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Phylogenomics informs a generic revision of the Australo-Papuan treefrogs (Anura: Pelodryadidae)

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ABSTRACT

The generic level classification of the Australo-Papuan hyloid family Pelodryadidae is contentious and unstable. The major issue is the lack of a well resolved and comprehensively sampled phylogeny for the family's 233 species, that are placed presently in only three genera. One of these genera, *Litoria*, comprises most of the species and has long been regarded as paraphyletic. We present a molecular phylogenetic framework for a revision of the family's generic level classification that is based on taxonomically comprehensive mitochondrial and phylogenomic scale DNA sequence datasets. Our analyses provided a well-resolved phylogeny and in combination with comprehensive morphological, acoustic, and life history data provide the basis for recognizing a total of 35 genera for the Pelodryadidae. We also identified a largely Melanesian clade that represents a rapid recent radiation comprising a number of phenotypically distinctive crown groups. Geographically, Australia and Melanesia each host 13 endemic genera and share another nine genera. Our classification provides a stable generic taxonomy for the Pelodryadidae and gives it a functional value for the wide range of scientists and community members who are concerned with biodiversity science and legislative conservation management.

Keywords: New Guinea; Melanesia; mtDNA; nuclear DNA; *Cyclorana*; *Litoria*; *Nyctimystes*

INTRODUCTION

The Australo-Papuan region comprises two quite contrasting environments for frogs. On one hand, the large tropical island of New Guinea is covered primarily with forests ranging from tropical savannah woodlands in the south to lowland and montane rainforests and alpine grasslands in the north and interior. On the other hand, a large proportion of the Australian landscape comprises arid and semi-arid habitats and wet-dry tropical savannahs, with moist forests being confined largely to the eastern coastal margin and the south-west of the continent. Since the Early Miocene when the leading edge of the Australian plate began to collide with the south-eastern margin of the Asian plate (Hall *et al.* 2011), Australia and New Guinea have had the opportunity for sharing of Gondwanan and Asian-derived anuran lineages. More recently both regions have been serially connected by land-bridges throughout the Plio-Pleistocene glacial cycles providing numerous opportunities for vicariant episodes.

Of the seven anuran families that occur in the Australo-Papuan region, the family Pelodryadidae Günther, 1858, a lineage within the larger Gondwanic radiation of hyloid frogs (Darst and

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Cannatella 2004, Faivovich *et al.* 2005, Frost *et al.* 2006, Zhang *et al.* 2013, Duellman *et al.* 2016, Streicher *et al.* 2018, Hime *et al.* 2021), has diversified into the widest range of habitats and occupies the widest geographic range, occurring from Seram and Timor in the west to the Solomon Islands in the east and throughout continental Australia and Tasmania, and has been introduced into New Zealand, New Caledonia, and Vanuatu (Ineich *et al.* 2015). The family comprises 233 species, of which roughly half occur in Australia and half in Melanesia and eastern Indonesia, and contributes 28% of anuran species diversity in the region. On a global scale Oliver *et al.* (2022) show that Melanesia has the world's most diverse insular amphibian fauna, with over 7% of frog species globally in less than 0.7% of the world's land area, and with over 97% of species endemic. The region encompasses three biodiversity hotspots (Myers *et al.* 2000) and falls within the governance of four countries: Australia, Indonesia, Papua New Guinea, and the Solomon Islands.

Unsurprisingly, given the ecological breadth of the Pelodryadidae, the group also displays a wide range of variation in morphological and life history traits that show strong associations with ecological specializations (Burton 1996, Menzies 2006, Vidal-García and Keogh 2015, Anstis 2017). Body size (SVL) shows a large range of variation from 2 cm to 13.5 cm (Tyler 1968a). Relative limb length in ground dwellers is long to very long, with the exception of the specialized burrowing *Cyclorana*. One clade of ground-dwellers has a rocket-shaped habitus characterized by a pointed snout, long legs, and long digits. Many arboreal and scansorial taxa are dorso-ventrally flattened and have enlarged finger and/or toe discs particularly in primarily arboreal taxa. Egg size and pigmentation, clutch size, and tadpole morphology correlate with egg deposition sites for which particular taxa show strong fidelity, including breeding in ephemeral or permanent still waters, flowing water, or torrents, or deposition of eggs on vegetation over water or in tree holes (Menzies 2006, Anstis 2017, Richards *et al.* 2023).

Until recently three genera, *Cyclorana* Steindachner, 1867, *Litoria* Tschudi, 1838, and *Nyctimystes* Stejneger, 1916, were used to taxonomically allocate diversity within the Pelodryadidae. Wells and Wellington (1985) described more genera, but the questionable scientific quality of their work has led to limited acceptance of their taxonomic changes. More recent revisions have included species groups split across separate genera despite strong genetic evidence of their monophyly (Duellman *et al.* 2016) or were not comprehensive treatments (Dubois and Frétey 2016). In comparison with the three other family level Australo-Papuan anuran groups, the generic level classification of diversity in pelodryadids is disparate. The 233 species in three genera of pelodryadids contrasts dramatically with the myobatrachids (14 genera, 91 species), limnodynastids (seven genera, 44 species) and microhylids—Asterophryinae (15 genera, 353 species).

Nyctimystes comprises a distinctive lineage of 31 species of tree frogs from the Australo-Papuan region that Tyler and Davies (1979a) distinguished from *Cyclorana* and *Litoria* in their extended diagnosis based on 39 characters. Menzies (2006) pointed out that all but two of the characters, pupil shape and patterning on the palpebral membrane, are not likely to be autapomorphic. Uncertainty regarding the affinities of frogs placed in *Nyctimystes* started to emerge with a review (Tyler and Davies 1979a) which inferred that *Nyctimystes* is related to a subset of lineages within the morphologically and ecologically diverse *Litoria*, a notion inconsistent with the continued use of *Litoria* as the single generic name for the pelodryadids exclusive of *Nyctimystes*. Haas and Richards (1998) showed that the larvae of the *Litoria nannotis* Group and *Nyctimystes dayi* (Günther, 1897) share a unique upper jaw-opening mechanism involving the adrostral cartilage as a pushing-rod element which is not present in three other pelodryadid species groups (*sensu* Tyler and Davies 1978), further suggesting paraphyly of *Litoria*. In a revision of amphibians world-wide, Frost *et al.* (2006) demonstrated that *Nyctimystes* is paraphyletic with *Litoria* and diphyletic as *N. dayi* from the north-eastern Australian wet tropics was allied with *L. nannotis* (Andersson, 1916) from the same geographic region. These findings were extended by Rosauer *et al.* (2009) and Richards *et al.* (2010) in taxonomically more comprehensive mitochondrial DNA-based phylogenies which confirmed the relationship of *N. dayi* with the *Litoria nannotis* Group and, further, showed a relationship of New Guinean *Nyctimystes* with *Litoria infrafrenata* (Günther, 1867). From a morphological perspective Kraus (2013a) and Menzies and Riyanto (2015) demonstrated that neither of the two extra-limital taxa, *Nyctimystes dayi* from Australia and *Nyctimystes rueppelli* (Boettger, 1895) from the Moluccan islands, conformed with a diagnosis for *Nyctimystes* that includes a combination of a vertical pupil, patterning of the palpebral membrane, and unpigmented ova. With the removal of the two extra-limital species, *Nyctimystes* has a distribution confined to New Guinea and its satellite islands.

The affinities of burrowing frogs of the genus *Cyclorana* also have undergone some revision. Based on their fossorial adaptations, *Cyclorana* were placed with burrowing groups of the myobatrachids (Parker 1940), but subsequently their evolutionary affinity with the pelodryadids was recognized by Tyler (1978) and King *et al.* (1979). Later molecular phylogenetic analyses demonstrated a paraphyletic relationship with *Litoria s.l.* and in particular a sister group relationship with the *Litoria aurea* Group (Maxson *et al.* 1982, Hutchinson and Maxson 1987). Phylogenetic analyses of nucleotide sequences (Frost *et al.* 2006, Rosauer *et al.* 2009, Duellman *et al.* 2016) also confirmed a close relationship of *Cyclorana* with the *Litoria aurea* Group *sensu* Tyler and Davies (1978) which included *Litoria dahlii* (Boulenger, 1895).

Molecular clock estimates of an Oligocene timing for the initial diversification within the Pelodryadidae (Brennan *et al.* 2024) are consistent with a long evolutionary history for *Litoria s.l.* The taxonomically comprehensive analysis (at that time) of Tyler and Davies (1978) was the first and only attempt so far to comprehensively recognize taxonomic units within the immensely morphologically and ecologically diverse *Litoria*. This is primarily because of the high level of convergence combined with a relatively conservative external morphology, which Vidal-Garcia and Keogh (2015) have demonstrated recently for convergence in body shape for pelodryadids from Australia. In comparison with other groups of vertebrates from the Australo-Papuan region that have diversified over a comparable timescale to the pelodryadids, the three-genus classification of pelodyradids does not adequately delineate the evolutionary diversity of the family. For instance, murine rodents are classified in 38 genera in < 10 Mya (Roycroft *et al.* 2022); the marsupials:

Dasyuridae 18 genera in < 30 Mya; Peramelidae six genera in < 20 Mya; Macropodinae 12 genera in < 20 Mya (Mitchell *et al.* 2014); elapid snakes 37 genera in < 15 Mya (Sanders *et al.* 2008); python snakes nine genera in < 25 Mya (Esquerré *et al.* 2020); agamid lizards 17 genera in < 25 Mya (Hugall *et al.* 2008); sphenomorphine skinks 16 genera in < 30 Mya (Rabosky *et al.* 2007); and microhylid frogs > 18 genera in < 20 Mya (Hill *et al.* 2022).

The substantial residual issues of resolving the relationships among *Cyclorana*, *Nyctimystes*, and the many deep lineages of *Litoria*, and demonstrating that the groups of *Litoria* (*sensu* Tyler and Davies 1978) represent lineages, are requirements for establishing a generic classification for the pelodryadids that is based on their evolutionary history. We also note that 101 species of pelodryadines have been described since the seminal work of Tyler and Davies (1978). To establish evolutionary relationships within the family, we employed a two-phase approach. We first sequenced as many taxa as were available to us with the mitochondrial *ND4* gene to identify crown groups [in most cases equivalent to the Groups of Tyler and Davies (1978)] that, in effect, are candidate genera. We then implemented a phylogenomic approach to test that the mitochondrial crown groups do indeed represent lineages and to establish relationships among these. To this end, we used a targeted sequence capture approach (Faircloth *et al.* 2012, Lemmon *et al.* 2012) to obtain sequences for more than 350 nuclear genes from a subset of the taxa that represent the crown groups and isolated lineages. In particular, we used the Anchored Hybrid Enrichment protocol [AHE—*Lemmon et al.* (2012)] that was specifically optimized for amphibian phylogenomics (Chen *et al.* 2020, Hime *et al.* 2021).

The phylogeny provides strong evidence of relationships and monophyly of groups which we then combine with large phenotypic datasets of egg, larval, and adult internal and external morphology, life history, and acoustic characters to define morphologically cohesive and distinctive groups as genera while minimizing the number of monotypic genera. We present a thorough revision of the Pelodryadidae where we recognize 35 genera in the Pelodryadidae based on comprehensive and diverse data sets, naming 20 new genera *Amnihyla* Richards, Mahony & Donnellan, *Carichyla* Mahony, Donnellan and Richards, *Chlorohyla* Mahony, Donnellan & Richards, *Eremnoculus* Mahony, Richards & Donnellan, *Exedrobatrachus* Richards, Mahony & Donnellan, *Exochohyla* Richards, Mahony & Donnellan, *Hyalotos* Richards, Mahony & Donnellan, *Ischnohyla* Richards, Mahony & Donnellan, *Kallistobatrachus* Richards, Mahony & Donnellan, *Lathrana* Richards, Mahony & Donnellan, *Leptobatrachus* Richards, Donnellan & Mahony, *Megatestis* Donnellan, Mahony & Richards, *Melvillihyla* Richards, Donnellan & Mahony, *Nasutibatrachus* Richards, Mahony & Donnellan, *Papuahyla* Donnellan, Mahony & Richards, *Rhyaconastes* Mahony, Donnellan & Richards, *Spicicalyx* Donnellan, Mahony & Richards, *Sylvagemma* Mahony, Donnellan & Richards, *Teretistes* Richards, Mahony & Donnellan and *Viridihyla* Richards, Mahony & Donnellan and raising a further 12 from synonymy..

In light of the plethora of recent publications proposing taxonomic changes for pelodryadids, we adopt the approach to nomenclatural precedence as articulated by the Australian Society of Herpetologists (ASH 2024) in which taxonomic decisions in herpetology and their nomenclatural consequences are acceptable only when supported by a body of evidence published within the peer-review process which is specified through a list of journals and other publications that meet the criteria for an acceptable peer review process.

MATERIAL AND METHODS

Mitochondrial DNA survey

We obtained mitochondrial *ND4* sequences from multiple individuals of all taxa (where samples were available) by Sanger nucleotide sequencing or from ‘bycatch’ from AHE experiments (Lemmon *et al.* 2012). A total of 344 sequences from 179 pelodryadid species were used along with 12 outgroups.

For sequences obtained by Sanger sequencing, DNA extraction, PCR, nucleotide sequencing, sequence editing, and alignment protocols are described in Anstis *et al.* (2016). PCR primer sequences are listed in Supporting Information, Table S1. Sequences were aligned with Muscle v.6.814b (Edgar 2004) implemented in Geneious Pro v.8.1.4 (Kearse *et al.* 2012) and GenBank accession numbers are listed in Supporting Information, Table S2. For sequences obtained from ‘bycatch’ from AHE experiments, we reconstructed the mitochondrial genomes from the raw reads for each sample using a wrapper R script based on MITObim v.1.9 (Hahn *et al.* 2013). As a reference, we used the mitochondrial genome of *Nyctimystes kubori* Zweifel, 1958 (GenBank accession no. JX564879). We aligned the reconstructed sequences using MAFFT v.7.3 (Katoh and Standley 2013) and then carefully inspected and edited the alignment by eye.

For model-based phylogenetic inference, we estimated the best substitution model and partition scheme from three data subsets comprising the 1st, 2^{nd}, and 3rd codon positions, with ModelFinder (Kalyaanamoorthy *et al.* 2017) following the Bayes Information Criterion (BIC). For maximum likelihood phylogenetic tree reconstruction, we used IQ-tree (Nguyen *et al.* 2015) on the IQ-TREE webserver (Trifinopoulos *et al.* 2016). We assessed branch support with 100 standard bootstrap pseudo-replicates (Hoang *et al.* 2018).

Anchored hybrid enrichment phylogenomic methods

We assembled an exon-capture dataset comprising 183 frog species spanning most major anuran clades with particular focus on the Australo-Papuan family Pelodryadidae (Supporting Information, Table S2). This dataset includes unprecedented species (72%) sampling of the Pelodryadidae. We generated new AHE (Lemmon *et al.* 2012) data for 167 samples and combined these with 21 outgroup samples from the amphibian phylogenomic dataset of Hime *et al.* (2021). Outgroup sampling was designed around maximizing commonly used anuran fossil calibrations to provide a consistent time-calibrated phylogenomic estimate of pelodryadid frogs. Data from different AHE projects (Supporting Information, Table S2) were combined using custom scripts which relied on *metablastr* to identify orthologous loci (*blast_best_reciprocal_hit*) (Benoit and Drost 2021), *mafft* to align them (*--add*, *--keeplength*) (Katoh and Standley 2013), and *AMAS* to manipulate alignments (Borowiec 2016). Final locus alignments are presented in Supporting Information, AHE locus alignments. We reconstructed individual genealogies for our exon-capture data ($N = 352$) under maximum-likelihood in IQTREE (Nguyen *et al.* 2015), allowing the program to assign the best fitting model of nucleotide substitution using ModelFinder (Kalyaanamoorthy *et al.* 2017) and then perform 1000 ultrafast bootstraps (Minh *et al.* 2013). We then estimated a species tree using the quartet-based summary method ASTRAL III (Zhang *et al.* 2018) with IQTREE gene trees as input. The local posterior probability (LPP) was used to assess support for branches (Sayyari and Mirarab 2016). To estimate divergence times among taxa we applied a series of fossil calibrations first compiled by Feng *et al.* (2017) (Supporting Information, Text S1) and used the Bayesian divergence time software MCMCtree (Rannala and Yang 2007). We started by concatenating all loci and considering them in two partitions, first and second codons together, and third codons separately. We then used *baseml* to estimate approximate likelihoods (dos Reis and Yang 2011) and branch lengths before running *mcmctree* on the gradient and Hessian (in.BV file) for five replicate analyses. We inspected Markov chain Monte Carlo (MCMC) files for stationarity and compared for convergence, then combined them using logCombiner (Drummond and Rambaut 2007) , and used this combined MCMC file to summarize divergence times on our tree (*print* = *-1* in.ctl file).

Adult morphological data

We summarized morphological data presented in numerous publications, and from our own observations and unpublished data from Dr Margaret Davies (summarized in Supporting Information, Table S3 along with data sources). In the diagnoses, where morphological characters have not been determined for particular species, we indicate the number of species for each genus for which the character state was determined. Where these numbers are not indicated the character state had been determined in all species of that genus.

For size (snout to vent length—SVL) we used the maximum SVL reported for a species. For relative hindlimb length—tibia length/snout to vent length (TL/SVL) and relative eye size—eye diameter/snout to vent length (ED/SVL), we tabulated or calculated the value of the mean for individual species from literature records and unpublished data of colleagues (Supporting Information, Table S3). Where literature records presented the range only for relative hindlimb length and eye size, we used the mid-point value of the range.

As verbal descriptions of relative size are not used in a consistent way in the literature, we evaluated the range of values for overall size, relative hindlimb length, and relative eye size, and assigned size range bins for each variable based on the 'medium' category encompassing the bin with the highest frequency. For snout to vent length (SVL), we followed Duellman (1970), in recognizing the following size categories in the diagnoses: 'small' (up to 30 mm), 'medium' (31–50 mm), 'large' (51–80 mm), and 'very large' (>80 mm). For relative hindlimb length (TL/SVL), we used the following ranges of ratios as categories in the diagnoses: 'small' (0.32–0.415), 'medium' (0.415–0.51), 'long' (0.51–0.605), and 'very long' (0.605–0.67). For relative eye size (ED/SVL), we used the following ranges of ratios as categories in the diagnoses: 'small' (0.065–0.093), 'medium' (0.094–0.122), and 'large' (0.123–0.152).

Adult external morphological characters that were assessed included: the degree of webbing of fingers: 'no webbing' [Tyler (1968: fig. 10)], 'reduced' (does not reach distal sub-articular tubercle on digit III [Tyler (1968: fig. 18)], 'fully webbed' (reaches terminal disc on finger III [Tyler (1968: fig. 4)]; and toe webbing: 'minimal' (reaches second most distal sub-articular tubercle on toe IV [Tyler (1968: fig. 48)], 'reduced' (reaches most distal sub-articular tubercle on toe IV [Tyler (1968: fig. 49)], 'fully webbed' [reaches terminal disc on toe IV- Tyler (1968: fig. 4)]; the size of terminal discs on fingers ('undeveloped'—not extending beyond fringe of penultimate phalanx, 'prominent'—obviously extending laterally beyond the fringe of penultimate phalanx); the size of finger discs relative to toe discs ('equal', 'smaller'); pupil shape (vertical or not vertical); inner metatarsal tubercule (IMT) length ('long'—equal to or longer than length of digit 1, 'short'—less than half the length of digit 1); the form of the nuptial pad (spinous—with enlarged conical or spine-shaped papillae vs. granular—fine, numerous densely arranged or pigmented papillae or larger, sometimes almost conical and more widely spaced papillae [Tyler 1968a: fig. 3, Cunningham 2002: fig. 2, Günther *et al.* 2023: fig. 2]); dorsal colour pattern; and the presence/absence characters: vomerine teeth, vocal sac (determined from the presence of vocal slits), rostral spike, transparency of the tympanum, patterning of the palpebral membrane, dermal ornamentation on the hindlimbs ('absent' or 'prominent pigmented tubercles' or 'crenulations'), and heel spike.

Internal and skeletal characters included presence or absence of the adductor mandibulae externus superficialis muscle (AMES), presence or absence of the alary process of the hyoid, and intercalary structure located between the terminal and subterminal (penultimate) phalanges in the digits (absent, cartilaginous or ossified) described by Tyler and Davies (1978) and Davies (unpublished data) and three hand muscle characters: m. extensor digitorum communis, m. extensor brevis medius digiti IV, and m. palmaris longus from Burton (1996). Although Burton (1996) described a number of other hand muscle characters we were unable to determine the character states for these from the text descriptions.

Colour images of individuals in life were available for 218 species, and are presented as part of the generic descriptions, to illustrate the general body habitus and colour pattern characters (image details are presented in Supporting Information, Table S4). Summary descriptions of generic dorsal colours and patterns were developed from species accounts in Menzies (2006) and Sanders (2021) and original species descriptions (Table 1; Supporting Information, Table S3).

Reproductive data

Egg and larval characters that were compiled included: egg size and pigmentation, and tadpole oral disc types and overall tadpole morphology type following Anstis's (2017) classification criteria and nomenclature for Australian species. We use a modified version of the size classification for eggs of Anstis (2017) so that literature records without measurements could be

Table 1. Morphological and reproductive data summary by genus for the Pelodryadidae. Character state frequency coding: normal font—most frequent character state, bold text—next most frequent character state, underlined text—least frequent character state. The species for which a particular character state was determined is detailed in Supporting Information, Table S3. Sources of data are listed in Supporting Information, Table S3, and literature references are included in the text

Genus	No. of species	Size	TL/SVL	ED/SVL	Pupil	Palpebral membrane patterning	Tympanum	Vocal sac	Vomerine teeth
Amnihyla	24	Small (18), medium (5), **large** (1)	Long (11), very long (13)	**Small** (1), medium (11), large (12)	Not vertical	Absent	Visible	Present	**Absent** (5), present (19)
Carichyla	2	Small	**Medium** (1), long (1)	**Small** (1), medium (1)	Not vertical	Absent	Visible	Present	**Absent** (1), present (1)
Chlorohyla	12	Small (7), medium (5)	Long	Medium (8), large (4)	Not vertical	Absent	Visible	Present	Present
Coggerdonia	1	Medium	**Medium**	**Small**	Not vertical	Absent	Visible	Present	Present
Colleeneremia	12	Small (8), medium (4)	Short (4), **medium** (6), long (2)	**Small** (5), medium (6), large (1)	Not vertical	**Well-developed** (1), **poorly developed** (1), absent (10)	Visible	Present	Present (11)
Cyclorana	14	Small (1), medium (9), **large** (2), very large (2)	Short (11), **medium** (3)	**Small** (1), medium (12), large (1)	Not vertical	Absent	Visible	Present	Present
Drymomantis	3	Small	**Medium** (2), long (1)	Medium	Not vertical	Absent	Visible	Present	**Absent** (2), present (1)
Dryopsophus	10	Small (6), medium (4)	**Medium** (3), long (7)	Medium	Not vertical	Absent	Visible	Present	Present (8)
Eremnoculus	1	Medium	Long	Large	Not vertical	**Well-developed**	Visible	Present	Present
Exedrobatrachus	1	Small	Long	Medium	Not vertical	Absent	Visible	Present	**Absent**
Exochohyla	4	Small (1), medium (3)	**Medium** (3), long (1)	**Small** (1), medium (2), large (1)	Not vertical	Absent	Visible	Present	Present
Hyalotos	3	Small	Long (2), very long (1)	Medium (2), large (1)	Not vertical	Absent	**Transparent**	Present	**Absent** (2), present (1)
Ischnohyla	5	Small	Long	Medium (4), large (1)	Not vertical	Absent	Visible	Present	**Absent** (2), present (1)
Kallistobatrachus	8	Small	**Medium** (1), long (7)	Medium (6), large (1)	Not vertical	Absent	Visible	Present	**Absent** (2), present (6)
Lathrana	1	Small	**Medium**	Medium	Not vertical	Absent	Visible	Present	Present

Table 1. Continued

Genus	No. of species	Size	TL/SVL	ED/SVL	Pupil	Palpebral membrane patterning	Tympanum	Vocal sac	Vomerine teeth
Leptobatrachus	5	Small (2), medium (3)	Long	**Small** (1), medium (3), large (1)	Not vertical	Absent	Visible	Present	Present
Litoria	13	Small (10), medium (2), **large** (1)	**Medium** (1), long (5), very long (7)	**Small** (1), medium (12)	Not vertical	Absent	Visible	Present	Present
Mahonabatrachus	6	Small	Long (5), very long (1)	Medium (5), large (2)	Not vertical	Absent	Visible	Present	**Absent** (1), present (5)
Megatestis	1	Medium	**Medium**	**Small**	Not vertical	Absent	Visible	**Absent**	Present
Melvillihyla	1	Very large	Long	Medium	Not vertical	Absent	Visible	**Absent**	Present
Mosleyia	4	Small (3), medium (1)	**Medium** (1), long (3)	Medium (3), large (1)	Not vertical	Absent	Visible	**Absent**	Present
Nasutibatrachus	5	Small	**Medium** (2), long (3)	Medium	Not vertical	Absent	Visible	Present	**Absent**
Nyctimystes	32	Small (4), medium (20), **large** (7), very large (1)	Long (24), very long (8)	**Small** (1), medium (21), large (8)	**Vertical**	**Well-developed**	Visible	**Absent** (5), present (24)	Present (27)
Papuahyla	9	Small	**Medium** (1), long (8)	Medium (5), large (3)	Not vertical	Absent (7)	Visible	Present (8)	**Absent** (6), present (3)
Pelodryas	5	Medium (2), **large** (2), very large (1),	**Medium**	**Small** (4), medium (1)	Not vertical	Absent	Visible	Present	Present
Pengilleyia	6	**Large**	**Medium** (3), long (3)	**Small** (3), medium (3)	Not vertical	Absent	Visible	Present	Present
Ranoidea	5	Medium	**Medium** (3), long (2)	**Small**	Not vertical	Absent	Visible	Present	Present
Rawlinsonia	8	Small (6), medium (1), **large** (1)	**Medium** (4), long (4)	Medium	Not vertical	Absent	Visible	Present	Present (7)
Rhyaconastes	4	Medium (2), **large** (2)	Long (2), very long (2)	Medium	Not vertical	Absent	Visible	**Absent**	Present
Saganura	1	Medium	Long	Medium	Not vertical	Absent	Visible	Present	Present
Sandyrana	14	Medium (5), **large** (7), very large (2)	Long (13)	**Small** (1), medium (12)	Not vertical	**Well-developed** (1), **poorly developed** (1), absent (12)	Visible	Present	Present

Table 1. Continued

Genus	No. of species	Size	TL/SVL	ED/SVL	Pupil	Palpebral membrane patterning	Tympanum	Vocal sac	Vomerine teeth
Spicicalyx	5	Small (2), medium (3)	Long	**Small** (1), medium (3), large (1)	Not vertical	Absent	Visible	**Absent**	Present
Sylvagemma	1	Medium	**Medium**	Medium	Not vertical	Absent	Visible	Present	Present
Teretistes	1	Small	Long	Medium	Not vertical	Absent	Visible	Present	**Absent**
Viridihyla	5	Small	**Medium** (1), long (5)	Medium (3), large (2)	Not vertical	Absent	Visible	Present	Present
Hyla jeudii	-	Small	**Medium**	Medium	ND	Absent	Visible	Nd	Present

Genus	No. of species	Nuptial pad	Rostral spike	Finger webbing	Toe webbing	Finger discs	Toe vs. finger discs	Ornamentation on hindlimb	Heel spike
Amnihyla	24	Granular (19)	Absent	**None** (7), reduced (16)	**Minimal** (4), reduced (16), fully (4)	Expanded	Equal (19), **smaller** (5)	Unornamented (5), **tubercles** (13), crenulations (4)	**Present** (4), absent (20)
Carichyla	2	Granular	Absent	**None** (1), reduced (1)	Reduced (1), fully (1)	Expanded	Equal	Unornamented	Absent
Chlorohyla	12	Granular (11)	Absent	Reduced	Reduced (8), fully (3)	Expanded	Equal (6), **smaller** (5)	Unornamented	Absent
Coggerdonia	1	Granular	Absent	Reduced	Reduced	Expanded	Equal	Unornamented	Absent
Colleeneremia	12	Granular (10)	Absent	**None** (1), reduced (11)	**Minimal** (3), reduced (9)	Expanded	Equal (11), **smaller** (1)	Unornamented (11), **tubercles** (1)	Absent
Cyclorana	14	Granular	Absent	**None**	**Minimal**	**Undeveloped**	Equal	Unornamented	Absent
Drymomantis	3	Granular	Absent	Reduced	Reduced (2), fully (1)	Expanded	Equal	Unornamented	Absent
Dryopsophus	10	Granular	Absent	**None** (1), reduced (9)	**Minimal**, reduced	Expanded	Equal (9), **smaller** (1)	Unornamented	Absent
Eremnoculus	1	Granular	Absent	Reduced	**Minimal**	Expanded	Equal	Unornamented	Absent
Exedrobatrachus	1	Granular	Absent	Reduced	Reduced	Expanded	**Smaller**	**Tubercles**	Absent
Exochohyla	4	Granular (3)	Present in both sexes	Reduced (1), fully (3)	Fully (3), reduced (1)	Expanded	Equal	**Tubercles** (3), crenulations (2)	Absent
Hyalotos	3	Granular	Absent	Reduced (1), fully (2)	**Minimal** (1), reduced (2)	Expanded	Equal	Crenulations	Absent
Ischnohyla	5	Granular	Absent	Reduced (4), fully (1)	Reduced (4), Fully (1),	Expanded	Equal (4), **smaller** (1)	Unornamented (1), **tubercles** (2), crenulations (2)	Absent
Kallistobatrachus	8	Granular (6)	Absent	**None** (1), reduced (6)	Reduced (7)	Expanded	Equal (6), **smaller** (2)	**Tubercles** (5), crenulations (2)	Absent

Table 1. Continued

Genus	No. of species	Nuptial pad	Rostral spike	Finger webbing	Toe webbing	Finger discs	Toe vs. finger discs	Ornamentation on hindlimb	Heel spike
Lathrana	1	Granular	Absent	Reduced	Reduced	Expanded	Smaller	**Tubercles**	Absent
Leptobatrachus	5	Granular	Absent	**None** (2), reduced (2), fully (1)	**Minimal** (1), reduced (2), fully (2)	Expanded	Equal (1), **smaller** (4)	Unornamented (3), **tubercles** (2)	Absent
Litoria	13	Granular	Absent	**None**	**Minimal**	**Undeveloped** (10), expanded (3)	Equal (11), **smaller** (2)	Unornamented	Absent
Mahonabatrachus	6	Granular	Absent	**None**	**Minimal** (4), reduced (1), fully (1)	**Undeveloped** (1), expanded (5)	Equal	Unornamented (3), **tubercles** (3)	Absent
Megatestis	1	Granular	Absent	**None**	Fully	**Undeveloped**	Equal	Unornamented	Absent
Melvillihyla	1	Granular	Absent	**None**	Reduced	Expanded	Equal	Unornamented	Absent
Mosleyia	4	**Spinous**	Absent	Reduced	Fully	Expanded	Equal, **smaller**	Unornamented (2), **tubercles** (2)	Absent
Nasutibatrachus	5	Granular	**Present** only in males	Reduced	Reduced	**Undeveloped** (1), expanded (4)	Equal	Unornamented (1), **tubercle** (4)	Absent
Nyctimystes	32	Granular (19), **spinous** (4)	Absent	Reduced	Reduced	Expanded (30)	Equal (18), **smaller** (5)	Unornamented (5), **tubercles** (19), crenulations (4)	**Present** (13), absent (18)
Papuahyla	9	Granular (7)	Absent	**None** (1), reduced (7)	Reduced (5), fully (3)	Expanded	Equal (7), **smaller** (1)	Unornamented	Absent (7)
Pelodryas	5	Granular	Absent	**None** (2), reduced (3)	Reduced	Expanded	Equal (3), **smaller** (2)	Unornamented	Absent
Pengilleyia	6	Granular	Absent	Reduced (4), fully (2)	Reduced (2), fully (4)	Expanded	Equal (3), **smaller** (3)r	Unornamented (4), crenulations (2)	Absent
Ranoidea	5	Granular	Absent	**None**	Reduced (3), fully (2)	**Undeveloped** (3), expanded (1)	Equal (3), **smaller** (1)	Unornamented	Absent
Rawlinsonia	8	Granular	Absent	**None** (3), reduced (4)	**Minimal** (1), reduced (7)	Expanded	Equal (4), **smaller** (4)	Unornamented	Absent
Rhyaconastes	4	Granular	Absent	**None**	Reduced	Expanded	Equal (1), **smaller** (3)	Unornamented	Absent
Saganura	1	Granular	Absent	**None**	**Minimal**	Expanded	Equal	Unornamented	Absent
Sandyrana	14	Granular (11)	Absent	Reduced (8), fully (6)	Reduced (3), fully (11)	Expanded	Equal (9), **smaller** (5)	Unornamented (4), **tubercles** (1), crenulations (7)	Absent
Spicicalyx	5	Granular	Absent	Reduced (4) fully (1)	Reduced (3), fully (2)	Expanded	Equal (3), **smaller** (2)	Crenulations	**Present**
Sylvagemma	1	Granular	Absent	**None**	**Minimal**	Expanded	Equal	Unornamented	Absent

Table 1. Continued

Genus	No. of species	Nuptial pad	Rostral spike	Finger webbing	Toe webbing	Finger discs	Toe vs. finger discs	Ornamentation on hindlimb	Heel spike
Teretistes	1	Granular	**Present** only in males	**None**	**Minimal**	Expanded	Equal	Unornamented	Absent
Viridihyla	5	Absent (3), granular (2)	Absent	Reduced (4), fully (1)	Reduced (4), fully (1)	Expanded	Equal	Unornamented (1), **tubercles** (1), crenulations (3)	Absent
Hyla jeudii	-	ND[a]	Absent	**None**	**Minimal**	Expanded	**Smaller**	Unornamented	Absent
Genus	**No. of species**	**Inner metatarsal tubercule**	**AMES[b]**	**Intercalary structures**	**Alary process of hyoid**	**Egg size**	**Egg pigmentation**	**Tadpole oral disc**	**Tadpole morph type**
Amnihyla	24	Small (23), **large** (2)	Absent (7)	Cartilaginous (1), ossified (13)	**Absent** (13)	**Large** (1), small (11)	**Unpigmented** (1), pigmented (11)	3 (2)	6 (2), 7 (2)
Carichyla	2	Small	Absent (1)	Ossified (1)	Present (1)	Small	Pigmented	1 (1)	1 (1)
Chlorohyla	12	Small	ND	Cartilaginous (1), ossified (3)	Present (4)	Small (5), medium (1)	Pigmented (6)	1 (3)	4 (3)
Coggerdonia	1	Small	Absent	Ossified	**Absent**	Small	Pigmented	1	1
Colleeneremia	12	Small	Absent (4)	Cartilaginous (2), ossified (5)	Present (1) **absent** (5)	Small (4), medium (1)	Pigmented (4)	1 (7)	1, 1A (7)
Cyclorana	14	**Large**	**Present** (1)	**Absent** (13), ossified (1)	Present (13)	Small (9)	Pigmented (9)	1	3
Drymomantis	3	Small	Absent (2)	Ossified (2)	Present (2), **absent** (1)	Small (2)	Pigmented	1	1
Dryopsophus	10	Small	Absent (5)	Cartilaginous (1), ossified (5)	Present (3), **absent** (2)	Small (4), medium (4)	Pigmented (8)	1 (6), 4 (1), 5 (2)	5 (6), 6 (3)
Eremnoculus	1	Small	**Present**	Cartilaginous	Present	**Large**	**Unpigmented**	6	7
Exedrobatrachus	1	Small	ND	Ossified	Present	Small	Pigmented	ND	ND
Exochohyla	4	Small (3)	ND	Ossified (1)	**Absent** (1)	**Large** (2)	**Unpigmented** (2), pigmented (2)	1A (1)	6 (1)
Hyalotos	3	Small (1), **large** (1)	ND	ND	ND	Medium (1), **large** (2)	Pigmented	ND	ND
Ischnohyla	5	Small	Absent (1)	Ossified (2)	Present (1), **absent** (2)	Small (1), medium (2), **large** (1)	**Unpigmented** (1), pigmented (4)	3 (1)	2A (1)

Table 1. Continued

Genus	No. of species	Inner metatarsal tubercule	AMES^{b}	Intercalary structures	Alary process of hyoid	Egg size	Egg pigmentation	Tadpole oral disc	Tadpole morph type
Kallistobatrachus	8	Small (6)	Absent (1)	Ossified (2)	**Absent** (1)	Small (2), medium (2)	Pigmented (4)	1B (1)	7 (1)
Lathrana	1	Small	ND	Ossified	**Absent**	Medium	Pigmented	1B (1)	ND
Leptobatrachus	5	Small	**Present** (3)	Cartilaginous (3)	Present (1)	Small (1)	Pigmented (1)	1, 1A (1)	4 (1)
Litoria	13	Small	Absent (7)	Ossified (10)	Present (10)	Small (6), medium (5)	Pigmented (11)	1 (9), 3 (3)	2, 2A (11), 6 (1)
Mahonabatrachus	6	Small	Absent (4)	Ossified (5)	Present (3), **absent** (1)	Small (4), **large** (1)	**Unpigmented** (1), pigmented (3)	1 (3), 3 (1)	2 (1), 5 (2), 6 (1)
Megatestis	1	Small	**Present**	Ossified	Present	Small	Pigmented	1	3
Melvillihyla	1	Small	ND	Ossified	Present	Small	Pigmented	1	5
Mosleyia	4	Small	Absent (3)	Cartilaginous (1), ossified (3)	Present	**Large** (3)	**Unpigmented** (3)	6	7
Nasutibatrachus	5	Small (3)	ND	ND	**Absent** (1)	ND	ND	ND	ND
Nyctimystes	32	Small	**Present** (9)	Cartilaginous (11)	**Absent** (8)	**Large** (5)	**Unpigmented** (6)	6A (2)	6 (2)
Papuahyla	9	Small	Absent (1)	Ossified (2)	**Absent** (3)	Small (5)	Pigmented (5)	1 (1)	1 (1)
Pelodryas	5	Small	**Present** (1)	Cartilaginous (3), ossified (1)	Present (1), **absent** (2)	Small (2), medium (2)	Pigmented (4)	1 (4)	1, 1A (4)
Pengilleyia	6	Small	Absent (5)	Cartilaginous	**Absent** (5)	Small (5)	Pigmented (6)	1 (5)	1 (5)
Ranoidea	5	Small	**Present**	Ossified	Present (2), **absent** (1)	Small (2)	Pigmented (3)	1	1
Rawlinsonia	8	Small	Absent (4)	Ossified (6)	**Absent** (5)	Small (3), medium (3)	Pigmented (6)	1 (7)	1 (7)
Rhyaconastes	4	Small	**Present** (2)	Cartilaginous (2)	Present (2)	Small (2), medium (2)	Pigmented (1)	3	6
Saganura	1	Small	Absent	Ossified	ND	**Large**	Pigmented	1	1
Sandyrana	14	Small	**Present** (1)	Cartilaginous (4)	Present (2)	Small (1), medium (1)	Pigmented (2)	1 (1)	1 (1)
Spicicalyx	5	Small	**Present** (2)	Cartilaginous (3)	Present (3)	**Large** (2)	Pigmented (4)	1 (3)	4 (3)
Sylvagemma	1	Small	**Present**	Ossified	Present	Medium,	Pigmented (4), **unpigmented** (1)	1A	1
Teretistes	1	ND	ND	ND	ND	**Large**	Pigmented	3	1
Viridihyla	5	Small	Absent (1)	Cartilaginous (1)	**Absent** (2)	ND	ND	ND	ND
Hyla jeudii	-	Small	ND	ND	ND	ND	ND	ND	ND

Table 1. Continued

Genus	No. of species	m. extensor digitorum communis	m. extensor brevis medius digiti IV	m. palmaris longus	Diploid number	Dorsal pattern
Amnihyla	24	2 slip (4)	Absent (4)	Multi-divided (4)	26 (4)	Base coloration green, dark brown, rufous brown, yellow-brown with green, olive, brown, or golden-yellow mottling or pale green spots or patches or sometimes with hour glass mark or lichen-like spots
Carichyla	2	2 slips (1)	Absent (1)	Multi-divided (1)	26 (1)	Yellow green to bright green or bronze and occasionally with small dark flecks
Chlorohyla	12	2 slips (3)	Absent (2), **present** (1)	Multi-divided (3)	26 (2)	Uniformly green, occasional scattered pale spots
Coggerdonia	1	ND	ND	ND	26	Commonly brown, less frequently grey or green, immaculate to peppered or with longitudinal patches
Colleeneremia	12	2 slips (2)	Absent (2)	Multi-divided (2)	26 (4)	Slate-grey to pale brown yellowish brown, brown to red-brown with broad irregular dark vertebral zone or two irregular dark transverse bands, or cream spots or vermiculations with or without pale mid-dorsal stripe or two dorso-lateral and lateral dark stripes and a thin dark mid-dorsal line
Cyclorana	14	2 slips (9)	**Present** (9)	**Reduced** (9)	26 (9)	Highly variable with maculations and with a discrete collar and or vertebral stripe in smaller taxa
Drymomantis	3	2 slips (1)	Absent (1)	Multi-divided (1)	26	Green or yellowish green or brown or grey or bronze, with faint patches or small dark flecks, or immaculate yellow green to bright green
Dryopsophus	10	2 slips (4)	Absent (4)	Multi-divided (4)	26 (6)	Brown or green but not uniform, with sparse scattered gold or black spots or irregular olive to green marbling
Eremnoculus	1	2 slips	Absent	Multi-divided	26	Shades of brown to red-brown, either immaculate or with pale brown patches or cream spots or blotches
Exedrobatrachus	1	ND	ND	ND	ND	Shades of olive, green to brown with a yellow or olive lateral stripe
Exochohyla	4	ND	ND	ND	ND	Flesh-toned, or light blue-grey, green, brown, or grey, greenish-grey, ochre with dark bands or patches
Hyalotos	3	ND	ND	ND	ND	Mottled light and dark green or predominately blue-grey merging into grey-green on upper dorsum with irregular black bars across the body
Ischnohyla	5	ND	ND	ND	26 (2)	Green or green-tinged ivory or pale creamy brown with green or black spots and flecks or mottled with brown, black or green, in one species a pair of irregular yellowish stripes from posterior margin of eye extending dorso-laterally to groin

Table 1. Continued

Genus	No. of species	m. extensor digitorum communis	m. extensor brevis medius digiti IV	m. palmaris longus	Diploid number	Dorsal pattern
Kallistobatrachus	8	ND	ND	ND	ND	Bright green or bright green occasionally yellow-green with brown markings or brown with green markings, peppered or vermiculated black occasionally with white spots, or scattered pale brown spots, or immaculate green or yellowish green mottled all over with darker green or sparse minute yellow spots
Lathrana	1	ND	ND	ND	ND	Greenish-brown with small dark green or dark brown spots
Leptobatrachus	5	2 slips (1)	Absent (1)	Multi-divided (1)	26 (2)	Yellowish, or beige or plain dark or light brown/olive yellow/pale jade green with or without white spots or irregular dark spots
Litoria	13	2 slips (8)	Absent (8)	Multi-divided (8)	26 (9)	Grey, brown and red tones, immaculate or with darker markings and smudges, or faint distinct or poorly defined darker blotches, sometimes with dark mid-dorsal streak or broad diffuse parallel band on latero-dorsal margin
Mahonabatrachus	6	2 slips (2)	Absent (2)	Multi-divided (2)	26 (3)	Diffuse mottling of brown, grey-brown, fawn, redish brown, or with grey brown or rusty tones and darker between mid-dorsum and flanks or pale tan to brown either immaculate or with irregular feint blotches
Megatestis	1	2 slips	Absent	**Reduced**	26	Pale or dark green, or olive or brown, immaculate or with darker patches, vertebral stripe, often with pale dorso-lateral band
Melvillihyla	1	ND	ND	ND	ND	With diffuse brown mottling with scattered grey or olive or pale yellow blotches
Mosleyia	4	2 slips (3)	Absent (3)	Multi-divided (3)	26 (3)	Grey, olive-grey or green or light brown, with pale or dark brown or black mottling or spots
Nasutibatrachus	5	ND	ND	ND	ND	Light to dark brown, olive, or yellowish-brown or green, with variable amounts of green or darker brown or black spotting, mottling or banding and in some green tubercles contrasting with base colour
Nyctimystes	32	**3 slips** (6)	Absent (6)	Multi-divided (6)	26 (9)	Various shades of brown, grey, green, blue-green, yellowish-golden with paler contrasting spots or rings or blotches or variously coloured lichen-like patches or dark edged brown or olive-green patches with small black spots or large tan mid-dorsal blotches sprinkled with small dark-brown flecks
Papuahyla	9	ND	ND	ND	26 (2)	Green or yellowish green or brown or grey or bronze sometimes with broad brown vertebral zone, or dark chocolate brown with faint patches or small dark flecks, or immaculate
Pelodryas	5	2 slips (2)	**Present** (2)	Multi-divided (2)	26 (2)	Uniform green or olive brown with scattered spots or blotches in some taxa
Pengilleyia	6	**3 slips** (3)	Absent (3)	Multi-divided (3)	526 (2)	Grey or light brown or orange-brown, with or without darker mottling, and tiny emerald-green spots, sometimes with pale mid-dorsal line
Ranoidea	5	ND	**Present (3)**	Multi-divided (3)	26 (4)	Metallic green with larger coppery gold patches and longitudinal ridges of black
Rawlinsonia	8	**3 slips** (2)	Absent (2)	Multi-divided (2)	26 (4)	Light brown, sometimes green, with two darker brown longitudinal bands or with dark speckling

Table 1. Continued

Genus	No. of species	m. extensor digitorum communis	m. extensor brevis medius digiti IV	m. palmaris longus	Diploid number	Dorsal pattern
Rhyaconastes	4	2 slips (2)	Absent (2)	Multi-divided (2)	26	Usually immaculate grey-brown to fawn, occasionally with darker spots or blotches or reticulations
Saganura	1	ND	ND	ND	ND	Marbled green, brown and grey
Sandyrana	14	ND	**Present** (1)	Multi-divided (1)	**24** (1)	Bright green to shades of olive-brown or yellow-green, usually immaculate, or rarely with dark spots
Spicicalyx	5	ND	Absent (1)	Multi-divided (1)	26 (2)	Mottled with greys, browns, green, pink, or red
Sylvagemma	1	ND	ND	ND	ND	Uniform chocolate brown, immaculate or with fine dark flecks
Teretistes	1	ND	ND	ND	ND	Green with few sparse dark spots and small blotches
Viridihyla	5	ND	ND	ND	ND	Uniform green with small, scattered, white-yellow or green spots
Hyla jeudii	-	ND	ND	ND	ND	Marbled

[a]ND—not determined. [b]AMES - adductor mandibulae externus superficialis muscle.

incorporated as follows: 'small' (≤ 1.4 mm), 'medium' (1.5–1.8 mm), and 'large' (≥1.9 mm).

To accommodate additional diversity in New Guinean species, we describe another three oral disc types, but have not used continuous numbers since they could be confused with numbering already used by Anstis (2017) that also included myobatrachid and microhylid morphologies. We have placed the three oral disc types with the most similar pelodryadid morphological types and numbered them as Types 1B, 6A, and 6B.

Type 1B. *Kallistobatrachus iris* (Tyler, 1962). Oral disc moderate. Papillae on anterior and lateral borders but absent from posterior border. Two anterior and three posterior tooth rows, wide medial gap in A^2 and P^1. Labial tooth row formula (LTRF) = 2(2)/4(1) (Tyler 1963a).

Type 6A. *Nyctimystes montanus* (Peters & Doria, 1878) and *Nyctimystes semipalmatus* Parker, 1936. Oral disc strongly suctorial and very large. No gap in row of close double marginal papillae, with the fine edge of the lower lip so small that it appears finely denticulate. Two anterior and four posterior entire tooth rows. Lower lip with up to 12 knob-like prominences divided into two by a wide interspace. Jaw sheaths medium, even width and upper tapered towards side (Parker 1936: figs 4, 6). LTRF = 2/4.

Type 6B. *Amnihyla angiana* (Boulenger, 1915) and *Amnihyla arfakiana* (Peters & Doria, 1878). Oral disc strongly suctorial, very large, and indistinctly marginate. No oral papillae but faint irregular serrations on the outer margin of the oral disc. Upper jaw sheath reduced to two very small, keratinized jaws situated laterally; lower jaw sheath is similar, but lower jaws are about twice as large as upper. A roundish ridge posterior to each upper jaw sheath and lobes lateral of the mouth are conspicuous. Two undivided anterior teeth rows with those in the centre of the anterior row double in number compared with that in the posterior row. Three undivided posterior tooth rows, the two outer rows have more numerous teeth than the inner row (Günther 2006a: fig. 8). LTRF = 2/3.

Acoustic data

Many calls are available on digital media and on-line applications (electronic field guides and web pages) and along with our own and recordings contributed by colleagues, we were able to obtain a comprehensive coverage of species, with data from over 80% of described pelodryadid species available (Supporting Information, Table S6).

For comparative analysis of the call characters of the pelodryadids, we used a 'call-centred' terminology based on the definitions and terminology for anuran acoustic analysis, with minor modifications, outlined by Köhler *et al.* (2017) (see Supporting Information, Table S5). As reproductive calls are spectrally and temporally characteristic for each species and a recorded call can be objectively measured, and structural features categorized (Köhler *et al.* 2017), then there is some utility in these data for comparative taxonomic purposes (Cocroft and Ryan 1995). Some level of intra-specific variation occurs in reproductive calls; however, this variation does not unduly affect the use of structural features of calls as taxonomic characters (see Köhler *et al.* 2017). There are no reported cases of female vocalization in the pelodryadids, and as such calls analysed are assumed to be from males. Temperature influences temporal components of calls and body size can affect frequency and both parameters can be observed in spectrograms (Gerhardt and Huber 2002), but we did not have sufficient information on the temperature for many recordings nor the body size of the individual recorded. However, temperature does not affect the call structure (call complexity, number of notes per call, call frequency and amplitude modulation, sound category, call envelope shape, number of notes per call, note rate change across the call) or the relative duration of these characters which we report as means, thus we do not consider that lack of temperature data unduly affects our taxonomic inferences. Also, we were unable to correct dominant frequency for body size but the variation in body size within genera is usually quite limited and thus body size does not unduly affect our taxonomic inferences. No examples of ultrahigh frequencies (above that detectable by the human ear) are known among the pelodryadids, and this remains a possibility especially among species that occur in habitats with high natural noise levels, but we did not test for the occurrence of such calls.

We focus on reproductive calls as the most relevant functional call category since these are the calls commonly heard and recorded, many species descriptions contain detailed information on them, and their role in mate attraction and social competition is well understood (reviewed in Gerhardt and Huber 2002, Wells 2007, Köhler *et al.* 2017). Other categories of calls such as distress calls (= defensive, warning, and alarm calls) and release calls occur among pelodryadids, but they are recorded rarely, and if they are, the behavioural context is often not described, so they are therefore less useful for taxonomic purposes, and we do not include them in our analysis.

In pelodryadids, the reproductive call (hereafter calls) may comprise an advertisement component alone (simple call) or combined advertisement and aggressive components (complex calls) (Littlejohn 1977, Gerhardt and Huber 2002). Where complex calls occur, we identify components by differences in the note structure and spectral properties (termed 'note type') (Supporting Information, Table S5). While the identification of the function of the components requires specific testing (Gerhardt *et al.* 2007) which has not been undertaken for any species of pelodryadid, we nevertheless report the occurrence of complex calls since they are often species specific.

Using the call-centred approach, calls comprise notes, which may be a single 'note' or 'note groups' (repeated notes with regular relative note and inter-note duration), to produce the characteristic species call. Notes comprise pulses which are so closely spaced that the human ear is not able to distinguish separate pulses (Fig. 3). In species with complex calls, the advertisement and aggressive components are discernible as at least two different and discrete note groups (Fig. 3).

In many species calls have a typical duration (expressed as mean duration) followed by a silent inter-call interval that is usually longer than the call, before the call is repeated (see for example Supporting Information, Figs S2, S5, S6, S7, S16; Table 2), which we classify as 'defined' calls. In other species, calls comprise 'long trains' of notes that may extend up to several minutes (see for example Supporting Information, Figs S4-1, S10-1, S11-1, S19-1; Table 2), and there is no defined end to the call, or typical call duration, which we classify as 'non-defined calls'. Since call duration cannot be measured in non-defined calls, we were not able to report the number of notes for non-defined calls. To facilitate comparisons among calls we grouped raw data on call characters into categories; for dominant frequency (Hz) (low < 1999, medium 2000–3999, high > 4000), call definition (defined, not defined), call duration (s) (short 0–0.9, medium 1.0–2.9, long > 3.0), call frequency modulation (yes, no), call amplitude modulation (yes, no), sound category (after Beeman 1998), call envelope shape (see Supporting Information, Table S5), number of notes (pulses) in the call (few 1–5, medium 6–19, many > 20), and note rate change across the call (yes, no) (Table 2; Supporting Information, Table S6).

As far as possible we used calls of individuals that could be isolated from choruses and other acoustic interference to produce oscillograms and spectrograms (see Supporting Information, Table S6 for data for each species). A selection of at least five sequential calls, with minimal interference from conspecifics was used for analysis. Calls were analysed with Raven Pro 1.6 software (http://www.birds.cornell.edu/raven), and spectrograms were produced with a fast-Fourier transform (FFT) of 512 points, 50% overlap, and 86.1 Hz grid-spacing, using Hanning windows.

In applying the call-centred approach, we relied on identifying the structure of calls, i.e. notes and inter-note intervals being discernible by the human ear, which can also be clearly identified in an oscillogram with the time unit of 2 s, i.e. a RavenPro 1.6 oscillogram window with the time axis set at 2 s. To analyse the overall pattern of calling, we set the oscillogram time axis window at 40 s, since we found that this interval encompassed five or more consecutive calls in most species. We analysed the following characters where applicable: dominant frequency, call definition, call complexity, call duration, call frequency modulation, call amplitude modulation, sound category based on the general sound categories of Beeman (1998), call envelope shape, number of notes in the call and note rate change across the call (see Supporting Information, Table S5 and Fig. 4 for details of analysis and definitions of the characters).

RESULTS

Owing to the large number of generic changes, we use an approach to naming the genera in the results section to make the paper easier for the reader to follow. We use the final generic names throughout the manuscript rather than use an initial group nomenclature that we would change to the final generic names in the systematics section. We use the Results section to examine the evidence for relationships within the pelodryadids and then to tabulate adult morphological, reproductive, and acoustic data to establish a final taxonomy.

Molecular analyses

We used phylogenetic analysis of mitochondrial sequences to identify crown groups based on a taxonomically near comprehensive *ND4* alignment (Fig. 1; Supporting Information, ND4 alignment), and published mitochondrial 12S rRNA (Richards *et al.* 2010, Günther and Richards 2005) and *COI* analyses (Hoskin *et al.* 2005, Sulaeman *et al.* 2021) that include the few

Table 2. Acoustic data summary by genus for the Pelodryadidae. Call characters. Character state frequncy coding: normal font—most frequent character state, bold text—next most frequent character state, underlined text—least frequent character state. The species for which a particular character state was determined is detailed in Supporting information, Table S6. Sources of data are listed in Supporting information, Table S6, and literature references are included in the text.

Genus	No. of species (no. of species with data)	Dominant frequency mean (Hz)[a]	Call duration definition	Call complexity	Call duration mean (s)[b]	Call frequency modulation	Call amplitude modulation	Sound category[c]	Call envelope shape	No. of notes (pulses) in call[d]	Note rate change across call
Amnihyla	24 (16)	**Low**, medium, high	Defined	Simple, **complex**	**Short**, medium, long	No, **yes**	**Different components—yes & no**	Note repetition, tonal & pulsatile	Rectangular, oval, spike, teardrop & fusiform	Few, **medium**, many	Yes
Carichyla	2 (2)	Medium, high	Defined	**Complex**	Medium	Both yes & no	**Different components—yes & no**	*Tonal & note repetition*	Spike-fusiform	Few, many	Yes
Chlorohyla	12 (9)	**Low**, medium	Defined	Simple, **complex**	Medium, long	**Yes**	Yes	Note repetition	Left teardrop, oval	Few, **medium**	**No**
Coggerdonia	1 (1)	Medium	Defined	**Complex**	**Short**	No	Yes	Note repetition	Right teardrop	Few	Yes
Colleeneremia	12 (7)	Medium	Defined	Simple	**Short**, medium, long	No, **yes**	Yes	Pulsatile & note repetition	Fusiform	**Medium**, many	**No**
Cyclorana	14 (14)	**Low**, medium	Defined	Simple	**Short**, medium	No	Yes	*Tonal with dense harmonics*	Left teardrop	Few	**No**
Drymomantis	3 (3)	Medium, high	Defined	**Complex**	**Short**, medium	**Yes**	**Different components—yes & no**	*Tonal & note repetition*	Fusiform-spike	Few, **medium**	Yes
Dryopsophus	10 (9)	Low, medium	Defined	Simple, **complex**	**Short**, medium, long	No	Yes	*Pulsatile and note repetition*	Fusiform, left triangular	Few, **medium**	Yes
Eremnoculus	1 (1)	Medium	**Not defined**	Simple	**Short**	**Yes**	Yes	**Tonal**	Oval	Few	**No**
Exedrobatrachus	1 (1)	High	Defined	**Complex**	**Short**	No	**Different components—yes & no**	Note repetition	Fusiform	Few	Yes
Exochohyla	5 (3)	**Low**, medium	Defined	**Complex**	Medium	ND	**Different components—yes & no**	Note repetition, **tonal**	ND[e]	Few, **medium**	Yes
Hyalotos	3 (1)	High	Defined	**Complex**	**Short**	No	No	*Pulsatile*	Teardrop	**Medium**	**No**
Ischnohyla	6 (5)	Medium	Defined	Simple, **complex**	**Short**, medium	ND	Yes	Note repetition, tonal & pulsatile	Left triangular, left teardrop, oval	Few, **medium**, many	**No**
Kallistobatrachus	9 (7)	Medium	Defined	Simple, **complex**	**Short**, medium	No	**Different components—yes & no**	Note repetition, tonal & pulsatile	Fusiform, teardrop, spike	Few	Yes
Lathrana	1 (1)	Medium	Defined	**Complex**	**Short**	No	**Different components—yes & no**	**Tonal**	Oval	Few	**No**

Table 2. Continued

Genus	No. of species (no. of species with data)	Dominant frequency mean (Hz)[a]	Call duration definition	Call complexity	Call duration mean (s)[b]	Call frequency modulation	Call amplitude modulation	Sound category[c]	Call envelope shape	No. of notes (pulses) in call[d]	Note rate change across call
Leptobatrachus	5 (4)	Medium	Defined	Simple	**Short**, medium	No	Yes	Note repetition	Teardrop	Few, many	**No**
Litoria	13 (13)	**Low**, medium, high	Defined, **not defined**	Simple, **complex**	Long	No, **yes**	**Different components—yes & no**	*Note repetition & tonal*	Fusiform, abrupt end, rectangular	**Medium**, many	Yes
Mahonabatrachus	6 (5)	High	**Not defined**	Simple, **complex**	**Short**, long	**Yes**	**Different components—yes & no**	Note repetition, tonal & pulsatile	Fusiform-spike & rectangular	Many	Yes
Megatestis	1 (1)	**Low**	Defined	Simple	Long	No	Yes	Note repetition	Rectangular	**Medium**	**No**
Melvillihyla	1 (1)	**Low**	**Not defined**	Simple	**Short**	No	No	**Tonal**	Spike	Few	**No**
Mosleyia	4 (3)	**Low**, medium	**Not defined**	Simple	**Short**, long	**Yes**	Yes	*Tonal & note repetition*	Oval	Few, many	**No**
Nasutibatrachus	5 (2)	Medium	Defined	**Complex**	**Short**	**Yes**	ND	*Pulsatile*	ND	Few, many	ND
Nyctimystes	32 (17)	**Low**, medium	**Not defined**	Simple	**Short**	No	Different components—yes & no	Note repetition	Left teardrop	Few	**No**
Papuahyla	5 (9)	Medium, high	Defined	**Complex**	**Short**	**Yes**	**Different components—yes & no**	**Tonal**, *pulsatile & note repetition*	Right triangular	Few	Yes
Pelodryas	5 (5)	**Low**, medium	Defined	Simple	Medium, long	No	Yes	Note repetition	Right teardrop	**Medium**, many	**No**
Pengilleyia	5 (4)	**Low**, medium	Defined	Simple	**Short**, medium, long	No	Yes	Note repetition	Fusiform, abrupt end	**Medium**, many	**No**
Ranoidea	5 (5)	**Low**	Defined	**Complex**	Medium, long	**Yes**	Yes	*Pulsatile*	Fusiform, abrupt end	Few	Yes
Rawlinsonia	8 (8)	Medium	Defined	Simple	Medium, long	**Yes**	Yes	Note repetition	Fusiform, abrupt end	Few, **medium**, many	**No**
Rhyaconastes	4 (4)	**Low**	Defined	Simple	Medium, long	No	Yes	Note repetition	Rectangular	Few, **medium**, many	Yes
Saganura	1 (1)	**Low**	**Not defined**	Simple	**Short**	No	Yes	**Tonal**	Teardrop	Few	**No**

Table 2. Continued

Genus	No. of species (no. of species with data)	Dominant frequency mean (Hz)[a]	Call duration definition	Call complexity	Call duration mean (s)[b]	Call frequency modulation	Call amplitude modulation	Sound category[c]	Call envelope shape	No. of notes (pulses) in call[d]	Note rate change across call
Sandyrana	14 (9)	**Low**	Defined, **not defined**	Simple, **complex**	**Short**, medium, long	No	Yes	**Tonal**	Oval or teardrop	Few, **medium**, many	Yes, **no**
Spicicalyx	5 (4)	**Low**	Defined, **not defined**	Simple	**Short**, medium	No	No	**Tonal**, note repetition	Left teardrop	Few, **medium**, many	**No**
Sylvagemma	1 (1)	Medium	**Not defined**	Simple	Long	No	No	**Tonal**	Rectangular	Many	Yes
Teretistes	1 (1)	High	Defined	**Complex**	**Short**	**Yes**	**Different components—yes & no**	Note repetition	Triangular	Few	Yes
Viridihyla	4 (4)	**Low**, medium	Defined	Simple, **complex**	**Short**, medium	No	**Different components—yes & no**	Note repetition	Fusiform, left teardrop, rectangular	Few, **medium**	Yes, **no**

[a]Dominant Frequency (Hz), low < 1999, medium 2000–3999, high > 4000. [b]Call duration (s), short 0–0.9, medium 1.0–2.9, long > 3.0. [c]after Beeman (1998). [d]Number of notes (pulses) in call (see Supporting information, Table S5, for designation of notes and pulses) few 1–5, medium 6–19, many > 20. [e]ND—not determined.

taxa missing from the *ND4* analysis. Our analysis includes 177 of the 233 described pelodryadid species.

Pelodryadid mitochondrial nucleotide sequences fall into three major clades: the *Cyclorana–Eremnoculus* Clade, the *Litoria–Rawlinsonia* Clade, and the *Sylvagemma–Nyctimystes* Clade (Fig. 1). Major features of the phylogeny resolve with high confidence two long standing issues in the Pelodryadidae.

First, the paraphyletic relationship of the former *Litoria* with *Cyclorana* is resolved with the restriction of *Litoria* to the *Litoria–Rawlinsonia* Clade and the placement of *Cyclorana* in the *Cyclorana–Eremnoculus* Clade. Second, the three lineages that represent the former concept of *Nyctimystes* are each placed in one of the three major clades. '*Nyctimystes*' *dayi* is the sister lineage to *Mosleyia* with which it is geographically co-distributed with both placed in the *Cyclorana–Eremnoculus* Clade. '*Nyctimystes*' *rueppelli* falls within *Colleeneremia* in the *Litoria–Rawlinsonia* Clade and our sample of sequences from 10 species of *Nyctimystes* form a sub-clade which is the sister lineage of *Sandyrana* within the *Sylvagemma–Nyctimystes* Clade.

For the genera that we recognize, branch support is uniformly high with bootstrap proportions of 100% in all but two cases: *Cyclorana* 91% and *Papuahyla* 95%.

There are also a number of deeply divergent monotypic lineages on long branches among the former *Litoria* and within the *Drymomantis* Sub-clade which contains the majority of New Guinean species. The divergence between these monotypic lineages and their sister lineages is within the range of divergence observed between well-supported crown groups to which we have assigned generic status. The monotypic lineages include: *Coggerdonia adelaidensis* (Gray, 1841), *Eremnoculus dayi* Günther, 1897), *Exedrobatrachus biakensis* (Günther, 2006b), *Lathrana verae* (Günther, 2004a), *Megatestis dahlii, Melvillihyla andiirrmalin* (McDonald, 1997), *Saganura burrowsae* (Scott, 1942), *Sylvagemma brevipalmata* (Tyler, Martin & Watson, 1972), and *Teretistes havina* (Menzies, 1993).

We then selected representatives from across the mitochondrial tree to confirm support for the crown groups and to test relationships among lineages using the AHE data (Fig. 2) and to establish a temporal scale for the diversification of the pelodryadids (Fig. 2 inset). All genera except *Lathrana* were represented in these analyses. The vast majority of branches received very strong support. None of the nine branches that received lesser support involved branches for generic clades. Taking into account the differences in taxon sampling between the mitochondrial and nuclear and phylogenetic analyses, there was a very high degree of concordance for relationships in particular for the composition of the generic clades. The three major clades observed in the mtDNA phylogeny were also present in the AHE phylogeny, but their inter-relationships differed with the *Sylvagemma–Nyctimystes* Clade sister to the other two major clades in the mtDNA phylogeny, whereas the *Cyclorana–Eremnoculus* Clade is the sister to the other two major clades in the AHE phylogeny.

Within the *Sylvagemma–Nyctimystes* Clade intergeneric relationships were consistent between the mitochondrial and AHE phylogenies. Within the *Cyclorana–Eremnoculus* Clade the placement of *Dryopsophus*, *Megatestis*, and *Leptobatrachus* differed between the mitochondrial and AHE phylogenies. When comparing the mitochondrial and AHE phylogenies for the

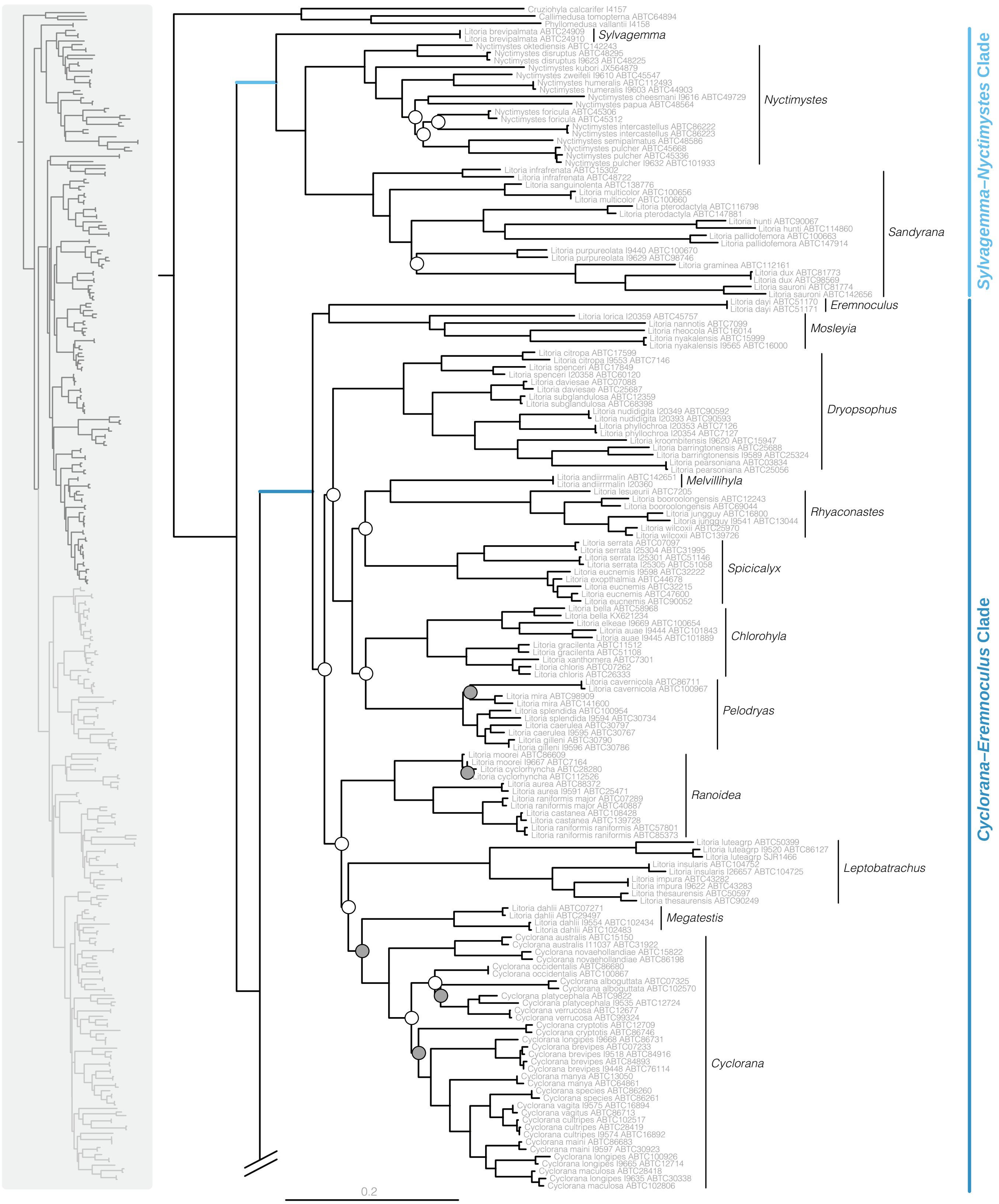


Figure 1. Maximum likelihood phylogram of mitochondrial *ND4* nucleotide sequences from the Pelodryadidae constructed with IQTree. Circles at nodes indicate ultrafast bootstrap pseudoreplicate proportions: none/ > 90 /high; grey/ > 70 < 90 /moderate; white/ <70 /low; legend tree at left indicates portion of whole tree. The tree is presented with the outgroups *Callimedusa tomopterna, Cruziohyla calcarifer,* and *Phyllomedusa vallantii*.

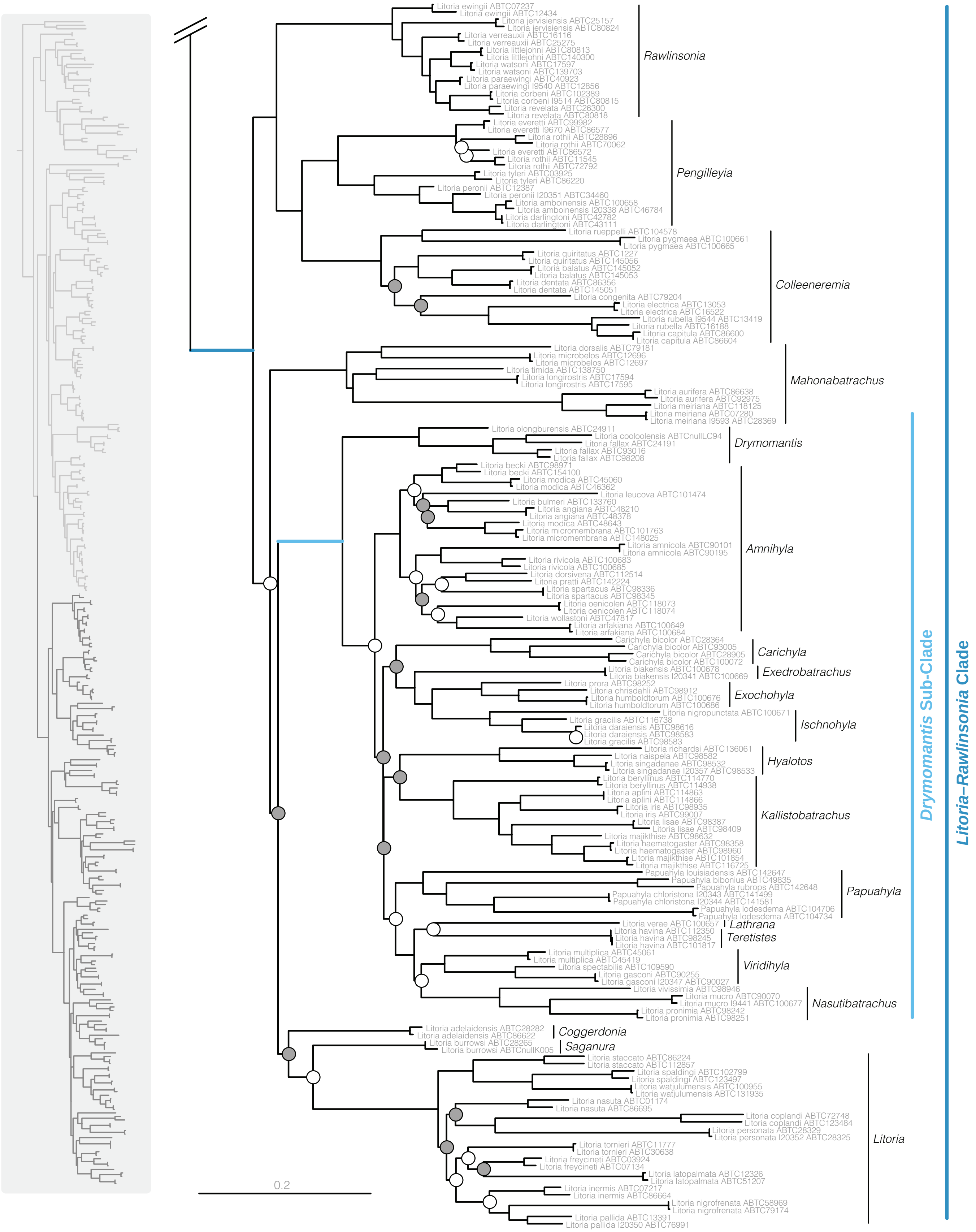


Figure 1. Continued

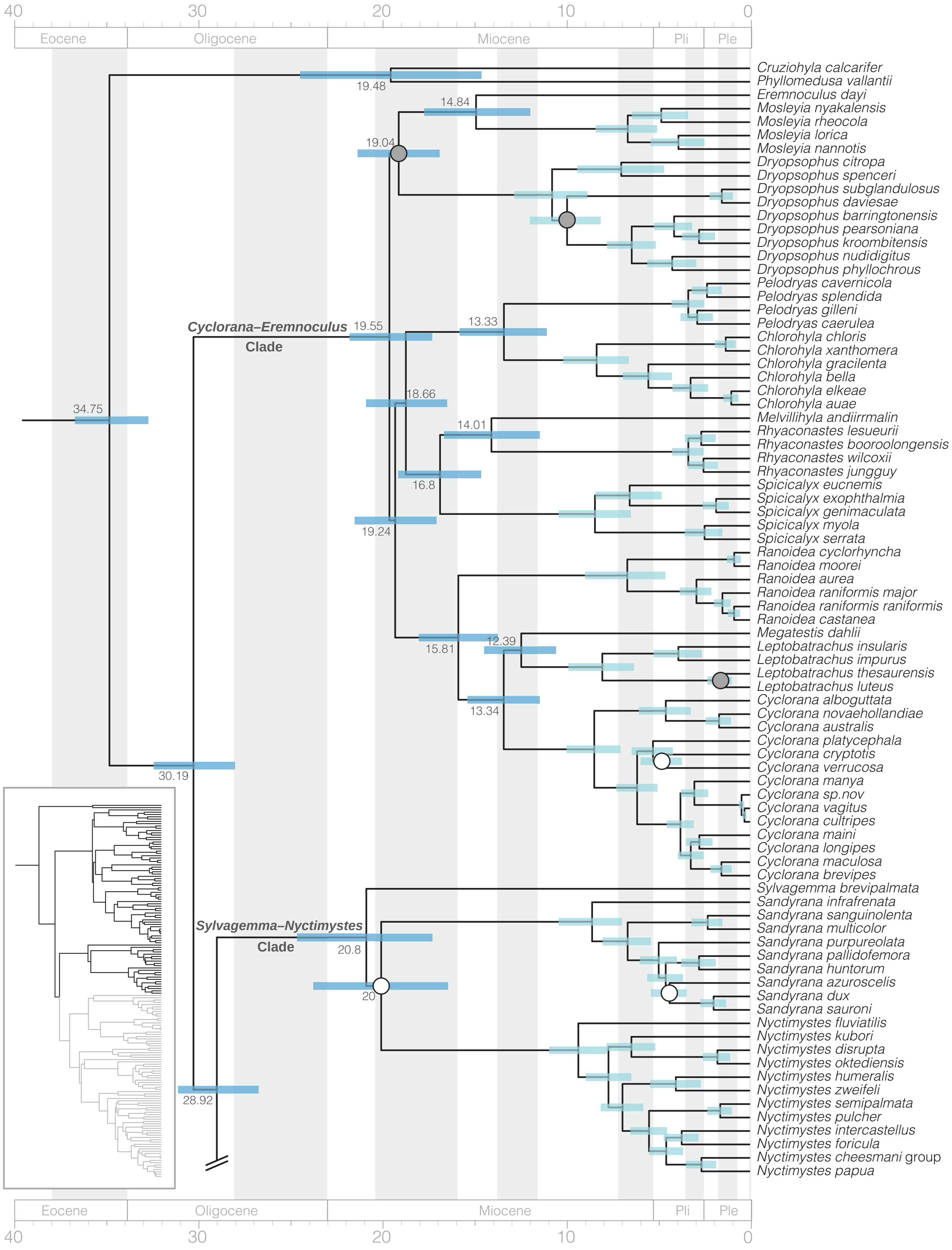
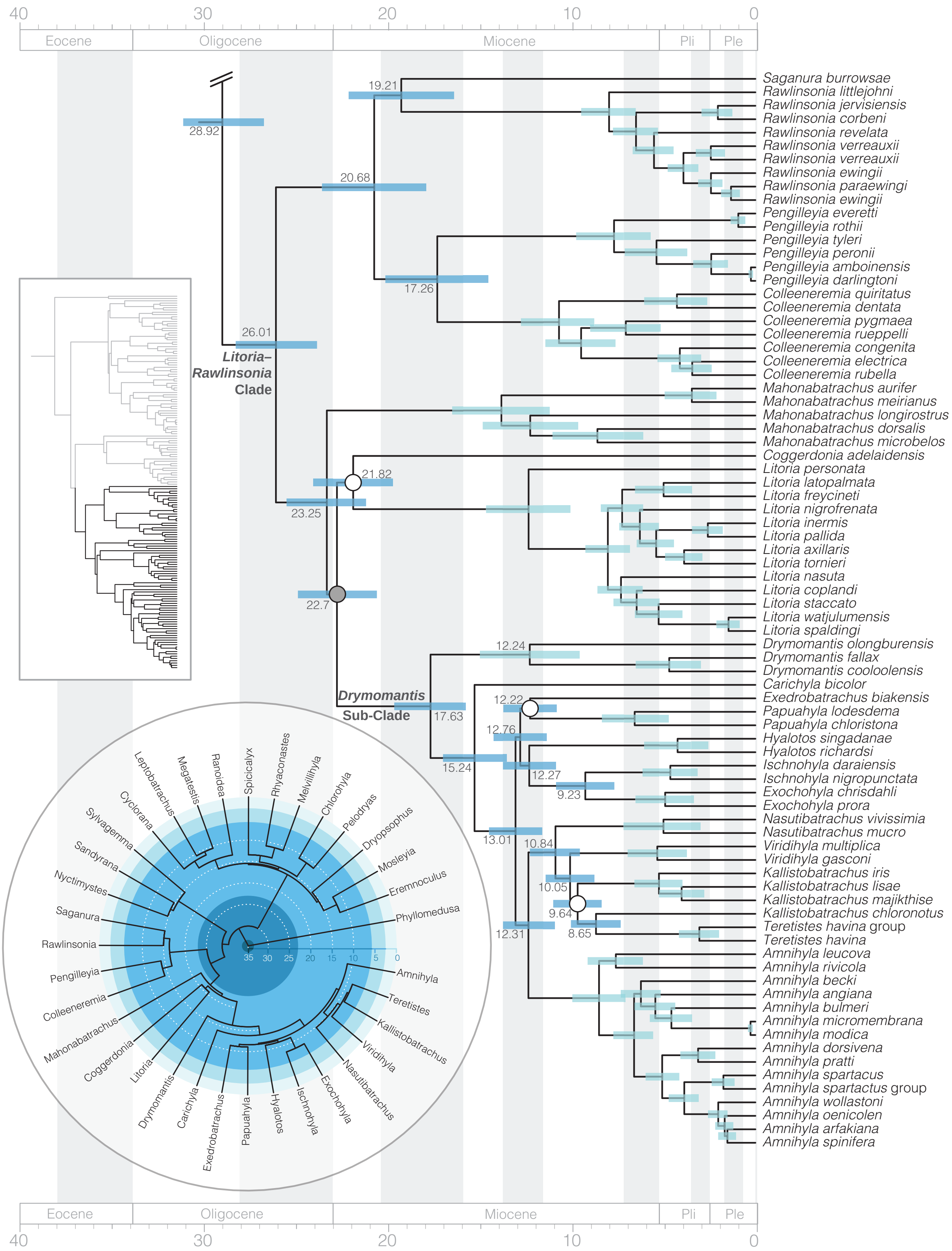


Figure 2. Markov chain Monte Carlo (MCMC) timetree based on Anchored Hybrid Enrichment nucleotide sequence data for the Pelodryadidae. Splits within genera have credibility intervals coloured light blue, splits above genera have credibility intervals coloured dark blue. Support (local posterior probabilities—LPP) for the vast majority of branches in the species tree (not presented) generated with ASTRAL III was 100 (branches not denoted). Branches that had an LPP > 90 < 95 are denoted with grey circles, and branches that had an LPP < 90 are denoted with white circles. The tree is presented with only two of the outgroups: *Cruziohyla calcarifer* and *Phyllomedusa vallantii*. An MCMC timetree with all outgroups included is presented in Supporting Information, Fig. S1. The inset is a summary chronogram for viewing convenience.



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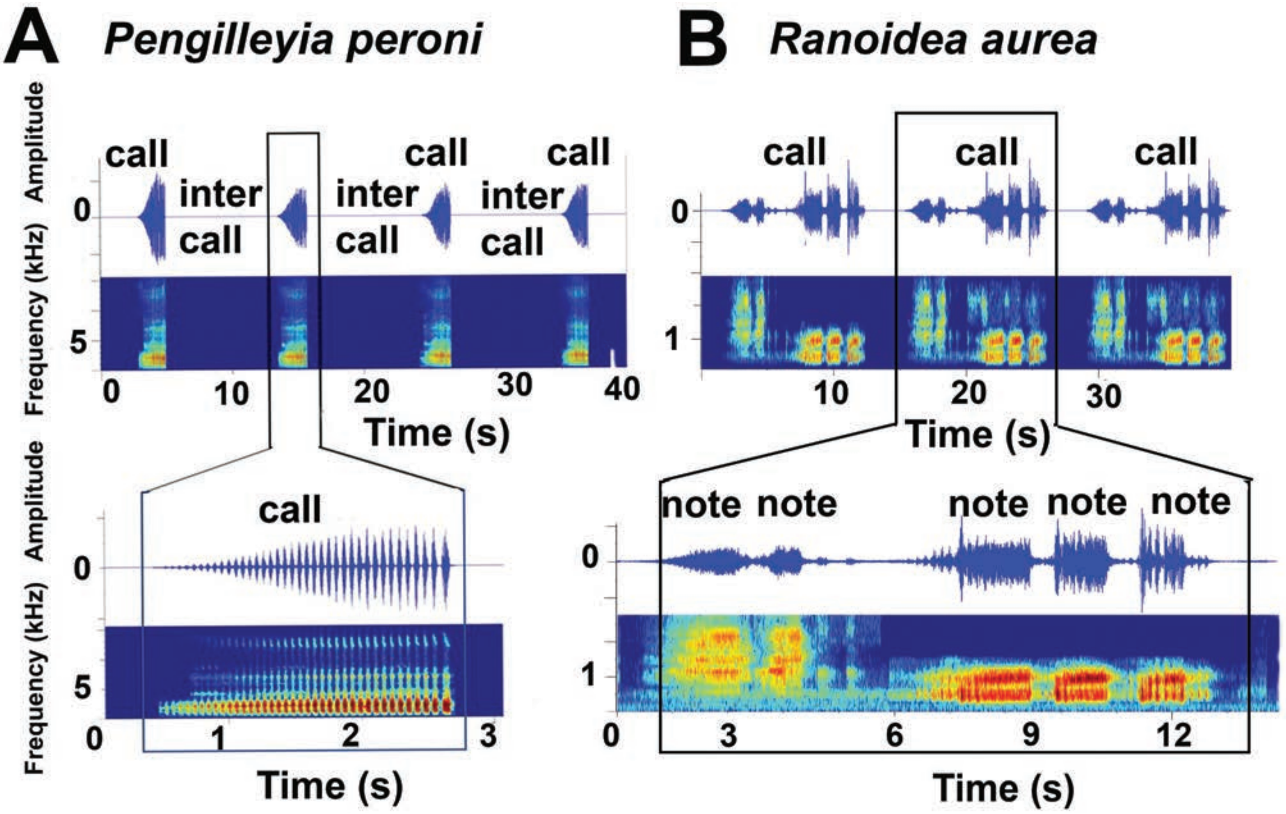

Figure 3. Illustration of the call-centred approach adopted to describe call characters in the Pelodryadidae. Reproductive calls of two species, (A) *Pengilleyia peronii* and (B) *Ranoidea aurea* are shown, with the upper oscillogram and spectrogram plotted on a window of 40 s to show several consecutive calls, and in the lower oscillograms and spectrograms an individual call from each species plotted on a window of 4 s (A) and 6 s (B) to show the note and pulse structure. (A) *P. peronii*. Four calls in 40 s, call duration is about 2 s, and inter-call interval about 7 s; simple call consisting of one note type with a note repetition call structure; notes are fully amplitude modulated; the call envelope has a fusiform shape, with the amplitude gradually rising across the call and ending abruptly; dominant frequency is at 2067 Hz with a secondary band of almost equal energy at 872 Hz, and two higher frequency bands at 6923 and 12 276 Hz, without evidence of frequency modulation. (B) *R. aurea*. Three calls in 40 s, call duration is about 5.5 s, and inter-call interval about 5 s. Complex call comprising five notes that are completely amplitude modulated, two note types both with a densely pulsatile note structure; the first two notes which are incompletely amplitude modulated are the first note type and have several frequency bands not observed in the second note type. The envelope shape of the first two notes is fusiform with the amplitude rising gradually to a peak before declining with an incomplete break between the two notes. This is followed by an inter-note interval prior to the third, fourth, and fifth notes which are of the second note type (only one of these notes is shown expanded on the 6-s window), which are also densely pulsatile, and fusiform in shape with some evidence of sub-notes that are incompletely amplitude modulated. Dominant frequency in the first two notes is 1464 Hz with sub-bands at 473, 1109, and 2136 Hz, whereas in the second note type the dominant frequency is 880 Hz with a low band at 473 Hz with approximately equal energy, this latter band is the fundamental frequency of the call. There is no evidence of frequency modulation in the first note type but there is a very slight rise in frequency across the pulses in the second note type.

Litoria–Rawlinsonia Clade the position of *Saganura* was inconsistent, and relationships among the lineages in the *Drymomantis* Sub-clade varied with the majority of branches (17 of 19) in the AHE phylogeny receiving strong support (> 90% bootstrap proportions). However, the mitochondrial tree was based on a relatively short sequence, the mitochondrial genome was effectively a single locus, and the evolutionary history of the mitochondrial genome may conflict with the organismal evolutionary history of the group that was estimated from the vastly more genomically representative nuclear dataset (> 350 loci).

The timetree estimate of the crown age for the Pelodryadidae was 30.19 Mya (Fig. 2 inset; Supporting Information, Fig. S1) consistent with the estimate based on wider sampling of other anuran families in Brennan *et al.* (2024). The estimated ages for polytypic crown groups, i.e. genera, ranged from 13.78 to 3.32 Mya, i.e. from the Early Miocene to the Mid-Pliocene (Fig. 2 inset; Supporting Information, Text S1). Ages of divergence of monotypic genera from their nearest relative ranged from 21.82 to 8.65 Mya.

Morphology

Rather than describe variation in each morphological or life history character, we illustrated with some examples how these character types have not provided the robust evidence needed to assess evolutionary relationships and hence to address generic level taxonomic revision in the Pelodryadidae. Our illustration was facilitated by the availability of a well-supported phylogeny for the Pelodryadidae (Figs 1, 2) which enabled us to identify clades to which phenotypic character descriptions can be assigned.

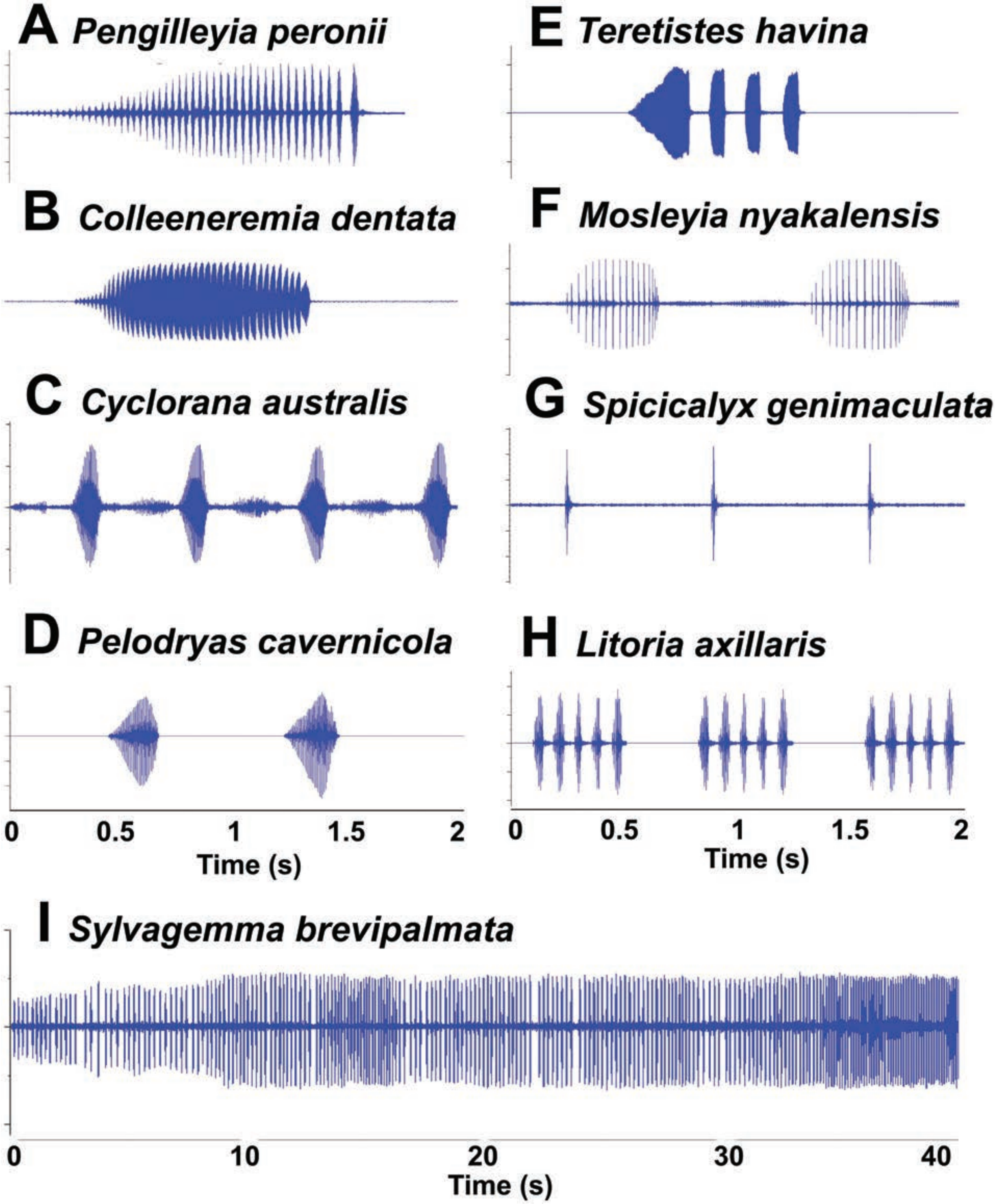

Figure 4. Call shape classification. Call shape (call envelope shape) summarizes the temporal structure and arrangement of notes in the waveform of the call and is a useful character that often shows a common pattern among congeners. Time is plotted on the *x*-axis (2 s in A–H, and 40 s in I), and the *y*-axis is the relative amplitude. Calls are classifiable into four call envelope shapes: fusiform, teardrop, square, and spike. (A) *Pengilleyia peronii*, simple call, defined duration, fusiform envelope with abrupt termination, note repetition, individual notes audible (100% amplitude modulate in waveform), Central Coast, NSW, Michael Mahony; (B) *Colleeneremia dentata*, simple call, defined duration, fusiform with tapered termination, note (pulse repetition), moderately pulsatile notes (not completely amplitude modulated), Dorrigo, NSW, Michael Mahony; (C) *Cyclorana australis*, simple call, defined duration, teardrop shape, note with dense pulses (pulsatile), Victoria River, NT, David Stewart; (D) *Pelodryas cavernicola*, simple call, defined duration, teardrop, note with dense pulses (pulsatile), Mitchell Falls, WA, Paul Doughty; (E) *Teretistes havina*, complex call (two different note structures), defined duration, teardrop (dense pulsatile), square shape three notes (note repetition), Western Province, PNG, Stephen Richards; (F) *Mosleyia nyakalensis*, simple call, defined duration, fusiform shape, pulses observable, Windsor Tableland, QLD, David Stewart; (G) *Spicicalyx genimaculata*, simple call, spike-shaped notes, note repetition, Mt Lewis, QLD, Michael Mahony; (H) *Litoria axillaris*, simple call, square shape, note repetition, individual notes distinguishable and audible, Prince Regent River, WA, Paul Doughty; (I) *Sylvagemma brevipalmata*, simple call, non-defined duration, square shape, note repetition, individual notes distinguishable and audible, but note rate is not always uniform, Coopernook, NSW, Michael Mahony.

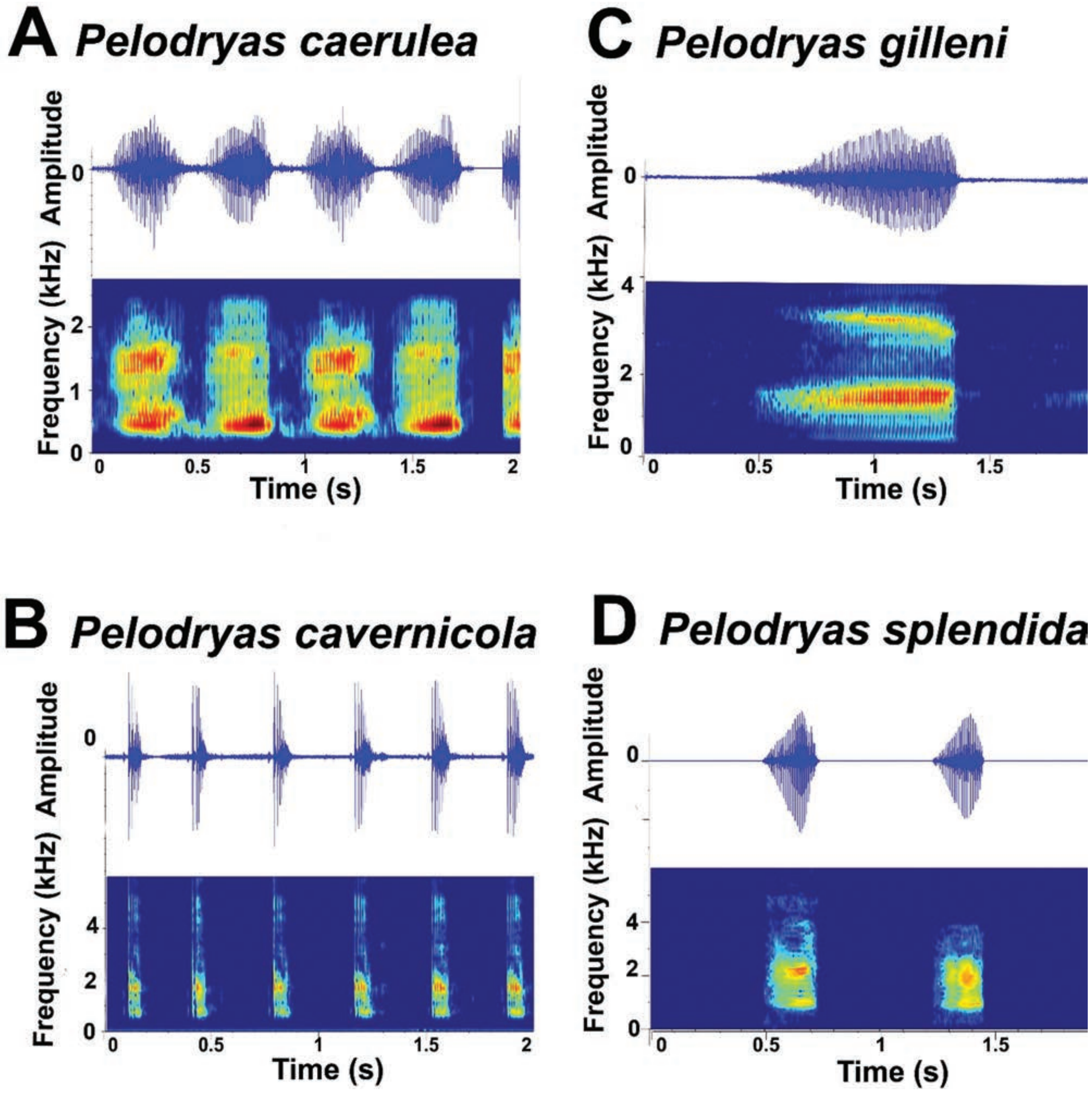

Figure 5. Representative oscillograms and spectrograms of *Pelodryas* reproductive calls. Calls are simple and comprise one note repeated at regular intervals. Calls have a defined duration, followed by a regular inter-call interval. In each species the notes are composed of dense pulses that cannot be distinguished by the human ear or the waveform oscillogram with a 2-s window. Differences among the species occur in the note repetition rate and in dominant frequency. In each species the call envelope shape is teardrop and two frequency bands occur. (A) *Pelodryas caerulea*, Central Coast Range, Michael Mahony; (B) *Pelodryas cavernicola*, Mitchell Plateau, Paul Doughty, the upper frequency band is modulated; (C) *Pelodryas gilleni*, Central Australia, Alastair Stewart; (D) *Pelodryas splendida*, Python Pool near Wyndham, Paul Doughty.

Each of the major Clades (Fig. 1) in the phylogeny had at least one genus that has the following distribution of character states: absence or reduction of finger and toe discs, absence of webbing on the hand, minimal or reduced webbing on the feet, limbs that are medium to very long relative to body size except for *Cyclorana* (TL/SVL), and small to medium eyes relative to body size (ED/SVL) (Table 1). Six of the 35 genera (*Cyclorana–Eremnoculus* Clade: *Cyclorana*, *Leptobatrachus*, *Ranoidea*, *Rhyaconastes*, the *Litoria–Rawlinsonia* Clade: *Litoria* and the *Sylvagemma–Nyctimystes* Clade: *Sylvagemma*) possessed these character states, and their phylogenetic placement was consistent with independent evolution of these character states (Figs 1, 2). Without the benefit of the phylogeny, one might infer a close relationship of the genera with this distinctive morphology.

Several genera expressed character states that were apparently unique and hence likely highly derived. *Cyclorana* was highly distinctive because of the following set of characters: complete absence of finger and toe discs, lack of intercalary structures (with the exception of one of 14 species), rounded bodies (Figs 13, 14)

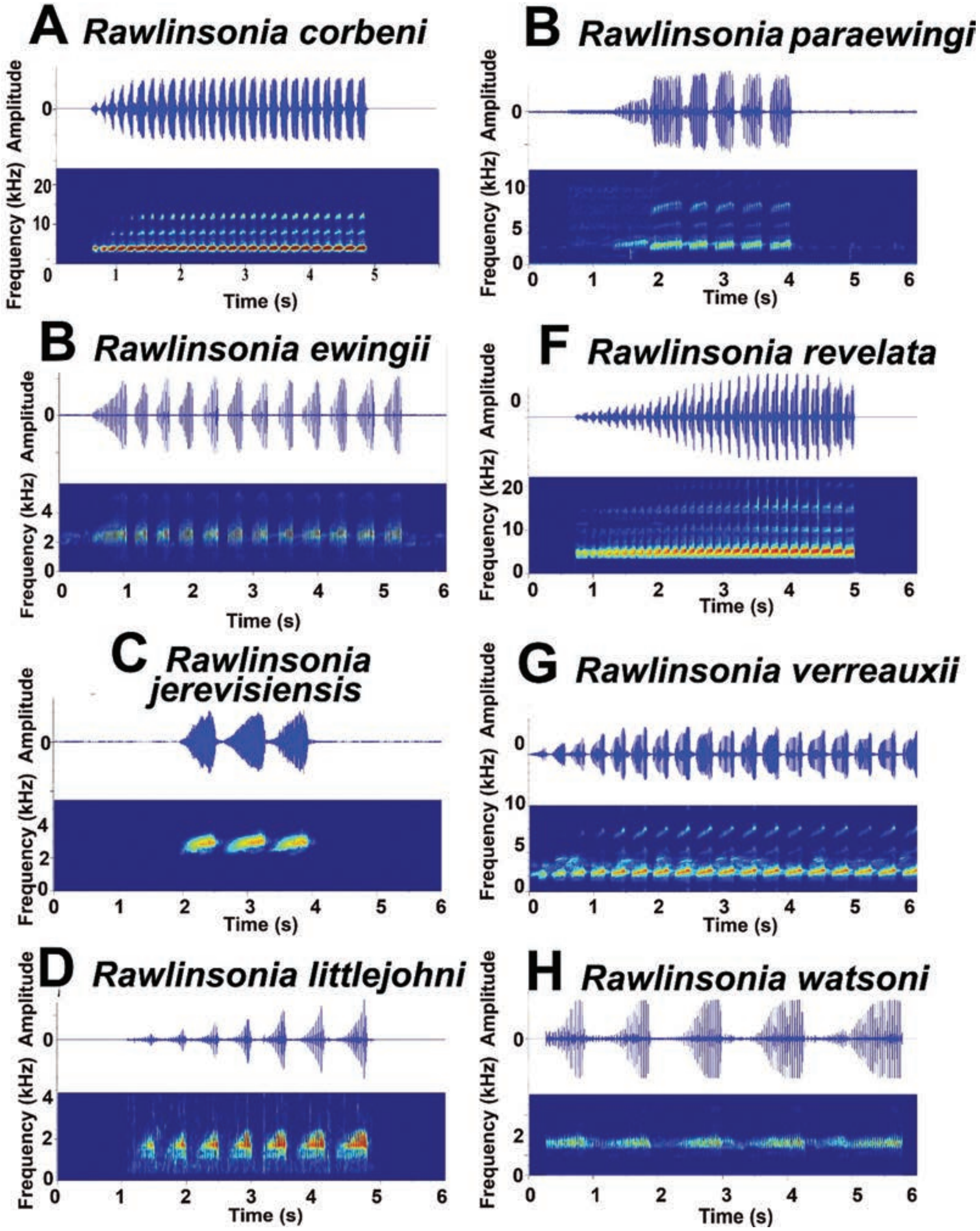

Figure 6. Representative oscillograms and spectrograms of reproductive calls of *Rawlinsonia.* Calls show a common structure of note repetition but the duration of notes and note repetition rate vary among species. In all species amplitude rises across the call to a plateau and concludes abruptly. The call is simple with notes of only one structure and frequency. Species differ in the number of repeated notes in the call, duration of notes and inter-note intervals (note repetition rate), and dominant frequency(DF). In five species, individual notes within the call can be distinguished by the human ear and the notes are densely pulsatile and can be readily seen in the waveform oscillogram with a 2-s window. Calls have a defined duration. (A) *Rawlinsonia corbeni* Atherton Tablelands, QLD, Luke Price, has a mean call duration of 4 s, with a mean of 38 repeated notes, fusiform call shape, moderate DF, and no evidence of frequency modulation, and is very similar to (F) *Rawlinsonia revelata*, Central Coast Range, NSW, Michael Mahony, except for the amplitude modulation of the call. (B) *Rawlinsonia ewingii*, (E) *Rawlinsonia paraewingi*, and (G) *Rawlinsonia verreauxii* are similar but differ in the mean number of notes in the call, have a similar mean DF and no frequency modulation. (D) *Rawlinsonia littlejohni*, Central Coast Range, NSW, Michael Mahony, and (H) *Rawlinsonia watsoni*, Parma Creek Nature Reserve, NSW, Michael Mahony, are similar to one another in structure and have fewer but longer notes than those above, have a similar DF and no frequency modulation. (C) *Rawlinsonia jervisiensis*, Myall Lakes, NSW, Michael Mahony, has a small number of notes (mean 3) of longer duration than all other congeners, the notes are densely pulsatile and frequency modulation occurs.

with short limbs (TL/SVL), mostly medium-sized eyes (ED/SVL), and a well-developed inner metatarsal tubercle. These highly distinctive and unique characters highlighted *Cyclorana* as a distinct crown group but did not provide substantial information on relationships with other crown groups.

Other examples occurred where several genera had a distinctive character that was apparently derived. Rostral spikes were a character that only occurs in three arboreal genera in New Guinea (*Exochohyla* occurs in both sexes, *Nasutibatrachus* occurs in males only, *Teretistes* occurs in males only). These three genera were in the *Litoria*–*Rawlinsonia* Clade; however, they were not sister lineages, and the implication is that development of the rostral spikes had occurred independently.

The occurrence of patterning on the palpebral membrane, a character previously considered to be unique to *Nyctimystes* (Kraus 2013a), occurs in three unrelated lineages (the *Cyclorana*–*Eremnoculus* Clade: *Eremnoculus dayi*, the *Litoria*–*Rawlinsonia* Clade: *Colleeneremia rueppelli*, and the *Sylvagemma*–*Nyctimystes* Clade: *Nyctimystes*) and two species of *Sandyrana*–*Sandyrana nullicedens* (Kraus, 2018) and *Sandyrana sauroni* (Richards and Oliver, 2006a) (Fig. 32O), indicating that the character had evolved independently at least four times (Menzies and Riyanto 2015, Kraus 2018). Close examination of the nature of the patterning showed that it was not equivalent in each case, with considerable variation in the pattern within the polytypic *Nyctimystes* and among the four lineages in which patterning occurred providing further evidence of independent origin of this character (Menzies 2006, Menzies and Riyanto 2015, Kraus 2018).

A wholly or partially transparent tympanum was a highly distinctive character found only in one crown group, *Hyalotos*, and while it distinguished this group provided no information on its relationships.

Acoustic data

Call characters data for each species, where available, are presented in Supporting Information, Table S6 and summarized at the genus level in Table 2.

Call duration

The duration of the reproductive call ranged from single note calls with a duration less than 0.5 s, to multi-note calls emitted over more than a minute. To categorize the variation, we arbitrarily classed calls that had a defined maximum duration of 25 s as having a 'defined duration' (measured as the mean duration). In most genera the inter-call interval was longer than the call duration. Genera where the call duration exceeded 30 s or more without an evident maximum duration were classed as 'non-defined' duration. Call duration is species-specific has a typical value for a species and the intra-specific variation is limited. Most genera had defined calls, and most congeners were similar in the duration of the call. All species of *Drymomantis, Kallistobatrachus, Mosleyia, and Nasutibatrachus* had calls of less than 1 s duration, species of *Ranoidea* and *Rawlinsonia* had calls of about 2–6 s duration, and *Pelodryas* 16–25 s. For species of three genera *Litoria*, *Sandyrana*, and *Sylvagemma* that had calls of non-defined duration, the call comprised short notes (< 0.5 s duration) repeated in long trains. *Cyclorana* did not fit neatly into the dichotomy of defined and non-defined call duration, since all species produced short notes (0.2–1.5 s) that were repeated over long periods (> 60 s), with a short interval between notes, such that it was not clear whether the call was a single note, or the call was a long series of repeated notes that proceeded for over 60 s. We chose to place them in defined calls, i.e. the single note was the call, because several species of *Cyclorana* had relatively long single note calls, e.g. *Cyclorana maculosa* Tyler and Martin, 1977 1.6 s and *Cyclorana verrucosa* Tyler and Martin, 1977 1.3 s, with longer inter-note intervals, typical of calls and note sequences in other genera. It is not uncommon for individuals to vary the number of notes in calls, which happens often at the commencement of a call series (see Köhler *et al.* 2017). To address this, where possible we analysed calls from the middle of calling sequences and calculated mean duration from up to five calls per individual and from several individuals, where the data were available.

Dominant frequency

Dominant frequency (DF) of reproductive calls in the Pelodryadidae ranged from < 500 to ≥ 7000 Hz. Dominant frequency had a narrow range within species, with a small amount of variation, and was a species-specific character. The general pattern, found in most anuran amphibians (Wells 2007), is that dominant frequency is correlated with body size. Pelodryadid genera with larger frogs had lower frequency calls, e.g. *Pelodryas* 500–2100 Hz, and *Sandyrana* 400–1800 Hz, and those genera with smaller species, e.g. *Carichyla*, *Drymomantis*, *Mahonabatrachus*, and *Papuahyla*, had higher frequency calls (2700–7300 Hz). The relationship between body size and frequency was well demonstrated in *Cyclorana* where the species ranged from medium to large body size, and the dominant frequency of the calls reflected that variation. The four largest species by SVL length had a DF < 800 Hz [*Cyclorana australis* (Gray, 1842) 665 Hz, *Cyclorana novaehollandiae* Steindachner, 1867 689 Hz, *Cyclorana occidentalis* Anstis, Price, Roberts, Catalano, Hines, Doughty & Donnellan, 2016 656 Hz, and *Cyclorana platycephalus* (Günther, 1873) 750 Hz], seven moderately sized species had a DF between 1000 and 2000 Hz [*Cyclorana alboguttata* (Günther, 1867) 1981 Hz, *Cyclorana brevipes* (Peters, 1871) 1712 Hz, *Cyclorana cultripes* Parker, 1940 1981 Hz, *Cyclorana longipes* Tyler & Martin, 1977 1875 Hz, *Cyclorana maini* Tyler & Martin, 1977 1875 Hz, *Cyclorana vagitus* Tyler, Davies & Martin, 1981 1780 Hz, and *Cyclorana verrucosa* 1031 Hz), and the smallest two species had a DF > 2000 Hz (*Cyclorana maculosa* 2191 Hz and *Cyclorana manya* Van Beurden & McDonald, 1980 2411 Hz). An exception was *Cyclorana cryptotis* Tyler & Martin, 1977 with a DF of 775 Hz and an SVL in the medium size range. Uniquely within *Cyclorana*, this species did not have a tympanic membrane. In species with complex calls the frequency of the different call components was often different and we report the DF of each component (Table 2).

Frequency modulation

The presence or absence of frequency modulation was generally invariant within genera with the exception of *Colleeneremia* and *Litoria*. Where frequency was modulated

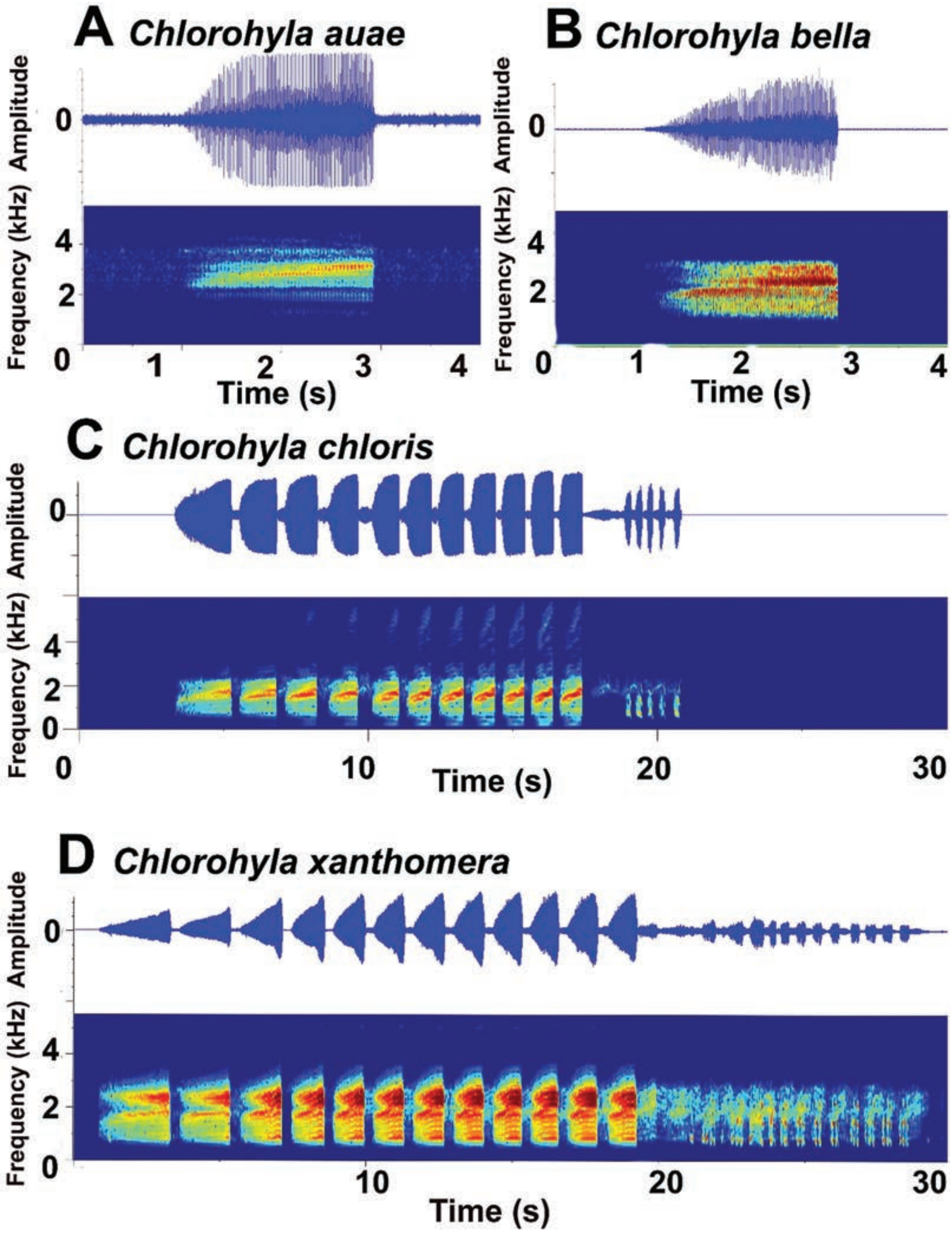

Figure 7. Representative oscillograms and spectrograms of reproductive calls of four species of *Chlorohyla*. Calls show differences in call and note structure. The calls of two of the species illustrated (A) *Chlorohyla auae*, Herowana, PNG, Stephen Richards, and (B) *Chlorohyla bella*, Iron Range, QLD, Conrad Hoskin, have a single note that is relatively long and comprises dense pulses, and is simple (comprising a one-note structure). In the other two species illustrated (C) *Chlorohyla chloris*, Nightcap Range, NSW, Michael Mahony, and (D) *Chlorohyla xanthomera* Lamb Range, QLD, Conrad Hoskin, the calls are complex with a different note structure and comprise two components, both with pulse repetition. The call comprises multiple notes with variable duration and inter-note interval. Individual notes within the call can be distinguished by the human ear and the notes are densely pulsatile and can be readily seen in the waveform oscillogram with a 2-s window. The call is amplitude modulated and has a fusiform shape, and each note is fully amplitude modulated. Frequency modulation occurs in all four species.

across the call, most typically the frequency increased over the call. The were no cases of large sweeps of frequency modulation in any species.

Call shape

Call structure and call envelope shape were a combination of temporal and physical characters, such as number of notes, duration of note and inter-note interval, note rate (notes per second), pulse structure within notes, and amplitude modulation (Fig. 3). Call structure showed similarities among congeners from being similar, to variation on a common call structure, or completely different in others. Genera where the calls of all congeners were similar in call shape were *Cyclorana*, *Leptobatrachus*, *Nasutibatrachus*, *Papuahyla*, *Pelodryas*, and *Rhyaconastes* (Figs

4 and 5; Supporting Information, Figs S6, S9, S13, S14, S18). Genera in which species showed variation on a common call structure included *Colleeneremia*, *Kallistobatrachus*, *Mosleyia*, *Pengilleyia*, *Ranoidea*, *Rawlinsonia*, and *Spicicalyx* (Figs 6, 8; Supporting Information, Figs S5, S9, S12, S15, S16, S17, S20). Genera in which some congeners showed different call structures included *Amnihyla*, *Chlorohyla*, *Dryopsophus*, *Exochohyla*, *Litoria*, and *Mahonabatrachus* (Supporting Information, Figs S1, S3, S8, S10, S11), but in most of these there were congeners that had structure that was similar or variation on a common structure and only one or two species had different call structure. For example, in *Chlorohyla* two species, *Chlorohyla chloris* (Boulenger, 1892) and *Chlorohyla xanthomera* (Davies, McDonald & Adams, 1986), had very similar call structure, which differed from their congeners, *Chlorohyla auae* (Menzies & Tyler, 2004), *Chlorohyla bella* (McDonald, Rowley, Richards & Frankham, 2016), and *Chlorohyla gracilenta* (Peters, 1869), which together had a very similar structure (Fig. 7; Supporting Information, Fig. S3).

Call complexity

Genera had either uniformly simple calls (15 genera), or uniformly complex calls (eight genera), or both states occurred within a genus (10 genera). Where complex calls occurred, the properties of the notes (number of notes, pulse structure, duration, and amplitude modulation) were often similar among congeners. As an example of congeners sharing a simple call, the calls of all eight species of *Rawlinsonia* comprised a series of notes repeated at a uniform interval, with amplitude modulation increasing across the call, and a fusiform-shaped envelope (Fig. 6; Supporting Information, Fig. S16). Species-specific differences occurred in the number of notes, duration of the note, note pulse structure, inter-note interval, and note repetition rate, but the overall call structure was conserved. In a second example, all 13 species of *Cyclorana* had single note calls with dense pulses and teardrop-shaped envelopes (Supporting Information, Figs S5, S6). Among the genera with complex calls congeners displayed similar overall call structure and call envelope shape, for example in *Ranoidea* (Fig. 8; Supporting Information, Fig. S15), all five species had a complex call with overall similar structure with a long drawn out densely pulsatile note commencing the call, followed by several moderately long repeated notes with dense pulses. Variation among species occurred in the total duration of the calls which in part was due to variation in the number of notes that were included in the second component of the call.

Systematics

In large generic-level revisions, there is the potential for incomplete resolution of the group's phylogeny even with phylogenomic scale data due to biological phenomena (e.g. rapid adaptive radiation with short internode intervals) or inadequate sampling (e.g. inadequate taxon representation, smaller molecular datasets) or inadequate analyses. The stability of a proposed taxonomy should be the primary criterion for its adoption. Vences *et al.* (2013) and Mahony *et al.* (2024) focus largely on the evidentiary basis of decisions to address the stability issue, which we examine in detail here for our proposed taxonomic revision of the Pelodryadidae, using their four criteria (monophyly, evidence, practice, and community consensus). Below we discuss taxa that required careful consideration in light of these criteria, before we outline our taxonomic actions.

(1) Monophyly—Monophyly should be the basis of supra-specific systematic revisions that have an evolutionary framework (Hennig 1966) and such a principle can be applied where the evidentiary basis is adequate (Vences *et al.* 2013), but see Seifert *et al.* (2016) for a discussion of the potential for discordance of the application of the monoplyetic criterion in a Linnean rank taxonomic system. In practice the strict adherence to the principle of monophyly has produced taxonomic instability in the Pelodryadidae. In particular, the generic revision of the Pelodryadidae by Duellman *et al.* (2016) has not received widespread acceptance. These authors applied the principle of strict monophyly to remove the paraphyletic nature of *Litoria*, a long-recognized issue, but in doing so synonymized *Cyclorana* (a genus that is eminently diagnosable and with long-standing usage) and produced an extended concept for *Nyctimystes*, creating a taxon that no longer had a clear diagnosis.

In practice, the scheme of Duellman *et al.* (2016) has been adopted inconsistently by database and taxon list managers. Rejection of the scheme of Duellman *et al.* (2016) has focused on how it interrupted longstanding usage and has viewed it as an interim arrangement that introduced instability (ASH 2024, Mahony *et al.* 2024) and does not represent a meaningful improvement for end users.

Furthermore, taxonomy can be viewed as an incremental process due to the limitations of the resolving power of particular datasets, the reality of the limitations of real-world data, and the implicit nature of the scientific process. It is thus an iterative process with new discoveries providing the basis for new hypotheses that require further investigation.

In our contribution to this process, we have resolved the long-standing issue of a paraphyletic *Litoria* and produced a generic arrangement that restores the use of *Cyclorana* and *Nyctimystes*.

For *Kallistobatrachus*, we discuss the uncertainty in relationships due to lack of comparable sampling between the mitochondrial and nuclear datasets and our conservative approach in the taxonomic account for the genus below.

(2) Evidence—Vences *et al.* (2013) provide a framework based on seven sub-criteria to assess the evidentiary basis for supra-specific taxonomic changes. Our work complies with all of these criteria. For sub-criteria (i), (ii), (v), (vi), and (vii): all taxa except *Kallistobatrachus* were recovered as robustly supported clades in an explicit phylogenetic analysis based on high-quality independent data sets with independent analytical methods. All polytypic genera received 100% support from both local posterior probability in the nuclear phylogenomic and bootstrap proportions in the mitochondrial maximum likelihood analyses. Phylogenetic relationships were established from a phylogenomic dataset [comprising > 350 nuclear genes] which is virtually the state of the art for phylogenetic reconstruction and therefore

for the robust identification of clades. For subcriterion (iv), we achieved dense taxon sampling. Our taxon sampling is 100% complete [all 233 species described at the time of manuscript finalization—July 2023] for a proportion of the phenotypic data, 94% complete for images in life (218 species), 74% complete for the acoustic data (173 species), 72% complete for the nuclear phylogenomic dataset (168 species), and 77% complete for the mitochondrial dataset (179 species). For the Australian pelodryadids, our coverage is 100% for the morphological datasets and 99% complete for the molecular datasets, only two species are missing from the acoustic dataset (one likely extinct) and four species lack information on tadpole morphology. The shortfall in taxon sampling for the non-morphological datasets is confined to the Melanesian Pelodryadidae.

For all genera but *Kallistobatrachus*, our data based on the sub-criteria (i), (ii), (v), (vi), and (vii) strongly support monophyly. For *Kallistobatrachus*, for sub-criterion (iii)—the absence of evidence for non-monophyly—the situation is less clear. The absence of *Lathrana* in our nuclear dataset and poor support for the branch uniting *Kallistobatrachus* and the *K. chloronotus*–*Teretistes* clade makes interpretation of the support for relationships uncertain. For *Kallistobatrachus*, we can consider stability not only of the focal taxon, but of the overall emerging classification of the Pelodryadidae. Some authors recommend avoiding naming well-supported taxa in parts of a phylogenetic tree where uncertainty affects neighbouring species at the same taxonomic level because it would create a paraphyletic situation for the latter (e.g. Orthia *et al.* 2005). A strict application of this recommendation could impede taxonomic progress because phylogenetic trees with robust support for all clades are rare, and likely to be a common occurrence for large radiations in which rapid adaptive bursts are a feature. Vences *et al.* (2013) recommend considering stability of the overall phylogenetic hypothesis when applying the principle of clade stability in alternative classification schemes.

(3) Practice—We are not the first to propose a generic rank dissection or its equivalent of the Pelodryadidae. Tyler (1968a) introduced morphologically defined species groups for *Litoria* that did not cover all of the species known at that time. Later, Tyler and Davies (1978) based on what appears to have been a gestalt impression of overall phenotypic similarity, nominated 37 species groups ('Group' in their terminology) among *Litoria* (their review did not consider the status of *Cyclorana* or *Nyctimystes*). Wells and Wellington (1985) assigned generic names to the Australian *Litoria*, largely reflecting the content of the Tyler and Davies (1978) Groups, but their generic nomina have not been adopted due to the contentious nature of the evidentiary basis for their determinations (ASH 2024).

(4) Community consensus—Numerous publications have used the Tyler and Davies (1978) Groups in some form or another (with amendments to incorporate species described since 1978) to functionally organize descriptions of the diversity in the Pelodryadidae as exemplified by (i) field guides—Clulow and Swann (2019); Tyler and Knight (2020); and Sanders (2021); and (ii) taxonomic descriptions—Courtice and Grigg (1975); Davies and McDonald (1979); Davies *et al.* (1983); Donnellan *et al.* (2020, 2021); Donnellan and Mahony (2004); Doughty (2011); Doughty and Anstis (2007); Günther and Richards (2000); Günther *et al.* (2023); Hoskin (2007), Hoskin *et al.* (2013); Ingram *et al.* (1982); Kraus (2013b); Kraus and Allison (2004a, 2009); Liem (1974a, b, 1977); Mahony *et al.* (2001, 2010, 2020); Martin *et al.* (1979); McDonald *et al.* (2016), Menzies (1972, 1993); Menzies *et al.* (2008); Menzies and Tyler (2004); Menzies and Zug (1979); Menzies and Zweifel (1974); Oliver *et al.* (2019, 2020, 2021a); Richards *et al.* (2007, 2010, 2021); Richards and Donnellan (2020); Richards and Oliver (2022); Rowley *et al.* (2021); Tyler and Anstis (1975); Tyler and Davies (1977, 1979, 1985); Tyler and Parker (1972, 1974); Tyler *et al.* (1978); Vörös *et al.* (2023), and Watson *et al.* (1971). Here we provide consistent lines of evidence (morphology, acoustics, genomics) that support taxonomic recognition for 17 of the 37 Groups of Tyler and Davies (1978). Under each generic account we indicate correspondence with the Groups of Tyler and Davies (1978) where applicable.

Taxonomic actions

Maintaining the usage of the three traditionally recognized genera, *Cyclorana*, *Litoria*, and *Nyctimystes*, in the Pelodryadidae has some consequences for the recognition of a minimal number of genera to accommodate their continued usage. Further, with the availability of a robust phylogenetic hypothesis of evolutionary relationship for the Pelodryadidae, and a comprehensive survey of a range of phenotypic characters, we can postulate a generic classification that recognizes the evolutionary diversity in the family.

Within the *Sylvagemma*–*Nyctimystes* Clade, *Nyctimystes* is diagnosable phenotypically from the two other lineages. Because *Sandyrana* shares a sister relationship with *Nyctimystes*, then *Sylvagemma* requires generic status as it is the sister to *Nyctimystes* + *Sandyrana* (Fig. 2). *Sylvagemma* is diagnosable from *Sandyrana*.

Within the *Cyclorana*–*Eremnoculus* Clade, *Cyclorana* is diagnosable from all other lineages within this clade and within the Pelodryadidae. *Megatestis* and *Leptobatrachus* are diagnosable from each other, requiring *Ranoidea* to have generic status. Within the clade that includes *Pelodryas* to *Spicicalyx*, all of the sister crown groups are diagnosable from each other resulting in the recognition of five genera: *Pelodryas*, *Chlorohyla*, *Melvillihyla*, *Rhyaconastes*, and *Spicicalyx*. Within the clade that includes *Eremnoculus* to *Dryopsophus*, all of the sister crown groups are diagnosable from each other resulting in the recognition of three genera: *Eremnoculus*, *Mosleyia*, and *Dryopsophus* (Fig. 2).

Within the *Litoria*–*Rawlinsonia* Clade, *Litoria* is diagnosable from its sister lineage *Coggerdonia* requiring the recognition of *Mahonabatrachus* and the *Drymomantis* Sub-Clade. A

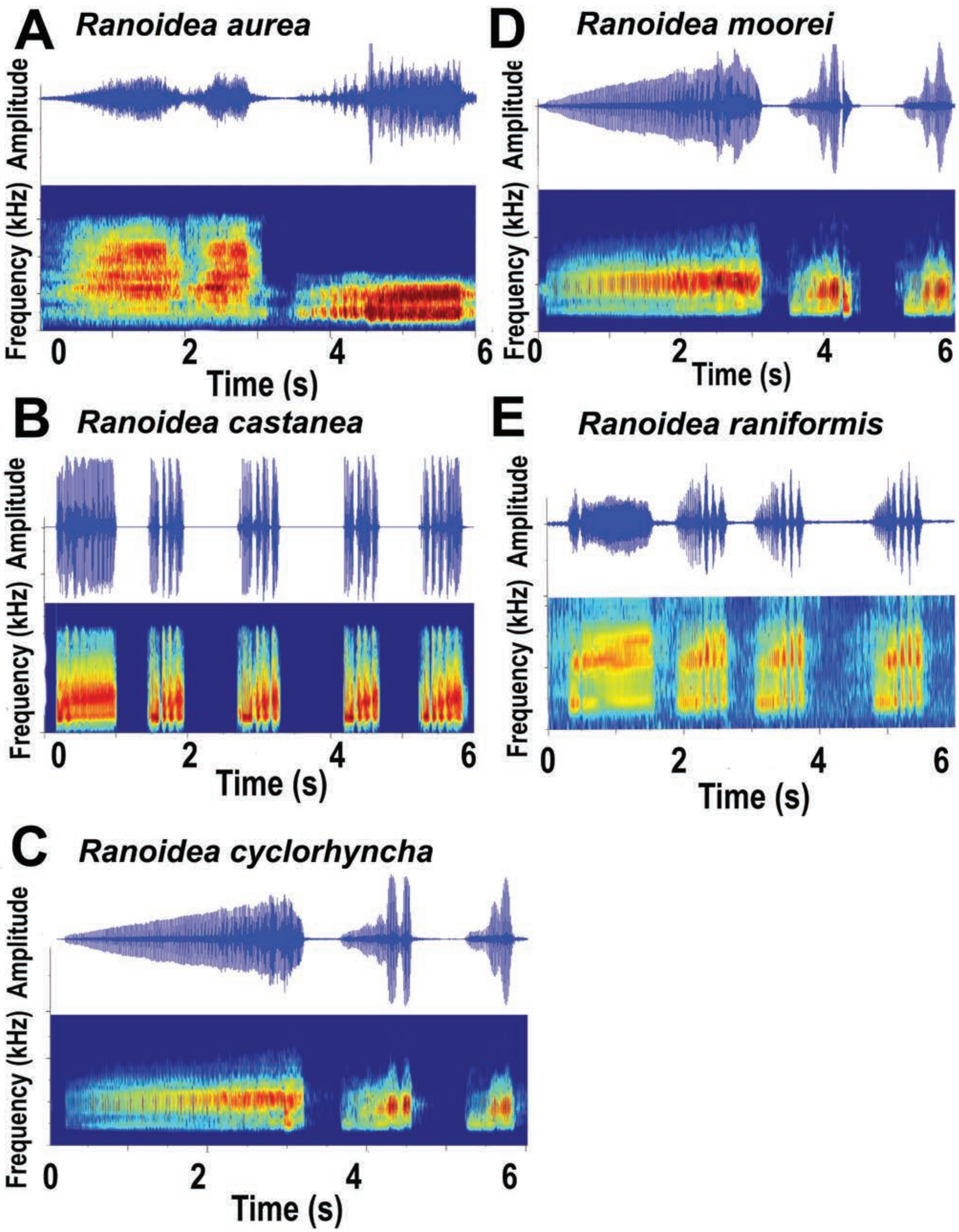

Figure 8. Representative oscillograms and spectrograms of reproductive calls of *Ranoidea*. (A) *Ranoidea aurea*, Yuraygir National Park, NSW, David Stewart; (B) *Ranoidea castanea*, Southern Tablelands, NSW, David Hunter; (C) *Ranoidea cyclorhyncha*, south-west WA, Dale Roberts; (D) *Ranoidea moorei*, south-west WA, Dale Roberts; (E) *Ranoidea raniformis*, Nampoo, SA, Judit Vörös. Calls are similar and illustrate complex calls with notes of two differing structures. All five species have relatively long notes that are densely pulsatile and cannot be distinguished by the human ear or in an oscillogram over a 6-s sound window. The first note is fully amplitude modulated and has a fusiform shape, and the second note, which is repeated, is not completely amplitude modulated and has a square shape. Frequency is broadband with evidence of frequency modulation in the first note.

substantial proportion of pelodryadid phenotypic diversity resides within the *Drymomantis* Sub-Clade (Tables 1, 2; Figs 9, 10, 11, 15, 16, 17, 18, 19, 23, 26, 33) resulting in 13 diagnosable lineages.

All of the remaining sister crown groups within the *Litoria–Rawlinsonia* Clade are diagnosable from each other resulting in the recognition of four genera: *Saganura*, *Rawlinsonia*, *Pengilleyia*, and *Colleeneremia* (Fig. 2).

General statement about the taxonomic accounts

Our approach is to provide a tabulation of morphological, acoustic, and molecular characters so that character state for all genera is explicitly presented, facilitating comparisons across genera (Tables 1, 2, 3; Supporting Information, Tables S3, S6). We also present an abridged diagnosis that covers some of the specific diagnostic characters with respect to sister-taxa and give reference to the Tables for diagnoses against other more distantly related genera, so that our generic accounts comply with Article 13.1.1 of the International Code of Zoological Nomenclature (ICZN 1999)which requires the name to 'be accompanied by a description or definition that states in words characters that are purported to differentiate the taxon'. We note that in many cases sister taxa will be single genera but in fewer cases a genus is sister to a clade that comprises two or more genera, e.g. *Sylvagemma* vs. *Nyctimystes* and *Sandyrana*, or *Ranoidea* vs. *Cyclorana*, *Leptobatrachus*, and *Megatestis*. In the cases of *Cyclorana* and *Nyctimystes* that are so distinctive, we have diagnosed them from all other pelodryadid genera. In view of the conservative nature of morphology for the Pelodryadidae, some genera will be diagnosed by a combination of a number of shared largely putative plesiomorphic character states rather than by one or more putatively apomorphic character states. Also, with a traditional text-based description, the character state of each character may not be apparent for all genera, making comparisons difficult, especially considering the very large number of genera involved. Tables 1, 2, and 3 and Supporting Information, Tables S3 and S6 provide that explicit comparison of character states across genera.

Molecular characters can also be used in generic diagnoses and may provide significant support in cases where phenotypic evolution has been constrained. Recent major taxonomic revisions have in some cases diagnosed genera solely from transformations in nucleotide character states at numerous positions in the alignments of mitochondrial and/or nuclear genes, e.g. Frost *et al.* (2006) and Faivovich *et al.* (2005). Recommended practice for 'barcode-based' diagnoses emphasizes that description of characters should be both contrastive and explicit with regard to character states (Rheindt *et al.* 2023). We present nucleotide character state transformations in the alignment of the mitochondrial *ND4* gene in Table 3 and in eight nuclear loci from among those with the longest alignments in Supporting Information, AHE loci diagnostic sites.

Authority for designation of type species of genera was taken from Amphibian Species of the World v.6.1 (Frost 2023) and from our own investigations. Where we have assigned type species to genera described in our paper, we have nominated the first described taxon irrespective of its original generic allocation.

There are a few species where material was not available for molecular genetic analysis (specimens missing or more than 110 years old) and either the only available material is in very poor condition, or the taxon is known only from the type specimen. In each of these cases, the species exhibit a unique combination of character states such that their affinities are uncertain. In these cases, we have placed the taxon in a genus based on available inferences of relationships (which admittedly are not robust) or in one case retained it in '*Hyla*' as a temporary assignment due to the lack of any semblance of information that could indicate its relationships, rather than arbitrarily erect a monotypic genus.

Distributions: For the information on the distribution of the genera we use the following definitions:

i Australia.
ii New Guinea and surrounding islands—including mainland New Guinea, land bridge islands of the D'Entrecasteaux group, Yapen, Aru Islands, Rajah Ampats and other continental islands of the Indonesian provinces of Central Papua, Highland Papua, Papua, West Papua, Southwest Papua, Maluku, and North Maluku.
iii New Guinea, Admiralty and Bismarck Archipelagos—including mainland New Guinea, the Bismarck and Admiralty Archipelagos.
iv New Guinea, Admiralty and Bismarck Archipelagos, and Solomons Islands—including the Bismarck and Admiralty Archipelagos and biogeographical Solomon Island chain, including Bougainville and Buka Islands.
v East Nusa Tenggara—the islands in the eastern portion of the Lesser Sunda Islands.

In the taxonomic accounts section below, we indicate the species for which molecular genetic data were available with *, details of which molecular genetic dataset was used for each species are presented in Supporting Information, Table S2.

Family Pelodryadidae Günther, 1859

Duellman *et al.* (2006) provided a definition for the family. Faivovich *et al.* (2010) discussed the lack of formal evidence for the monophyly of the pelodryadine frogs based on the limited range of species represented in molecular phylogenetic studies to that time and the absence of a morphological diagnosis. Elias-Costa *et al.* (2021) discussed the evolution of submandibular musculature in Anura and provided morphological synapomorphies for the Pelodryadidae, for which Faivovich *et al.* (2011) had previously defined the homology of structures for these muscles. Bossuyt and Roelants (2009) considered that the pelodryadine frogs should be regarded as a distinct family based on the age of their divergence from their sister lineage the Phyllomedusidae, while Dubois *et al.* (2021) argued for sub-family status on the basis of fitting a rank-based classification to a hypothesis of phylogenetic relationships, generated largely from mitochondrial DNA nucleotide sequences. Our comprehensive molecular phylogenetic analyses demonstrate the monophyly of the pelodryadine frogs and Hime *et al.*

Table 3. Diagnostic sites in *ND4* gene alignment. Site numbering follows the full alignment (Supporting Information, ND4 alignment)

		1	1	1	1	1	1	1	1	2	2	2	2	3	3	3	3	3	4	4
	9	1	1	4	5	6	6	6	8	2	2	9	9	2	2	8	8	9	5	6
	3	8	9	9	8	1	2	7	5	4	7	1	3	0	3	6	9	8	3	7
Drymomantis cooloolensis	**G**	**C**	**C**	**C**	**T**	**A**	**A**	**A**	**A**	**T**	**T**	**C**	**T**	**T**	**C**	**A**	**G**	**T**	**A**	**T**
Drymomantis fallax	**G**	**C**	**C**	**T**	**T**	**A**	**A**	**A**	**A/G**	**T**	**G/T**	**C**	**T**	**T**	**C**	**A**	**A/G**	**T**	**A**	**T**
Drymomantis olongburensis	**G**	**C**	**T**	**C**	**T**	**A**	**A**	**A**	**G**	**T**	**T**	**C**	**T**	**C**	**T**	**A**	**C**	**C**	**A**	**T**
Carichyla bicolor ABTC28364	**A**	**T**	G	T	**A**	**T**	**C**	**C**	**T**	**A**	**A**	**A**	**A**	**A**	**C**	**T**	**T**	**A**	**A**	**A**
Carichyla bicolor ABTC28905	**A**	**T**	T	A	**A**	**T**	**C**	**C**	**C**	**A**	**A**	**A**	**A**	**A**	**C**	**T**	**T**	**A**	**A**	**C**
Carichyla bicolor ABTC93005	**A**	**T**	A	C	**A**	**T**	**C**	**T**	**C**	**A**	**A**	**A**	**A**	**A**	**C**	**T**	**T**	**A**	**A**	**C**
Carichyla bicolor ABTC100072	**A**	**T**	T	A	**A**	**T**	**C**	**C**	**T**	**A**	**A**	**A**	**G**	**A**	**C**	**T**	**T**	**A**	**A**	**C**
Papuahyla lodesdema	A	**T**	**G**	**A**	A	**T**	C	**T**	A	A	C	**G**	**C**	**T**	**T**	**T**	**T**	**T**	**C**	**C**
Papuahyla bibonius	G	**T**	**A**	**A**	T	**T**	C	**T**	T	T	T	**A**	**T**	**A**	**T**	**C**	**T**	**A**	**T**	**A**
Papuahyla chloristona	G	**T**	**A**	**A**	T	**T**	C	**T**	A	T	A	**A**	**T**	**G**	**T**	**C**	**T**	**A**	**T**	**A**
Papuahyla louisiadensis	G	**T**	**A**	**A**	T	**T**	A	**G**	A	T	C	**A**	**T**	**C**	**T**	**T**	**T**	**T**	**C**	**T**
Papuahyla rubrops	G	**C**	**A**	**A**	T	**T**	C	**T**	T	C	T	**A**	**T**	**A**	**T**	**T**	**T**	**A**	**T**	**G**
Exedrobatrachus biakensis	G	T	A	T	G	T	C	A	A	A	T	A	T	A	T	T	T	C	A	C
Exochohyla chrisdahli	A	T	T	T	A	A	A	T	A	A	T	A	C	A	C	C	T	T	A	A
Exochohyla humboldtorum	A	T	A	T	A	A	A	C	A	A	T	A	T	G	C	T	T	T	A	A
Exochohyla	G	T	T	T	A	A	A	T	A	A	T	G	T	A	T	T	A	T	A	A
Ischnohyla daraiensis	G	T	A	A	G	A	A	T	A	A	A	A	T	A	T	T	T	T	A	A
Ischnohyla gracilis	G	T	A	A	G	T	A	T	A	A	A, C	A	T	A	C/T	T	T	T	A/T	A/G
Ischnohyla nigropunctata	A	T	A	A	G	A	A	C	A	A	T	A	T	T	C	T	T	T	A	A
Amnihyla amnicola	G	T	A	A	T	T	C	T	A	A	G	A	T	T	T	T	T	T	A	A
Amnihyla angiana	A	T	A	A	A	G	C	A	G	T	A	A	T	G	A	T	T	C	A	A
Amnihyla arfakiana	G	T	G	G	A	G	C	A	A	A	A	A	T	T	C	T	T	A	A	C
Amnihyla becki	G	T	G	A	G	T	C	T	T	T	T	A	T	A/G	C	T	T	C	A	A
Amnihyla bulmeri	G	T	A	A	A	G	C	A	A	T	G	A	C	G	T	T	T	C	A	A
Amnihyla dorsivena	G	T	A	A	G	A	C	C	A	T	A	A	T	G	C	T	T	A	A	T
Amnihyla haematogaster	G	T	G	G	A	T	C	A	T	T	T	A	T	A	C	T	A	T	A	A
Amnihyla leucova	A	T	A	A	G	A	C	T	A	C	A	A	T	A	C	T	T	A	A	C
Amnihyla micromembrana	G	T	A	A	A	G	C	A	A	T	A	A	C	A	C	A	A	C	A	C
Amnihyla modica	G	T	A	A	A	T	C	A,C	A	C	A/T	A	C/T	G	C	A/T	A/T	C/T	A	G
Amnihyla oenicolen	G	T	A	A	A	A	C	C	T	T	A	A	T	G	T	T	T	C	A	T
Amnihyla pratti	G	T	A	A	G	A	C	A	A	C	A	A	T	A	C	T	T	A	A	C
Amnihyla rivicola	G	T	A	A	G	T	C	T	A	T	A	A	T	A	C/T	T	T	T	A	T
Amnihyla spartacus	G	T	G	T	G	A	C	T	A	T	A	A	T	A	T	T	T	C	A	T

Table 3. Continued

	93	118	119	149	158	161	162	167	185	224	227	291	293	320	323	386	389	398	453	467
Amnihyla wollastoni	G	T	A	C	G	A	C	T	A	T	A	A	T	G	C	A	T	T	A	T
Hyalotos naispela	-	T	A	A	A	T	G	G	A	T	C	A	T	G	T	T	A	C	A	A
Hyalotos richardsi	G	T	G	G	A	A	G	T	A	T	C	G	C	A	T	T	A	T	A	A
Hyalotos singadanae	G	T	A	A	G	T	G	T	A	T	T	A	T	A/G	T	T	T	C	A	A
Kallistobatrachus aplini	G	T	A	A	A	T	C	A	T	T	T	A	C	A	C	T	G	T	A	A
Kallistobatrachus beryllinus	G	T	A	A	A	C	C	A	A	A	T	G	C	C	C	T	A	A	A	T
Kallistobatrachus iris	G	T	A	A	G	T	C	C	T	T	T	A	T	G	T	T	A	T	A	G
Kallistobatrachus lisae	G	T	A	A	A	T	C	A	C/T	C	T	A	T	A	T	T	A/G	T	A	T
Kallistobatrachus majikthise	G	T	A	A	A	T	C	A	T	T	C	A	T	A	C	T	A	T	A	A
Lathrana verae	G	T	A	A	T	A	T	A	A	T	T	A	C	G	C	T	C	T	T	A
Nasutibatrachus mucro	A	C	A	C	A	T	C	A	T	C	A	A	C	A	T	T	T	T	C	C
Nasutibatrachus pronimius	A	C	A	A	G/T	T	C	A	T	T	A	A	T	A	T	T	T	T	T	C
Nasutibatrachus vivissimia	A	T	A	A	A	T	C	A	A	T	T	A	A	A	C	T	T	T	C	T
Teretistes havina	A	T	A	A	G	T	C	T	G	C	T	A	T	G	T	T	T	A	T	C
Viridihyla gasconi	G	T	A	C	A	T	A	T	T	T	T	A	T	T	T	T	T	A	C/T	T
Viridihyla multiplica	G	T	A	T	A	G	C	T	T	T	A	A	A	T	T	T	T	T	T	T
Viridihyla spectabilis	G	C	A	T	A	T	A	T	T	T	C	A	T	T	T	T	T	T	T	T
Coggerdonia adelaidensis	G	T	G	T	A	T	C	A	A	T	C/T	A	T	A	T	A	T	C	A	A
Litoria personata	A	C	C	A	T	T	G	A	A	T	T	A	A	A	T	C	A	A	A	A
Litoria spaldingi	A	T	C	T	G	T	C	A	A	T	A/G	A	G	A	C	T	G	A	A	A

	472	491	494	530	543	548	551	552	611	614	615	616	639	641	675	678	701	711	719
Drymomantis cooloolensis	**C**	**A**	**A**	**T**	**A**	A	**T**	**G**	**G**	**C**	**C**	**T**	**T**	**C**	**A**	**T**	**A**	**A**	**T**
Drymomantis fallax	**C**	**A**	**G**	**T**	**A**	A	**T**	**G**	**A**	**C**	**C**	**T**	**T**	**C**	**A**	**T**	**A**	**A**	**T**
Drymomantis olongburensis	**C**	**A**	**A**	**C**	**A**	T	**T**	**G**	**A**	**C**	**A**	**T**	**T**	**C**	**A**	**T**	**A**	**A**	**T**
Carichyla bicolor ABTC28364	**C**	**T**	**T**	**A**	**A**	**A**	**A**	**A**	**T**	**T**	**T**	**C**	**A**	**T**	**A**	**A**	**T**	**C**	**C**
Carichyla bicolor ABTC28905	**C**	**T**	**C**	**A**	**A**	**A**	**A**	**A**	**C**	**T**	**T**	**C**	**A**	**T**	**A**	**C**	**T**	**C**	**C**
Carichyla bicolor ABTC93005	**C**	**T**	**C**	**G**	**A**	**A**	**A**	**A**	**C**	**T**	**T**	**C**	**A**	**A**	**A**	**C**	**C**	**C**	**C**
Carichyla bicolor ABTC100072	**C**	**T**	**C**	**A**	**A**	**A**	**A**	**A**	**T**	**T**	**T**	**C**	**A**	**T**	**A**	**C**	**T**	**C**	**C**
Papuahyla lodesdema	**T**	**G**	**C**	**T**	**G**	**G**	**T**	**G**	A	C	G	C	T	**T**	**G**	**C**	**T**	**C**	T
Papuahyla bibonius	**T**	**A**	**T**	**T**	**G**	**T**	**G**	**G**	C	T	A	T	T	**T**	**G**	**C**	**C**	**C**	T
Papuahyla chloristona	**T**	**A**	**A**	**T**	**G**	**G**	**T**	**G**	T	T	T	C	T	**T**	**G**	**C**	**T**	**C**	C

Table 3. Continued

	472	**491**	**494**	**530**	**543**	**548**	**551**	**552**	**611**	**614**	**615**	**616**	**639**	**641**	**675**	**678**	**701**	**711**	**719**
Papuahyla louisiadensis	**T**	**A**	**A**	**C**	**G**	**C**	**A**	**G**	C	T	C	T	A	**T**	**G**	**C**	**T**	**C**	C
Papuahyla rubrops	**T**	**A**	**T**	**T**	**G**	**T**	**G**	**G**	T	T	G	T	T	**T**	**G**	**C**	**C**	**C**	T
Exedrobatrachus biakensis	C	A	A	C	A	C	A	A	T	T	T	C	A	C	A	T	T	C	T
Exochohyla chrisdahli	T	A	A	T	A	A	A	G	A	A	T	C	T	G	A	T	C	C	C
Exochohyla humboldtorum	T	A	A	T	A	A	A	G	A	A	T	C	T	A	A	C	C	C	T
Exochohyla	C	G	G	T	A	T	G	G	T	A	T	C	A	G	A	C	T	C	T
Ischnohyla daraiensis	C	A	A	T	A	T	G	G	T	T	T	C	T	T	A	T	T	A	T
Ischnohyla gracilis	C	A	A	T	A	C/T	A	G	T	T	T	C	T	T	A	T	T	A	C/T
Ischnohyla nigropunctata	T	A	A	C	A	G	C	G	C	T	T	C	A	T	A	T	T	A	C
Amnihyla amnicola	T	A	C	T	A	A	G	G	T	T	A	C	A	T	A	T	T	A	T
Amnihyla angiana	C	A	A	C	A	G	G	G	C	A	A	C	A	T	A	C	C	T	T
Amnihyla arfakiana	C	A	T	T	A	A	G	A	C	A	A	T	A	T	G	C	T	C/T	T
Amnihyla becki	C	A	A	C	A	G	G	A	C	A	A	C	A	T	A	C/T	T	T	T
Amnihyla bulmeri	C	A	A	C	A	C	A	A	A	A	A	C	A	T	A	C	T	T	T
Amnihyla dorsivena	C	A	C	C	A	G	A	A	T	T	A	C	A	T	G	T	T	T	C
Amnihyla haematogaster	C	A	A	T	A	A	T	A	A	A	G	C	A/G	T	A	T	A	C	C
Amnihyla leucova	C	G	T	C	A	A	G	A	C	T	T	C	A	T	A	T	T	T	T
Amnihyla micromembrana	T	A	A	C	A	T	A	A	T	T	A	T	A	C	A	A	C	T	T
Amnihyla modica	C/T	G	A	C	A	A/T	A/G	A	C/T	A	A	C	A	T	A	A/C/T	T	T	T
Amnihyla oenicolen	C	A	C	T	A	A	A	A	C	T	A	C	A	T	G	C	T	A	T
Amnihyla pratti	C	A	T	C	A	A	A	G	C	C	A	C	A	T	G	T	T	A	C
Amnihyla rivicola	C	A	T	A	A	A	A	G	C/T	C	T	T	T	T	G	T	T	T	T
Amnihyla spartacus	C	A	T	C	A	T	G	G	C	C	A	C	A	T	A	T	A	G	C
Amnihyla wollastoni	C	A	T	T	A	C	G	G	A	T	A	T	A	T	A	T	C	C	T
Hyalotos naispela	C	A	A	C	A	A	A	A	C	A	A	T	A	T	A	T	C	C	T
Hyalotos richardsi	C	A	A	C	A	A	G	A	T	C	A	C	A	C	A	T	T	C	T
Hyalotos singadanae	T	A	A	C	A	A	A	A	C	G	A	T	A	T	A	T	C	C	T
Kallistobatrachus aplini	T	A	A	T	A	T	A	G	A	A	A	T	A	T	A	T	C	C	T
Kallistobatrachus beryllinus	T	A	A	T	A	T	G	G	A	A	A	C	A	T	A	T	C	C	T
Kallistobatrachus iris	C/T	A	A	C	A	C	A	G	A	A	A	T	A	T	A	T	T	C	C
Kallistobatrachus lisae	C	A	A	T	A	A	A	A	A	A	A	C/T	A	T	A	T	T	C	T
Kallistobatrachus majikthise	C	A	A	C/T	A	A/G	T	A/G	A	A	A/G	C	A	T	A	T	C	C	T
Lathrana verae	T	A	A	T	A	A	G	A	C	T	A	C	A	T	A	C	C	T	T
Nasutibatrachus mucro	T	A	T	A	A	A	A	A	T	T	A	T	A	T	A	T	A	C	T

Table 3. Continued

	472	491	494	530	543	548	551	552	611	614	615	616	639	641	675	678	701	711	719
Nasutibatrachus pronimius	T	A	A	C	A	A	A	A	C	A	A	T	A	T	A	C/T	A	C	T
Nasutibatrachus vivissimia	T	A	A	T	A	G	A	A	C	A	A	C	A	T	A	C	A	C	T
Teretistes havina	T	A	A	T	A	G	T	A	C	T	A	T	A	T	A	T	T	C	C
Viridihyla gasconi	C	G	A	T	A	A	A	A	C	T	G	T	A	T	A	T	A	C	T
Viridihyla multiplica	T	A	A	T	A	T	A	A	T	G	A	C	A	T	A	T	T	G	T
Viridihyla spectabilis	C	A	A	T	G	A	A	A	A	T	A	C	A	T	A	T	T	C	T
Coggerdonia adelaidensis	C	A	A	A	A	A	A	A	C	C	T	T	A	T	A	C	A	C	T
Litoria personata	T	A	A	T	G	G	A	A	C	T	A	A	T	C	G	C	T	C	C
Litoria spaldingi	C	A/G	A	T	G	A/G	C/T	A	G	G	A	T	A	C	A	C	A	C	C

(2021) provide robust phylogenomic evidence of the relationships of the Pelodryadidae with other hyloid families.

Amnihyla Richards, Mahony & Donnellan, **gen. nov.**

(Figs 9, 10)

ZooBank LSID: urn:lsid:zoobank.org:act:4A0ADBA7-AE39-43FC-A114-78063102556E Type species: Hyla (Litoria) arfakiana (Peters & Doria, 1878).

Content: 24 species—*Amnihyla amnicola** (Richards, Tjaturadi, Krey & Donnellan, 2021) comb. nov., *Amnihyla angiana** (Boulenger, 1915) comb. nov., *Amnihyla arfakiana** (Peters & Doria, 1878) comb. nov., *Amnihyla becki** (Loveridge, 1945) comb. nov., *Amnihyla brongersmai* (Loveridge, 1945) comb. nov., *Amnihyla bulmeri** (Tyler, 1968a) comb. nov., *Amnihyla dorsivena** (Tyler, 1968a) comb. nov., *Amnihyla fuscula* (Oliver & Richards, 2007) comb. nov., *Amnihyla lakekamu* (Richards & Bickford, 2023) comb. nov., *Amnihyla leucova** (Tyler, 1968a) comb. nov., *Amnihyla longicrus* (Boulenger, 1911) comb. nov., *Amnihyla macki* (Richards, 2001) comb. nov., *Amnihyla megalops* (Richards & Iskander, 2006) comb. nov., *Amnihyla micromembrana** (Tyler, 1963a) comb. nov., *Amnihyla modica** (Tyler, 1968a) comb. nov., *Amnihyla napaea* (Tyler, 1968a) comb. nov., *Amnihyla oenicolen** (Menzies & Zweifel, 1974) comb. nov., *Amnihyla pratti** (Boulenger, 1911) comb. nov., *Amnihyla rara* (Günther & Richards, 2005) comb. nov., *Amnihyla rivicola** (Günther & Richards, 2005) comb. nov., *Amnihyla scabra* (Günther & Richards, 2005) comb. nov., *Amnihyla spartacus** (Richards and Oliver, 2006b) comb. nov., *Amnihyla spinifera**(Tyler, 1968a) comb. nov., *Amnihyla wollastoni** (Boulenger, 1914) comb. nov.

Diagnosis: All *Amnihyla* can be diagnosed from *Exochohyla*, *Nasutibatrachus*, and *Teretistes* by the absence of a rostral spike; all except *A. amnicola* from *Carichyla*, *Drymomantis*, *Exedrobatrachus*, and *Papuahyla* by large pale vs. small pigmented ova (*A. amnicola* can be diagnosed from *Exedrobatrachus* by toe and finger discs equal in size vs. smaller; and from *Carichyla*, *Drymomantis*, and *Papuahyla* by the presence of tubercles on the hindlimb vs. absence); from *Drymomantis* and *Papuahyla* by a Type 3 vs. Type 1 tadpole oral disc, and Type 6 or 7 vs. Type 1 overall tadpole morphology; from *Hyalotos* by pigmented vs. transparent tympanum; from *Ischnohyla* by Type 6 or 7 vs. Type 2A overall tadpole morphology; from *Lathrana* by frequency modulated vs. unmodulated calls, by medium duration vs. long duration calls, and by calls with few vs. medium number of notes; from *Papuahyla* by fusiform, oval, rectangular, spike, or teardrop vs. a right triangular call envelope shape; from *Viridihyla* by a highly variable dorsal pattern vs. a uniform green dorsum. *Amnihyla*, except *A. amnicola*, can be diagnosed from *Kallistobatrachus* by large unpigmented eggs vs. small or medium pigmented eggs. *Amnihyla amnicola* can be diagnosed from *Kallistobatrachus* by lacking bright colours ventrally and/or in axilla and groin. Refer to Tables 1 and 2.

Distribution and ecology: New Guinea and surrounding islands, lowland forests to alpine meadows. Arboreal or semi-aquatic frogs that breed in clear-flowing, often torrential, streams. All

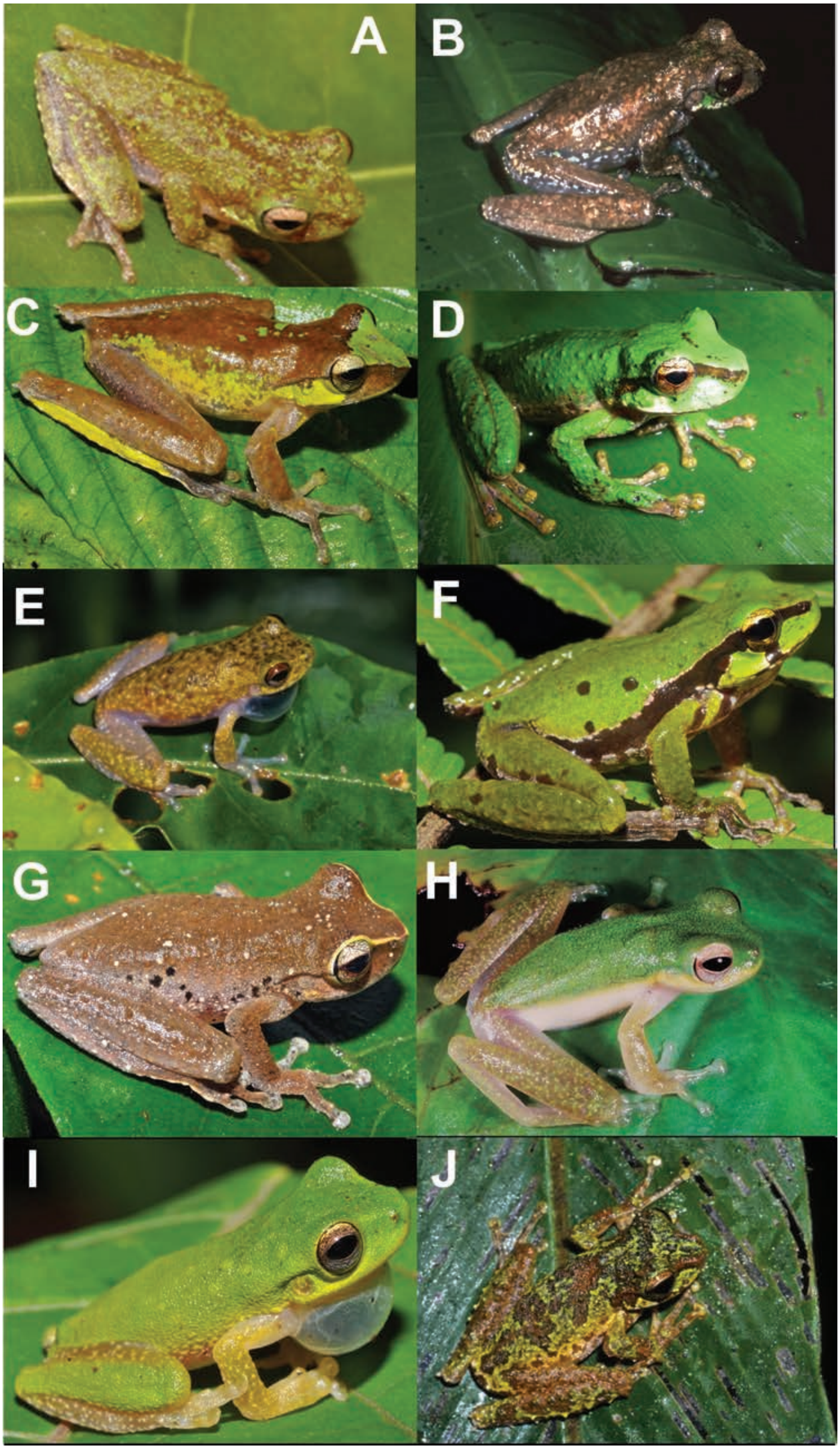

Figure 9. Images in life of *Amnihyla*: (A) *Amnihyla amnicola* Stephen Richards, (B) *Amnihyla angiana* Stephen Donnellan, (C) *Amnihyla arfakiana* Stephen Richards, (D) *Amnihyla becki* Chris Dahl, (E) *Amnihyla brongersmai* Stephen Richards, (F) *Amnihyla bulmeri* Stephen Richards, (G) *Amnihyla dorsivena* Stephen Richards, (H) *Amnihyla lakekamu* Stephen Richards, (I) *Amnihyla leucova* Stephen Richards, (J) *Amnihyla macki* Stephen Richards.

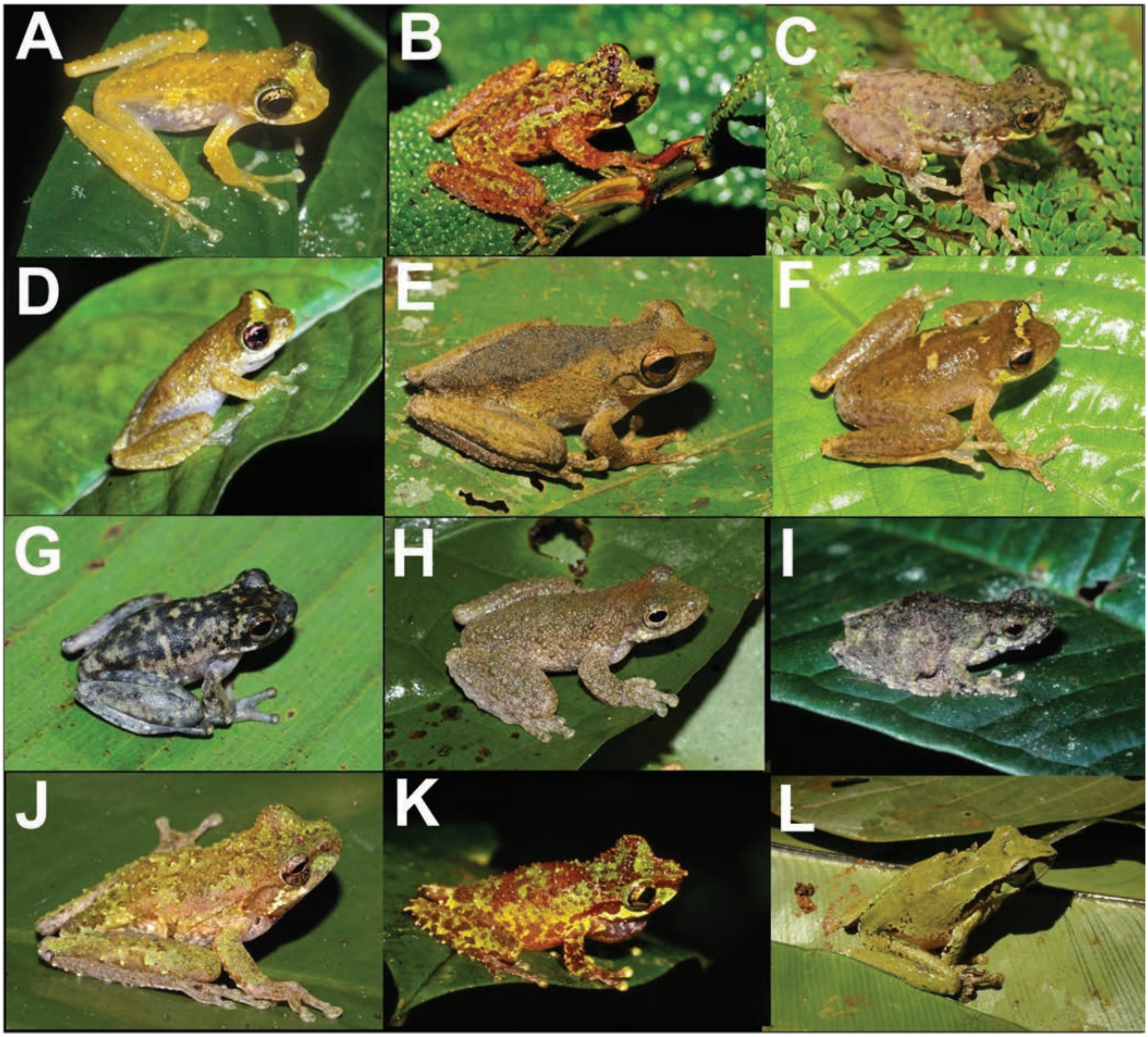

Figure 10. Images in life of *Amnihyla*: (A) *Amnihyla megalops* Stephen Richards, (B) *Amnihyla micromembrana* Stephen Richards, (C) *Amnihyla modica* Stephen Richards, (D) *Amnihyla napaea* Stephen Richards, (E) *Amnihyla oenicolon* Stephen Richards, (F) *Amnihyla* cf. *pratti* Stephen Richards, (G) *Amnihyla rara* Rainer Günther, (H) *Amnihyla rivicola* Stephen Richards, (I) *Amnihyla scabra* Stephen Richards, (J) *Amnihyla spartacus* Stephen Richards, (K) *Amnihyla spinifera* Stephen Richards, (L) *Amnihyla wollastoni* Fred Kraus.

species for which eggs are known, with the exception of *A. amnicola*, have large unpigmented eggs. Tadpoles are known or presumed to have large, ventrally oriented suctorial mouthparts. Calls often with narrow frequency bands to enhance detection above the sound of running water.

Etymology: From the Latin *amnis* (a river) and *Hyla* Laurenti, 1768, the earliest generic name for a tree frog, itself derived from Ύλας (*Hylas*), companion of Hercules in Greek mythology. While the original *Hylas* was a boy, and Copland (1962) treated the generic name derived from *Hylas* as masculine (incorrectly emending numerous adjectival species epithets to match), the generic name is feminine in its original formation (Myers and Stothers 2006) and remains so as the root for *Amnihyla*. The name alludes to the riverine habitat of the species in the genus.

Remarks: Amnihyla is the equivalent of the *Litoria angiana*, *Litoria arfakiana*, *Litoria becki*, *Litoria bulmeri*, *Litoria dorsivena*, *Litoria leucova*, and *Litoria napaea* Groups of Tyler and Davies (1978). Small to large New Guinea stream-dwelling frogs. The following nine species are all closely associated with clear-flowing streams and are included in *Amnihyla* in the absence of genetic data pending genetic material becoming available. *Hyla brongersmai* was not treated by Tyler and Davies (1978) but Menzies (2006) noted that its 'habitat and morphology indicate that this species is correctly placed among the torrent breeders'. Oliver and Richards (2007) argued that based on its morphology and ecology *Litoria fuscula* is allied to the *L. dorsivena* species group. Richards and Bickford (2023) noted that the ecology of *L. lakekamu* 'suggests that it is more likely to be related to the clade of torrent dwelling frogs including *L. leucova*'. *Litoria macki* was described by Richards (2001) as a torrent dwelling species most similar to *L. spinifera*, a species within *Amnihyla*. Richards and Iskandar (2006) considered *Litoria megalops* to be most similar to *L. micromembrana* and *L. modica*, both within *Amnihyla*. Günther and Richards (2005) demonstrated that *L. rara* is closely related to *L. rivicola* within *Amnihyla* based on mitochondrial 12S rDNA nucleotide sequences, and that *L. scabra* is morphologically most similar to *L. rivicola*. *Hyla napaea* has large unpigmented eggs and was considered probably a 'stream-breeding species' (Tyler and Davies 1978). Tyler and Davies (1978) placed *Hylella longicrus* Boulenger, 1911 in their *Litoria bicolor* Group. With unpigmented eggs, a truncate vs. rounded snout and close association with clear-flowing streams it is clearly not in the *Litoria bicolor* Group, and we assign it tentatively to *Amnihyla* pending further studies.

Carichyla Mahony, Donnellan & Richards, **gen. nov.**

(Fig. 11)

ZooBank LSID: urn:lsid:zoobank.org:act:565D5CC3-9C17-4BB6-8C76-D7DA56C0D699 Type species: Eucnemis bicolor Gray, 1842.

Content: Two species—*Carichyla bicolor** (Gray, 1842) comb. nov., *Carichyla viranula* (Menzies, Richards & Tyler, 2008) comb. nov.

Diagnosis: Carichyla can be diagnosed from members of the *Drymomantis* Sub-clade as follows: from *Amnihyla* except *A. amnicola* by pigmented vs. unpigmented eggs. It can be diagnosed from *A. amnicola* by the absence vs. presence of prominent tubercles on the hindlimb. It can be diagnosed from *Exochohyla* by a Type 1 vs. Type 1A tadpole oral disc and Type 1 vs. Type 6 overall tadpole morphology; from *Exedrobatrachus* by unornamented vs. tubercules on hindlimb, and toe disc equal to finger discs vs. smaller; from *Hyalotos* by a pigmented vs. transparent tympanum, small vs. medium or large eggs, absent vs. crenulated hindlimbs and spike, and fusiform vs. teardrop call envelope shape, a note rate change across the call vs. none; from *Ischnohyla* by a Type 1 vs. Type 3 tadpole oral disc, Type 1 vs. Type 2A overall tadpole morphology, and by spike-fusiform vs. left triangular, or left teardrop or oval call envelope shape, a note rate change across the call vs. none; from *Kallistobatrachus* by a Type 1 vs. Type 1B tadpole oral disc, Type 1 vs. Type 7 overall tadpole morphology, unornamented vs. tubercles or crenulations on the hindlimbs, and presence vs. absence of the alary process of the hyoid; from *Lathrana* by unornamented vs. tubercules on hindlimb, small vs. medium eggs, toe disc equal to finger discs vs. smaller, and presence vs. absence of the alary process of the hyoid, and spike-fusiform vs. oval call envelope shape, a note rate change across the call vs. none; from *Nasutibatrachus* and *Teretistes* by the absence of a rostral spike; further from *Teretistes* by small vs. large eggs, toe webbing reduced or fully webbed vs. minimally webbed, small vs. large egg size, a Type 1 vs. Type 3 tadpole oral disc, and spike-fusiform vs. triangular call envelope shape; from *Viridihyla* by small vs. large egg size, ossified vs. cartilaginous intercalary structure and presence vs. absence of the alary process of the hyoid. *Carichyla* can be diagnosed from *Drymomantis* by the presence vs. the absence of an unbroken lateral white stripe from the under the eye to the groin (Figs 11, 15), by a spike-fusiform vs. fusiform-spike call envelope shape (Table 2) and by 31 sites in the mitochondrial *ND4* alignment (Table 3). *Carichyla* can be diagnosed from *Papuahyla* by presence vs. absence of the alary process of the hyoid, and a spike-fusiform vs. right triangular call envelope shape (Table 2) and by 13 sites in the mitochondrial *ND4* alignment (Table 3). Refer to Tables 1, 2, and 3. Diagnosis of *Carichyla* from all other genera in the *Drymomantis* Sub-clade is supported by 189 sites distributed across eight AHE loci (Supporting Information, AHE loci diagnostic sites).

Distribution and ecology: Northern and eastern Australia and southern New Guinea. Arboreal frogs that are found in open permanent or seasonal grassy, sedge, or sago swamps in natural or altered lowland habitats, usually not in closed forests (Menzies 2006, Anstis 2017).

Etymology: The generic name for sedges, *Carex* (Latin) refers to a common name for the group 'sedge frogs'. The stem for combining with other nouns is *caric-* (the study of sedges is caricology). See etymology for *Amnihyla* above for the derivation of *Hyla*.

Remarks: Carichyla is the equivalent to part of the *Litoria bicolor* Group of Tyler and Davies (1978). In the absence of genetic data for *Litoria viranula*, conservatively we have included it in *Carichyla* on the basis that Menzies *et al.* (2008) found it closest to *L. bicolor* in their multivariate analysis of morphometric variables. We also note that James' (1997) analysis of genetic data showed that *C. bicolor* is an unresolved species complex which is also consistent with the diversity for this taxon in our *ND4* data (Fig. 1).

Chlorohyla Mahony, Donnellan & Richards, **gen. nov.**

(Fig. 11)

ZooBank LSID: urn:lsid:zoobank.org:act:395E8CA0-986F-4F81-913B-3239EBB0B7DE Type species: Hyla gracilenta Peters, 1869.

Content: 12 species—*Chlorohyla aruensis* (Horst, 1883) comb. nov., *Chlorohyla auae** (Menzies & Tyler, 2004) comb. nov., *Chlorohyla bella** (McDonald, Rowley, Richards & Frankham, 2016) comb. nov., *Chlorohyla callista* (Kraus, 2013b) comb. nov., *Chlorohyla chloris** (Boulenger, 1892) comb. nov., *Chlorohyla elkeae** (Günther & Richards, 2000) comb. nov., *Chlorohyla eschata* (Kraus and Allison, 2009) comb. nov., *Chlorohyla gracilenta** (Peters, 1869) comb. nov., *Chlorohyla kumae* (Menzies & Tyler, 2004) comb. nov., *Chlorohyla robinsonae* (Oliver, Stuart-Fox & Richards, 2008) comb. nov., *Chlorohyla vagabunda* (Peters & Doria, 1878) comb. nov., *Chlorohyla xanthomera** (Davies, McDonald & Adams, 1986) comb. nov.

Diagnosis: Chlorohyla can be diagnosed from the sister taxon *Pelodryas* by overall tadpole morphology Type 4 vs. Type 1,

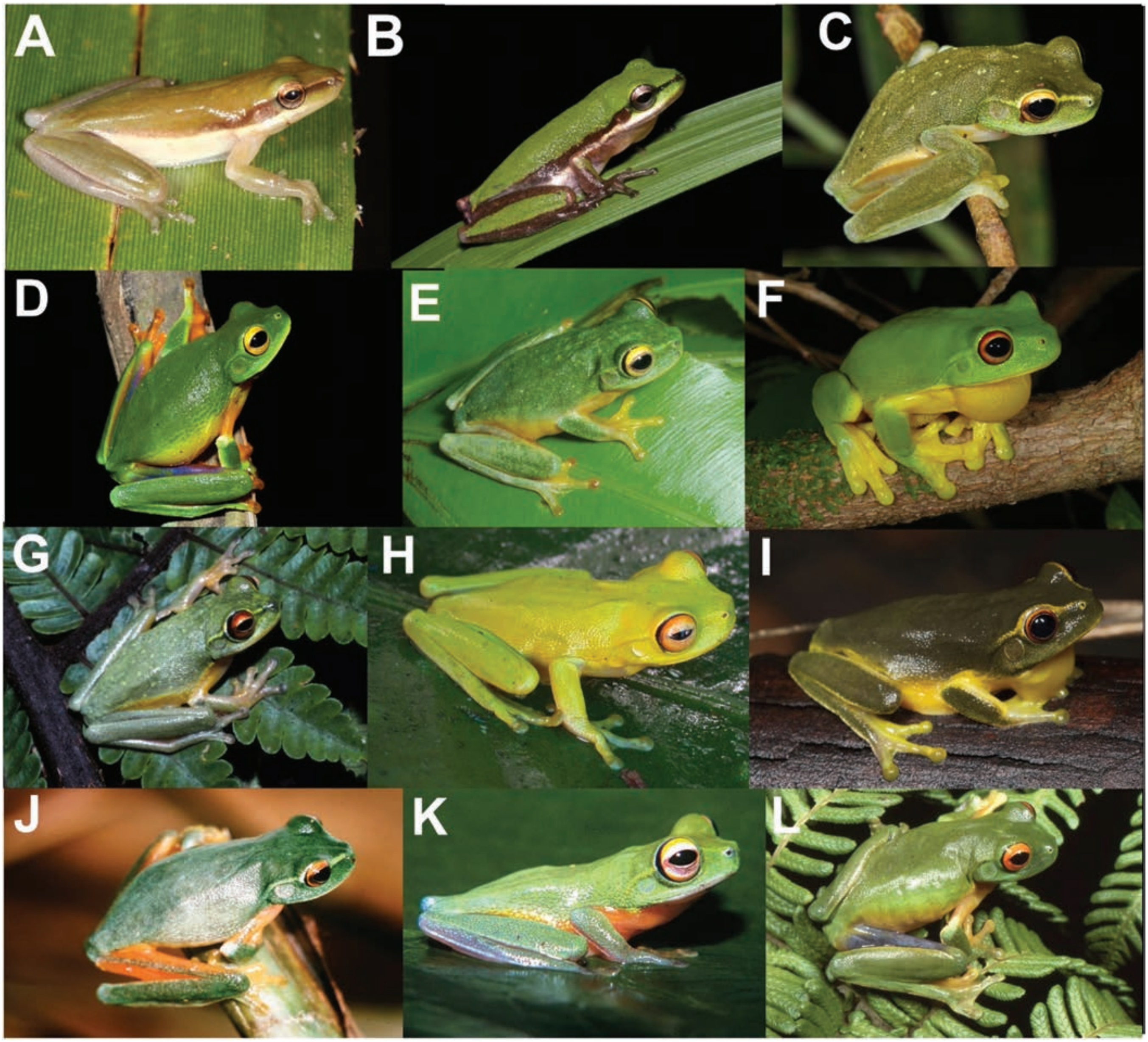

Figure 11. Images in life of *Carichyla* and *Chlorohyla*: (A) *Carichyla bicolor* Stephen Mahony, (B) *Carichyla viranula* Stephen Richards, (C) *Chlorohyla auae* Stephen Richards, (D) *Chlorohyla bella* Keith McDonald, (E) *Chlorohyla callista* Fred Kraus, (F) *Chlorohyla chloris* Stephen Mahony, (G) *Chlorohyla elkeae* Stephen Richards, (H) *Chlorohyla eschata* Fred Kraus, (I) *Chlorohyla gracilenta* Stephen Mahony, (J) *Chlorohyla kumae* James Menzies, (K) *Chlorohyla robinsonae* Devi Stuart-Fox, (L) *Chlorohyla xanthomera* Stephen Donnellan.

and by frequency modulated vs. non-modulated calls. Refer to Tables 1 and 2.

Distribution and ecology: Arboreal frogs that breed in ponds, found in forest and savannah habitats and modified landscapes in eastern Australia and New Guinea and surrounding islands.

Etymology: Refers to the bright green colour (Greek *chlōrós*) of frogs (Greek *Hyla*) in this lineage. The gender is feminine.

Remarks: Chlorohyla corresponds in part to the *Litoria aruensis* Group (*C. aruensis*, *C. chloris* and *C. gracilenta*) of Tyler and Davies (1978). We have conservatively placed *Hyla vagabunda* Peters & Doria, 1878 in *Chlorohyla* based on Menzies' (2006) discussion of its affinities. Menzies (2006) suggested affinity with *Litoria gracilenta* based on a pale canthal stripe, but also indicated that the hands are unwebbed (S.J.R. observations also confirm reduced toe webbing), whereas *Chlorohyla* have finger webbing. It is known only from two specimens from Seram, Maluku Province, and Sorong, Southwest Papua Province, Indonesia. Tyler and Davies (1978) placed it in their monotypic *Litoria vagabunda* Group. A confident understanding of the affinities of *H. vagabunda* awaits the availability of further material. Five additional species lacking genetic data are included within *Chlorohyla*: *C. aruensis*, *C. callista*, *C. eschata*, *C. kumae*, and *C. robinsonae*. *Hyla aruensis* was considered a member of the *Litoria gracilenta* group by Menzies (2006). All of the others are moderately small green frogs with a pale canthal stripe that were assigned to the *L. gracilenta* group or considered related to that species in their original descriptions (Menzies and Tyler 2004, Oliver *et al*. 2008, Kraus and Allison 2009, Kraus 2013b).

Coggerdonia Wells & Wellington, 1985: 4

(Fig. 12)

Type species: Hyla adelaidensis Gray, 1841, by original designation.

Content: One species—*Coggerdonia adelaidensis** (Gray, 1841).

Diagnosis: Coggerdonia can be diagnosed from *Mahonabatrachus* by medium vs. small size; from *Litoria* and *Mahonabatrachus* by reduced finger webbing vs. none; and from *Litoria* by the absence vs. presence of an alary process of hyoid. Refer to Tables 1 and 2.

Distribution and ecology: Arboreal frogs that call from emergent reeds in permanent ponds or slow-moving water, found in forests and woodlands and modified landscapes in south-western Australia.

Etymology: According to Wells and Wellington (1985), named for Harold Cogger, in recognition of his contributions to Australian herpetology. The gender is feminine.

Remarks: Coggerdonia is the equivalent of the *Litoria adelaidensis* Group of Tyler and Davies (1978).

Colleeneremia Wells and Wellington, 1985: 4

(Fig. 12)

Type species: Hyla rubella Gray, 1842, by original designation.

Content: 12 species—*Colleeneremia balatus** (Rowley, Mahony, Hines, Myers, Price, Shea & Donnellan, 2021) comb. nov., *Colleeneremia capitula** (Tyler, 1968) comb. nov., *Colleeneremia congenita** (Peters & Doria, 1878) comb. nov., *Colleeneremia dentata** (Keferstein, 1868) comb. nov., *Colleeneremia electrica** (Ingram & Corben, 1990) comb. nov., *Colleeneremia pygmaea** (Meyer, 1874) comb. nov., *Colleeneremia quadrilineata* (Tyler & Parker, 1974) comb. nov., *Colleeneremia quiritatus** (Rowley, Mahony, Hines, Myers, Price, Shea & Donnellan, 2021) comb. nov., *Colleeneremia rubella** (Gray, 1842), *Colleeneremia rueppelli** (Boettger, 1895) comb. nov., *Colleeneremia umbonata* (Tyler & Davies, 1983) comb. nov., *Colleeneremia wisselensis* (Tyler, 1968a) comb. nov.

Diagnosis: Colleeneremia can be diagnosed from the sister taxon *Pengilleyia* by small to medium vs. large size and calls with a densely pulsatile structure in which the notes are not fully amplitude modulated compared with note repetition in which the notes are fully amplitude modulated. Refer to Tables 1 and 2.

Distribution and ecology: Arboreal frogs that breed in ephemeral ponds and are found in forests, woodlands, arid shrublands, and modified landscapes in the northern two-thirds of Australia, New Guinea and surrounding islands, and the province of East Nusa Tenggara, Indonesia.

Etymology: According to Wells and Wellington (1985), named for Miss Colleen Montgomery of Sydney in appreciation for her interest in wildlife conservation. The gender is feminine.

Remarks: Colleeneremia is the equivalent of the *Litoria rubella* and *L. quadrilineata* Groups of Tyler and Davies (1978). Three species lacking genetic data are included in *Colleeneremia*: *C. quadrilineata*, *C. umbonata*, and *C. wisselensis*. Tyler and Davies (1978) included *L. wisselensis* in the *Litoria rubella* Group (= *Colleeneremia*) and *L. quadrilineata* in a separate, monotypic group. Tyler and Davies (1983) subsequently placed *L. umbonata* and *L. wisselensis* in a separate group. However, based on their very short legs Menzies (2006) included all three species in the *Litoria rubella* 'complex' and we follow this arrangement pending availability of genetic data.

Cyclorana Steindachner 1867: 29(Figs 13, 14)

Synonymy

Chiroleptes Günther 1859: 34 (type species *australis* Gray, 1842) (name unavailable due to *Chiroleptes* Kirby 1837: 280).

Phractops Peters 1867: 30 [type species *alutaceus* Peters, 1867 (= *novaehollandiae* Steindachner, 1867)].

Mitrolysis Cope 1889: 312 (type species *alboguttata* Günther, 1867).

Brendanura Wells and Wellington 1985: 4 (type species *alboguttata* Günther, 1867).

Neophractops Wells and Wellington 1985: 5 (type species *platycephalus* Günther, 1873) [mis-spelt as *Neophracops* by Duellman *et al.* (2016)].

Type species: Cyclorana novaehollandiae Steindachner, 1867, by monotypy.

Content: 14 species—*Cyclorana alboguttata** (Günther, 1867), *Cyclorana australis** (Gray, 1842), *Cyclorana brevipes** (Peters, 1871), *Cyclorana cryptotis** Tyler & Martin, 1977, *Cyclorana cultripes** Parker, 1940, *Cyclorana longipes** Tyler & Martin, 1977, *Cyclorana maculosa** Tyler & Martin, 1977, *Cyclorana maini** Tyler & Martin, 1977, *Cyclorana manya** Van Beurden & McDonald, 1980, *Cyclorana novaehollandiae** Steindachner, 1867, *Cyclorana occidentalis** Anstis, Price, Roberts, Catalano, Hines, Doughty & Donnellan, 2016, *Cyclorana platycephalus** (Günther, 1873), *Cyclorana vagitus** Tyler, Davies & Martin, 1981, *Cyclorana verrucosa** Tyler & Martin, 1977.

Diagnosis: Cyclorana can be diagnosed from other pelodryadids by a combination of the absence of the intercalary structure (except for *C. alboguttata*), large inner metatarsal tubercle, absence of finger webbing, and unexpanded finger and toe discs. It can be diagnosed from all other pelodryadids with the exception of *Megatestis* by overall tadpole morphology Type 3. It can be diagnosed from *Leptobatrachus* and *Megatestis* by the presence of

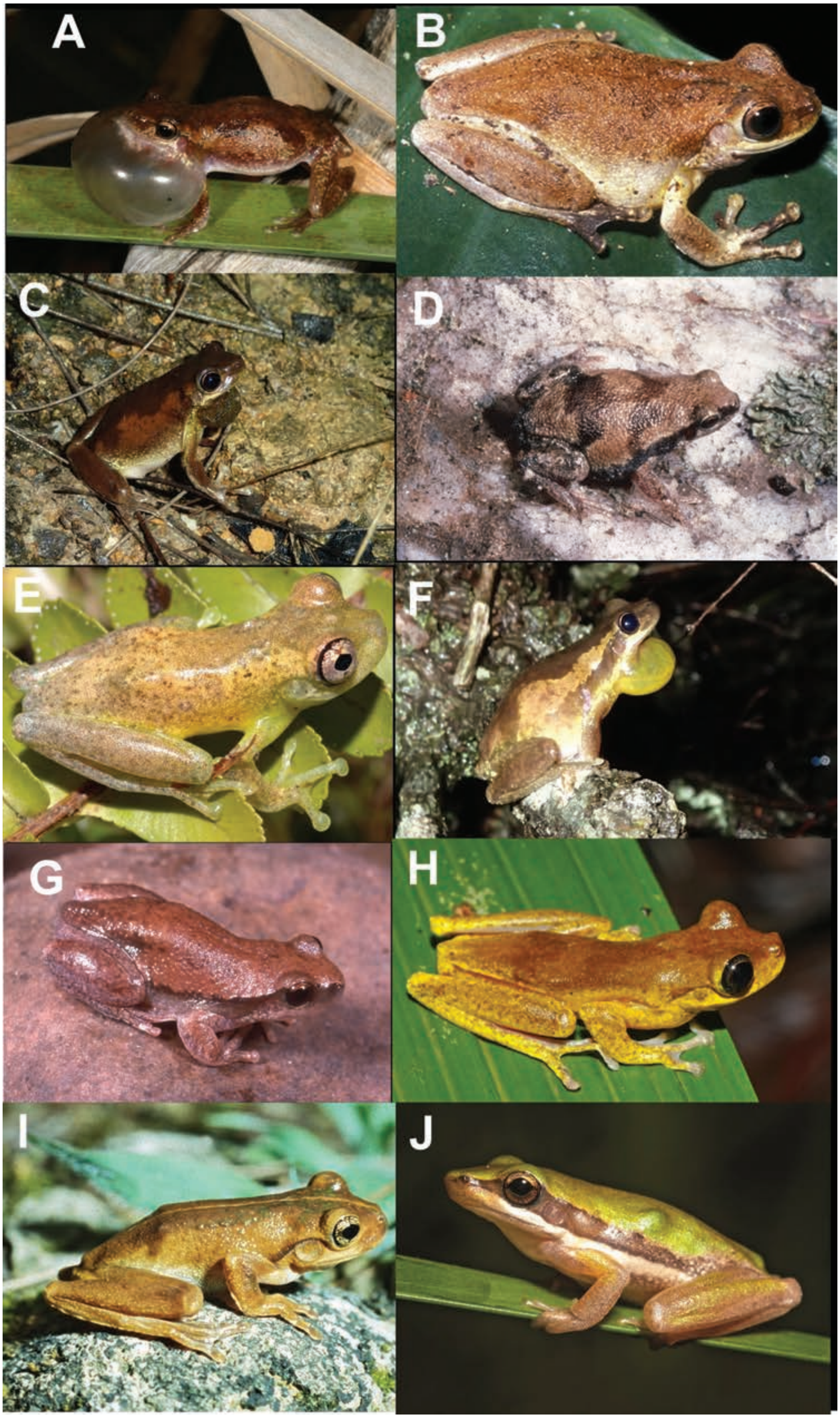

Figure 12. Images in life of *Colleeneremia* and *Coggerdonia*: (A) *Colleeneremia balatus* Harry Hines, (B) *Colleeneremia congenita* Stephen Richards, (C) *Colleeneremia dentata* Jodi Rowley, (D) *Colleeneremia electrica* Stephen Donnellan, (E) *Colleeneremia pygmaea* Stephen Richards, (F) *Colleeneremia quiritatus* Jodi Rowley, (G) *Colleeneremia rubella* Stephen Donnellan, (H) *Colleeneremia rueppelli* Stephen Richards, (I) *Colleeneremia umbonata* Rainer Günther, (J) *Coggerdonia adelaidensis* Marion Anstis.

Figure 13. Images in life of *Cyclorana*: (A) *Cyclorana alboguttata* Stephen Mahony, (B) *Cyclorana australis* Marion Anstis, (C) *Cyclorana brevipes* Marion Anstis, (D) *Cyclorana cryptotis* Marion Anstis, (E) *Cyclorana cultripes* Marion Anstis, (F) *Cyclorana longipes* Michael Mahony, (G) *Cyclorana maculosa* Marion Anstis, (H) *Cyclorana maini* Marion Anstis.

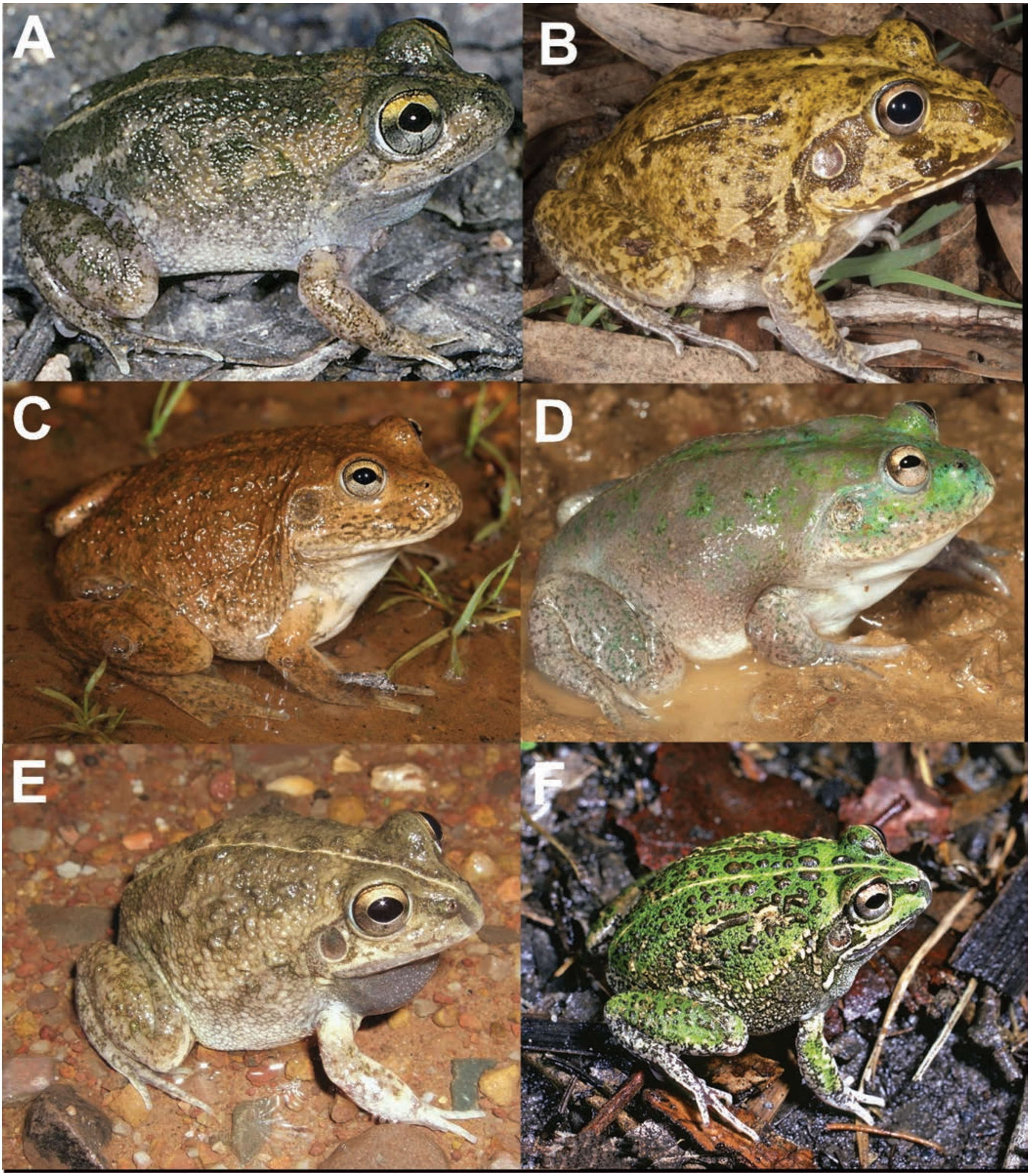

Figure 14. Images in life of *Cyclorana*: (A) *Cyclorana manya* Stephen Richards, (B) *Cyclorana novaehollandiae* Stephen Mahony, (C) *Cyclorana occidentalis* Stephen Mahony, (D) *Cyclorana platycephalus* Marion Anstis, (E) *Cyclorana vagitus* Marion Anstis, (F) *Cyclorana verrucosa* Marion Anstis.

the m. extensor brevis medius digiti IV vs. its absence. Refer to Tables 1 and 2.

Distribution and ecology: Fossorial frogs that breed in ephemeral and permanent waterbodies especially after heavy rainfall, from deserts, savannah woodlands, grasslands, and woodlands, found in northern two-thirds of Australia.

Etymology: Derivation not stated by Steindachner (1867), but presumably from the Latin *cyclus* (circle) and *Rana* (frog), in allusion to the rounded shape of these burrowing frogs. Gender, based on *Rana*, is feminine.

Remarks: Cyclorana is the most specialized burrowing taxon in the pelodryadids. *Cyclorana* form cocoons and demonstrate metabolic depression during aestivation (Withers and Thompson 2000), characters that are associated with their burrowing lifestyle in semi-arid, arid, and savannah ecosystems.

Drymomantis **Peters, 1882: 8**

(Fig. 15)

Synonymy

Hylomantis Peters 1880: 224, based on *fallax*, is preoccupied by *Hylomantis* Peters, 1873: 293 (type species, *Hylomantis aspera* Peters, 1873 from Bahia).

Drymomantis Peters 1882: 8 is a replacement name for *Hylomantis* Peters, 1880.

Duellman *et al.* (2016) mis-spelt *Drymomantis* as *Dryomiantis*.

Type species: Hylomantis fallax Peters, 1880.

Content: Three species—*Drymomantis cooloolensis** (Liem, 1974), *Drymomantis fallax** (Peters, 1880), *Drymomantis olongburensis** (Liem & Ingram, 1977).

Diagnosis: Drymomantis can be diagnosed from the other members of the *Drymomantis* Sub-clade as follows: from *Amnihyla* except *A. amnicola* by pigmented vs. unpigmented eggs, by a Type 1 vs. Type 3 tadpole oral disc, and Type 1 vs. Type 6 or 7 overall tadpole morphology. It can be diagnosed from *A. amnicola* by the unornamented vs. prominent tubercles on the hindlimb. It can be diagnosed from *Exedrobatrachus* by small vs. medium body size, presence vs. absence of vomerine teeth, unornamented vs. tubercules on hindlimb, toe disc equal to finger discs vs. smaller, and unornamented vs. tubercules on the hindlimb; from *Exochohyla* by absent vs. present rostral spike, unornamented vs. tubercules or crenulations on hindlimb, small vs. large egg size, and a Type 1 vs. Type 1A tadpole oral disc, and Type 1 vs. Type 6 overall tadpole morphology; from *Hyalotos* by a pigmented vs. transparent tympanum, small vs. medium or large egg size, unornamented vs. tubercules and crenulations on the hindlimb, and fusiform-spike vs. teardrop call envelope shape, a note rate change across the call vs. none; from *Ischnohyla* by a Type 1 vs. Type 3 tadpole oral disc, Type 1 vs. Type 2A overall tadpole morphology, and fusiform-spike vs. left triangular, left teardrop, or oval call envelope shape, a note rate change across the call vs. none; from *Kallistobatrachus* by unornamented vs. tubercules or crenulations on the hindlimb, a Type 1 vs. Type 1B tadpole oral disc, and Type 1 vs. Type 7 overall tadpole morphology; from *Lathrana* by small vs. medium body size, unornamented vs. tubercules on hindlimb, toe disc equal to finger discs vs. smaller, small vs. medium eggs, and fusiform-spike vs. oval call envelope shape, a note rate change across the call vs. none; from *Nasutibatrachus* and *Teretistes* by the absence of a rostral spike; further from *Teretistes* by reduced vs. no finger webbing, full or reduced vs. minimal toe webbing, small vs. large eggs, by a Type 1 vs. Type 3 tadpole oral disc, and fusiform-spike vs. triangular call envelope shape; from *Viridihyla* by ossified vs. cartilaginous intercalary structures, small vs. large eggs. *Drymomantis* can be diagnosed from *Carichyla* by the absence vs. the presence of an unbroken lateral white stripe from the under the eye to the groin (Figs 11, 15) by a fusiform-spike vs. spike-fusiform call envelope shape (Table 2), and by 31 sites in the mitochondrial *ND4* alignment (Table 3). *Drymomantis* can be diagnosed from *Papuahyla* by a fusiform-spike vs. right triangular call envelope shape (Table 2) and by 16 sites in the mitochondrial *ND4* alignment (Table 3). Refer to Tables 1, 2, and 3. Diagnosis of *Drymomantis* from all other genera in the *Drymomantis* Sub-clade is supported by 18 sites distributed across eight AHE loci (Supporting Information, AHE loci diagnostic sites).

Distribution and ecology: Eastern Australia. Arboreal frogs that are found in lowland open permanent or seasonal grassy or reedy swamps in natural or altered habitats, usually not in closed forests (Menzies 2006, Anstis 2017).

Etymology: Not stated by Peters, but presumably from the combination of the Greek Δρυμός (*drymos*, forest) and μᾰ́ντῐς (*mantis*, the green tree frog, *Hyla arborea*, of Ancient Greece). *Mantis* is masculine.

Remarks: Drymomantis is the equivalent to part of the *Litoria bicolor* Group of Tyler and Davies (1978).

Dryopsophus **Fitzinger 1843: 30**

(Fig. 15)

Type species: '*Hyla citropa* Péron' (=*Hyla citripoda* Péron, 1807 = *Hyla citropa* Duméril & Bibron 1841), by original designation.

Content: 10 species— *Dryopsophus barringtonensis** (Copland, 1957), *Dryopsophus citropa** (Péron, 1807), *Dryopsophus daviesae** (Mahony, Knowles, Foster & Donnellan, 2001), *Dryopsophus kroombitensis** (Hoskin, Hines, Meyer, Clarke & Cunningham, 2013) comb. nov., *Dryopsophus nudidigitus** (Copland, 1963), *Dryopsophus pearsoniana** (Copland, 1961), *Dryopsophus phyllochrous** (Günther, 1863), *Dryopsophus piperata* (Tyler & Davies, 1985), *Dryopsophus spenceri** (Dubois, 1984), *Dryopsophus subglandulosus** (Tyler & Anstis, 1983).

Diagnosis: Dryopsophus can be diagnosed from the other members of the *Cyclorana–Eremnoculus* Clade as follows: from *Chlorohyla* by the absence of the AMES vs. presence, by overall tadpole

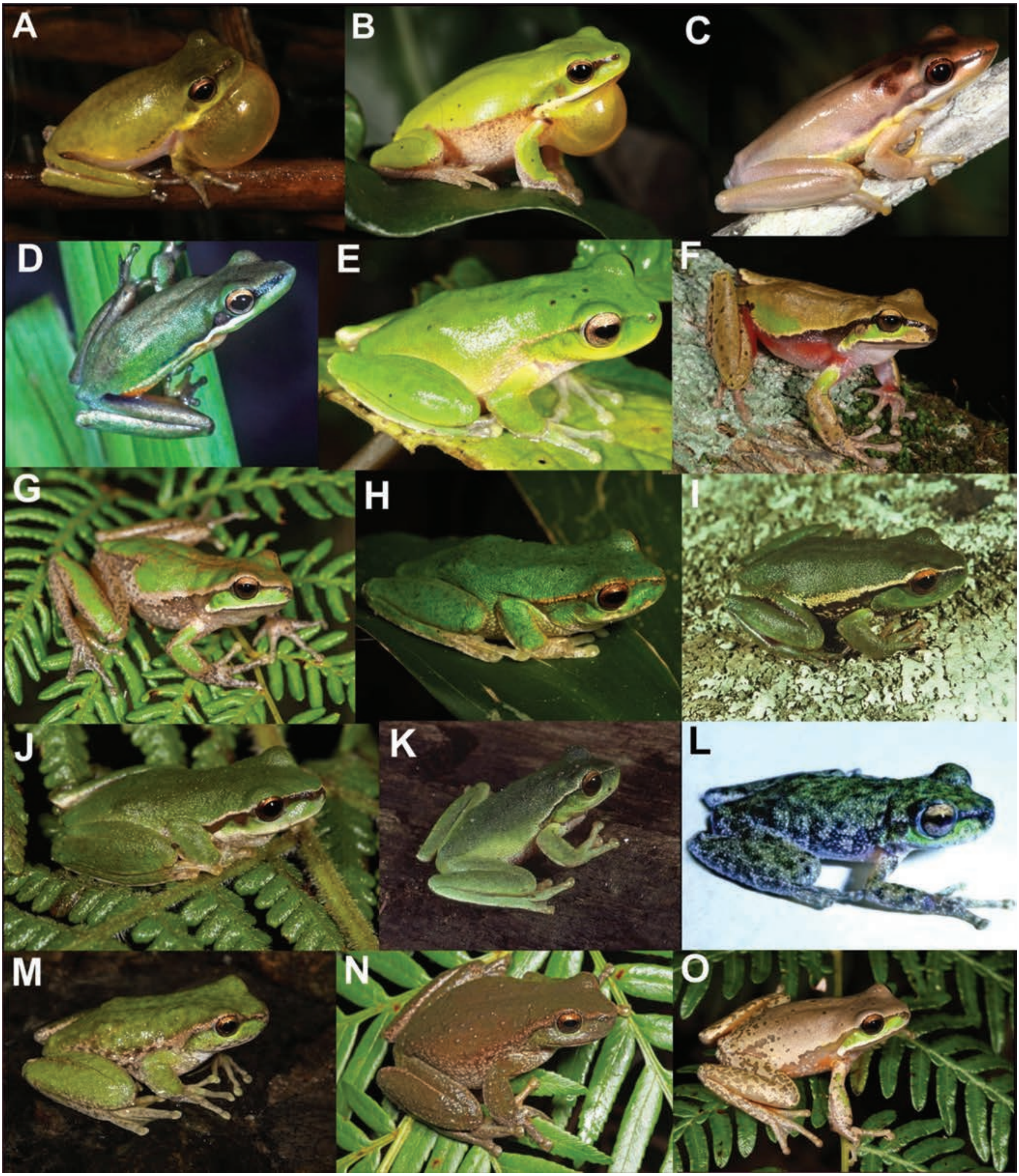

Figure 15. Images in life of *Drymomantis* and *Dryopsophus*: (A) *Drymomantis cooloolensis* Harry Hines, (B) *Drymomantis fallax* Stephen Mahony, (C) *Drymomantis olongburensis* Stephen Mahony, (D) *Drymomantis olongburensis* Michael Mahony, (E) *Dryopsophus barringtonensis* Stephen Mahony, (F) *Dryopsophus citropa* Stephen Mahony, (G) *Dryopsophus daviesae* Stephen Mahony, (H) *Dryopsophus kroombitensis* Stephen Mahony, (I) *Dryopsophus nudidigitus* Marion Anstis, (J) *Dryopsophus pearsoniana* Stephen Mahony, (K) *Dryopsophus phyllochrous* Stephen Donnellan, (L) *Dryopsophus piperata* Marion Anstis, (M) *Dryopsophus spenceri* Stephen Mahony, (N) *Dryopsophus spenceri* Michael Mahony, (O) *Dryopsophus subglandulosus* Stephen Mahony.

morphology Type 5 or 6 vs. 4; from *Cyclorana* by presence of the intercalary structure vs. absent except for *C. alboguttata*, small vs. large inner metatarsal tubercle, expanded vs. and unexpanded finger and toe discs, overall tadpole morphology Type 5 or 6 vs. Type 3; from *Eremnoculus* by medium vs. large ED/SVL, absent vs. well-developed palpebral reticulum, tadpole oral disc Type 1, 4, or 5 vs. Type 6, overall tadpole morphology Type 5 or 6 vs. Type 7; from *Leptobatrachus* by overall tadpole morphology Type 5 or 6 vs. Type 4; from *Megatestis* by medium vs. small ED/SVL, minimally or reduced vs. fully webbed toes, developed vs. undeveloped finger discs, absence of the AMES vs. presence, a multi-divided vs. reduced m. palmaris longus, a high vs. low call dominant frequency; from *Melvillihyla* by a multiple note vs. single note call, by a complex call in seven of the 10 species vs. a simple call; from *Mosleyia* by granular vs. spinous nuptial pads, small or medium pigmented eggs vs. large unpigmented eggs, tadpole oral disc Type 1, 4, or 5 vs. Type 6, overall tadpole morphology Type 5 or 6 vs. Type 7; from *Pelodryas* by overall tadpole morphology Type 5 or 6 vs. Type 1 or 1A, absence vs. presence of the m. extensor brevis medius digiti IV, by a complex call in seven of the 10 species vs. a simple call; *Ranoidea* by the production of short higher pitched calls with fully amplitude modulated notes compared to relatively long low pitched calls of densely pulsatile notes, overall tadpole morphology Type 5 or 6 vs. Type 1, note repetition vs. densely pulsatile call, a high vs. low call dominant frequency; from *Rhyaconastes* by presence vs. absence of a vocal sac, absence of the AMES vs. presence, tadpole oral disc Type 1, 4, or 5 vs. Type 3; from *Spicicalyx* by unornamented hindlimb vs. crenulations on hindlimb, absence vs. presence of a heel spike, overall tadpole morphology Type 5 or 6 vs. Type 4, by a complex call in seven of the 10 species vs. a simple call. Refer to Tables 1 and 2.

Distribution and ecology: Forests in eastern Australia. Arboreal frogs found in lower riparian vegetation along flowing streams where they breed.

Etymology: Not stated by Fitzinger (1843), but presumably from the Greek δρῦς (*drys*, oak tree) and ψόφος (*psophos*, a sound not produced by the human voice), so a sound calling from the trees. Both the original Greek noun and the Latinized version *psophus* are masculine (Article 30.1.3).

Remarks: Dryopsophus is the equivalent of the *Litoria citropa* and the *Litoria maculata* (*D. spenceri*) Groups of Tyler and Davies (1978).

Eremnoculus Mahony, Richards & Donnellan, **gen. nov.**

(Fig. 16)

ZooBank LSID: urn:lsid:zoobank.org:act:3FD4893D-79A5-4DE5-B308-E9C6EB520849 Type species: Hyla dayi Günther, 1897.

Content: One species—*Eremnoculus dayi** (Günther, 1897) comb. nov.

Diagnosis: Eremnoculus can be diagnosed from its sister lineage, *Mosleyia*, by presence of a vocal sac, presence of a well-developed palpebral reticulum, granular nuptial pads, and the presence of the AMES. Refer to Tables 1 and 2.

Distribution and ecology: Australian Wet Tropics in north-eastern Queensland. Semi-aquatic frogs that breed in streams in tropical rainforest. Large unpigmented eggs laid under or glued to rocks; tadpoles with large, ventrally located suctorial oral discs.

Etymology: From the Greek ἐρεμνός (*eremnos*, = black) and Latin *oculus* (eye), referring to large dark eye in the species. The gender of *oculus* is masculine.

Remarks: A monotypic lineage on a long branch associated with the torrent frogs, *Mosleyia*, also from the Australian Wet Tropics in north-eastern Queensland.

Exedrobatrachus Richards, Mahony & Donnellan, **gen. nov.**

(Fig. 16)

ZooBank LSID: urn:lsid:zoobank.org:act:71F5CD28-163F-474F-97BF-66ADD805188E Type species: Litoria biakensis Günther, 2006.

Content: One species—*Exedrobatrachus biakensis** (Günther, 2006) comb. nov.

Diagnosis: Exedrobatrachus can be diagnosed from *Papuahyla* by tubercules on the hindlimb vs. an unornamented hindlimb, by a fusiform vs. right triangular call envelope shape, and 13 sites in the mitochondrial *ND4* alignment (Table 3). *Exedrobatrachus* can be diagnosed from *Exochohyla* by the absence vs. presence of a rostral spike, the occurrence of small pigmented vs. large unpigmented ova; and from each species of *Ischnohyla* by species specific combination of each of the four following characters: by small vs. medium (*I. nigropunctata and I. umarensis*) or large (*I. daraiensis* and *I. gracilis*) eggs; pigmented vs. unpigmented (*I. gracilis*) eggs; absence vs. presence (*I. gracilis and I. nigropunctata*) of the vomerine teeth; toe discs smaller than finger disc vs. equal (*I. gracilis, I. nigropunctata, I. umarensis*, and *I. vocivincens*). Refer to Tables 1 and 2.

Distribution and ecology: Arboreal frogs that are found in swamps with thickets of trees and brush on Biak Island, Papua Province, Indonesia (Günther 2006b).

Etymology: From the Greek ἔξεδρος (*exedros*, away from home) and βάτραχος (*batrachos*, frog). Both the original *batrachos* and the Latinized *batrachus* are masculine (Article 30.1.3). The name alludes to the biogeographically and phylogenetically isolated nature of the lineage.

Remarks: A monotypic genus with a distribution confined to Biak Island, a continental island which harbours a number of endemic vertebrates (Bergmans and Sarbini 1985, Groves and Flannery 1994, Jacobs 2002).

Exochohyla Richards, Mahony & Donnellan, **gen. nov.**

(Fig. 16)

ZooBank LSID: urn:lsid:zoobank.org:act:68B6B5AB-2585-4ED0-8EC2-4A22D7174157 Type species: Hyla prora (Menzies, 1969).

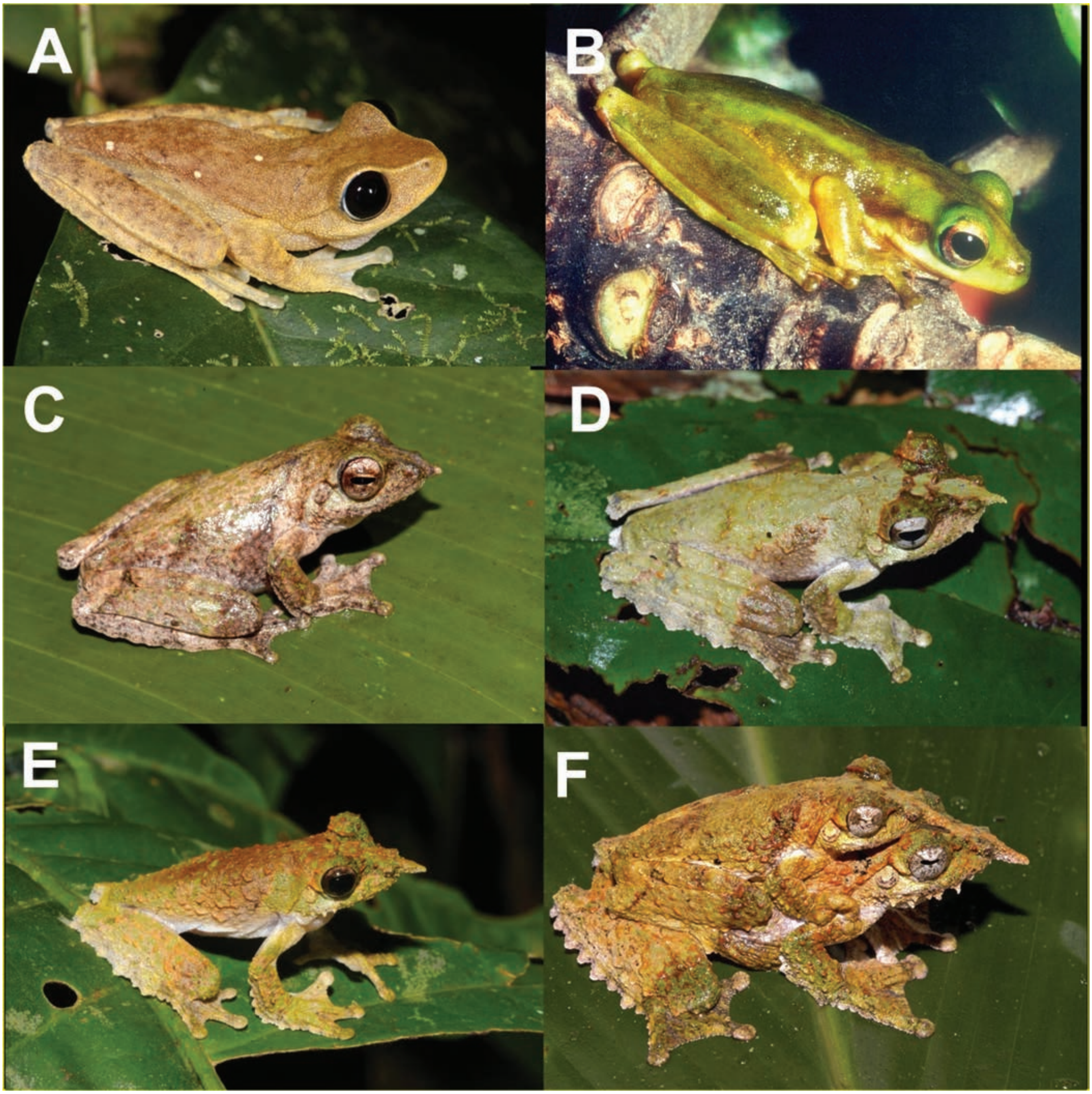

Figure 16. Images in life of *Eremnoculus*, *Exedrobatrachus*, and *Exochohyla*: (A) *Eremnoculus dayi* Stephen Mahony, (B) *Exedrobatrachus biakensis* Rainer Günther, (C) *Exochohyla chrisdahli* Stephen Richards, (D) *Exochohyla humboldtorum* Stephen Richards, (E) *Exochohyla prora* Stephen Richards, (F) *Exochohyla prora* in amplexus Stephen Richards.

Content: Four species—*Exochohyla chrisdahli** (Richards, 2007a) comb. nov., *Exochohyla hilli* (Hiaso & Richards, 2006) comb. nov., *Exochohyla humboldtorum** (Günther, 2006c) comb. nov., *Exochohyla prora** (Menzies, 1969) comb. nov.

Diagnosis: Exochohyla can be diagnosed from other pelodryadids by a combination of rostral spike present in both sexes and enlarged tubercles or crenulated ornamentation of the hindlimbs. It can be further diagnosed from *Ischnohyla* by tadpole oral disc Type 1A vs. 3, and overall tadpole body morphology Type 6 vs. Type 2, a note rate change across the call vs. none. Refer to Tables 1 and 2.

Distribution and ecology: New Guinea and surrounding islands. Arboreal frogs that breed in small forest pools where eggs are known or expected to be glued to leaves overhanging the water until free-swimming tadpoles drop into water to complete development.

Etymology: From the Greek ἔξοχος (*exochos*, projecting or jutting out) and *Hyla* (the frog genus). The name is feminine.

Remarks: Exochohyla is the equivalent of the *Litoria prora* Group of Tyler and Davies (1978). A rostral spike is present in both sexes, a unique character among pelodryadids. *Litoria rostandi* Kraus, 2007 is a junior synonym of *Litoria hilli* (IUCN SSC Amphibian Specialist Group 2020). Genetic data for *L. hilli* are not available but its similarity to *E. prora* was noted in the original description and to *E. humboldtorum* in Kraus (2007).

Hyalotos Richards, Mahony & Donnellan, **gen. nov.**

(Fig. 17)

ZooBank LSID: urn:lsid:zoobank.org:act:7C1C360B-D81D-4985-A93C-D065C201ED53 Type species: Litoria richardsi Dennis & Cunningham, 2006.

Content: Three species—*Hyalotos naispela** (Richards, Donnellan & Oliver, 2023) comb. nov., *Hyalotos richardsi** (Dennis & Cunningham, 2006) comb. nov., *Hyalotos singadanae** (Richards, 2005) comb. nov.

Diagnosis: Hyalotos can be diagnosed from other pelodryadids by a combination of a wholly or substantially transparent tympanum, crenulated ornamentation of the hindlimb, and medium to large, pigmented eggs, high dominant call frequency, absence of call frequency modulation, tear drop call envelope shape, none vs. a note rate change across the call. Refer to Tables 1 and 2.

Distribution and ecology: New Guinea lowlands to lower montane species. Arboreal frogs known or expected to lay eggs on tree trunks over tree-holes (Richards *et al.* 2023).

Etymology: From the Greek ὕαλος (*hyalos*, glass) and ωτός (*otos*, ear), alluding to the transparent tympanum. The name, based on *otos*, is neuter.

Remarks: The tympanum is predominantly transparent, a character unique among pelodryadids (Richards 2005, Denis and Cunningham 2006, Richards *et al.* 2023).

Ischnohyla Richards, Mahony & Donnellan, **gen. nov.**

(Fig. 17)

ZooBank LSID: urn:lsid:zoobank.org:act:7E77AC9B-CD9C-40B3-B7CD-1F1CBC5F492E Type species: Litoria nigropunctata (Meyer, 1874).

Content: Five species—*Ischnohyla daraiensis** (Richards, Donnellan & Oliver, 2023) comb. nov., *Ischnohyla gracilis** (Richards, Donnellan & Oliver, 2023) comb. nov., *Ischnohyla nigropunctata** (Meyer, 1874) comb. nov., *Ischnohyla umarensis* (Günther, 2004a) comb. nov., *Ischnohyla vocivincens* (Menzies, 1972) comb. nov.

Diagnosis: Ischnohyla can be diagnosed from its sister taxon *Exochohyla* by the absence of a heel and rostral spikes, the occurrence of large unpigmented ova vs. either the presence of small pigmented ova (one species) or medium-sized pigmented ova (two species) or large unpigmented ova (two species), no note rate change across the call vs. present. Refer to Tables 1 and 2.

Distribution and ecology: New Guinea and surrounding islands. Arboreal frogs that are found in forests, predominantly in lowland and foothill habitats. At least one species (*gracilis*) glues unpigmented eggs to leaves above forest pools or pools within slow-flowing streams, and one (*vocivincens*) lays small, pigmented eggs in water.

Etymology: From the Greek ισχνός (*ischnos*, weak, thin, or meagre) and the frog genus name *Hyla*, alluding to the slender body form of this genus. The gender, based on *Hyla*, is feminine.

Remarks: Ischnohyla is the equivalent in part (*I. nigropunctata* and *I. vocivincens*) to the *Litoria nigropunctata* Group of Tyler and Davies (1978). *Litoria obtusirostris* Meyer, 1874 was described from Ansus, Yapen Island, the same type locality as *I. nigropunctata*. It is the same size as that species, and with the exception of being reported to have exceptionally long legs—possibly in error—and poorly developed vomerine teeth there is little to distinguish the two taxa (colour variation in *nigropunctata* is more extensive than previously recognized). Given that the holotype (and only known) specimen was destroyed during the Second World War, and that extensive collections of pelodryadids on Yapen Island in recent decades have failed to detect a species distinct from *nigropunctata* (D. Price, personal communication, R. Günther, personal observations), we tentatively place this species in the synonymy of *I. nigropunctata*.

We placed *I. vocivincens* in *Ischnohyla* because of Menzies' (1972) diagnosis of a *Litoria nigropunctata* group that included both *I. nigropunctata* and *I. vocivincens*, the only two species of *Ischnohyla* described at that time. We also placed *L. umarensis* in *Ischnohyla* following Menzies' (2006) placement of this species in the *L. nigropunctata* 'complex'. A robust determination of these species' relationships requires molecular genetic evidence.

Kallistobatrachus Richards, Mahony & Donnellan, **gen. nov.**

(Fig. 18)

ZooBank LSID: urn:lsid:zoobank.org:act:07817ADB-A3E8-4B1F-B97F-86293EBFA986 Type species: Hyla iris Tyler, 1962. 1897.

Content: Eight species—*Kallistobatrachus aplini** (Richards & Donnellan, 2020) comb. nov., *Kallistobatrachus beryllinus** (Richards & Donnellan, 2023) comb. nov., *Kallistobatrachus chloronotus** (Boulenger, 1911) comb. nov., *Kallistobatrachus haematogaster** (Richards, Donnellan & Oliver, 2023) comb. nov., *Kallistobatrachus iris** (Tyler, 1962) comb. nov., *Kallistobatrachus lisae** (Richards, Donnellan & Oliver, 2023) comb. nov., *Kallistobatrachus majikthise** (Johnston & Richards, 1994) comb. nov., *Kallistobatrachus ollauro* (Menzies, 1993) comb. nov.

Diagnosis: Kallistobatrachus can be diagnosed from *Lathrana* by medium vs. short call duration and by variable vs. constant

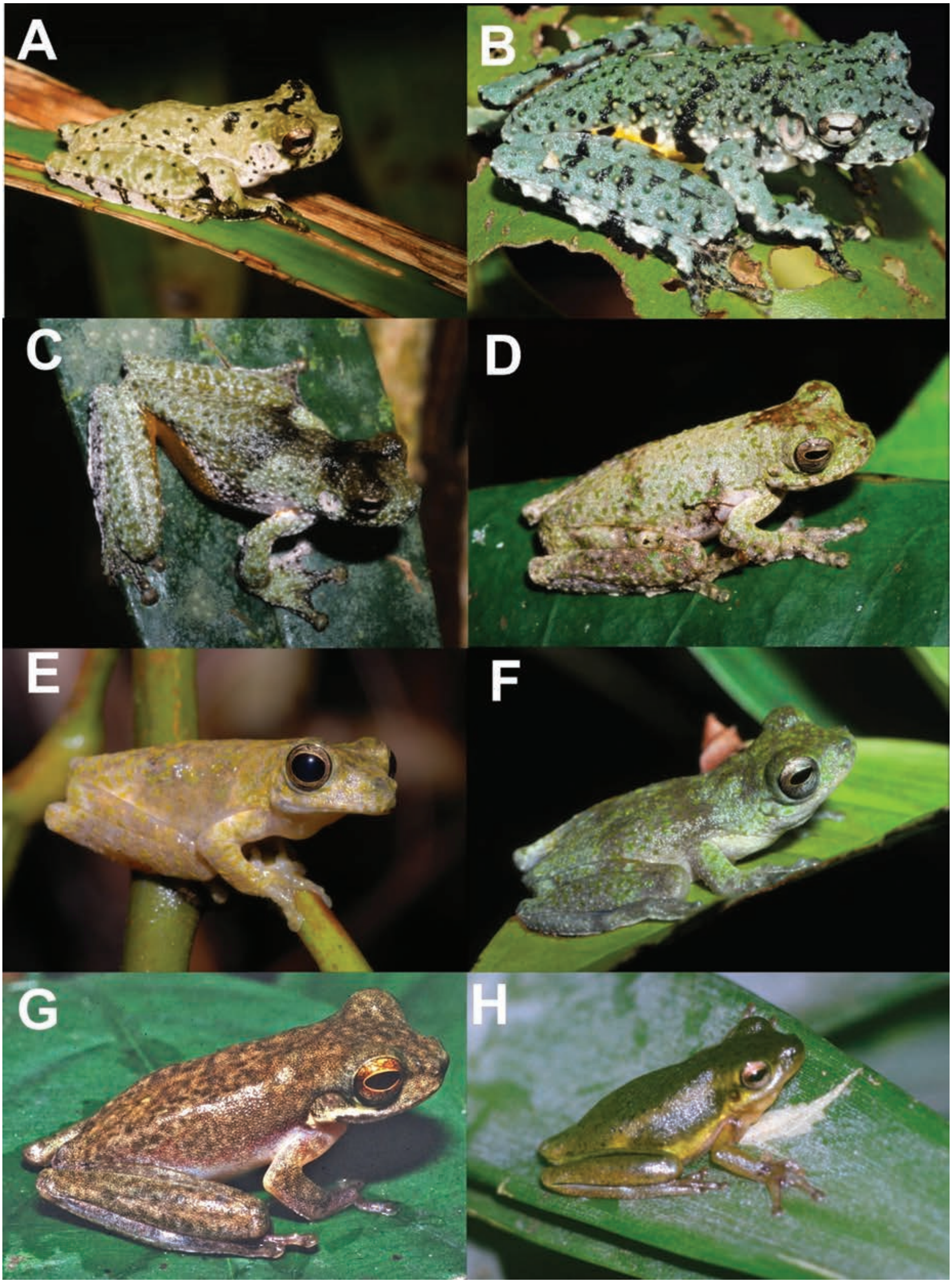

Figure 17. Images in life of *Hyalotos* and *Ischnohyla*: (A) *Hyalotos naispela* Stephen Richards, (B) *Hyalotos richardsi* Stephen Richards, (C) *Hyalotos singadanae* Stephen Richards, (D) *Ischnohyla daraiensis* Stephen Richards, (E) *Ischnohyla gracilis* Stephen Richards, (F) *Ischnohyla nigropunctata* Stephen Richards, (G) *Ischnohyla umarensis* Rainer Günther, (H) *Ischnohyla vocivincens* James Menzies.

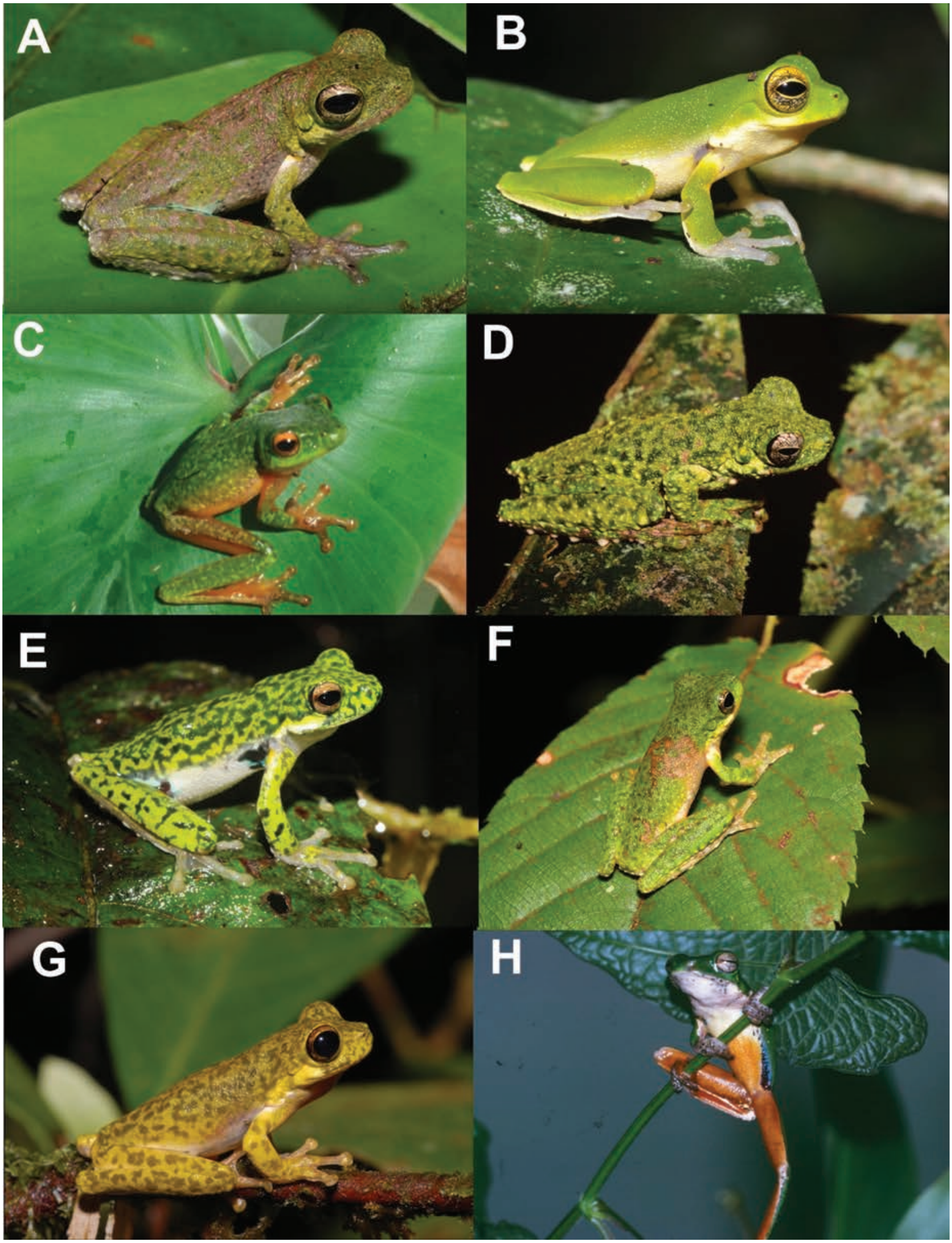

Figure 18. Images in life of *Kallistobatrachus*: (A) *Kallistobatrachus aplini* Stephen Richards, (B) *Kallistobatrachus beryllinus* Stephen Richards, (C) *Kallistobatrachus chloronotus* James Menzies, (D) *Kallistobatrachus haematogaster* Stephen Richards, (E) *Kallistobatrachus iris* Stephen Richards, (F) *Kallistobatrachus lisae* Stephen Richards, (G) *Kallistobatrachus majikthise* Stephen Richards, (H) *Kallistobatrachus ollauro* James Menzies.

pulse rate; from *Nasutibatrachus* and *Teretistes* by the absence of a rostral spike vs. the presence in males only; and further from *Teretistes* by medium vs. high call dominant, fusiform or teardrop or spike vs. triangular call envelope shape and from *Viridihyla* by small to medium vs. large eggs, variable dorsal pattern (all species except *K. beryllinus*) vs. uniform green dorsum (Figs 18, 33). Refer to Tables 1 and 2.

Distribution and ecology: New Guinea lowland to montane arboreal frogs that are found in association with ponds. Some, and probably all, lay eggs on leaves over water (Richards *et al.* 2023).

Etymology: From the Greek κάλλιστος (*kallistos*, very beautiful) and βάτραχος (*batrachus*, frog), alluding to the beautiful coloration of the species. Both the original *batrachos* and the Latinized *batrachus* are masculine (Article 30.1.3).

Remarks: Kallistobatrachus is the equivalent in part (*K. chloronota*) to the *Litoria bicolor* Group and in part (*K. iris*) to the *L. nigropunctata* Group of Tyler and Davies (1978).

We here emend the specific epithet *chloronota to chloronotus*. The name refers to the green dorsum of the species, using the Greek *notos* (back) for the name. While it could be considered the name is being treated as a noun, the Greek noun 'back' is *noton* (neuter) or *notos* (masculine). There is no feminine form (*nota* is the plural of both *noton* and *notos*). Hence, by using the term *nota* in combination with the original feminine *Hylella*, Boulenger (1911) was using gender agreement to change the original source word into a Latinized feminine form, so it could be argued that he was using it as an adjective (green-backed).

We have conservatively placed *Hylella chloronota* Boulenger in *Kallistobatrachus* despite its sister relationship with *Teretistes* in the nuclear phylogenetic analysis (Fig. 2), which together are the sister to the other species of *Kallistobatrachus*. *Kallistobatrachus chloronotus* lacks a rostral spike, the presence of which is diagnostic for *Teretistes*, but we are unable on the available data to diagnose it from the remainder of *Kallistobatrachus*. Resolution of the generic allocation for *Kallistobatrachus chloronotus* awaits more comprehensive phenotypic data and the inclusion of *Lathrana* (the sister lineage of *Teretistes* in our mitochondrial phylogeny, Fig. 1) in the nuclear gene phylogenomic analysis. Although genetic data are not available for *L. ollauro* that species is placed in *Kallistobatrachus* on the basis of its overall morphology, likely breeding strategy (eggs fixed to leaves over water), and its proposed relationship to *L. iris* by Menzies (2006).

While as a general principal we have used the first named species to be the type species for genera erected herein, we depart from this practice for *Kallistobatrachus* in view of the uncertainty for the relationships of *Hylella chloronota* Boulenger 1911 and instead instate *Hyla iris* Tyler 1962 as the type species.

Lathrana Richards, Mahony & Donnellan, **gen. nov.**

(Fig. 19)

ZooBank LSID: urn:lsid:zoobank.org:act:47A793B5-4B74-45A4-A2AC-824365227066 Type species: Litoria verae Günther, 2004.

Content: One species—*Lathrana verae** (Günther, 2004) comb. nov.

Diagnosis: Lathrana can be diagnosed from *Teretistes* by the absence of a rostral spike, the presence of tubercle ornamentations on hindlimb, reduced vs. no webbing between the fingers, and medium vs. large egg size, medium vs. high call dominant frequency, oval vs. triangular call envelope shape, no note rate change across the call vs. present. Refer to Tables 1 and 2.

Distribution and ecology: Wondiwoi Mountains, Wandammen Peninsula in western Cenderawasih Bay, Papua Province, Indonesia (Günther 2004a). Arboreal frogs that breed in small swamps close to periodically flowing mountain streams.

Etymology: Based on the Greek λάθριος (*lathrios*, hidden or concealed, referring to the 'hidden, unexpected' divergence of this species) and Latin *Rana* (frog). The latter word is feminine.

Remarks: A monotypic lineage on a long branch associated with another monotypic and distinctive genus, *Teretistes* on another long branch.

Leptobatrachus Richards, Donnellan & Mahony, **gen. nov.**

(Fig. 19)

ZooBank LSID: urn:lsid:zoobank.org:act:E426591D-82ED-443F-B500-DF10DF135A0F Type species: Hyla impura Peters & Doria, 1878.

Content: Five species—*Leptobatrachus flavescens* (Kraus and Allison, 2004a) comb. nov., *Leptobatrachus impurus** (Peters & Doria, 1878) comb. nov., *Leptobatrachus insularis** (Richards and Oliver, 2023) comb. nov., *Leptobatrachus luteus** (Boulenger, 1887) comb. nov., *Leptobatrachus thesaurensis** (Peters, 1877) comb. nov.

Diagnosis: Leptobatrachus can be diagnosed from *Cyclorana* and *Megatestis* by the multi-divided state of the m. palmaris longus vs. a reduced state, overall tadpole morphology Type 4 vs. Type 3, and further from *Megatestis* by long vs. medium legs; from *Cyclorana* by long vs. short or medium length legs, small vs. large inner metatarsal tubercles, and presence vs. absence (in 12 of 13 species of *Cyclorana*) of intercalary structures. Refer to Tables 1 and 2.

Distribution and ecology: Arboreal frogs that are found in New Guinea and surrounding islands, Bismarck Archipelago, Solomon Islands. *Leptobatrachus luteus* is known to lay its eggs over tree hollows and bamboo stems (Zug and Fisher 2018; S. Richards, personal observations). Other species known or expected to lay eggs in small, slow-flowing streams or forest pools.

Etymology: From the Greek λεπτός (*leptos*, slender) and βάτραχος (*batrachos*, frog), in reference to the slender body form of the species. The gender is masculine.

Remarks: Leptobatrachus is the equivalent of the *Litoria thesaurensis* Group of Tyler and Davies (1978). *Leptobatrachus luteus* and *L. thesaurensis* are unusual in pelodryadids in that they have green pigmented bones that can be seen in life through the ventral skin. The bones of both *L. flavescens* and *L. impurus* lack the green coloration (Kraus and Allison 2004a, Menzies 2006). Genetic data are not available for *Litoria flavescens*, but it was placed in the *Litoria thesaurensis* group in the original description (Kraus and Allison 2004a) and in the *Litoria thesaurensis* complex by Menzies (2006).

Litoria Tschudi 1838: 77

(Fig. 20)

Synonymy

Lepthyla Duméril and Bibron 1841: 504 (manuscript name listed in synonymy of *Litoria* by Duméril and Bibron, abandoned by them due to the priority of Tschudi's *Litoria*).

Pelobius Fitzinger 1843: 31 (type species also *freycineti*).

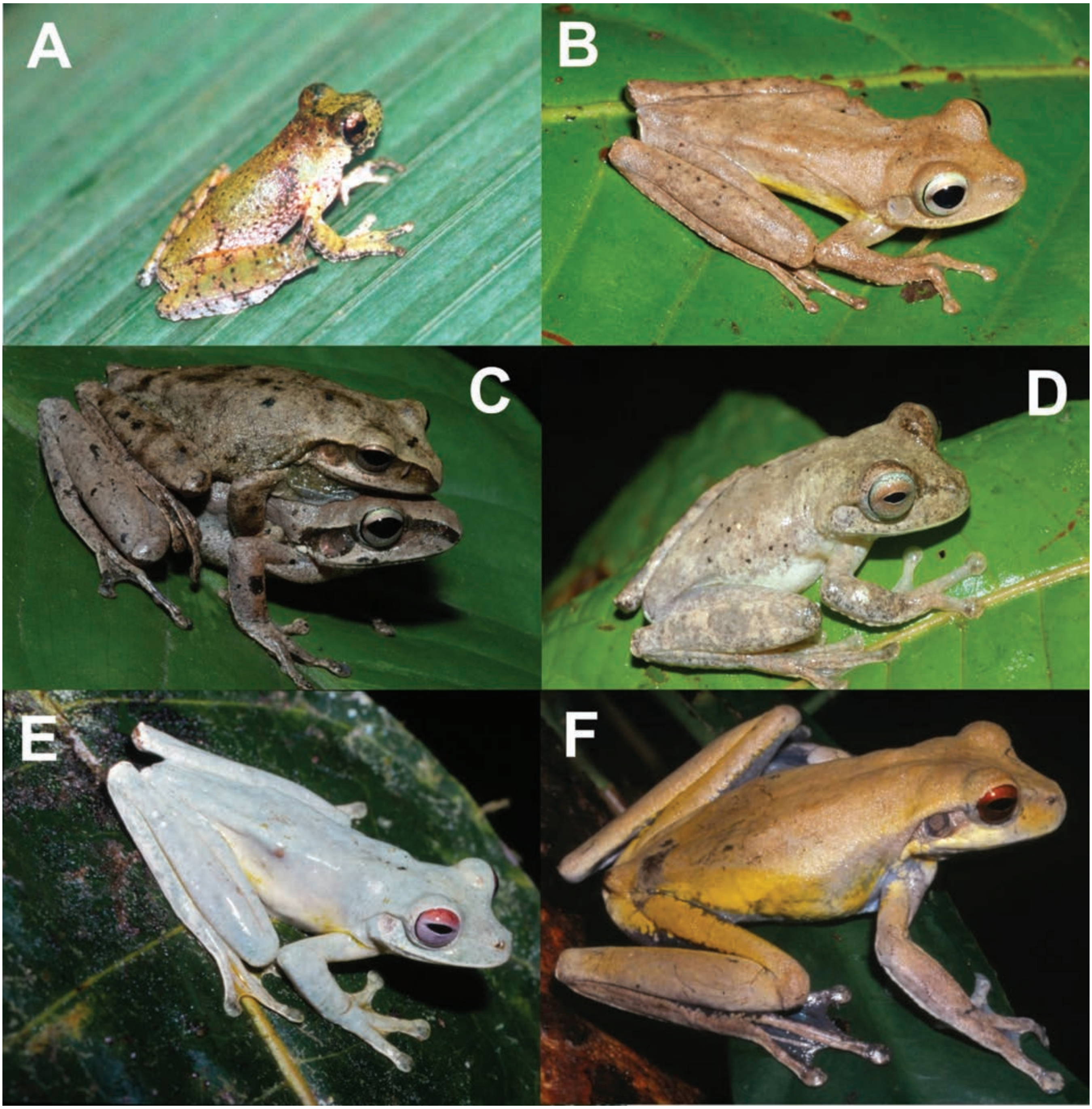

Figure 19. Images in life of *Lathrana* and *Leptobatrachus*: (A) *Lathrana verae* Rainer Günther, (B) *Leptobatrachus flavescens* Fred Kraus, (C) *Leptobatrachus impurus* Chris Austin, (D) *Leptobatrachus insularis* Stephen Richards, (E) *Leptobatrachus luteus* Stephen Richards, (F) *Leptobatrachus thesaurensis* Stephen Richards.

Type species: Litoria freycineti Tschudi, 1838, by monotypy.

Content: 13 species—*Litoria axillaris** Doughty, 2011, *Litoria coplandi** (Tyler, 1968b), *Litoria freycineti** Tschudi, 1838, *Litoria inermis** (Peters, 1867), *Litoria latopalmata** (Günther, 1867), *Litoria nasuta** (Gray, 1842), *Litoria nigrofrenata** (Günther, 1867), *Litoria pallida** Davies, Martin & Watson, 1983, *Litoria personata** Tyler, Davies & Martin, 1978, *Litoria spaldingi** (Hosmer, 1964), *Litoria staccato** Doughty & Anstis, 2007, *Litoria tornieri** (Nieden, 1923), *Litoria watjulumensis** (Copland, 1957).

Diagnosis: Litoria can be diagnosed from the sister taxon *Coggerdonia* by the absence of finger webbing, minimal vs. reduced toe webbing, the presence of an alary process of the hyoid, overall tadpole morphology Type 2, 2A or 6 vs. Type 1, and defined vs. non-defined call duration (nine of 13 species). Refer to Tables 1 and 2.

Figure 20. Images in life of *Litoria*: (A) *Litoria axillaris* Paul Doughty, (B) *Litoria coplandi* Stephen Donnellan, (C) *Litoria freycineti* Harry Hines, (D) *Litoria inermis* Stephen Mahony, (E) *Litoria latopalmata* Stephen Donnellan, (F) *Litoria nasuta* Stephen Donnellan, (G) *Litoria nasuta* Stephen Donnellan, (H) *Litoria nigrofrenata* Marion Anstis, (I) *Litoria pallida* Stephen Donnellan, (J) *Litoria personata* Marion Anstis, (K) *Litoria personata* Harry Hines, (L) *Litoria spaldingi* Stephen Richards, (M) *Litoria staccato* Marion Anstis, (N) *Litoria tornieri* Marion Anstis, (O) *Litoria watjulumensis* Stephen Mahony.

Distribution and ecology: Terrestrial frogs that breed in ponds, streams, and flooded areas, found in grasslands, forests, woodlands, and heaths or rocky habitats in ranges in eastern and northern Australia and southern New Guinean mainland.

Etymology: Tschudi (1838) did not provide an etymology, and Duméril and Bibron (1841) were also unclear of its meaning, suggesting that it was either derived from the Greek λĩθος (*lithos*, which they translate as 'terre légère', or thin soil) or Latin *litos* meaning is or is on the shore (presumably meaning the Latin *litus*/*litoris*, which has that meaning). According to Duellman *et al.* (2016), 'the generic name is the Latin noun '*litoris*' meaning shore. Inasmuch as Tschudi's (1838) description was based on material he observed in Paris that was plundered from a British ship leaving Australia, he may have assumed that the frog lived near the shore'. Meagher (2013) also notes the potential for a derivation from the coastline [stating the formation of *litoris* as being from Greek, as with all other Tschudi generic names: λῑτός (*litos*, which he translated as shore, although it actually means simple) and ὅρος (*oros*, boundary)], but also suggests potential for the name being derived from the Greek 'simple' in allusion to the appearance of the frog. However, it is also possible that Duméril and Bibron were partially correct with their first suggestion, with a derivation from the Greek for stone potentially relating to the mottled brown coloration and rough skin texture of the species. Whatever the origin, assuming a derivation from Greek [either *lithos* or *litos*, Latinized with the addition of the suffix –*ia*, determines the gender as feminine (Article 30.1.3)].

Remarks: Litoria comprises the *Litoria coplandi*, *L. freycineti*, *L. latopalmata*, and *L. nigrofrenata* Groups of Tyler and Davies (1978).

Mahonabatrachus Wells & Wellington, 1985: 5

(Fig. 21)

Synonymy

Llewellynura Wells and Wellington, 1985: 5.

Type species: Hyla meiriana Tyler, 1969, by original designation.

Content: Six species—*Mahonabatrachus aurifer** (Anstis, Tyler, Roberts, Price & Doughty, 2010) comb. nov., *Mahonabatrachus dorsalis** (Macleay, 1878) comb. nov., *Mahonabatrachus longirostris** (Tyler & Davies, 1977) comb. nov., *Mahonabatrachus meirianus** (Tyler, 1969), *Mahonabatrachus microbelos** (Cogger, 1966) comb. nov., *Mahonabatrachus timidus** (Tyler & Parker, 1972) comb. nov.

Diagnosis: Mahonabatrachus can be diagnosed from *Coggerdonia* by small vs. medium body size, medium vs. small ED/SVL, overall tadpole morphology Type 2, 5, or 6 vs. Type 1, and none vs. reduced finger webbing. *Mahonabatrachus* can be diagnosed from *Litoria* by small vs. medium body size, defined vs. non-defined call duration (nine of 13 species). All *Mahonabatrachus* except *M. microbelos* can be diagnosed from *Amnihyla* by the presence vs. absence of an alary process of the hyoid. *Mahonabatrachus microbelos* can be diagnosed from *Amnihyla* by an oral dics Type 1 vs. Type 3 or 6B and by an overall tadpole morphology Type 2 vs. Type 6 or 7. It can be diagnosed from the other members of the *Drymomantis* Sub-clade as follows: from *Carichyla*, *Drymomantis*, and *Papuahyla* by overall tadpole morphology Type 2, 5, or 6 vs. Type 1; from *Exochohyla*, *Nasutibatrachus*, and *Teretistes* by the absence of a rostral spike vs. presence; from *Exedrobatrachus* and *Viridihyla* by small vs. medium body size, by no vs. reduced or fully webbed fingers, further from *Exedrobatrachus* by toe discs equal to finger discs in size vs. smaller; from *Hyalotos* by pigmented vs. transparent tympanum, small pigmented vs. medium to large pigmented eggs; from *Ischnohyla* by overall tadpole morphology Type 2, 5, or 6 vs. Type 2A, by no vs. reduced or fully webbed fingers; from *Kallistobatrachus* by small vs. medium body size, overall tadpole morphology Type 2, 5, or 6 vs. Type 7; from *Lathrana* by small vs. medium body size, no vs. reduced finger webbing, toe discs equal to finger discs in size vs. smaller, and small vs. medium eggs. Refer to Tables 1 and 2.

Distribution and ecology: Terrestrial and saxicoline frogs that breed in ephemeral and permanent streams and still water in grasslands, forests, and savannah woodlands, and rocky terrains in northern Australia and the southern New Guinean mainland.

Etymology: According to Wells and Wellington (1985), named for Michael Mahony in recognition of his research on Australia's amphibians. The gender, based on *batrachus* (frog), is masculine.

Remarks: Mahonabatrachus is the equivalent of the *Litoria dorsalis* and *L. meiriana* Groups of Tyler and Davies (1978).

For *Litoria aurifera* Anstis, Tyler, Roberts, Price and Doughty 2010, the specific epithet is feminine, but becomes *aurifer* (masculine) in combination with a generic name based on *batrachus*.

Information on the derivation of the specific epithet was not provided in the original description of *Litoria meiriana* Tyler 1969. Our investigations would indicate that it is derived from *meiri* = waterhole as listed in Baldwin Spencer's book 'Native Tribes of the Northern Territory of Australia' (Spencer, 1914: 460). As such *meiriana* is an adjective and becomes *meirianus* in a masculine genus.

Megatestis Donnellan, Mahony & Richards, **gen. nov.**

(Fig. 22)

ZooBank LSID: urn:lsid:zoobank.org:act:F90744D2-FE44-49F8-8765-81A1D77F863D Type species: Chiroleptes dahlii Boulenger, 1896.

Content: One species—*Megatestis dahlii** (Boulenger, 1896) comb. nov.

Diagnosis: Megatestis can be diagnosed from the sister taxon *Leptobatrachus* by medium vs. long legs, undeveloped vs. expanded finger discs, and the reduced state of the m. palmaris longus vs. a multi-divided state; from *Cyclorana* by fully vs. minimal toe webbing, small vs. large inner metatarsal tubercles, presence vs. absence (in 13 of 14 species of *Cyclorana*) of intercalary structures, and by defined vs. non-defined call duration. Refer to Tables 1 and 2.

Distribution and ecology: Semi-aquatic frogs that breed in large permanent waterbodies in grasslands and savannah forest in northern Australia.

Etymology: From the Greek μέγᾰς (*megas*, large, mighty, marvellous) and Latin *testis* (the organ, itself based on the Latin noun meaning witness, in reference to the Roman legal system which permitted only males to testify; Field and Harrison 1968), referring to the spectacularly large testis to body mass ratio exhibited

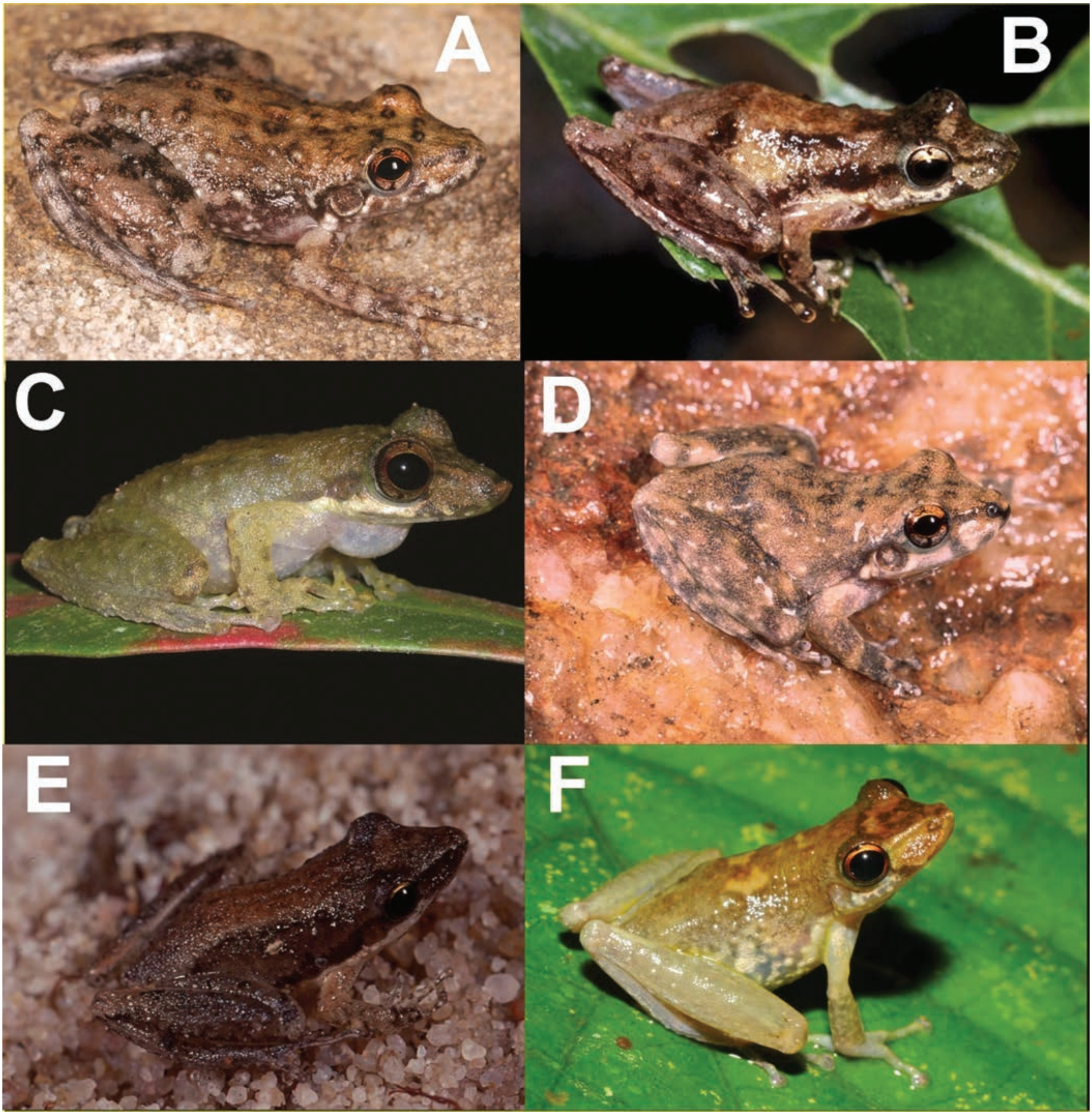

Figure 21. Images in life of *Mahonabatrachus*: (A) *Mahonabatrachus aurifer* Marion Anstis, (B) *Mahonabatrachus dorsalis* Stephen Richards, (C) *Mahonabatrachus longirostris* Marion Anstis, (D) *Mahonabatrachus meirianus* Stephen Donnellan, (E) *Mahonabatrachus microbelos* Stephen Donnellan, (F) *Mahonabatrachus timida* Stephen Richards.

by this species, among the largest in the animal kingdom. The gender is masculine.

Remarks: Megatestis was included in the *Litoria aurea* Group of Tyler and Davies (1978). Males of *Megatestis* can have one of the largest relative testis masses of any animal, with values of 7.3–12.6% (Donnellan *et al.*, unpublished data). While our data are not in accord with published values, 0.102% for *M. dahlii* in Byrne *et al.* (2002), in the absence of specimen voucher numbers in Byrne *et al.* (2002) we are unable to evaluate the reasons for the different observations. Currently monotypic but molecular genetic analyses indicate that *Megatestis dahlii* is a species complex (Donnellan and Mahony unpublished data).

Melvillihyla Richards, Donnellan & Mahony, **gen. nov.**

(Fig. 22)

ZooBank LSID: urn:lsid:zoobank.org:act:30C05CFB-255B-4889-A162-FEC1C99BAF73 Type species: Litoria andiirrmalin McDonald, 1997.

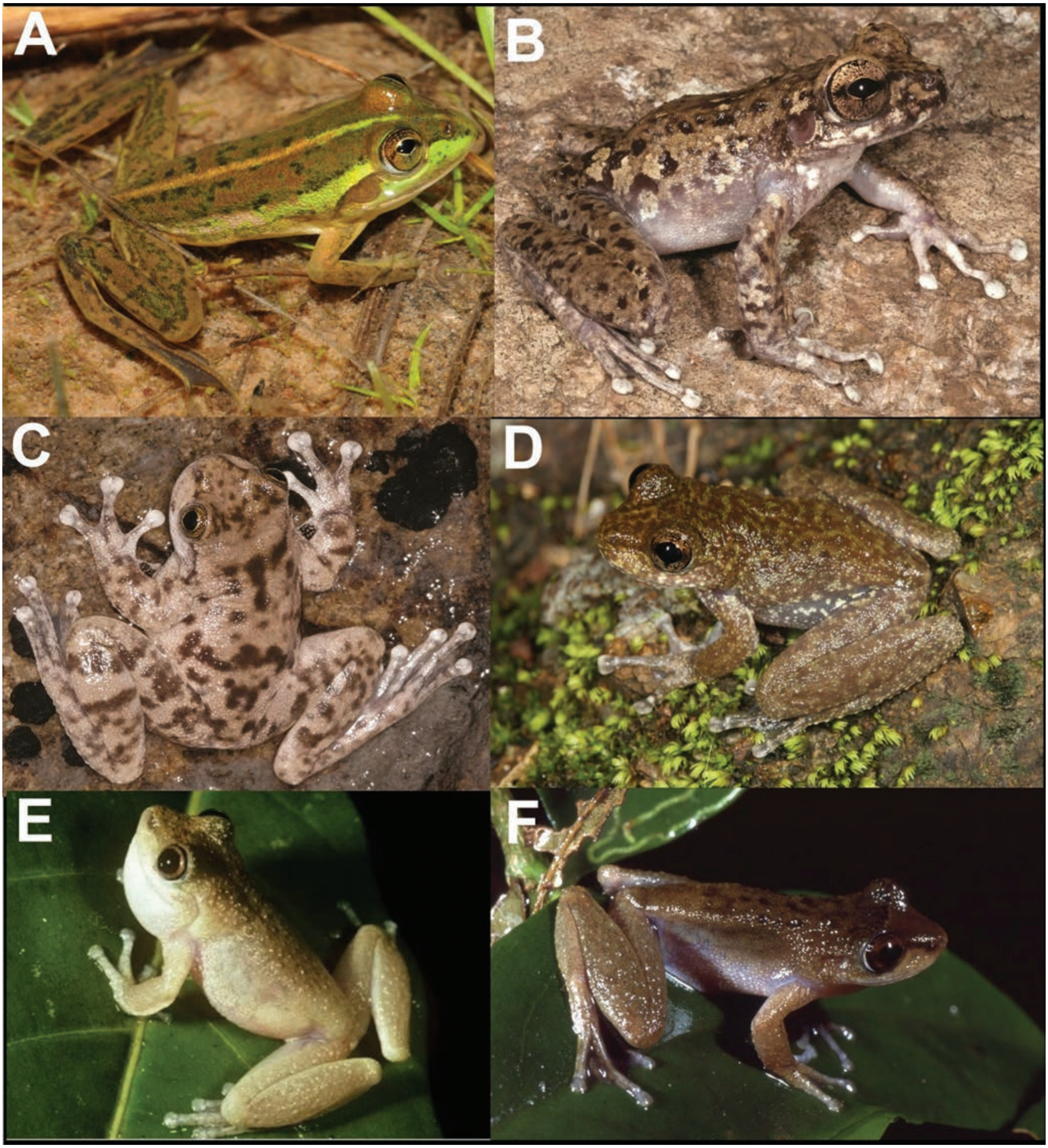

Figure 22. Images in life of *Megatestis*, *Melvillihyla*, and *Mosleyia*: (A) *Megatestis dahlii* Stephen Richards, (B) *Melvillihyla andiirrmalin* Marion Anstis, (C) *Mosleyia lorica* Marion Anstis, (D) *Mosleyia nannotis* Stephen Mahony, (E) *Mosleyia nyakalensis* Stephen Richards, (F) *Mosleyia rheocola* Stephen Donnellan.

Content: One species—*Melvillihyla andiirrmalin** (McDonald, 1997) comb. nov.

Diagnosis: Melvillihyla can be diagnosed from *Rhyaconastes* by its large vs. medium size, ossified vs. cartilaginous intercalary structures, tadpole oral disc Type 1 vs. Type 3, overall tadpole morphology Type 5 vs. Type 6, and single vs. multiple notes per reproductive call. Refer to Tables 1 and 2.

Distribution and ecology: Terrestrial boulder dwelling frogs that breed in streams within rainforest in Cape Melville in north-eastern Australia.

Etymology: Named for Cape Melville, north Queensland which contains the species' entire distribution. The gender, based on the frog generic name *Hyla*, is feminine.

Remarks: A monotypic genus with a distribution restricted to Cape Melville which has a unique combination of geology, rainforest and sclerophyll forest communities, and climate (McDonald 1997).

Mosleyia Wells & Wellington, 1985: 5

(Fig. 22)

Type species: Hyla nannotis Andersson, 1916, by original designation.

Content: Four species—*Mosleyia lorica** (Davies & McDonald, 1979) comb. nov., *Mosleyia nannotis** (Andersson, 1916), *Mosleyia nyakalensis** (Liem 1974b), *Mosleyia rheocola** (Liem 1974b).

Diagnosis: Mosleyia can be diagnosed from its sister taxon, *Eremnoculus*, by absence of a vocal sac, absence of a well-developed palpebral reticulum, spinous nuptial pads, fully vs. minimal webbed toes, and the absence vs. presence of the AMES. Refer to Tables 1 and 2.

Distribution and ecology: Semi-aquatic frogs that are found along and breed in fast-flowing rocky streams in rainforests in north-eastern Australia. Large unpigmented eggs laid under or glued to rocks; tadpoles with large, ventrally located suctorial oral discs.

Etymology: According to Wells and Wellington (1985), named for Geoff Mosley, director of the Australian Conservation Foundation. Wells and Wellington did not specify a gender for the genus and did not include species with an adjectival specific epithet that would establish gender. In this circumstance, the generic name is considered feminine, following Article 30.2.4.

Remarks: Mosleyia is the equivalent of the *Litoria nannotis* Group of Tyler and Davies (1978). *Eremnoculus* and *Mosleyia* have suctorial tadpoles (Anstis 2017) that have a large adrostral cartilage (Haas and Richards 1998). In *Eremnoculus dayi* the adrostral cartilage is flexibly and synchondrotically connected to the pars alaris, whereas, in *M. nannotis* and *M. rheocola*, it is connected by ligaments.

Nasutibatrachus Richards, Mahony & Donnellan, **gen. nov.**

(Fig. 23)

ZooBank LSID: urn:lsid:zoobank.org:act:7DF4855C-6953-4D04-B969-C15F8D8B2013 Type species: Litoria mucro (Menzies, 1993).

Content: Five species—*Nasutibatrachus mareku* (Günther, 2008) comb. nov., *Nasutibatrachus mucro** (Menzies, 1993) comb. nov., *Nasutibatrachus pinocchio* (Oliver *et al.*, 2019) comb. nov., *Nasutibatrachus pronimius** (Menzies, 1993) comb. nov., *Nasutibatrachus vivissimia** (Oliver, Richards & Donnellan, 2019) comb. nov.

Diagnosis: Nasutibatrachus can be diagnosed from members of the *Drymomantis* Sub-clade except *Exochohyla* and *Teretistes*, by the presence of a rostral spike. It can be diagnosed from *Exochohyla* by the absence of the rostral spike in females vs. presence in both genders, short vs. medium mean call duration; from *Teretistes* by reduced vs. no finger webbing and reduced vs. minimal toe webbing. Refer to Tables 1 and 2.

Distribution and ecology: New Guinea mainland, near sea level up to at least 2200 m a.s.l. Arboreal frogs that breed in ponds and ditches but eggs and tadpoles unknown. Males call from foliage adjacent to lentic waterbodies in forest.

Etymology: From the adjectival form of the Latin *nasus* (nose) and the Greek βάτραχος (*batrachos*, frog), alluding to the rostral projection. As with other generic names based on *batrachus*, the gender is masculine.

Remarks: Menzies (2006) considered *havina*, *mucro*, and *pronimia* to belong to the *Litoria* (= *Kallistobatrachus*) *iris* group. Description of the tadpole of *K. pronimia* by Menzies may refer to *Teretistes havina*. Genetic data are unavailable for *Nasutibatrachus mareku* and *N. pinocchio* but these are small, slender species in which the male has a rostral spike and Oliver *et al.* (2019) placed them in a phenetic group containing both *N. mucro* and *N. pronimia*.

Nyctimystes Stejneger 1916: 85

(Figs 24, 25)

Type species: Nyctimantis papua Boulenger, 1897, by monotypy.

Content: 32 species—*Nyctimystes avocalis* Zweifel, 1958, *Nyctimystes bivocalis* Kraus, 2012a, *Nyctimystes calcaratus* Menzies, 2014, *Nyctimystes cheesmani** Tyler, 1964a, *Nyctimystes cryptochrysos* Kraus, 2012b, *Nyctimystes daymani* Zweifel, 1958, *Nyctimystes disruptus** Tyler, 1963b, *Nyctimystes eucavatus* Menzies, 2014, *Nyctimystes fluviatilis** Zweifel, 1958, *Nyctimystes foricula** Tyler, 1963b, *Nyctimystes granti* (Boulenger, 1914), *Nyctimystes gularis* Parker, 1936, *Nyctimystes humeralis** (Boulenger, 1912), *Nyctimystes intercastellus** Kraus, 2012a, *Nyctimystes kubori** Zweifel, 1958, *Nyctimystes kuduki* Richards, 2007b, *Nyctimystes latratus* Menzies, 2014, *Nyctimystes montanus* (Peters & Doria, 1878), *Nyctimystes myolae* Menzies, 2014b, *Nyctimystes narinosus* Zweifel, 1958, *N. obsoletus* (Lönnberg, 1900), *Nyctimystes ocreptus* Menzies, 2014b, *Nyctimystes oktediensis** Richards & Johnston, 1993, *Nyctimystes papua** (Boulenger, 1897a), *Nyctimystes perimetri* Zweifel, 1958, *Nyctimystes persimilis* Zweifel, 1958, *Nyctimystes pulcher** (Wandolleck, 1911), *Nyctimystes semipalmatus** Parker, 1936, *Nyctimystes trachydermis* Zweifel, 1983, *Nyctimystes traunae* Menzies, 2014, *Nyctimystes tyleri* Zweifel, 1983, *Nyctimystes zweifeli** Tyler, 1967.

Diagnosis: Nyctimystes can be diagnosed from all other pelodryadids by a combination of a vertical pupil, patterning on

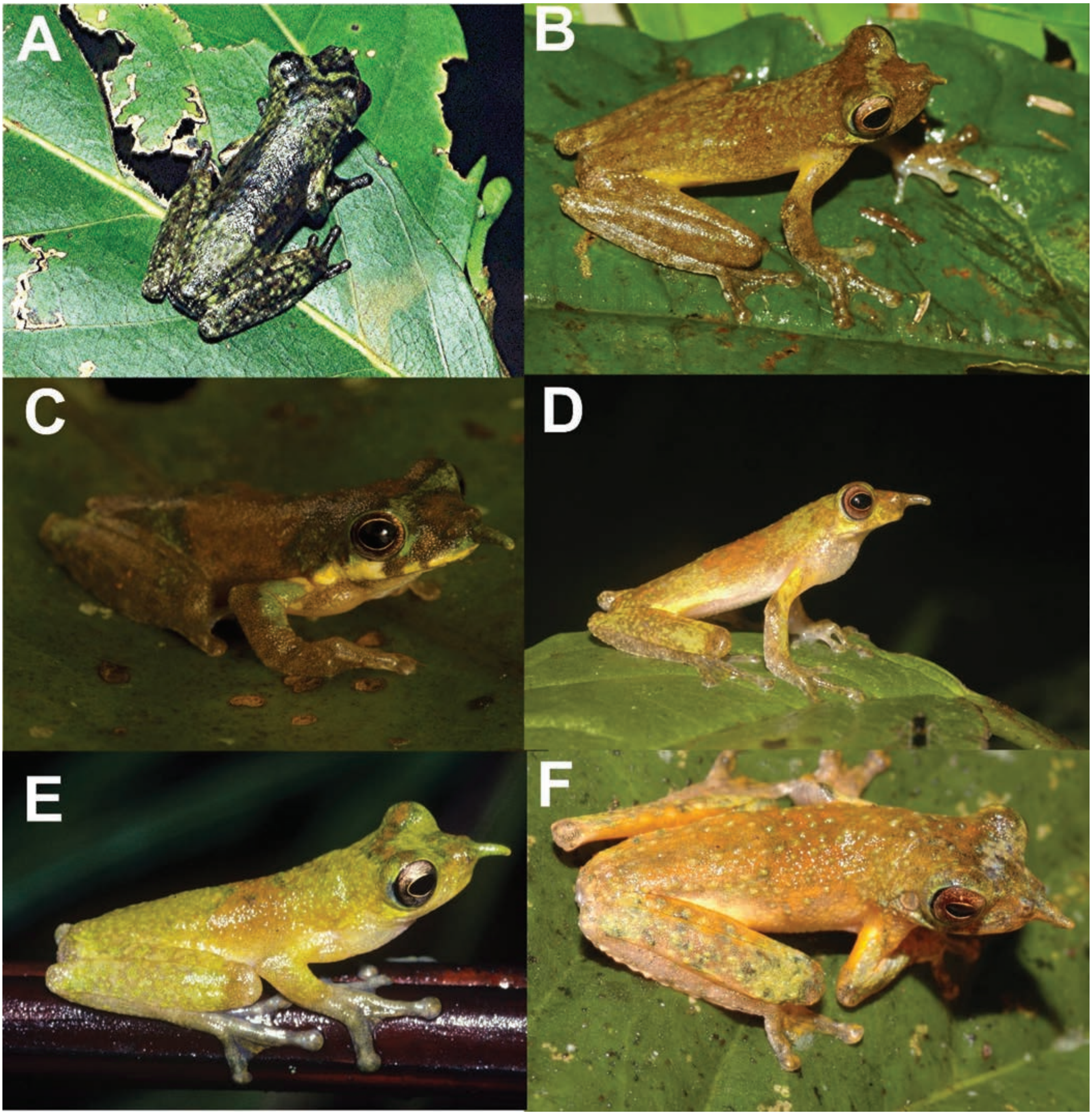

Figure 23. Images in life of *Nasutibatrachus*: (A) *Nasutibatrachus mareku* Rainer Günther, (B) *Nasutibatrachus mucro* Stephen Richards, (C) *Nasutibatrachus pinocchio* Stephen Richards, (D) *Nasutibatrachus pronimius* Stephen Richards, (E) *Nasutibatrachus pronimius*, Stephen Richards, (F) *Nasutibatrachus vivissimia* Stephen Richards.

the palpebral membrane, and large unpigmented eggs. It can be diagnosed further from *Sandyrana* by the absence vs. presence of the m. extensor brevis medius digiti IV; from *Sylvagemma* by tadpole oral disc Type 6A (oral disc reported for only two species of *Nyctimystes*) vs. Type 1A. Refer to Tables 1 and 2.

Distribution and ecology: Arboreal frogs that are found in New Guinea and surrounding islands. These frogs are found across a wide elevational range from near sea level to 3200 m a.s.l. and have the highest species diversity in lower montane habitats (Menzies 2006). All species for which reproduction is known produce large unpigmented eggs that are laid in clear-flowing, often torrential, rocky streams. Tadpoles of only two species have been documented (Table 1); these have large, ventrally oriented suctorial mouthparts; all species in the genus are expected to exhibit this character.

Etymology: From the Greek νυκτός (*nyktos*), the genitive singular of νύξ (*nyx*, the night) and μῦστης (*mystes*, a mystic, one who has been initiated). The name is a parallel to the genus

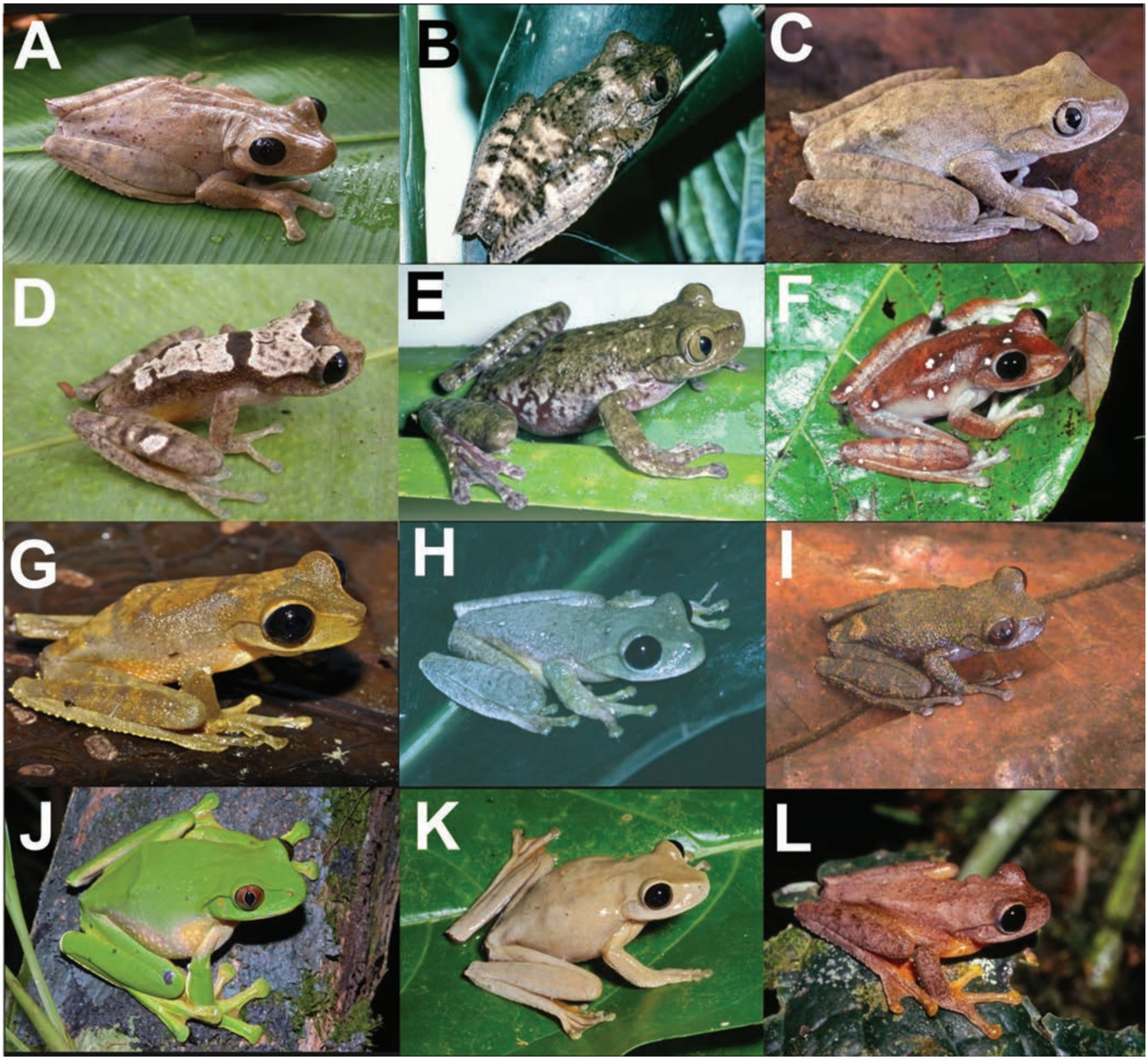

Figure 24. Images in life of *Nyctimystes*: (A) *Nyctimystes bivocalis* Fred Kraus, (B) *Nyctimystes calcaratus* James Menzies, (C) *Nyctimystes cheesmani* Fred Kraus, (D) *Nyctimystes cryptochrysos* Fred Kraus, (E) *Nyctimystes disruptus* James Menzies, (F) *Nyctimystes eucavatus* Stephen Richards, (G) *Nyctimystes fluviatilis* Stephen Richards, (H) *Nyctimystes foricula* James Menzies, (I) *Nyctimystes gularis* Fred Kraus, (J) *Nyctimystes humeralis* Stephen Richards, (K) *Nyctimystes intercastellus* Fred Kraus, (L) *Nyctimystes kubori* Stephen Richards.

Nyctimantis, from which Stejneger separated the species (Meagher 2013). However, Stejneger assumed that *mantis* was from the Greek word meaning seer or prophet, instead of the alternate meaning of a tree frog, though linked to the first meaning through the belief that the tree frog was able to predict the weather (Liddell and Scott 1897). The gender is masculine.

Remarks: Nyctimystes is found only on the main island of New Guinea and the high islands of the D'Entrecasteaux group and the Louisiade Archipelago in the south-east. Few species have been recorded from the western half of New Guinea to date but whether the difference in species diversity with the eastern half of the island reflects a biogeographic pattern or sampling opportunities remains to be determined (Menzies 2014a). *Nyctimystes oktediensis* was synonymized with *N. disruptus* by Menzies (2014b) but it differs from that species in aspects of size and colour pattern (unspotted vs. spotted), and the two species are deeply divergent genetically (Fig. 1). Numerous species remain to be described (Menzies 2006; S. Richards, personal observations).

Species included in *Nyctimystes* in the absence of genetic data are placed in this genus on the basis of having a vertical pupil, a palpebral reticulum and, where known, large, unpigmented eggs.

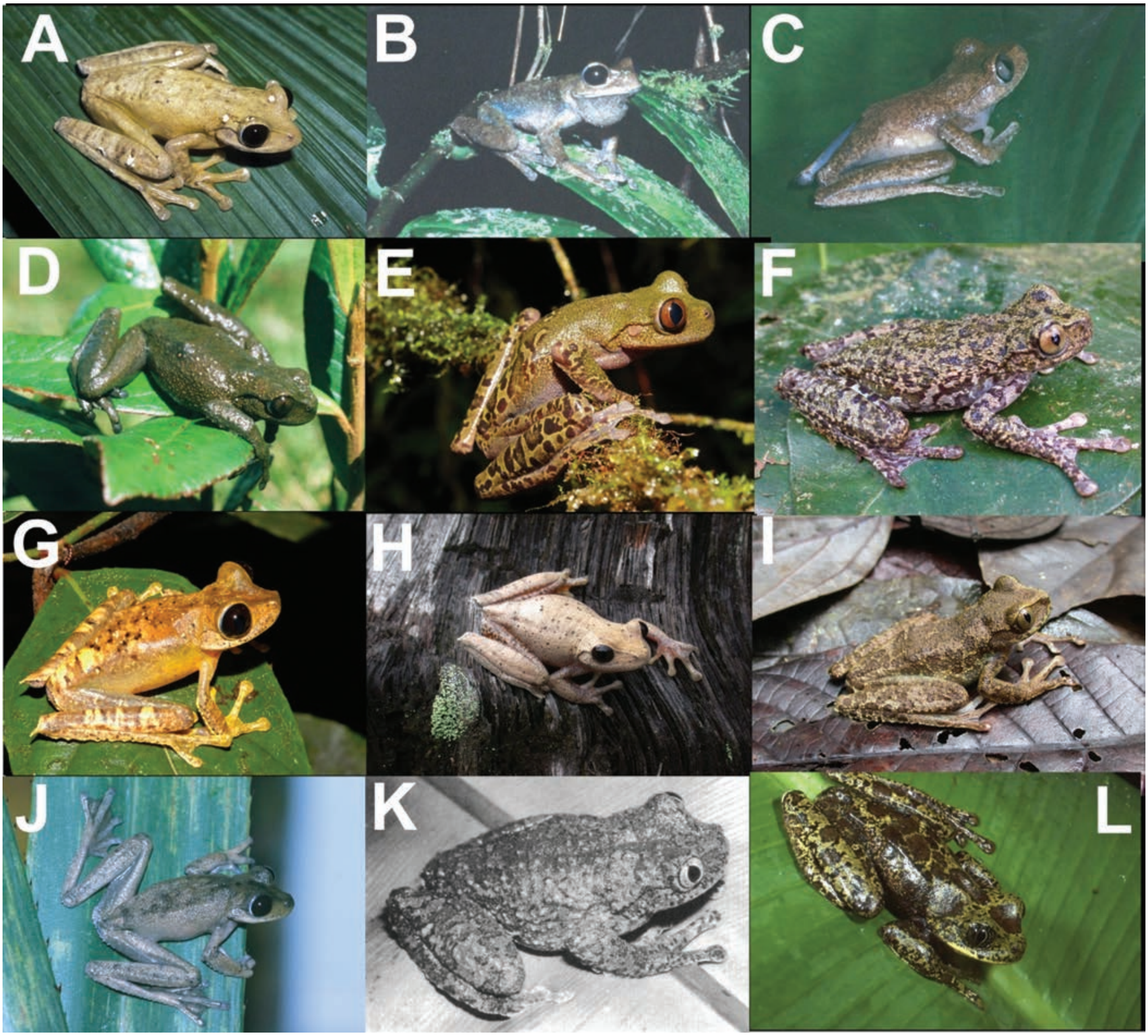

Figure 25. Images in life of *Nyctimystes*: (A) *Nyctimystes kuduki* Stephen Richards, (B) *Nyctimystes myolae* James Menzies, (C) *Nyctimystes obsoletus* James Menzies, (D) *Nyctimystes ocreptus* James Menzies, (E) *Nyctimystes oktediensis* Stephen Richards, (F) *Nyctimystes papua* Fred Kraus, (G) *Nyctimystes pulcher* Stephen Richards, (H) *Nyctimystes semipalmatus* Fred Kraus, (I) *Nyctimystes trachydermis* Fred Kraus, (J) *Nyctimystes traunae* James Menzies, (K) *Nyctimystes tyleri* Richard Zweifel, (L) *Nyctimystes zweifeli* Stephen Donnellan.

Papuahyla **Donnellan, Mahony & Richards, gen. nov.**

(Fig. 26)

ZooBank LSID: urn:lsid:zoobank.org:act:D17E72ED-A24F-49F0-B9FE-45A99516009D Type species: Litoria chloristona Menzies, Richards & Tyler, 2008.

Content: Nine species—*Papuahyla albolabris* (Wandolleck, 1911) comb. nov., *Papuahyla bibonius** (Kraus and Allison, 2004a) comb. nov., *Papuahyla chloristona** (Menzies, Richards & Tyler, 2008) comb. nov., *Papuahyla contrastens* (Tyler, 1968a) comb. nov., *Papuahyla eurynastes* (Menzies, Richards & Tyler, 2008) comb. nov., *Papuahyla lodesdema** (Menzies, Richards & Tyler, 2008) comb. nov., *Papuahyla louisiadensis** (Tyler, 1968a) comb. nov., *Papuahyla mystax* (Van Kampen, 1906) comb. nov., *Papuahyla rubrops** (Kraus and Allison, 2004b) comb. nov.

Diagnosis: Papuahyla can be diagnosed from the other members of the *Drymomantis* Sub-clade as follows: from *Amnihyla* by a Type 1 vs. Type 3 tadpole oral disc, Type 1 vs. Type 6 or 7 overall tadpole morphology; and by a right triangular vs. fusiform, oval, rectangular, spike, or teardrop call envelope shape. It can be diagnosed further from *A. amnicola* by unornamented vs. prominent tubercles on the hindlimb. It can be diagnosed from *Exedrobatrachus* by unornamented vs. tubercules on hindlimb, by a right triangular vs. fusiform call envelope shape, and 13 sites in the mitochondrial *ND4* alignment (Table 3); from *Exochohyla*

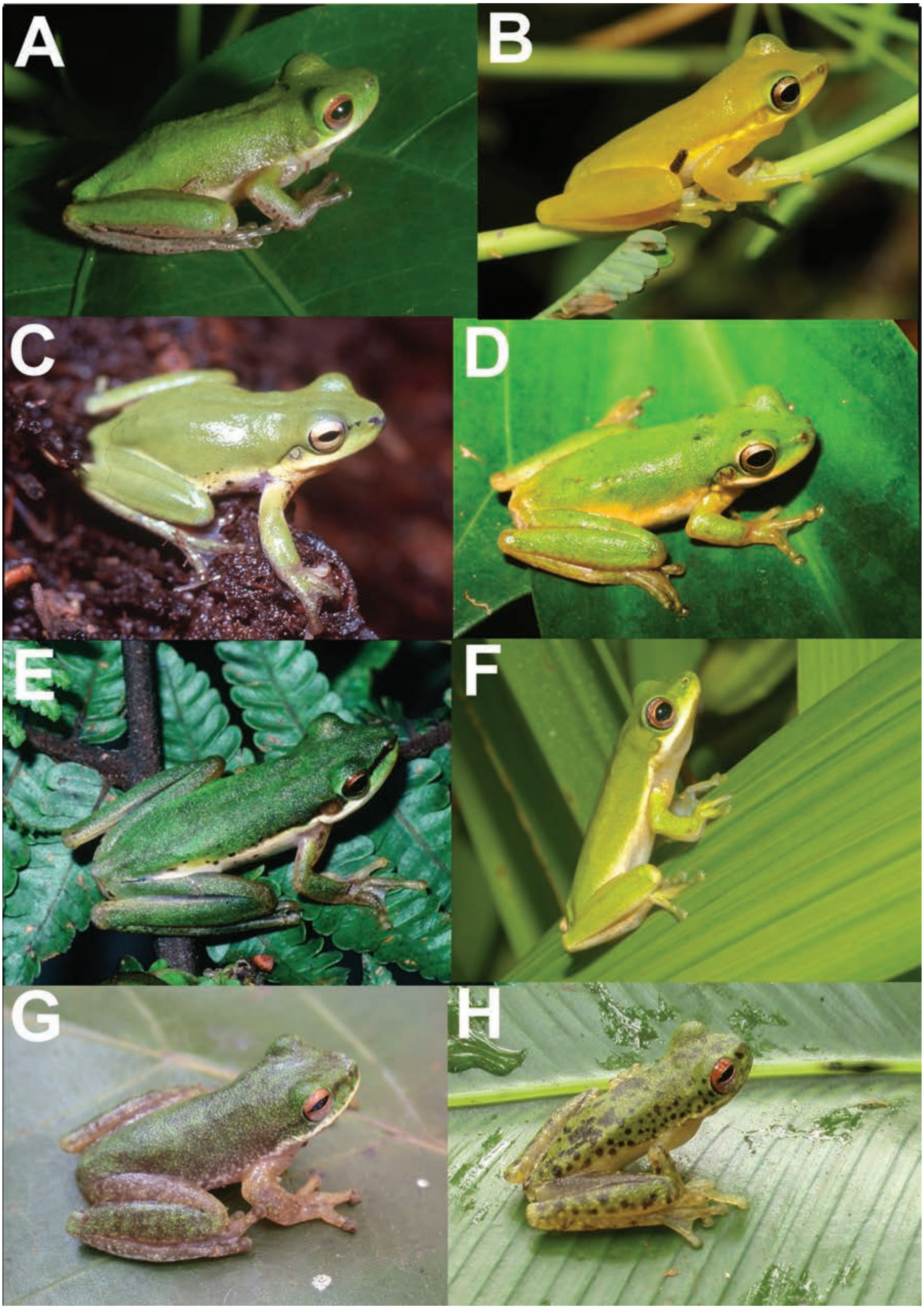

Figure 26. Images in life of *Papuahyla*: (A) *Papuahyla bibonius* Fred Kraus, (B) *Papuahyla chloristona* Stephen Richards, (C) *Papuahyla contrastens* Roy Mackay, (D) *Papuahyla eurynastes* Stephen Richards, (E) *Papuahyla eurynastes* Stephen Richards, (F) *Papuahyla lodesdema* Stephen Richards, (G) *Papuahyla louisiadensis* Fred Kraus, (H) *Papuahyla rubrops* Fred Kraus.

by absence of the rostral spike, unornamented vs. tubercles or crenulations on hindlimb, small vs. large egg size, a Type 1 vs. Type 1A tadpole oral disc, and Type 1 vs. Type 6 overall tadpole morphology; from *Hyalotos* by a pigmented vs. transparent tympanum, unornamented vs. crenulations on hindlimb, small vs. medium or large eggs, and by a right triangular vs. teardrop call envelope shape; from *Ischnohyla* by a Type 1 vs. Type 3 tadpole oral disc, Type 1 vs. Type 2A overall tadpole morphology, and by a right triangular vs. left triangular, left teardrop, or oval call envelope shape; from *Kallistobatrachus* by unornamented vs. tubercles or crenulations on hindlimb, a Type 1 vs. Type 1B tadpole oral disc, Type 1 vs. Type 7 overall tadpole morphology, and by a right triangular vs. fusiform, spike, or teardrop call envelope shape; from *Lathrana* by unornamented vs. tubercules on hindlimb, small vs. medium eggs, and by a right triangular vs. oval call envelope shape, and a note rate change across the call vs. none; from *Nasutibatrachus* and *Teretistes* by the absence of a rostral spike; further from *Teretistes* by full or reduced vs. minimal toe webbing, small vs. large eggs, and a Type 1 vs. Type 3 tadpole oral disc; from *Viridihyla* by ossified vs. cartilaginous intercalary structures, small vs. large eggs, and by a right triangular vs. fusiform, left teardrop, or rectangular call envelope shape. *Papuahyla* can be diagnosed by a right triangular call envelope shape vs. a spike-fusiform in *Carichyla* and fusiform-spike in *Drymomantis*, respectively (Table 2), and from *Carichyla* and *Drymomantis* by 13 and 16 sites, respectively, in the mitochondrial *ND4* alignment (Table 3). Refer to Tables 1, 2, and 3. Diagnosis of *Papuahyla* from all other genera in the *Drymomantis* Sub-clade is supported by 94 sites distributed across eight AHE loci (Supporting Information, AHE loci diagnostic sites).

Distribution and ecology: New Guinea and surrounding islands, Bismarck and Admiralty Archipelagos, and the Maluku and East Nusa Tenggara provinces of Indonesia. Arboreal frogs that are found in open permanent or seasonal grassy, reedy, or sago swamps in natural or altered habitats, usually not in closed forests (Menzies 2006, Anstis 2017), with most species in lowlands, except for *D. contrastens* which is a New Guinean highland species.

Etymology: Papua is a non-Latin non-Greek place name, a noun in apposition to a second noun (*Hyla*), without any need to modify either word. See etymology for *Amnihyla* above for the derivation of *Hyla*.

Remarks: Papuahyla is the equivalent to part of the *Litoria bicolor* Group and to the *Litoria albolabris* Group of Tyler and Davies (1978).

In the absence of molecular genetic data and clear evidence of affinity from morphology for *Hyla mystax* Van Kampen, 1906 and *Hyla albolabris* Wandolleck, 1911, we placed these two taxa conservatively in *Papuahyla*.

For *Hyla mystax*, Menzies (2006) discussed its relationships with the *Litoria bicolor* assemblage. Tyler (1968a) compared it with other green in life New Guinean species within or near to the size range of *H. mystax* which served to distinguish it from these species without providing direction for its affinities. Tyler and Davies (1978) placed it, without discussion, in the *Litoria bicolor* Group. Richards and Donnellan (2023) demonstrated that *H. mystax* is morphologically similar to *Kallistobatrachus beryllinus*.

Hyla albolabris Wandolleck, 1911 is a small green species with spotted ventral surfaces and a SVL of 20–22mm (Menzies 2006). Most of the original specimens are lost and the remaining two are in such poor condition being extremely dehydrated, distorted, and brittle that comparison with other species is not achievable (Menzies 2006). Tyler (1968a) discussed the original series in detail and concluded it may have been composite as there appears to have been at least two size classes represented. Tyler and Davies (1978) placed it in their *Litoria albolabris* Group.

Two species, *Hyla contrastens* and *Litoria eurynastes*, that lack genetic data presently are conservatively included in *Papuahyla* because they were considered to be closely related to *L. bicolor* in their original descriptions (Tyler 1968a, Menzies *et al.* 2008) and these associations have not been refuted subsequently, and because they are more geographically allied with *Papuahyla* being remote from *Drymomantis* that is exclusively Australian and do not share distribution with *Carichyla* which in New Guinea only occurs in the Trans-Fly region. *Papuahyla eurynastes* is likely to be a species complex (Menzies *et al.* 2008).

Pelodryas Günther, 1859: 119

(Fig. 27)

Type species: Rana caerulea White, 1790, by monotypy.

Content: Five species—*Pelodryas caerulea** (White, 1790), *Pelodryas cavernicola** (Tyler and Davies 1979b), *Pelodryas gilleni** (Spencer, 1896), *Pelodryas mira** (Oliver *et al.* 2021b) comb. nov., *Pelodryas splendida** (Tyler, Davies & Martin, 1977).

Diagnosis: Pelodryas can be diagnosed from the sister taxon *Chlorohyla* by medium to very large vs. small to medium body size, medium vs. long TL/SVL, overall tadpole morphology Type 1 vs. Type 4, and non-modulated vs. frequency modulated calls. Refer to Tables 1 and 2.

Distribution and ecology: Arboreal and saxicoline frogs that breed in still or slowly flowing waters in streams, permanent and ephemeral waterbodies in arid and semi-arid woodlands and grasslands, forests, and tropical savannah in central, eastern, and northern Australia, southern and northern mainland New Guinea.

Etymology: Günther (1859) did not provide an etymology for the name, but it is presumably from the Greek πέλωρος (*peloros*, huge or immense) and δρύας (*dryas*, a nymph or spirit of the woods), alluding to the large size of these tree frogs. *Dryas* is feminine. Duellman *et al.* (2016) incorrectly gave the derivation as from the Greek *pelo* meaning clay or mud and *dryos* meaning tree, and unsurprisingly were unable to identify the allusion.

Remarks: Pelodryas is the equivalent of the *Litoria caerulea* Group of Tyler and Davies (1978).

Pengilleyia Wells & Wellington, 1985: 5

(Fig. 28)

Type species: Litoria tyleri Martin, Watson, Gartside, Littlejohn & Loftus-Hills, 1979, by original designation.

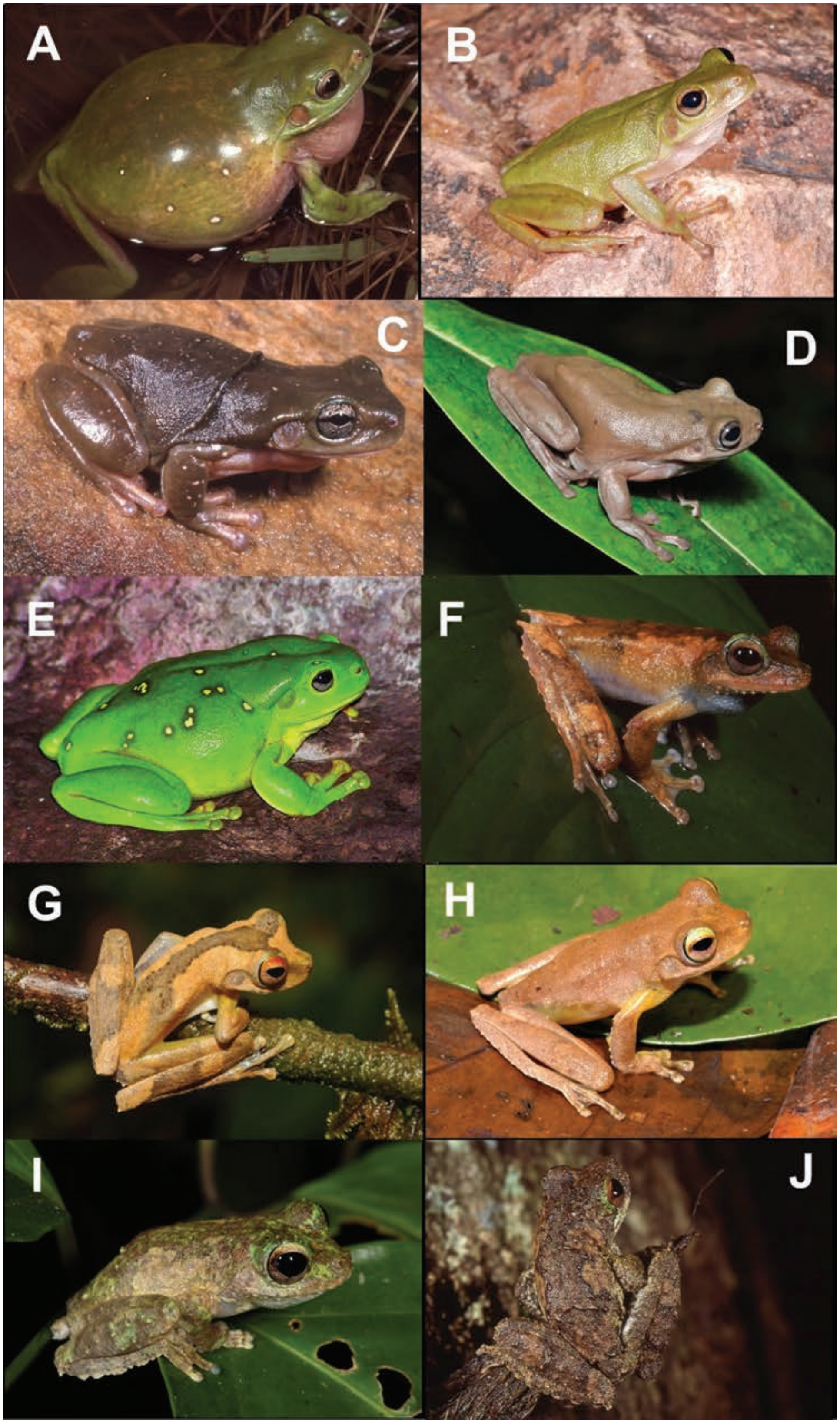

Figure 27. Images in life of *Pelodryas* and *Spicicalyx*: (A) *Pelodryas caerulea* Stephen Donnellan, (B) *Pelodryas cavernicola* Marion Anstis, (C) *Pelodryas gilleni* Stephen Donnellan, (D) *Pelodryas mira* Stephen Richards, (E) *Pelodryas splendida* Marion Anstis, (F) *Spicicalyx eucnemis* Stephen Donnellan, (G) *Spicicalyx exophthalmia* Stephen Richards, (H) *Spicicalyx genimaculata* Stephen Richards, (I) *Spicicalyx myola* Stephen Mahony, (J) *Spicicalyx serrata* Stephen Donnellan.

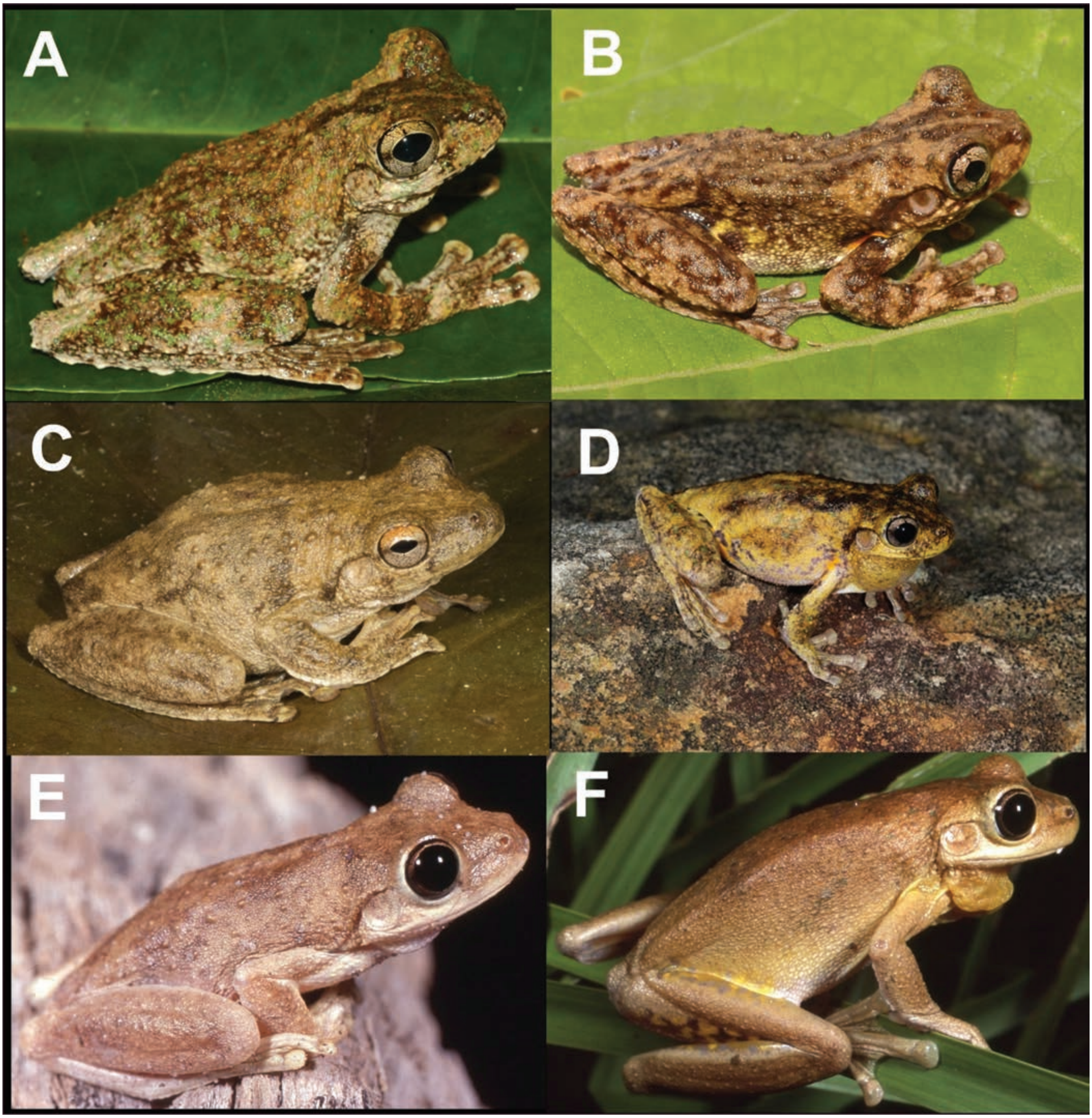

Figure 28. Images in life of *Pengilleyia*: (A) *Pengilleyia amboinensis* Stephen Richards, (B) *Pengilleyia darlingtoni* Stephen Richards, (C) *Pengilleyia everetti* Hinrich Kaiser, (D) *Pengilleyia peronii* Stephen Mahony, (E) *Pengilleyia rothii* Stephen Donnellan, (F) *Pengilleyia tyleri* Stephen Donnellan.

Content: Six species—*Pengilleyia amboinensis** (Horst, 1883) comb. nov., *Pengilleyia darlingtoni** (Loveridge, 1945) comb. nov., *Pengilleyia everetti** (Boulenger 1897b) comb. nov., *Pengilleyia peronii** (Tschudi, 1938), *Pengilleyia rothii** (De Vis, 1884), *Pengilleyia tyleri** (Martin, Watson, Gartside, Littlejohn & Loftus-Hill, 1979).

Diagnosis: Pengilleyia can be diagnosed from *Colleeneremia* by large vs. small or medium body size, three vs. two slips of the m. extensor digitorum communis, a call type that has note repetition vs. densely pulsatile, and a call that is fully amplitude modulated vs. without full amplitude modulation. Refer to Tables 1 and 2.

Distribution and ecology: Arboreal frogs that breed in permanent ponds and flooded areas in forests, woodlands, and savannahs in eastern and northern Australia, New Guinea, and the Indonesian provinces of East Nusa Tenggara and Maluku.

Etymology: According to Wells and Wellington (1985), named for David Pengilley, in recognition of his interest in the effects of urbanization on herpetofauna. By their original inclusion of the feminine adjectival specific epithet *serrata* in the genus, Wells and Wellington treated the name as feminine (Article 30.2.3).

Remarks: Pengilleyia is the equivalent of the *Litoria peronii* Group of Tyler and Davies (1978).

Ranoidea Tschudi, 1838: 76

(Fig. 29)

Synonymy

Polyphone Gistel, 1848:xi (replacement name for *Ranoidea*, created because Gistel did not like *Ranoidea*, not for any nomenclatural invalidity of *Ranoidea*).

Ranhyla M'Coy, 1867: 182 (type species *aurea*, although M'Coy's use of the name *aurea* would have been a misidentification of *raniformis*).

Chirodryas Keferstein, 1867: 358 (type species *raniformis*).

Fanchonia Werner, 1893: 82 (type species *elegans* [= *aurea*]).

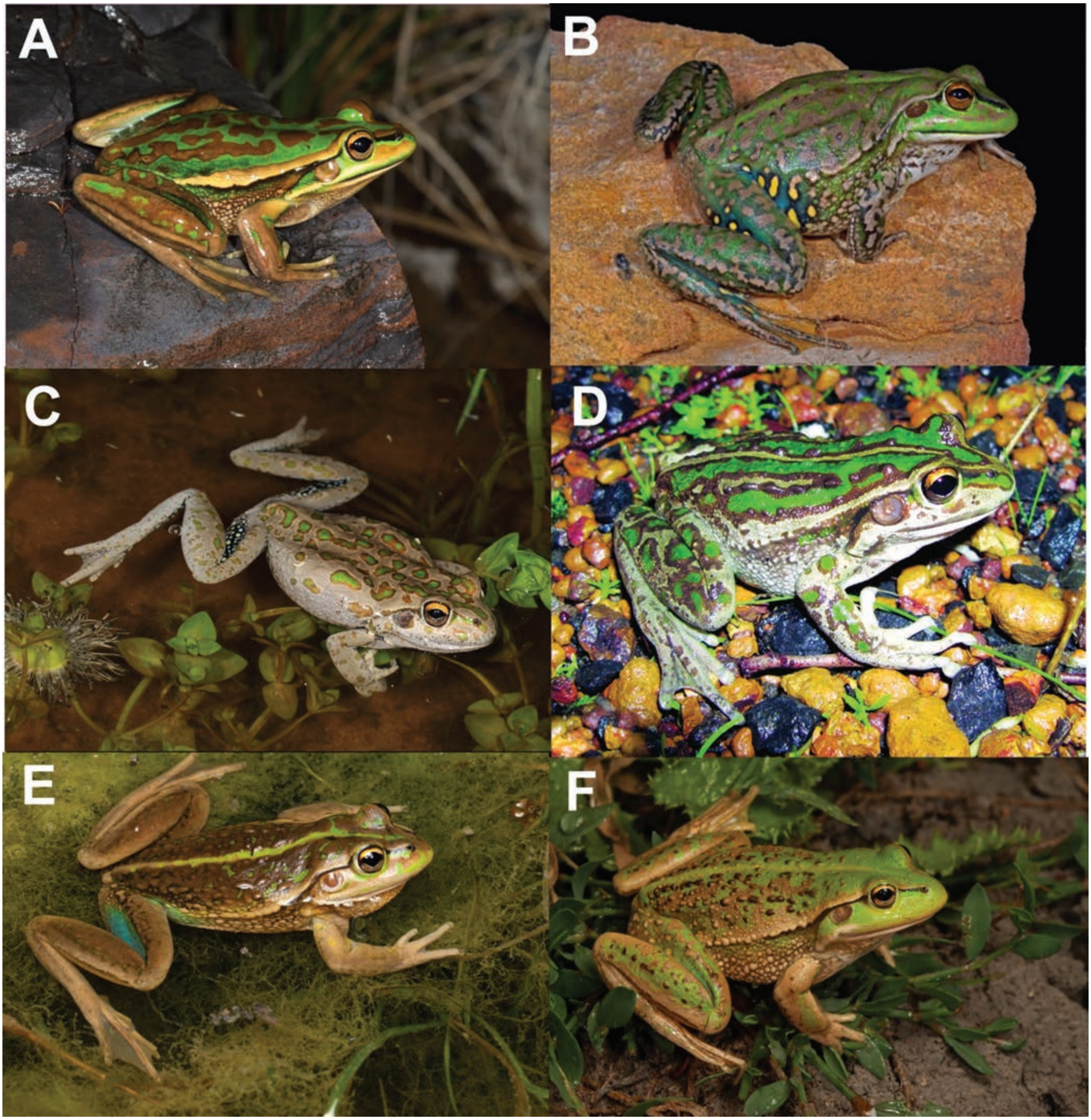

Figure 29. Images in life of *Ranoidea*: (A) *Ranoidea aurea* Stephen Mahony, (B) *Ranoidea castanea* David Hunter, (C) *Ranoidea cyclorhyncha* Stephen Mahony, (D) *Ranoidea moorei* Stephen Mahony, (E) *Ranoidea raniformis major* Stephen Mahony, (F) *Ranoidea raniformis raniformis* Stephen Mahony.

Type species: Ranoidea jacksoniensis Tschudi, 1838, by monotypy. *Ranoidea jacksoniensis* is a synonym of *Rana aurea* Lesson, 1829 (Cogger *et al*. 1983).

Content: Five species—*Ranoidea aurea** (Lesson, 1829), *Ranoidea castanea** (Steindachner, 1867) comb. nov., *Ranoidea cyclorhyncha** (Boulenger, 1882), *Ranoidea moorei** (Copland, 1957), *Ranoidea raniformis** (Keferstein, 1867).

Diagnosis: Ranoidea can be diagnosed from members of its sister clade comprising *Cyclorana*, *Leptobatrachus*, and *Megatestis* as follows: from *Cyclorana* by small vs. large inner metatarsal tubercles; by ossified intercalary structures vs. their absence in *Cyclorana* (13 species) and vs. cartilaginous in *Leptobatrachus*; by the presence of a vocal sac vs. absence in *Megatestis*; by overall tadpole morphology Type 1 vs. Type 3 or 4 in *Cyclorana*, *Leptobatrachus*, and *Megatestis*; by a tonal call type vs. pulsatile in *Cyclorana* and pulse repetition in *Megatestis*. *Ranoidea* can be diagnosed further from *Leptobatrachus* and *Megatestis* by the presence of the m. extensor brevis medius digiti IV vs. absence. Refer to Tables 1 and 2.

Distribution and ecology: Terrestrial frogs that breed in still or slowly flowing water in ephemeral and permanent waterbodies in grasslands, riverine billabongs, and forests in south-western and south-eastern Australia.

Etymology: Tschudi (1838) did not give an explicit etymology but referred to the superficial similarity of his species *jacksoniensis* to the true frogs (*Rana*), and the name presumably means *Rana*-like. The suffix *–oidea* is neo-Latin, and the neuter plural of *–oideus*. However, as the Code only includes ancient and medieval Latin in its definition of Latin, the gender must be determined by Article 30.2. With the only included species having a gender that could be either masculine or feminine, but not neuter, Article 30.2.4 must be invoked to consider the gender feminine.

Remarks: Ranoidea is in part the equivalent of the *Litoria aurea* Group of Tyler and Davies (1978) in which *M. dahlii* and *C. alboguttata* also were included.

For *Hyla aurea* var. *cyclorhynchus* Boulenger, 1882, the specific epithet ends in the neuter Greek term *rhynchos* (= nose, a noun), but Boulenger used it with the masculine ending *rhynchus*. Subsequently, the epithet has been treated consistently as an adjective, becoming *cyclorhyncha* in *Litoria*, which we have retained for its association with *Ranoidea*.

Rawlinsonia Wells & Wellington, 1985: 5

(Fig. 30)

Type species: Hyla ewingii Duméril & Bibron, 1841, by original designation.

Content: Eight species—*Rawlinsonia corbeni** (Wells & Wellington, 1985), *Rawlinsonia ewingii** (Duméril & Bibron, 1841), *Rawlinsonia jervisiensis** (Duméril & Bibron, 1841), *Rawlinsonia littlejohni** (White *et al.*, 1994), *Rawlinsonia paraewingi** (Watson, Loftus-Hills & Littlejohn, 1971) comb. nov., *Rawlinsonia revelata** (Ingram, Corben & Hosmer, 1982), *Rawlinsonia verreauxii** (Duméril, 1853), *Rawlinsonia watsoni** (Mahony, Moses, Mahony, Lemckert & Donnellan, 2020) comb. nov.

Diagnosis: Rawlinsonia can be diagnosed from *Colleeneremia* by three vs. two slips of the m. extensor digitorum communis, by a call type that is only pulse repetition vs. a combined pulse repetition and pulsatile call type; from *Pengilleyia* by ossified vs. cartilaginous intercalary structures; from *Saganura* by small to medium vs. large eggs, and by a pulse repetition vs. tonal call type. Refer to Tables 1 and 2.

Distribution and ecology: Arboreal frogs that breed in permanent ponds and slow flowing water in streams in forests, woodlands, heaths, grasslands, and modified habitats in eastern Australia.

Etymology: According to Wells and Wellington (1985), named for Peter Rawlinson in recognition of his contributions to Australian herpetology. By their inclusion of the feminine adjectival species epithets *alpina*, *dentata*, and *revelata* in their genus, the gender is to be treated as feminine (Article 30.2.3).

Remarks: Rawlinsonia is the equivalent of the *Litoria ewingii* Group of Tyler and Davies (1978).

Rhyaconastes Mahony, Donnellan & Richards, **gen. nov.**

(Fig. 31)

ZooBank LSID: urn:lsid:zoobank.org:act:82FC7DE1-19E8-4EB4-B16C-A27134640EA8

Synonymy
Euscelis Fitzinger 1843: 31 (type species *lesueurii*). Unavailable as its preoccupied by *Euscelis* Brullé 1832: 109.

Type species: Hyla lesueurii Duméril & Bibron 1841.

Content: Four species—*Rhyaconastes booroolongensis** (Moore, 1961) comb. nov., *Rhyaconastes jungguy** (Donnellan & Mahony, 2004) comb. nov., *Rhyaconastes lesueurii** (Duméril & Bibron, 1841) comb. nov., *Rhyaconastes wilcoxii** (Günther, 1864) comb. nov.

Diagnosis: Rhyaconastes can be diagnosed from *Melvillihyla* by its medium to large vs. very large body size, cartilaginous vs. ossified intercalary structures, tadpole oral disc Type 3 vs. Type 1, and overall tadpole morphology Type 6 vs. Type 5, and multiple vs. single notes per reproductive call. Refer to Tables 1 and 2.

Distribution and ecology: Terrestrial frogs that breed in streams and rivers in forests and woodlands in eastern Australia. All species lack a vocal sac but produce a low amplitude call.

Etymology: From the Greek ῥύακος (*rhyakos*, a stream or torrent) and ναστής (*nastes*, inhabitant), alluding to the stream-breeding habits of the species in the genus. The name, based on *nastes*, is masculine.

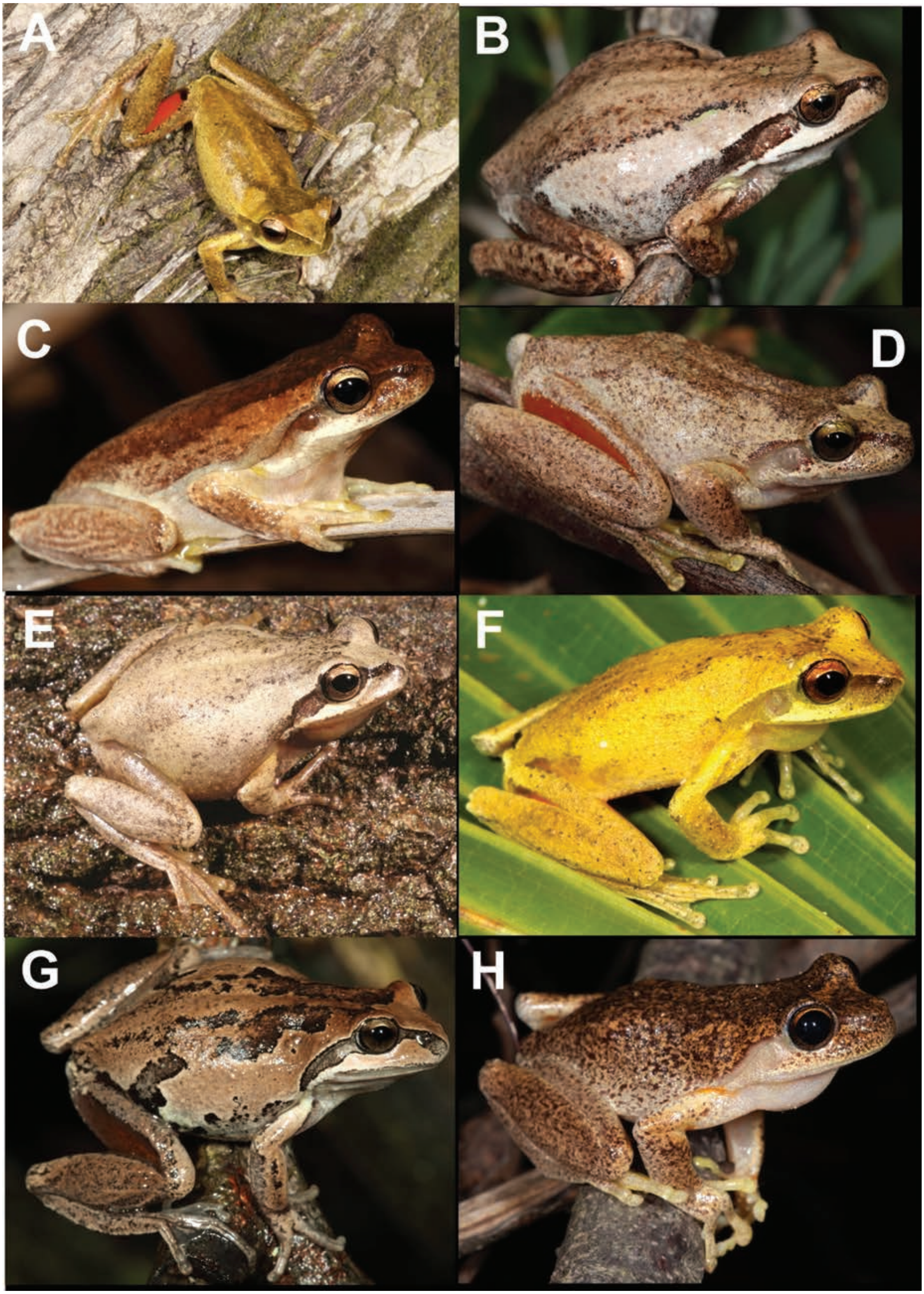

Figure 30. Images in life of *Rawlinsonia*: (A) *Rawlinsonia corbeni* Conrad Hoskin, (B) *Rawlinsonia ewingii* Stephen Mahony, (C) *Rawlinsonia jervisiensis* Stephen Mahony, (D) *Rawlinsonia littlejohni* Stephen Mahony, (E) *Rawlinsonia paraewingi* Marion Anstis, (F) *Rawlinsonia revelata* Stephen Mahony, (G) *Rawlinsonia verreauxii* Stephen Mahony, (H) *Rawlinsonia watsoni* Stephen Mahony.

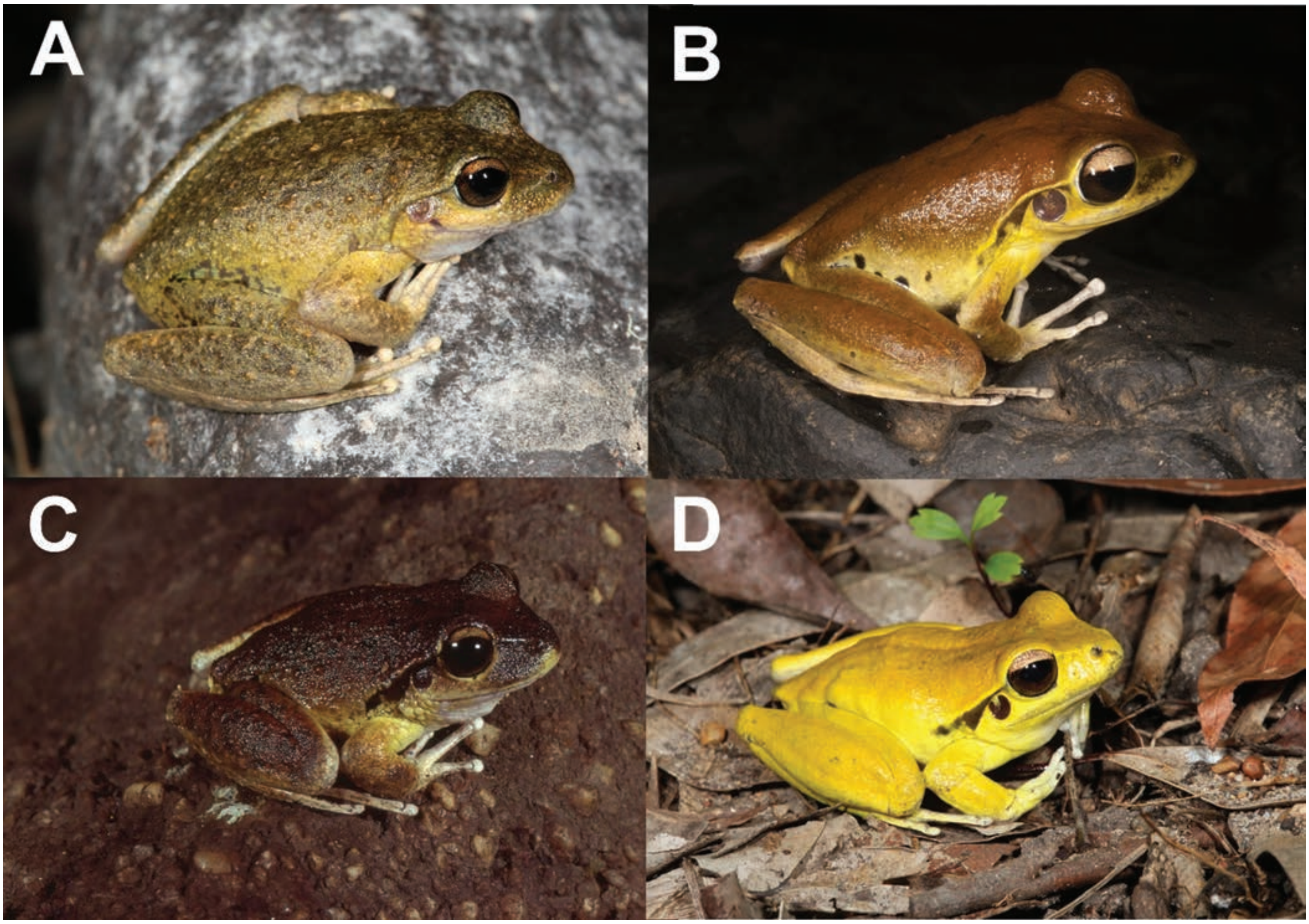

Figure 31. Images in life of *Rhyaconastes*: (A) *Rhyaconastes booroolongensis* Stephen Mahony, (B) *Rhyaconastes jungguy* Stephen Mahony, (C) *Rhyaconastes lesueuri* Stephen Donnellan, (D) *Rhyaconastes wilcoxii* Stephen Mahony showing yellow wash of breeding males.

Remarks: Rhyaconastes is the equivalent of the *Litoria booroolongensis* and *L. lesueurii* Groups of Tyler and Davies (1978). All *Rhyaconastes* species lack a vocal sac which distinguishes them from other ground-dwelling genera such as *Cyclorana* and *Litoria*.

Saganura Wells and Wellington 1985: 6

(Fig. 33)

Type species: Hyla burrowsi Scott, 1942, by original designation.

Content: One species—*Saganura burrowsae** (Scott, 1942).

Diagnosis: Saganura can be diagnosed from *Rawlinsonia* by large vs. small to medium eggs, and by a tonal vs. pulse repetition call type. Refer to Tables 1 and 2.

Distribution and ecology: An arboreal frog that breeds in static or slow-flowing ephemeral or permanent waterbodies in moorlands, sedgelands, and forests in Tasmania.

Etymology: According to Wells and Wellington (1985), named for Carl Sagan of Cornell University. The '*ura*' component of the name is not explained but could be considered to be derived from the Greek οὐρᾱ (*oura*, tail, feminine, often Latinized as '*ura*'). While this makes little sense in itself, it is likely a play on words, derived from the ordinal name for frogs, Anura, the first two letters of which are shared with the last two letters of Sagan's name, the name thereby meaning Sagan's frog. The gender is therefore to be treated as feminine.

Remarks: Saganura is the equivalent in part to the *Litoria maculata* [= *spenceri*] Group of Tyler and Davies (1978).

Sandyrana Wells and Wellington, 1985: 6

(Fig. 32)

Type species: Hyla infrafrenata Günther, 1867, by original designation.

Content: 14 species—*Sandyrana azuroscelis** (Günther, Richards, Hamidy, Trilaksono, Sulaeman & Oliver, 2023) comb. nov., *Sandyrana dux** (Richards and Oliver 2006a) comb. nov., *Sandyrana graminea** (Boulenger, 1905) comb. nov., *Sandyrana hunti** (Richards *et al.*, 2006) comb. nov., *Sandyrana infrafrenata** (Günther, 1867), *Sandyrana lubisi* (Oliver *et al.*, 2021a) comb. nov., *Sandyrana multicolor** (Günther, 2004b) comb. nov., *Sandyrana nullicedens* (Kraus, 2018) comb. nov.,

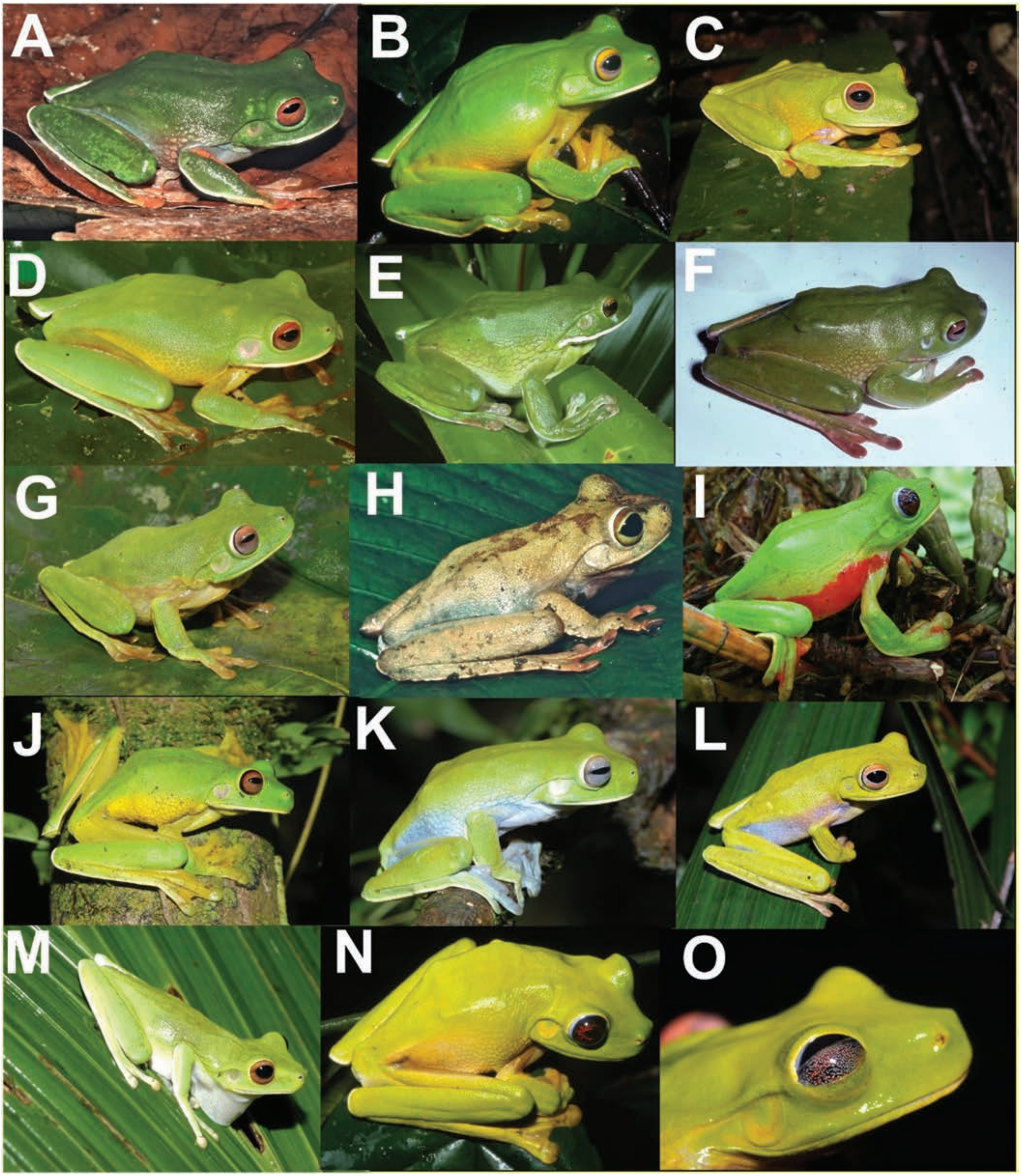

Figure 32. Images in life of *Sandyrana*: (A) *Sandyrana azuroscelis* Rainer Günther, (B) *Sandyrana dux* Stephen Richards, (C) *Sandyrana graminea* Chris Dahl, (D) *Sandyrana hunti* Stephen Richards, (E) *Sandyrana infrafrenata infrafrenata* Stephen Donnellan, (F) *Sandyrana infrafrenata militaria* Fred Parker, (G) *Sandyrana lubisi* Stephen Richards, (H) *Sandyrana multicolor* Rainer Günther, (I) *Sandyrana nullicedens* Fred Kraus, (J) *Sandyrana pallidofemora* Stephen Richards, (K) *Sandyrana pterodactyla* Stephen Richards, (L) *Sandyrana purpureolata* Stephen Richards, (M) *Sandyrana sanguinolenta* Stephen Richards, (N) *Sandyrana sauroni* Stephen Richards, (O) *Sandyrana sauroni* Stephen Richards showing patterning on the palpebral membrane.

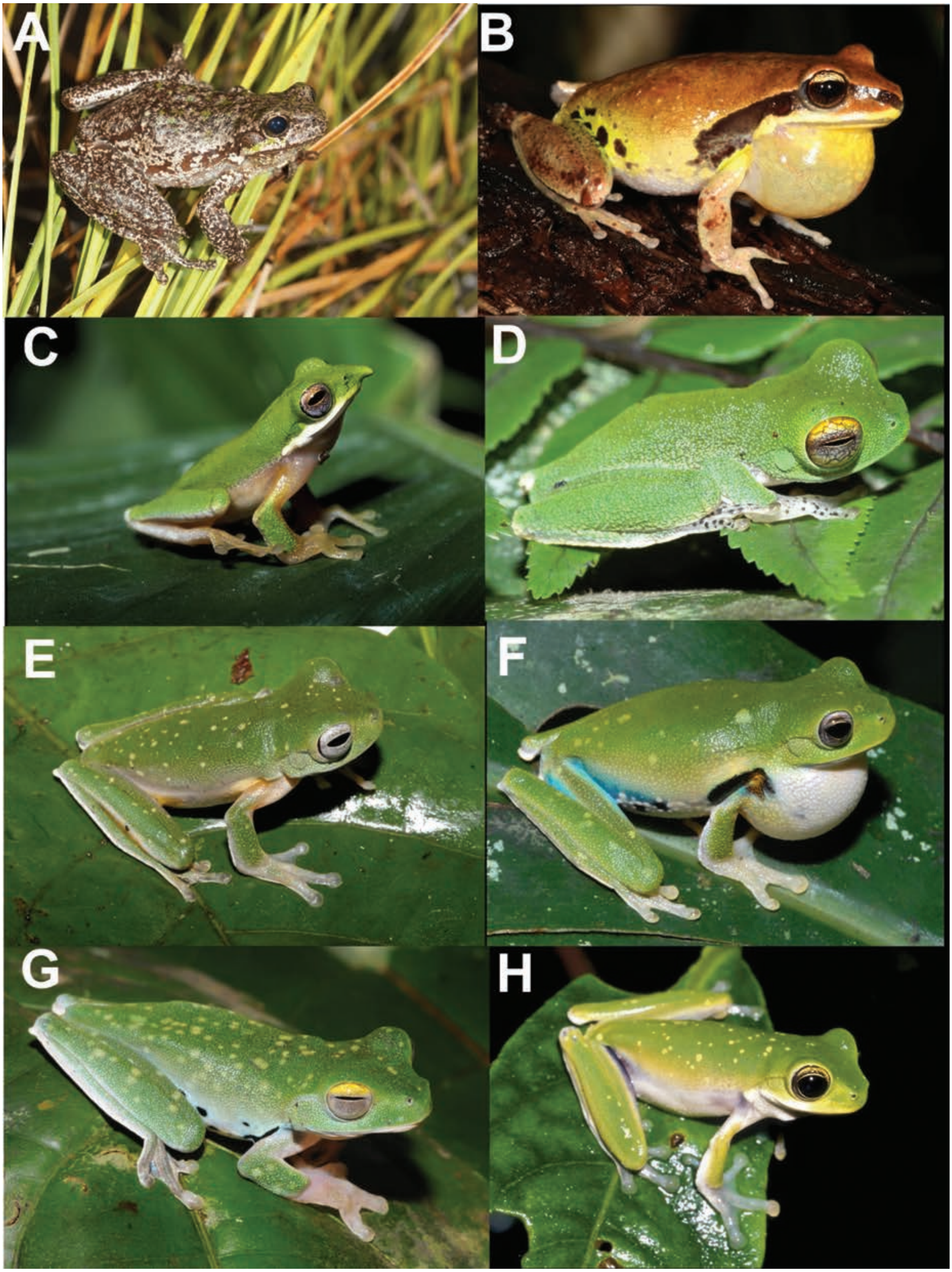

Figure 33. Images in life of *Saganura*, *Sylvagemma*, *Teretistes*, and *Viridihyla*: (A) *Saganura burrowsae* Mark Sanders, (B) *Sylvagemma brevipalmata* Stephen Mahony, (C) *Teretistes havina* Stephen Richards, (D) *Viridihyla christianbergmanni* Stephen Richards, (E) *Viridihyla gasconi* Stephen Richards, (F) *Viridihyla multiplica* Stephen Richards, (G) *Viridihyla spectabilis* Stephen Richards, (H) *Viridihyla wapogaensis* Stephen Richards.

*Sandyrana pallidofemora** (Kraus, 2018) comb. nov., *Sandyrana pterodactyla** (Oliver, Richards & Donnellan, 2019) comb. nov., *Sandyrana purpureolata** (Oliver *et al.*, 2007) comb. nov., *Sandyrana sanguinolenta** (Van Kampen, 1909) comb. nov., *Sandyrana sauroni** (Richards and Oliver, 2006a) comb. nov., *Sandyrana tenuigranulata** (Boettger, 1895) comb. nov.

Diagnosis: Sandyrana can be diagnosed from *Nyctimystes* by small to medum pigmented vs. large unpigmented eggs, tadpole oral disc Type 1 vs. Type 6A, overall tadpole morphology Type 1 vs. Type 6, by the presence of the m. extensor brevis medius digiti IV vs. absence, by non-vertical vs. vertical pupil; and from *Sylvagemma* by long vs. medium TL/SVL, reduced to fully vs. no finger webbing, reduced or fully vs. minimally webbed toes, cartilaginous vs. ossified intercalary structures, tadpole oral disc Type 1 vs. 1A. Refer to Tables 1 and 2.

Distribution and ecology: Arboreal frogs that are found in north-eastern Australia, New Guinea and surrounding islands, the Bismarck and Admiralty Archipelagos, the Indonesian provinces of East Nusa Tenggara and Maluku, and introduced into Java. *Sandyrana* display two contrasting lifestyles: dwelling and calling high in the canopy (Günther *et al.* 2023) and in some species observations of parachuting (Kraus 2018) or calling close to ponds and other water bodies on the ground (Günther *et al.* 2023).

Etymology: According to Wells and Wellington (1985), named for Sandy Ingleby, Sydney. The gender, based on *Rana*, is feminine.

Remarks: Sandyrana is the equivalent (*S. infrafrenata*) of the *Litoria infrafrenata* Group and in part (*S. graminea*) of the *L. aruensis* Group of Tyler and Davies (1978). The diploid chromosome number of $2n = 24$ for *Sandyrana infrafrenata* is unique amongst pelodryadids which otherwise have a $2n = 26$ karyotype among the 21 genera for which data are presently available (Supporting Information, Table S3; Stephenson and Stephenson 1970, Menzies and Tippet 1976, Tyler *et al.* 1978, King *et al.* 1979, 1990, King 1980, 1981, Kuramoto and Allison 1991, Donnellan and Mahony 2004, Kakampuy *et al.* 2013, Mollard 2018, Mollard *et al.* 2018, 2024, Schmid *et al.* 2018).

Shea and Kraus (2007) emended the name *hunti* to *huntorum* on the basis that it was named in recognition of the Hunt family (by implication, more than one person). However, Frost (2023) considered this to be an unjustified emendation. We retain *hunti* here while acknowledging that not all authors of this paper agree with this interpretation.

Sulaeman *et al.* (2021) include colour images in life of *Sandyrana tenuigranulata* (which they mis-spelt as *tennuigranulata*) from Ternate and Halmahera in the North Moluccas, Indonesia.

Genetic data for *Litoria lubisi* and *L. nullicedens* were not available. They are placed in *Sandyrana* on the basis of their very large size, green coloration, extensively webbed fingers, and canopy-dwelling habit (Kraus 2018, Oliver *et al.* 2021a).

Spicicalyx Donnellan, Mahony & Richards, **gen. nov.**

(Fig. 27)

ZooBank LSID: urn:lsid:zoobank.org:act:CC448528-5A9C-4851-9371-13AA9D2CECCB Type species: Hyla genimaculata Horst, 1883.

Content: Five species—*Spicicalyx eucnemis** (Lönnberg, 1900) comb. nov., *Spicicalyx exophthalmia** (Tyler, Davies & Aplin 1986) comb. nov., *Spicicalyx genimaculata** (Horst, 1883) comb. nov., *Spicicalyx myola** (Hoskin, 2007) comb. nov., *Spicicalyx serrata** (Andersson, 1916) comb. nov.

Diagnosis: Spicicalyx can be diagnosed from members of the sister clade as follows: from *Melvillihyla* and *Rhyaconastes* by the presence vs. absence of a vocal sac, presence vs. absence of crenulated ornamentation of the hindlimbs, presence vs. absence of a heel spike, reduced or fully webbed vs. no finger webbing, and further from *Melvillihyla* by cartilaginous vs. ossified intercalary structures, overall tadpole morphology Type 4 vs. Type 5, large vs. small eggs, and further from *Rhyaconastes* by overall tadpole morphology Type 4 vs. Type 6, and oral disc Type 1 vs. Type 3. Refer to Tables 1 and 2.

Distribution and ecology: Arboreal frogs that breed in slow-flowing permanent streams in rainforest in north-eastern Australia and New Guinea and surrounding islands.

Etymology: From the Latin *spica* (point or spear) and *calx* (heel), referring to the spike on the heel that is generally present in members of this genus. We emended *calx* to the more euphonious *calyx* for use in the name. *Calx* is feminine.

Remarks: Spicicalyx is the equivalent of the *Litoria eucnemis* Group of Tyler and Davies (1978).

Sylvagemma Mahony, Donnellan & Richards, **gen. nov.**

(Fig. 33)

ZooBank LSID: urn:lsid:zoobank.org:act:4BC89999-3291-4843-8D1C-40BEA3201B86 Type species: Litoria brevipalmata Tyler, Martin & Watson, 1972.

Content: One species—*Sylvagemma brevipalmata** (Tyler, Martin & Watson, 1972) comb. nov.

Diagnosis: Sylvagemma can be diagnosed from *Nyctimystes* by a non-vertical vs. vertical pupil, absence vs. presence of crenulated ornamentation on the hindlimbs, absence vs. presence of patterning of the palpebral membrane, by medium-sized pigmented vs. large sized unpigmented eggs, tadpole oral disc Type 1A vs. Type 6A (oral disc reported for only two species of *Nyctimystes*); from *Sandyrana* by medium vs. long TL/SVL, no webbing vs. reduced to fully webbed fingers, minimally webbed vs. reduced or fully webbed toes, ossified vs. cartilaginous intercalary structures, tadpole oral disc Type 1A vs. Type 1. Refer to Tables 1 and 2.

Distribution and ecology: Terrestrial frogs that breed in static ephemeral pools in forests, heathlands, grasslands, and modified landscapes in mid-eastern Australia.

Etymology: From the Latin *sylva* (forest) and *gemma* (a jewel), referring to the conspicuously coloured nature of this inhabitant of wet sclerophyll forests. The gender, based on *gemma*, is feminine.

Remarks: Sylvagemma is the equivalent of the *Litoria brevipalmata* Group of Tyler and Davies (1978). *Sylvagemma brevipalmata* is the only Australian pelodryadid in which the vent of the tadpoles has a medial position (Anstis 2017).

Teretistes Richards, Mahony & Donnellan, **gen. nov.**

(Fig. 33)

ZooBank LSID: urn:lsid:zoobank.org:act:1C8072BD-3776-4D70-BBA2-8ACE4E1A3495 Type species: Litoria havina Menzies, 1993.

Content: One species—*Teretistes havina** (Menzies, 1993) comb. nov.

Diagnosis: Teretistes can be diagnosed from other members of the *Drymomantis* Sub-clade by a combination of rostral spike only present in males, expanded finger and toe discs, large pigmented eggs, a Type 3 tadpole oral disc, high call dominant frequency, call frequency modulation, and triangular call envelope shape. Refer to Tables 1 and 2.

Distribution and ecology: Arboreal frogs that breed in small ponds in rainforest on mainland New Guinea. Eggs are deposited on leaves above water and following development free-swimming tadpoles drop into water below (Richards 2002). Tadpoles have striking black and gold pattern (Richards 2002).

Etymology: From the Greek τερέτισμα (*teretisma*, a whistling), with the masculine suffix -ἴστής (*-istes*, an agent, one who), alluding to the whistling call that also provides the specific epithet.

Remarks: A rostral spike is present only in males. While presently conceived as a monotypic lineage, a wide geographic survey of mitochondrial DNA sequence variation in *Teretistes havina* indicates that it is a species complex (Richards and Donnellan, unpublished data).

Viridihyla Richards, Mahony & Donnellan, **gen. nov.**

(Fig. 33)

ZooBank LSID: urn:lsid:zoobank.org:act:7E5988C6-9AAC-43DB-A5B8-B3BEE7281448 Type species: Hyla multiplica (Tyler, 1964b).

Content: Five species—*Viridihyla christianbergmanni* (Günther, 2008) comb. nov., *Viridihyla gasconi** (Richards *et al.*, 2009) comb. nov., *Viridihyla multiplica** (Tyler, 1964b) comb. nov., *Viridihyla spectabilis** (Richards & Donnellan, 2023) comb. nov., *Viridihyla wapogaensis* (Richards & Iskander, 2001) comb. nov.

Diagnosis: Viridihyla can be diagnosed from *Nasutibatrachus* and *Teretistes* by the absence of a rostral spike; from *Kallistobatrachus* by cartilaginous vs. ossified intercalary structures, large vs. small or medium egg size, by having dorsum uniform green with small scattered white-yellow or green spots vs. bright green or occasionally yellow-green with brown markings or brown with green markings, peppered or vermiculated black occasionally with white spots, or scattered pale brown spots, or immaculate green or yellowish green mottled all over with darker green or sparse minute yellow spots; and from *Lathrana* by finger and toe discs of equal size vs. smaller toe discs, cartilaginous vs. ossified intercalary structures, large vs. medium egg size, fusiform or left teardrop, or rectangular vs. oval call envelope shape. Refer to Tables 1 and 2.

Distribution and ecology: Arboreal frogs that are found typically along or near small clear-flowing streams in mainland New Guinea. The tadpole of *V. multiplica* is boldly marked with black (Anstis and Richards 2014).

Etymology: From the Latin *viridis* (green) and *Hyla*. The gender is feminine.

Remarks: Viridihyla corresponds in part (*V. multiplica*) to the *Litoria aruensis* Group of Tyler and Davies (1978). Genetic data were not available for *Litoria christianbergmanni* and *L. wapogaensis* and they are placed tentatively in *Viridihyla* based on the morphologically diagnostic characters outlined above. However, adult males of these two species have distinct brown nuptial pads (vs. absent in the remaining three species) so molecular genetic studies may require a reassessment of their relationships.

Incertae sedis

'Hyla jeudii' Werner, 1901 is known only from the holotype and lacks a precise type locality (= 'German New Guinea', now the northern part of Papua New Guinea). This species exhibits an unusual combination of characters including an elongate head, extremely short limbs, and reduced webbing between the toes, summarized in Tyler (1968a) and Menzies (2006). Tyler and Davies (1978) placed it in the *Litoria jeudii* Group, but its relationships remain obscure, and it was considered *incertae sedis* within Pelodryadidae by Duellman *et al.* (2016).

CONCLUSION

Our comprehensive phylogenomic and phenotypic surveys have formed the basis of the stabilization of the generic level classification of pelodryadines, providing an evolutionary classification of pelodryadines that recognizes the biological and ecological diversity of one of the three major anuran families of the Australo-Papuan region. This was principally achieved by eliminating paraphyly of *Litoria* which up until now contained 187 species or 80% of the pelodryadines that encompassed much of the biological and ecological diversity in the family. Our study, with a comprehensive species level survey and a phylogenomic dataset, also confirms the relationships that underlie the sub-family classification of the pelodryadines by Duellman *et al.* (2016).

Given the scale of our generic revision, some biologists, resource managers, and community scientists may find the introduction of a large number of genera in place of just three an unwieldy and a difficult transition. We fully expect that the end-user community will rapidly develop or produce new editions of field guides. We are aware of two that are currently in revision and are awaiting publication of our revision. We also appreciate that a standard dichotomous key likely will not be very easy to produce and that an illustrated Lucid-type identification and diagnostic key is likely to provide a much better practical approach for identification.

For any particular region in Australia or Melanesia a small to moderate number of genera are present. Using the biogeographic sub-regions as delineated by Burbidge *et al.* (2009), only three genera occur in the south-western semi-arid Eyrean sub-region, seven genera in the eastern semi-arid Eyrean sub-region, four genera in the arid Eyrean subregion, 11 genera in the Bassian subregion, 17 genera in the Torresian subregion, and 20 in Melanesia. In terms of endemicity, 13 genera are found only in New Guinea, four genera are found only in southern Australia, and four in the Torresian subregion. A similar apportioning of diversity could be applied to the various biogeographic regions of Melanesia, and furthermore many digital identification applications have a geolocation capacity that can further narrow identification options.

In terms of future species discovery, the description of large numbers of New Guinean taxa that are undocumented presently, particularly in the *Drymomantis* Sub-clade and *Nyctimystes* (Richards unpublished obs.), will make the largest contribution. These studies will render some monotypic genera such as *Megatestis* and *Teretistes* polytypic. The principal issue to resolve at the generic level is the paraphyletic genus *Kallistobatrachus* and the species without available genetic data that are placed currently in genera without strong phenotypic support which all require more nuclear phylogenomic data. The New Guinean endemic *Nyctimystes* aside from the high number of undescribed taxa also lacks a comprehensive molecular genetic survey and comprehensive documentation of mating call, egg, and larval data.

Our revision provides a much more informative perspective on the diversity of a major vertebrate lineage from the Australo-Papuan region that will be extremely useful for ecologists, comparative biologists, and agencies with responsibility for conservation policy development and government and non-government investment.

We have provided a summary list of the new generic allocations based on our reclassification of the Pelodryadidae for convenience of the general scientific and community science audience in Supporting Information, Text S3, New Names WebLinks.

SUPPORTING INFORMATION

Supplementary data is available at *Zoological Journal of the Linnean Society* online.

Figures S1 (and S1-1) to S20 (and S20-1). Diagrammatic representation of typical sequences of reproductive calls plotted at two timescales.

Figures S1 & S1-1. *Amnihyla, Exochohyla, Hyalotos, Ischnohyla.*
Figures S2 & S2-1. *Carichyla*
Figures S3 & S3-1. *Chlorohyla.*
Figures S4 & S4-1. Monotypic genera. *Coggerdonia, Eremnoculus, Melvillihyla, Saganura, Sylvagemma, and Teretistes.*
Figure S5 & S5-1. *Colleeneremia.*
Figures S6 & S6-1. *Cyclorana.*
Figure S7 & S7-1. *Drymomantis.*
Figures S8 & S8-1. *Dryopsophus.*
Figures S9 & S9-1. *Kallistobatrachus, Leptobatrachus, Megatestes, Nasutibatrachus.*
Figures S10 & S10-1. *Litoria.*
Figures S11 & S11-1. *Mahonabatrachus.*
Figures S12 & S12-1. *Mosleyia.*
Figures S13 & S13-1. *Papuahyla.*
Figures S14 & S14-1. *Pelodryas.*
Figures S15 & S15-1. *Pengilleyia.*
Figures S16 & S16-1. *Ranoidea.*
Figures S17 & S17-1. *Rawlinsonia.*
Figures S18 & S18-1. *Rhyaconastes.*
Figures S19 & S19-1. *Sandyrana.*
Figures S20 & S20-1. *Spicicalyx.*
Table S1. PCR primers.
Table S2. Genetic samples used.
Table S3. Character descriptions.
Table S4. Details of images in life.
Table S5. Definitions of call characters.
Table S6. Call character information for each species.
Text S1. Molecular clock.
Text S2. References for Supporting Information
Text S3. New Names, Weblinks
ND4 alignment.
AHE locus alignments.
AHE Loci diagnostic sites.

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CONFLICT OF INTEREST

The authors declare that they have no conflicts of interest in relation to this work.

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DATA AVAILABILITY

Datasets used for morphological (re)analysis, as well as molecular alignments and tree files are available from the Zenodo repository (https://doi.org/10.5281/zenodo.15302843).

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Note that the literature sources for data in the Supporting Information files are in Text S2. References for Supporting Information.

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