrachus*, with elaborately casqued skull morphology and dermal horns above the eyelids).

As implied by the name, the wide range of morphological and ecological variation in this clade renders an unambiguously exclusive diagnosis of *Aenigmanura* impossible. We are unaware of morphological synapomorphies for this group, although our phylogenetic analysis provides very strong support for this phenotypically and ecologically diverse clade (Fig. 2, Clade J).

Phylogenetic definition

Aenigmanura (NCN) is a maximum crown-clade name referring to the crown clade (Fig. 2, Clade J) originating with the most recent common ancestor of *Co. papuensis* and all extant species that share a more recent common ancestor with *Co. papuensis* than with any of the other species of the clade *Cornufer*. Alternatively it can be conceived of as the largest crown clade containing *Co. papuensis*, but not any other species of the clade *Cornufer*.

Content

Cornufer adiastolus, *Co. admiraltiensis*, *Co. akarithymus*, *Co. boulengeri*, *Co. citrinospilus*, *Co. custos*, *Co. desticans*, *Co. gilliardi*, *Co. hedigeri* (formerly *Pl. guppyi*; see below), *Co. latro*, *Co. macrosceles*, *Co. magnus*, *Co. mamusiorum*, *Co. nakanaiorum*, *Co. neckeri*, *Co. nexipus*, *Co. parilis*, *Co. papuensis*, *Co. pelewensis*, *Co. schmidti*, *Co. solomonis*, *Co. sulcatus*, *Co. weberi*, the newly described *Co. custos* (Richards *et al.*, 2014), and two undescribed species from Manus Island (sp. B Manus and sp. C Manus; Fig. 2., Clade J).

Comment

The range of body sizes in this large clade is striking. From miniaturized terrestrial species such as *Co. sulcatus* and *Co. akarithymus* (males 17–27 mm SVL), to giant ground species such as *Co. magnus* (males 75–150 mm SVL), to large canopy frogs such as *Co. neckeri* and *Co. hedigeri* (formerly *Pl. guppyi*; see below), to delicate, high-elevation, arboreal shrub species such as *Co. macrosceles* and *Co. mamusiorum*, to widespread terrestrial generalists such as *Co. papuensis*, *Co. weberi*, *Co. schmidti*, and *Co. solomonis* – the subgenus *Aenigmanura* exhibits nearly the full range of ceratobatrachid ecomorphological diversity (Brown, 2004), all within one clade of closely related species.

As noted above, allocation of *Pl. guppyi* Boulenger, 1884 (not to be confused with *D. guppyi*) to the genus *Cornufer* presented a case of secondary homonymy with respect to *R. guppyi* Boulenger, 1884. Given that no available junior synonym exists for the latter and that it is also the type species of *Discodeles*, we elected not to alter this name, and we have given *R. guppyi* precedence over *Pl. guppyi* following the principle of first reviser (ICZN, 1999:30). Thus, the establishment of a replacement name for *Pl. guppyi* Boulenger, 1884, is necessary. Accordingly, we designate *Co. hedigeri* as a *nomen novum* for *Pl. guppyi* Boulenger, 1884. The epithet *hedigeri* is a patronym for Heine Hediger (1908–1992) in recognition of his contributions (Hediger, 1933, 1934) to the taxonomy of the genus *Cornufer sensu lato* and the biology of the South Pacific.

Etymology

From the Latin *enigma*, meaning something 'obscure or unknown, a riddle', and *anura*, meaning 'frog', in reference to the unanticipated and confusing range of morphological and ecological variation represented by the closely related species of the new subgenus. The name is masculine in gender. Suggested common name: Pacific Island riddle frogs.

DISCUSSION

Phenotypic characters and diagnoses

The phylogenetic framework for our new ceratobatrachid classification was derived from a new multilocus DNA sequence data set. Although some phenotypic characters are easily identified as synapomorphies (e.g. the dermal 'horns' of *Ceratobatrachus*), we have not comprehensively surveyed phenotypic characters to determine their value as possible synapomorphies, and in many cases it is not possible to provide information that will place a species within a clade without using DNA sequences. As a result, some unsampled species and/or species of uncertain phylogenetic affinities (Figs. 2, 3), are not yet referable to subgenera (Table 3).

Our approach takes a top-down perspective in that we have begun with a phylogeny and will progressively incorporate information about phenotype. The next steps in our studies of ceratobatrachid evolution include the description of many new species, with a comprehensive survey of external morphology and phylogenetic analysis of advertisement calls. Our experience with these frogs suggests that we will glean many synapomorphies from the phenotype and acoustic data. Integrating these new data into this phylogenetic framework will provide a broader view of ceratobatrachid evolution.

TAXONOMY

Our phylogeny of the Ceratobatrachidae is a major step towards the development of a stable taxonomy for this poorly understood clade of frogs from Southeast Asia and the Pacific islands. Clearly *Platymantis* as previously defined is not monophyletic (Fig. 3A). Setting aside for the moment the genus *Alcalus* (formerly Southeast Asian species of *Ingerana*) as uncontroversial, we carefully considered the following options for the taxonomy of Clade D (Fig. 2).

1. Recognizeone genus *Platymantis* for Clade D, with no subgenera. This would subsume several species-poor genera such as *Discodeles*, *Palmatorappia*, etc. as junior synonyms of *Platymantis*. However, a 'flat' taxonomy such as this would conceal the phylogenetic hierarchy elucidated by this study. Because > 80% of ceratobatrachid species are *Platymantis*, few genus-species combinations would change.
2. Recognize one genus *Platymantis* for Clade D, with several subgenera, many of them new. This would convey both phylogenetic hierarchy and diversity in morphology, ecology, and biogeography. It would also retain the use of well-known clade names such as *Discodeles*, *Ceratobatrachus*, *Batrachylodes*, and *Palmatorappia*, which are associated with widely appreciated and distinct phenotypes. Similar to (1), few genus-species combinations would change.
3. Split Clade D into several genera. This would dissolve *Platymantis*, reduce its content, and so

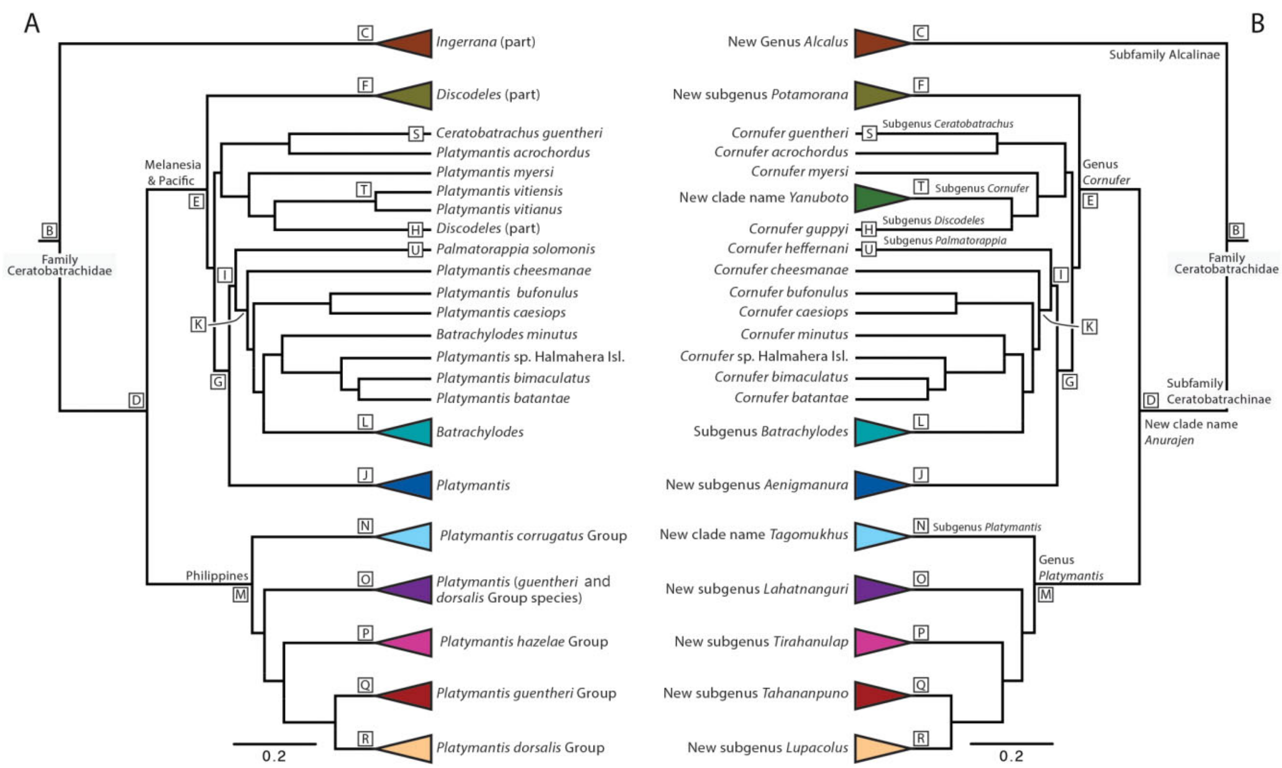


Figure 3. A schematic representation of ceratobatrachid phylogeny (based on Fig. 2), summarizing (A) the previous taxonomy of ceratobatrachid frogs and (B) the new classification scheme proposed here.

re-allocate many species to different genera. Numerous genus-species combinations would change.

4. Adopt an intermediate option, which is to recognize two genera, *Cornufer* and *Platymantis*, for Clade D. Subgenera would be used to reflect hierarchical structure and biotic diversity. The number of changes in genus-species combinations would be fewer than in option (3) but more than in (1) and (2).

We have adopted option (4), but we can be criticized for not using option (2), and in fact some of the authors (D. C. C. vs. R. M. B.) disagree on this choice. The latter would maintain the generic name *Platymantis* for the large number of species in Clade J (*Aenigmanura*) and minimize changes in combinations. Our use of the *Cornufer–Platymantis* arrangement (Fig. 3B) increases the number of changes in genus-species combination, although not as much as option (3), but emphasizes a trenchant biogeographical pattern between Clade M and Clade E, each situated on either side of Wallace's Line.

Under options (2) and (4) subgeneric ranks could be used. Under option (2), one might use two subgenera, *Platymantis* and *Cornufer*, with smaller taxa within each. These less inclusive taxa might be ranked as sections or series. According to the Code (Article 10.4; ICZN, 1999) such ranks are treated as subgenera. Nested levels of subgenera are an ideal but underused way to provide additional hierarchical information that is not evident in 'flat' taxonomies; for an example see Hillis *et al*. (2001). However, the use of nested subgenera is problematic under the Code (see Dubois, 2007; Hillis, 2007), which reflects the Code's non-evolutionary origins.

Although subgenera are an excellent means of enhancing phylogenetic information in taxonomy, they have problems that derive from the Code's emphasis on ranks. For example, although the proper form of *Ceratobatrachus guentheri* under our taxonomy is *Cornufer* (*Ceratobatrachus*) *guentheri*, *Ce. guentheri* alone unambiguously refers to that species without explicit mention of the subgenus rank. Unfortunately, the Code prohibits omission of the genus name when the subgenus name is used (Article 4.2), but ignoring this rule has little negative effect if the name is used in context. Additionally, monotypic subgenera (e.g. *Ceratobatrachus* in our taxonomy) add no information about relationships to other taxa, but we retain these names to connect the species epithets to previous taxonomies.

A second problem is that a subgenus containing the type species of the genus must be denoted by the same name as the genus (Articles 43.1 and 44.1). For example, from its creation *Platymantis* exists both as a genus and subgenus name, and simple reference to '*Platymantis*' is ambiguous as to rank. A simple solution is to define a new, unranked name in place of the subgeneric name, as we have done (Table 4), so that the name *Platymantis* refers to only one node.

It is possible that a future worker will propose raising the subgenera to generic rank. We feel that this action would be ill-advised and unwarranted because it would result in changes in a large number of genus–species couplet names. The practice of unnecessarily splitting a genus into several genera destabilizes taxonomy and hides nested phylogenetic information [see for example the proposal to split *Anolis* by Nicholson *et al*. (2012) and responses by Poe (2013) and R. Glor (unpubl. data)]. In many cases of oversplitting, the possibility of using subgenera is typically not considered or is rejected without discussion.

In weighing the goals of naming diversity that corresponds to phenotypic or geographical distinctiveness (and with the goals, some may feel, of optimizing educational and conservation benefits that may be associated with more atomized classification), vs. avoiding an excess of names of equal rank owing to the splitting of clades (Cannatella & de Queiroz, 1989; Glaw, Vences & Böhme, 1998; Vences *et al*., 2000; Vences & Glaw, 2001; Glaw & Vences, 2006; Glaw, Hoegg & Vences, 2006; Pauly, Hillis & Cannatella, 2009; Poe, 2013), we have adopted a compromise between changing genus–species couplets and retaining the presumed intentions of earlier taxonomists (Tschudi, 1838; Günther, 1858; Boulenger, 1884, 1887, 1896, 1918a; Ahl, 1927) who apparently recognized, appreciated, and formally named the morphological, biogeographical, and ecological distinctiveness of the taxa (Noble, 1931; Gorham, 1965). We feel that this compromise both recognizes the marked diversity within the Ceratobatrachidae, and also imparts a stable hierarchical classification that is conservative in that it requires relatively few changes to existing species names (Fig. 3).

Challenges exist for improved understanding of the relationships of ceratobatrachids. First, additional taxon sampling will provide new information to this initial estimate of phylogeny. With the addition of possibly 40–65 undescribed species (R. M. Brown, S. J. Richards, A. C. Diesmos & C. D. Siler, unpubl. data), some relationships and classification schemes will probably change. Additionally, poor resolution amongst the subgenera *Ceratobatrachus*, *Discodeles*, *Potamorana*, *Batrachylodes*, *Palmatorappia*, *Aenigmanura*, and the species of *Cornufer* not assigned to subgenera will require additional gene sampling and taxonomic revision. For the meantime, we consider the classification of Ceratobatrachidae to be a work in progress (*sensu* Graybeal & Cannatella, 1995; Linkem, Diesmos & Brown, 2011) and we anxiously await future studies that will address the remaining problems identified here.

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APPENDIX

Taxa, field collector number, museum repository catalog numbers, localities, and Genbank catalog numbers for samples included in this study. See Tables 3 & 4 and Figure 3 for summaries of updated classification

Genus	Species	Field No.	Catalog No.	Country	Region/State	Island	General locality	Specific locality	12S–16S	RAG1	Tyr	POMC
Alcalus	*rajae*	RMBR 8.2007	FN RMBR unnumbered	Indonesia	West Kalimantan Province	Borneo		Kecamatan Menukung, Kabupaten Melawi	KP298026		KP298324	KP298161
Alcalus	*rajae*	RMBR 1127	FN RMBR 001127	Indonesia	West Kalimantan Province	Borneo		Kecamatan Menukung, Kabupaten Melawi	KP298027		KP298325	KP298162
Alcalus	*rajae*	RMBR.01153	FN RMBR 01153	Indonesia	West Kalimantan Province	Borneo			KP298028		KP298326	KP298163
Alcalus	*baluensis*	FMNH 41428	FMNH 235604	Malaysia	Sabah	Borneo	Kota Marudu District		KP298029			
Alcalus	*mariae*	RMB 7803	KU 309518	Philippines	Palawan PAIC, Palawan Province	Palawan	Municipality of Brooke's Point	Boundary of Barangay Samarinana and Saulog: Mt. Mantalingahan Range; Area = "Pitang"	KP298038	KP298263		KP298166
Cornufer	cf *wolfi* sp. 2	CCA 2619	LSUMZ 94038	Papua New Guinea	North Solomons Province	Bougainville	Central Bougainville	Togarau Two Village, SE Slope of Mt. Balbi	KP298015	KP298255	KP298317	KP298150
Cornufer	*minutus*	ABTC 49504	ABTC 49504	Papua New Guinea	North Solomons Province	Bougainville	Central Bougainville		KP298016	KP298256	KP298318	KP298151
Cornufer	cf *trossulus*	CCA 2606	LSUMZ 94035	Papua New Guinea	North Solomons Province	Bougainville	Central Bougainville	Togarau Two Village, SE Slope of Mt. Balbi	KP298017	KP298257	KP298319	KP298152
Cornufer	*vertebralis*	CCA 2581	LSUMZ 94018	Papua New Guinea	North Solomons Province	Bougainville	Central Bougainville	Togarau Two Village, SE Slope of Mt. Balbi	KP298018	KP298258	KP298320	KP298153
Cornufer	cf *wolfi* sp. 1	CCA 2622	LSUMZ 94039	Papua New Guinea	North Solomons Province	Bougainville	Central Bougainville	Togarau Two Village, SE Slope of Mt. Balbi	KP298019	KP298259	KP298321	KP298154
Cornufer	*guentheri*	CCA 2583	LSUMZ 93759	Papua New Guinea	North Solomons Province	Bougainville	Central Bougainville	Togarau Two Village, SE Slope of Mt. Balbi	KP298021	KP298261		KP298156
Cornufer	*bufoniformis*	CCA 2585	LSUMZ 94046	Papua New Guinea	North Solomons Province	Bougainville	Central Bougainville	Togarau Two Village, SE Slope of Mt. Balbi	KP298022			KP298157
Cornufer	*bufoniformis*	RMB 6925	KU 307203	Solomon Islands	Western Province	Ranongga	Ranongga	Village of Poroi	KP298023			KP298158
Cornufer	*guppyi*	CCA 2586	LSUMZ 94047	Papua New Guinea	North Solomons Province	Bougainville	Central Bougainville	Togarau Two Village, SE Slope of Mt. Balbi	KP298024	KP298262	KP298322	KP298159
Cornufer	*malukuna*	A169052	AMNH A169052	Solomon Islands	Western Province	Kolambangara	New Georgia Island group	Kolambangara Volcano	KP298025		KP298323	KP298160
Cornufer	*minutus*	A84	ABTC 50388	Solomon Islands	Choiseul Province	Choiseul		Pavora River	KP298030			
Cornufer	*wolfi*	SJR 5324	SAMA R56813	Solomon Islands	Isabel Province	Barora Faa	Barora Faa Island, off the western tip of Isabel Island		KP298033		KP298328	KP298164
Cornufer	*trossulus*	A43	ABTC 50347	Solomon Islands	Choiseul Province	Choiseul		Pavora River	KP298034			
Cornufer	*guppyi*	JF 016	UWZM unnumbered	Papua New Guinea	Bismarck Archipelago, West New Britain Province	New Britain	northern Nakanai Mountains	Nakanai Plateau, ridge between the Ivule and Sigole river	KP298035		KP298329	KP298165

Cornufer	*heffernani*	SJR 5303	SAMA R56799	Solomon Islands	Isabel Province	Barora Faa	Barora Faa, off the western tip of Isabel		KP298042			KP298167
Cornufer	*neckeri*	A57	ABTC 50361	Solomon Islands	Choiseul Province	Choiseul		Pavora River	KP298044			
Cornufer	*pelewensis*	CCA 1307		Palau		Palau			KP298045		KP298330	KP298168
Cornufer	*adiastolus*	FK 10762	BPBM 22365	Papua New Guinea	Bismarck Archipelago, East New Britain Province	New Britain	New Britain	9 km NNW of Marmar (Camp 1)	KP298052		KP298331	KP298169
Cornufer	*admiraltiensis*	SJR 2603	SAMA R62801	Papua New Guinea	Admiralty Archipelago, Manus Province	Manus		Chachuau Camp near Tulu 1 Village	KP298053			KP298170
Cornufer	*boulengeri*	A9681	A9681	Papua New Guinea	Bismarck Archipelago, East New Britain Province	New Britain			KP298056	KP298266	KP298333	KP298173
Cornufer	*acrochordus*	SJR 5457	SAMA R56900	Solomon Islands	Isabel Province	Isabel	Kolopakisa Island	Kolopakisa Village	KP298057			KP298174
Cornufer	*gilliardi*	FK 10830	BPBM 22261	Papua New Guinea	Bismarck Archipelago, East New Britain Province	New Britain	Eastern New Britain	8.8 km NNW of Marmar (Bulisa's trail)	KP298060		KP298335	KP298177
Cornufer	*macrosceles*	FK 10809	BPBM 22273	Papua New Guinea	East New Britain Province	New Britain	New Britain	9.2 km NNW Marmar (cave near Camp 1)	KP298064			KP298181
Cornufer	*magnus*	SJR 5132	SAMA R60240	Papua New Guinea	Admiraty Archipelago, East New Britain Province	New Britain	Wanui River Valley	Wanui Camp	KP298065			KP298182
Cornufer	*desticans*	A81	ABTC 50385	Solomon Islands	Choiseul Province	Choiseul		Pavora River	KP298068			KP298184
Cornufer	*nakanaiorum*	JF 136	UPNG 10010	New Guinea	Bismarck Archipelago, West New Britain Province	New Britain	northern Nakanai Mountains	northern edge of Nakanai Plateau	KP298069			KP298185
Cornufer	*nexipus*	JF 009	UWZM 23893	New Guinea	Bismarck Archipelago, West New Britain Province	New Britain	northern Nakanai Mountains	Nakanai Plateau, ridge between the Ivule and Sigole river	KP298070			KP298186
Cornufer	*occidentalis*	RMB 2025	TNHC 59677	Indonesia	Sulawesi, Eastern Sulawesi Province	Peleng		Kecamatan Tinangkung, Desa Saiyang, 3 km S of Saiyang on rd to Ambelang	KP298071		KP298339	KP298187
Cornufer	*papuensis*	ABTC 48181	ABTC 48181	Papua New Guinea	Madang Province	New Guinea		Madang Caves	KP298072		KP298340	KP298188
Cornufer	*parilis*	SJR 5469	SAMA R56910	Solomons	Isabel Province	Isabel	northern Isabel	Kolopakisa Village,	KP298074			KP298341
Cornufer	*custos*	SJR 2611	SAMA R63511	Papua New Guinea	Admiralty Archipelago, Manus Province	Manus	Manus Province		KP298077			KP298192
Cornufer	*manus*	SJR 2591	UP10016	Papua New Guinea	Admiralty Archipelago, Manus Province	Manus	Manus Province		KP298078			
Cornufer	*vitianus*	CM 1498	no voucher	Fiji		Waisa			KP298079	KP298271	KP298343	KP298193
Cornufer	*vitiensis*	CM F7P	no voucher	Fiji		Savuru			KP298080	KP298272	KP298344	KP298272
Cornufer	*caesiops*	FK 10773	BPBM 22233	Papua New Guinea	Bismarck Archipelago, East New Britain Province	New Britain	New Britain	9 km NNW of Marmar (Camp 1 +/− 200 m)	KP298081		KP298345	KP298195
Cornufer	*bufonulus*	FK 10918	BPBM 22187	Papua New Guinea	Bismarck Archipelago, East New Britain Province	New Britain	New Britain	11.8 km NNW of Marmar (Point 14)	KP298082		KP298346	KP298196
Cornufer	*hedigeri*	AMSR 36662	AMNH	Solomon Islands	Malaita Province	Malaita			KP298083	KP298273	KP298347	KP298197
Cornufer	*akarithymus*	FK 11275	BPBM 22209	Papua New Guinea	Bismarck Archipelago, East New Britain Province	New Britain	New Britain	2.6 km NNW of Marmar (Camp 2)	KP298084		KP298348	KP298198
Cornufer	*solomonis*	CCA 2656	LSUMZ 93777	Papua New Guinea	North Solomons Province	Bougainville	Central Bougainville	South East SlopeMt. Balbi	KP298088	KP298275	KP298350	KP298202
Cornufer	*batantae*	RG 7812		Indonesia	West Papua Province	New Guinea	Manokwari, Gunung Meja		KP298090			
Cornufer	*bimaculatus*	RG 7600		Indonesia		New Guinea			KP298092			
Cornufer	*cheesemanae*	ABTC 3692	ABTC 3692	Papua New Guinea	Sandaun Province	New Guinea	Northern New Guinea	Utai	KP298096		KP298355	KP298208

APPENDIX *Continued*

Genus	Species	Field No.	Catalog No.	Country	Region/State	Island	General locality	Specific locality	12S–16S	RAG1	Tyr	POMC
Cornufer	*hedigeri*		ABTC 50356	Solomon Islands	Choiseul Province	Choiseul		Pavora River	KP298104		KP298362	KP298216
Cornufer	*latro*	CCA 2116	SAMA R62824	Papua New Guinea	Admiralty Archipelago, Manus Province	Manus		Tingau Village, 27 km south-west of Lorengau	KP298113			
Cornufer	*myersi*	CCA 2651	LSUMZ 93784	Papua New Guinea	North Solomons Province	Bougainville	Central Bougainville	Togarau Two Village, SE Slope of Mt. Balbi	KP298121	KP298298	KP298373	KP298231
Cornufer	*parilis*	CCA 2629	LSUMZ 93769	Papua New Guinea	North Solomons Province	Bougainville	Central Bougainville	Togarau Two Village, SE Slope of Mt. Balbi	KP298122	KP298299	KP298374	KP298232
Cornufer	*boulengeri*	FK 10744	BPBM 22329	Papua New Guinea	Bismarck Archipelago, East New Britain Province	New Britain	New Britain	9 km NNW of Marmar (Camp 1)	KP298133	KP298309	KP298385	KP298242
Cornufer	*schmidti*	FK 10897	BPBM 22366	Papua New Guinea	Bismarck Archipelago, East New Britain Province	New Britain	New Britain	11.3 km NNW of Marmar (Point 15)	KP298135			KP298244
Cornufer	sp. Halmahera	BJE 1606	MZB. Amph. 12962	Indonesia	Eastern Indonesia	Halmahera	North Maluku Province, Jailolo		KP298140			KP298249
Cornufer	*desticans*	SJR 5363	SAMA R56850	Solomon Islands	Isabel Province	Barora Faa	Barora Faa Island, off the western tip of Isabel		KP298145			
Cornufer	*weberi*		ABTC 50493	Solomon Islands	Guadalcanal Province	Guadalcanal		Mt. Austen	KP298149		KP298394	KP298254
Cornufer	*mamusiorum*	JF 132	UPNG 9992	Papua New Guinea	Admiralty Archipelago, West New Britain Province	New Britain	northern Nakanai Mountains	northern edge of Nakanai Plateau	KP298066			
Cornufer	sp. "arboreal"	SJR 2639	SAMA R63533	Papua New Guinea	Admiralty Archipelago, Manus Province	Manus	Manus Province	Chachuau Camp near Tulu 1 Village	KP298075	KP298270	KP298342	KP298190
Cornufer	sp. A "clicker"	SJR 2627	SAMA R63528	Papua New Guinea	Admiralty Archipelago, Manus Province	Manus	Manus Province	Chachuau Camp near Tulu 1 Village	KP298076			KP298191
Cornufer	*sulcatus*	SJR 5125	SAMA R5125	Papua New Guinea	Admiralty Archipelago, East New Britain Province	New Britain	Wanui River Valley	Wanui Camp	KP298147			
Platymantis	sp. 43	ACD 2033	PNM Unnumbered	Philippines	Luzon PAIC, Isabela Province	Luzon	Municipality of San Mariano	Barangay Dibuluan, Sitio Apaya	KP298020	KP298260		KP298155
Platymantis	sp. 31	ACD 2431	PNM unnumbered	Philippines	Luzon PAIC, Isabela Province	Luzon	Municipality of San Mariano	Barangay Del Pilar	KP298054	KP298264		KP298171
Platymantis	sp. 3	RMB 2218	FMNH 259000	Philippines	Luzon PAIC, Kalinga Province	Luzon	Municipality of Balbalasang	Barangay Balbalasang	KP298055	KP298265	KP298332	KP298172
Platymantis	*corrugatus*	RMB 3605	TNHC 62111	Philippines	Luzon PAIC, Albay Province	Luzon	Municipality of Tobaco	Barangay Bongabong	KP298058	KP298267	KP298334	KP298175
Platymantis	sp. 10	ACD 661	PNM 6521	Philippines	Luzon PAIC, Isabalea Province	Luzon	Municipality of Palanan	Barangay Didian, Sitio Natapdukan	KP298059			KP298176
Platymantis	*hazelae*	RMB 3316	TNHC 62160	Philippines	West Visayan PAIC, Negros Oriental Province	Negros		Municipality of Valencia, Sitio Nasuji, Mt. Talinis range	KP298061	KP298268	KP298336	KP298178
Platymantis	*insulatus*	CDS 032	KU 300338	Philippines	West Visayan PAIC, Iloilo Province	Gigantes	Muncipality of Carles	Gigante South Island	KP298062		KP298337	KP298179
Platymantis	*isarog*	RMB 3360	PNM 7273	Philippines	Luzon PAIC, Camarines Sur Province	Luzon	Municipality of Naga City	Barangay Panicuason, Mt. Isarog	KP298063		KP298338	KP298180
Platymantis	*montanus*	ACD 1012	PNM 7398	Philippines	Luzon PAIC, Quezon Province	Luzon	Municipality of Tayabas	Barangay Lalo, Area = 'Hasaan'	KP298067			KP298183
Platymantis	sp. 4	RMB 2206	FMNH 259017	Philippines	Luzon PAIC, Kalinga Province	Luzon	Municipality of Balbalasang	Barangay Balbalasang	KP298073	KP298269	KP298341	KP298189

Platymantis	sp. 29	RMB 426	FMNH 266270	Philippines	Luzon PAIC, Zambales Province	Luzon	Municipality of Masinloc	Mt. HighPeak	KP298085	KP298274		KP298199
Platymantis	cf. *montanus*	ACD 772	PNM 8464	Philippines	Luzon PAIC, Quezon Province	Luzon	Municipality of Tayabas	Barangay Lalo, Mt. Banahao	KP298086			KP298200
Platymantis	sp. 15	GVAG 303	FMNH 263460	Philippines	Luzon PAIC, Kalinga Province	Luzon	Municipality of Balbalasang	Barangay Balbalasang, Mapga	KP298087		KP298349	KP298201
Platymantis	*banahao*	RMB 3713	TNHC 61968	Philippines	Luzon PAIC, Quezon Province	Luzon	Municipality of Tayabas	Barangay Lalo, Mt. Banahao	KP298089		KP298351	KP298203
Platymantis	*bayani*	CDS 2757	KU 309252	Philippines	Mindanao PAIC, Eastern Samar Province	Samar	Municipality of Taft	Barangay San Rafael	KP298091	KP298276	KP298352	KP298204
Platymantis	sp. 30	RMB 4219	PNM 7497	Philippines	Luzon PAIC, Cagayan Province	Luzon	Municipality of Gattaran	Gattaran Forest Reserve	KP298093	KP298277		KP298205
Platymantis	*cagayanensis*	RMB 4231	PNM 7479	Philippines	Luzon PAIC, Cagayan Province	Palaui	Municipality of Santa Ana	Barangay Palaui	KP298094	KP298278	KP298353	KP298206
Platymantis	sp. 9	RMB 3601	TNHC 62078	Philippines	Luzon PAIC, Albay Province	Luzon	Municipality of Tobaco	Barangay Bongabong	KP298095	KP298279	KP298354	KP298207
Platymantis	*diesmosi*	RMB 3525	PNM 8500	Philippines	Luzon PAIC, Albay Province	Luzon	Municipality of Malinao	Barangay, Sugcad, area known locally as 'Sugcad Plaza'	KP298097	KP298280	KP298356	KP298209
Platymantis	*dorsalis*	ACD 902	PNM unnumbered	Philippines	Luzon PAIC, Laguna Province	Luzon	Municipality of Los Baños	Barangay Batong Malake, Mt. Makiling	KP298098	KP298281	KP298357	KP298210
Platymantis	*dorsalis*	CDS 1708	KU 304301	Philippines	Luzon PAIC, Catanduanes Province	Catanduanes	Municipality of San Miguel	Barangay San Roque	KP298099	KP298282	KP298358	KP298211
Platymantis	sp. 6	JAM 967	TNHC 54977	Philippines	Luzon PAIC, Quezon Province	Polillo	Municipality of Polillo	Barangay Sibucan, Sitio Watershed-Tambangin side	KP298100	KP298283	KP298359	KP298212
Platymantis	sp. 7	RMB 729	CMNH 8128	Philippines	Luzon PAIC, Aurora Province	Luzon	Municipality of San Luis	Barangay Villa Aurora	KP298101	KP298284	KP298360	KP298213
Platymantis	sp. 24		FMNH 270229	Philippines	Luzon PAIC, Camarines Norte Province	Luzon	Municipality of Labo	Barangay Tulay na Luba, Mt. Labo	KP298102	KP298285		KP298214
Platymantis	*guentheri*	CDS 3127	KU 311022	Philippines	Mindanao PAIC, Leyte Province	Leyte	Municipality of Baybay	Barangay Pilim, San Vicente	KP298103	KP298286	KP298361	KP298215
Platymantis	sp. 27	RMB 4063	TNHC 61989	Philippines	Luzon PAIC, Quezon Province	Luzon	Municipality of Atimonan	Barangay Malinao Ilaya	KP298105	KP298287	KP298363	KP298217
Platymantis	sp. 8	RMB 4005	TNHC 62018	Philippines	Luzon PAIC, Sorsogun Province	Luzon	Municipality of Irosin	Barangay San Rogue, Mt. Bulusan, Bulusan Lake	KP298106	KP298288	KP298364	KP298218
Platymantis	sp. 18	CDS 438	No voucher	Philippines	Luzon PAIC, Masbate Province	Ticao	Municipality of San Fernando		KP298107	KP298289	KP298365	KP298219
Platymantis	*indeprensus*	RMB 3643	TNHC 61956	Philippines	Luzon PAIC, Quezon Province	Luzon	Municipality of Tayabas	Barangay Lalo, Mt. Banahao	KP298108	KP298290	KP298366	KP298220
Platymantis	sp. 21	CDS 2906	KU 310464	Philippines	Mindanao PAIC, Eastern Samar Province,	Samar	Municipality of Taft	Barangay San Rafael	KP298109	KP298291	KP298367	KP298221
Platymantis	sp. 14	ACD 783	PNM 8842	Philippines	Luzon PAIC, Quezon Province	Luzon	Municipality of Lucban	Barangay Samil, Mt. Banahao	KP298110	KP298292		KP298222
Platymantis	sp. 19	ACD 855	PNM 8834	Philippines	West Visayan PAIC, Cebu Province	Cebu		Barangay Tabunan, Tabunan National Park	KP298111		KP298368	KP298223
Platymantis	sp. 20	RMB 3796	PNM unnumbered	Philippines	Mindanao PAIC, Davao City Province	Mindanao	Municipality of Calinan	Barangay Malagos, Malagos Eagle Station	KP298112			KP298224
Platymantis	*lawtoni*	RMB 8836	KU 315281	Philippines	Romblon Island Group, Romblon Province	Tablas	Municipality of Calatrava	Barangay Balogo: Sitio Piqueno	KP298114	KP298293	KP298369	KP298293

APPENDIX *Continued*

Genus	Species	Field No.	Catalog No.	Country	Region/State	Island	General locality	Specific locality	12S–16S	RAG1	Tyr	POMC
Platymantis	*levigatus*	RMB 5169	KU 304548	Philippines	Romblon Island Group, Romblon Province,	Sibuyan	Municipality of Magdiwang	Barangay Talaba, Mount Guiting-Guiting Natural Park	KP298115	KP298294	KP298370	KP298225
Platymantis	sp. 33	RMB 5307	KU 304973	Philippines	Mindoro PAIC, Occidental Mindoro Province	Lubang	Municipality of Lubang	Between Barangays Binakyas and Agkawayan	KP298116	KP298295		KP298226
Platymantis	*luzonensis*	CDS 1712	KU 304505	Philippines	Luzon PAIC, Catanduanes Province	Catanduanes	Municipality of San Miguel	Barangay San Roque	KP298117		KP298371	KP298227
Platymantis	sp. 22	CDS 752	KU 304386	Philippines	Romblon Island Group, Romblon Province	Tablas	Municipality of Magdiwang	Barangay Poblacion	KP298118	KP298296	KP298372	KP298228
Platymantis	sp. 35	ELR 376	PNM unnumbred	Philippines	Mindoro PAIC, Occidental Mindoro Province	Mindoro	Municipality of Sablayan	Barangay Batong Buhay, Batulai, Mt. Siburan	KP298119			KP298229
Platymantis	*mimulus*	RMB 4187	PNM 7453	Philippines	Luzon PAIC, Nueva Ecija Province	Luzon		Dalton Pass	KP298120	KP298297		KP298230
Platymantis	*negrosensis*	CDS 913	KU 300442	Philippines	West Visayan PAIC, Negros Oriental Province	Negros		Municipality of Valencia, Sitio Nasuji, Mt. Talinis range	KP298123	KP298300	KP298375	KP298233
Platymantis	*naomii*	RMB 3662	PNM 7356	Philippines	Luzon PAIC, Quezon Province,	Luzon	Municipality of Tayabas	Barangay Lalo, Mt. Banahao	KP298124	KP298301	KP298376	KP298234
Platymantis	*paengi*	CDS 1537	PNM 9241	Philippines	West Visayan PAIC, Antique Province,	Panay	Municipality of Pandan	Barangay Duyong	KP298125	KP298302	KP298377	KP298235
Platymantis	*panayensis*	H631	CMNH 4117	Philippines	West Visayan PAIC, Antique Province,	Panay	Municipality of Culasi	Mt. Madja-as	KP298126	KP298303	KP298378	KP298236
Platymantis	sp. 34	RMB 7952	KU 309728	Philippines	Mindanao PAIC, Camiguin Province	Caminguin Sur	Municipality of Mambajao	Barangay Pandan, Sitio Kampana	KP298127	KP298304	KP298379	KP298237
Platymantis	*polillensis*	RMB 8887	KU 326063	Philippines	Luzon PAIC, Quezon Province	Polillo	Municipality of Burdeos	Barangay Aluyon, Sitio Malinao	KP298128	KP298305	KP298380	
Platymantis	*pseudodorsalis*	ACD 826	PNM 6690	Philippines	Luzon PAIC, Quezon Province	Luzon	Municipality of Lucban	Barangay Samil, Mt. Banahao	KP298129		KP298381	KP298238
Platymantis	*pygmaeus*	ACD 2067	PNM 6456	Philippines	Luzon PAIC, Isabalea Province	Luzon	Municipality of Palanan	Barangay.Didian, Sitio.Natapdukan	KP298130	KP298306	KP298382	KP298239
Platymantis	*rabori*	CDS 2874	KU 309123	Philippines	Mindanao PAIC, Eastern Samar Province	Samar	Municipality of Taft	Barangay San Rafael	KP298131	KP298307	KP298383	KP298240
Platymantis	sp. 12	RMB 3641	TNHC 62070	Philippines	Luzon PAIC, Quezon Province	Luzon	Municipality of Tayabas	Barangay Lalo, Mt. Banahao	KP298132	KP298308	KP298384	KP298241
Platymantis	sp. 5	RMB 4625	FMNH 266271	Philippines	Luzon PAIC, Zambales Province	Luzon	Municipality of Masinloc	Mt. HighPeak	KP298134		KP298386	KP298243
Platymantis	sp. 25	ELR 234	PNM unnumbered	Philippines	Luzon PAIC, Nueva Vizcaya Province	Luzon	Municipality of Quezon	Barangay Maddiangat, Mount Palali	KP298136	KP298310	KP298387	KP298245
Platymantis	sp. 23	RMB 4220	PNM 7561	Philippines	Luzon PAIC, Cagayan Province	Luzon	Municipality of Gattaran	Gattaran Forest Reserve	KP298137	KP298311		KP298246
Platymantis	sp. 2	RMB 957	PNM 5780	Philippines	Luzon PAIC, Aurora Province	Luzon	Municipality of San Luis	Barangay Villa Aurora	KP298138	KP298312	KP298388	KP298247
Platymantis	*sierramadrensis*	RMB 973	CMNH 5904	Philippines	Luzon PAIC, Aurora Province	Luzon	Municipality of San Luis	Barangay Villa Aurora	KP298139		KP298389	KP298248
Platymantis	sp. 40	RMB 10235	KU 315214	Philippines	Mindanao PAIC, Zamboanga City Province	Mindanao	Municipality of Pasonanca		KP298141			
Platymantis	sp. 42	ELR 1147	KU 308682	Philippines	Luzon PAIC, Nueva Vizcaya Province	Luzon	Municipality of Quezon	Barangay Maddiangat, Mount Palali	KP298142			KP298250

Platymantis	*spelaeus*	CDS 265	KU 300435	Philippines	West Visayan PAIC, Negros Oriental Province	Negros		Barangay Cauayan	KP298143	KP298313	KP298390	KP298251
Platymantis	sp. 36	RMB 5764	KU 304644	Philippines	Luzon PAIC, Cagayan Province	Luzon	Municipality of Calayan	Barangay Balatabat; Local area name = 'Limandok'	KP298144	KP298314	KP298391	KP298252
Platymantis	*subterrestris*	RMB 3186	FMNH 259594	Philippines	Luzon PAIC, Kalinga Province	Luzon	Municipality of Balbalasang	Barangay Balbalasang, Mapga	KP298146	KP298315	KP298392	KP298253
Platymantis	*taylori*	ACD 1931	PNM 6524	Philippines	Luzon PAIC, Isabela Province	Luzon	Municipality of Palanan,	Barangay Didian, Sitio Natapdukan	KP298148	KP298316	KP298393	
Ingerana	*tenasserimensis*		CAS 205064	Myanmar	Rakhine State		Indochina	Gwa Township, ca 0.5 mi S of Pleasant Beach Resort	DQ347030		AY322308	
Sanguirana	*luzonensis*	RMB 3160	FMHH 259478	Philippines	Luzon PAIC, Kalinga Province	Luzon	Municipality of Balbalasang	Barangay Balbalasang, Mapga	KF477636			
Sanguirana	*sanguinea*	RMB 3075	KU 329484	Philippines	Palawan PAIC	Palawan	Municipality of Brooke's Point	Barangay Mainit, Mainit Falls	KP298051	DQ347273	DQ347180	
Hoplobatrachus	*rugulosus*	ACD 912	PNM 7827	Philippines	Luzon PAIC, Laguna Province	Luzon	Municipality of Los Baños	Barangay Batong Malake, Mt. Makiling	AY313685			
Huia	*masonii*	RMB 2124	TNHC 59914	Indonesia	Sundaland, West Java Province	Java	Kecamatan Kadudampit	Kabupaten Gede Panagrango Kelurahan Pangrango, Cigunung River, 6 km N Cisaat		EF088247	EU076770	
Hylarana	*grandocula*	RMB 2842	PNM 7588	Philippines	Eastern Visayan Islands	Bohol	Bohol Province, Municipality of Atequera	Barangay Poblacion	KF477675		KF477546	KF477814
Hylarana	*moellendorffi*	RMB 3077	PNM 7598	Philippines	Palawan PAIC	Palawan	Municipality of Brooke's Point	Boundary of Barangay Samarinana and Saulog: Mt. Mantalingahan Range	KF477699		KF477569	KF477836
Hylarana	*nicobariensis*	RMB 2086	TNHC 59856	Indonesia	West Java Province	Java	Sundaland	Depok City; University of Indonesia campus	AY326062		DQ347181	
Kaloula	*picta*	DLSUD 021	DLSUD 021	Philippines	Luzon PAIC, Cavite Province	Luzon		Mt. Palay -palay National Park	KC822553			
Limnonectes	*microtympanum*	RMB 1559	TNHC 59256	Indonesia	Eastern Indonesia, Sulawesi Tengah Province	Sulawesi	Kabupatan Banggai	Kecamatan Bagimana, Desa Siuna, Dusun Satu, Kampung Siuna, 4 km E of town at base of Mt. Tompotika	AY313745			
Limnonectes	*woodworthi*	ACD 949	PNM Unnumbered	Philippines	Luzon PAIC, Quezon Province	Luzon	Municipality of Atimonan,	Barangay Malinao Ilaya	AY313712			

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Figure S1. Partitioned Bayesian analyses (letters denote nodes of interest; see text and Figs. 2 and 3). Strongly supported conflict between nuclear [left; four partitions: recombinase activating gene 1 (RAG1), tyrosinase (Tyr), proopiomelanocortin (POMC), third codon positions combined) and mitochondrial (right; two partitions: 12S and 16S) gene partitions is most probably an artefact of missing 12S data.