



A new species of Australian frog (Myobatrachidae: *Uperoleia*) from the New South Wales mid-north coast sandplains

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Abstract

The discovery of new vertebrate species in developed countries is still occurring at surprising rates for some taxonomic groups, especially the amphibians and reptiles. While this most often occurs in under-explored areas, it occasionally still happens in well-inhabited regions. We report such a case with the discovery and description of *U. mahonyi* sp. nov., a new species of frog from a highly populated region of New South Wales, Australia. We provide details of its morphology, calls, embryos and tadpoles, and phylogenetic relationships to other species of eastern *Uperoleia*. We also provide the results of targeted surveys to establish its distribution and provide observations of its habitat associations. As a consequence of these surveys, we comment on the likely restricted nature of the species' distribution and habitat, and place this in the context of a preliminary assessment of its putative conservation status, which should be assessed for listing under the IUCN's red list. We note this species, which is morphologically distinct, has gone unnoticed for many decades despite numerous ecological surveys for local development applications.

Key words: Amphibia, Anura, cryptic species, toadlet, *Uperoleia mahonyi* sp. nov.

Introduction

A surprising proportion of species may remain undiscovered for extended periods, even when the clade has long been recognised, sometimes for more than a century. Discrete species often remain unrecognised for a common set of reasons. A case in point is the genus *Uperoleia* Gray, 1841; a genus of small, fossorial frogs endemic to Australia and New Guinea (Tyler & Davies 1984). Commonly referred to as 'toadlets', the genus comprises 27 species, making it the largest myobatrachid genus. Much of this taxonomic diversity has been recognised only recently. Only six species of *Uperoleia* were described prior to 1981 (Tyler *et al.* 1981a) with the majority subsequently described in the early to mid-1980s (Tyler *et al.* 1981a, 1981b, 1981c; Davies *et al.* 1985; Davies & Littlejohn 1986; Davies *et al.* 1986). More recently, advanced molecular genetic and morphological work has resulted in the description of a further four species in the past decade and another put in to synonymy (Young *et al.* 2005; Doughty & Roberts 2008; Catullo *et al.* 2011; Catullo & Keogh 2014; Catullo *et al.* 2014a). These molecular studies identified genetic and acoustic divergence in the absence of morphological divergence, supporting the hypothesis that the genus contains a number of morphologically cryptic species.

There are several reasons for so many species within this genus remaining cryptic; not least being that the morphology is highly conserved among these species, making many superficially similar (Tyler *et al.* 1981a; Cogger 2014). They are also highly secretive; individuals remain well camouflaged and hidden, often found only by following the male advertisement call, limiting the ability for morphological comparisons in the field. Calls between closely related species can sound superficially similar to the human ear, often requiring spectral analyses to confirm species identification (Catullo *et al.* 2014b).

The cryptic morphology and secretive nature of the group suggests that new species of *Uperoleia* could

potentially occur in well-inhabited regions, where currently recognised *Uperoleia* species can be common. We here present the surprising case of a new, previously overlooked, species from the densely inhabited eastern seaboard of Australia. The new species occurs in regions subject to frequent surveys for environmental assessments, which failed to recognise this superficially similar, but morphologically and acoustically distinct species.

In March 2007, specimens of an undescribed species of *Uperoleia* were discovered in a coastal sandplain swamp at Oyster Cove, NSW, Australia (-32.7394, 151.9557) by one of the authors (SC). It was immediately apparent that these specimens did not conform to any species of *Uperoleia* described at the time based upon the markings and, in particular, ventral patterns, and subsequent analyses of the morphology and calls of several of the specimens confirmed these to be a previously undescribed species. Genetic tests carried out at the time using ND2 mitochondrial DNA (mtDNA) sequencing provided further confirmation that the specimens belonged to an undescribed species.

Herein, we describe *Uperoleia mahonyi* **sp. nov.** and provide details of its morphology, calls, embryos and tadpoles, and phylogenetic relationships to other species of eastern *Uperoleia*. We also provide the results of targeted surveys to establish its distribution on the NSW mid-north coast and provide observations of its habitat associations. As a consequence of these surveys, we comment on the likely restricted nature of the species' distribution and habitat and place this in the context of a preliminary assessment of its conservation status.

Methods

External morphology. Specimens of *U. mahonyi* **sp. nov.** were collected, along with a number of specimens of other eastern *Uperoleia*, from various localities (Appendix 1). Individuals were examined for external morphology and colouration to record traits that might be useful in distinguishing the various species, and to confirm the level of variation within and between species. In particular, inspections focussed upon the ventral pigmentation, patterning and colouration; dorsal colouration and patterning; the presence and absence of glands (in particular the paratoid, inguinal and coccygeal glands); and the colour and location of groin and femoral colour patches (present in most *Uperoleia*).

The presence or absence of maxillary teeth was determined externally for all *U. mahonyi* **sp. nov.** specimens by the methods of Davies & Littlejohn (1986), and were confirmed by using fine forceps to check for the presence of serrations. The presence or absence of vomerine teeth was also checked.

Morphometrics. Morphological measurements were obtained for 11 male and 3 female specimens. Details and abbreviations for measurements taken are provided in Table 1. Tympanum diameter was not recorded due to the presence of paratoid glands that cover the tympana. Measurements were taken using digital callipers (accurate to 0.1 mm) or using an eyepiece micrometre on a dissecting microscope. Results are expressed in mm as mean \pm standard deviation for the two sexes separately.

Call recording and analysis. Advertisement calls of 9 specimens were recorded in the field on a Marantz PMD660 Professional Solid State Recorder using a RØDE NTG-2 directional condenser microphone at a distance of approximately 30 cm. The air temperature was measured at the recording site. The location of the recordings and numbers of individuals are shown in Table 2.

For each call recorded, five call properties were analysed: pulse rate (s^{-1}); dominant frequency (kHz); pulses per call; calls per minute and call duration (ms) using Raven Pro v.1.3 software. For each calling male, between three and thirteen calls were recorded. These were averaged and used to calculate means with ranges given in parentheses. These call properties were compared to those obtained from other eastern *Uperoleia* that might occur in sympatry or are close relatives with *U. mahonyi* **sp. nov.** as per the phylogeny.

Phylogenetic analysis. We determined the set of closest relatives of the new species by building a mitochondrial phylogeny incorporating the new species, and all other *Uperoleia* species with available mitochondrial data (26 additional species, not shown). Based on that analysis, we completed the below analyses incorporating specimens of *U. mahonyi* **sp. nov.**, and multiple specimens from all described *Uperoleia* species in New South Wales (NSW). Using all NSW species incorporated all the closest relatives of *U. mahonyi* **sp. nov.** into the analysis, as well as *U. rugosa*, a more distant relative also present in NSW (Appendix 1, and see Catullo & Keogh 2014). DNA extraction, amplification, and sequencing followed the protocols as per Catullo and Keogh (2014). In addition to the five nuclear genes (*A2AB*, *BDNF*, *BMP2*, *NTF3*, and *RAG1*) and the *16S rRNA*

mitochondrial gene used in that study, we also sequenced the mitochondrial *ND2* gene using primers and PCR protocols from Catullo *et al.* (2011).

TABLE 1. Description and abbreviation of morphometric measurements taken from (A) adult and (B) tadpoles of *Uperoleia mahonyi* **sp. nov.** Tadpole measurements follow Anstis (2013).

Abbreviation	Description
(A)	
SVL	snout-vent length
TibL	length of tibia
E	eye diameter from anterior to posterior corner of the eye
E-N	eye to naris distance from the anterior corner of the eye to the outer edge of the nostril
IN	inter-narial span, distance from the two inner-edges of the nares
HW	head width measured at the widest point of the jaws
CP	femoral colour patch diameter measured horizontally due to irregularity in shape
CP-K	femoral colour patch to knee distance measured from outer edge of colour patch to knee joint
CP-V	femoral colour patch to vent distance measured from inner edge of colour patch to vent
(B)	
TL	total length from the tip of the snout to the tip of the tail
BL	body length from the tip of the snout to the body-tail junction
BW	maximum body width in dorsal view
BD	maximum body depth in lateral view
EBW	body width measured in dorsal view in line with the middle of the eyes
IO	inter-orbital span, distance between eyes
IN	inter-narial span, distance between inner edges of nares
ED	maximum eye diameter measured in lateral view
EN	eye to naris from posterior edge of naris to anterior corner of eye, measured in dorsal view
SS	snout to spiracle distance, from tip of snout to dorsal corner of spiracular opening
SN	snout to naris distance measured in lateral view from tip of snout to anterior edge of narial opening
SE	snout to eye distance measured in lateral view from tip of snout to anterior edge of eye
TD	Maximum depth of tail measured in lateral view
BTM	Maximum depth of anterior end of tail muscle
ODW	Maximum width of oral disc measured in ventral view

Due to a history of known mitochondrial-nuclear discordance in the genus (see Catullo & Keogh 2014), phylogenies of the mitochondrial and concatenated nuclear datasets were estimated independently. Alignments were created using the MAFFT algorithm (Katoh *et al.* 2002) in GENEIOUS 6.1.8 (Biomatters Ltd.). Bayesian inference was performed using BEAST 2.3.0 (Bouckaert *et al.* 2014). Partitions and models were selected using the programme PARTITIONFINDER 1.1 (Lanfear *et al.*, 2012) (Appendix 1), and were selected using the lowest BIC score and a greedy algorithm. The concatenated mitochondrial and nuclear datasets were run for 10 million and 20 million generations respectively. Each analysis was run three times and the first 10% discarded as burning. Convergence of parameter values within runs was assessed using Tracer 1.6.0 (<http://tree.bio.ed.ac.uk/software/tracer/>), and convergence of independent runs on the same topology was assessed using an R version of AWTY (Nylander *et al.* 2008); <https://github.com/danlwarren/RWTY>). Edges with a posterior probability of 0.90 or more were considered significant.

Phylogenetic relationships were assessed under maximum likelihood using the multiparallel version of IQ-TREE (Minh *et al.* 2013), using 10,000 bootstrap replicates of the ultrafast bootstrap approximation. Analyses were conducted using the models and partitions selected under the TESTLINK function. Edges with bootstrap proportions of 70 or more were considered significant.

TABLE 2. Advertisement call characteristics of *Uperoleia mahomyi* sp. nov. and five other south eastern *Uperoleia* that overlap broadly in range. Values are given as means with ranges in parentheses. * values given are medians rather than means as only the range was provided in the original source.

Species	Location (Date)	N	Temperature (°C)	Pulse rate (s ⁻¹)	Dominant frequency (kHz)	Pulses per call (n)	Call duration (ms)	Calls per minute (n)	Reference
<i>Uperoleia mahomyi</i> sp. nov.	Type locality (4/10/2007)	4	14 (-)	92.7 (77.8–101.5)	2.15 (1.95–2.31)	39.9 (31–46)	432 (336–540)	26.3 (23–33)	This study
	Type locality (12/02/2008)	2	18 (17.5–18.5)	115.8 (107.1–125.5)	2.56 (2.30–2.78)	33.4 (27–37)	288 (250–325)	30.5 (29–32)	
	Tomago swale, NSW (22/10/2009)	1	14.6 (-)	104.2 (94.5–109.8)	2.42 (2.36–2.49)	26.1 (24–28)	250 (240–260)	24 (-)	
	Nelson Bay Golf Course, NSW (5/10/2009)	1	15.5 (-)	79.6 (74.1–86.5)	2.37 (2.35–2.40)	31 (27–34)	390 (310–460)	18 (-)	
	Tomago swamp, NSW (7/10/2009)	1	11 (-)	87.7 (73.8–107.9)	2.36 (2.28–2.42)	33.7 (33–34)	390 (320–460)	15 (-)	
<i>Uperoleia fusca</i>	Eungella, QLD (26/01/1984)	5	22.3* (21.5–23.1)	68.41 (64.86–73.08)	2.7 (-)	19.5* (11–28)	302 (220–360)	-	Davies et al. (1986)
<i>Uperoleia laevigata</i>	Oakdale, NSW (30/09/1975)	5	12 (11.7–12.7)	80.7 (77.0–83.0)	2.24 (2.10–2.37)	52 (48–55)	637 (572–680)	-	Davies & Littlejohn (1986)
	Walwa, VIC (2/09/1964)	5	10 (-)	73.8 (69.4–78.0)	2.24 (1.92–2.40)	39.6 (32–44)	531 (405–608)	-	
	Delegate, NSW (15/11/1965)	8	11.1 (10.6–11.5)	80.8 (69.7–95.0)	2.3 (2.15–2.36)	48.8 (42–56)	603 (499–723)	-	
	Nowa Nowa, VIC (7/12/1963)	5	15.8 (15–16.5)	80.8 (72.2–87.3)	2.01 (1.99–2.05)	49.8 (43–62)	610 (517–713)	-	Davies & Littlejohn (1986)
<i>Uperoleia martini</i>	Narrabarra, NSW (24/09/1985)	2	14.5 (14.2–14.8)	75.1 (72.8–77.4)	2.3 (2.21–2.38)	51 (47–55)	674 (603–746)	-	
	Marlo, VIC (26/09/1985)	3	7.9 (7.2–8.4)	62.1 (58.0–67.7)	2.11 (2.07–2.17)	37 (32–42)	596 (468–716)	-	
	Yarram, VIC (1/12/1980)	5	16.5 (15.5–17.1)	91.5 (87.7–96.0)	2.09 (2.05–2.16)	44.4 (42–46)	483 (463–523)	-	
	Colosseum, QLD (12/12/1984)	3	22.5 (22.2–22.8)	34.4 (33.33–36.55)	2.58 (2.50–2.75)	4 (4–4)	117 (110–120)	-	Davies & McDonald (1985)
	Savernake, NSW (27/07/1969)	5	13.3 (12.6–14.3)	31.1 (22.8–40.8)	2.05 (1.94–2.20)	3.4 (3–4)	94 (81–103)	-	Davies & Littlejohn (1986)
<i>Uperoleia tyleri</i>	Narrabarra, NSW (24/09/1985)	4	14.4 (13.7–14.8)	92.2 (82.1–95.9)	2.1 (2.01–2.24)	21.8 (19–25)	230 (212–253)	-	Davies & Littlejohn (1986)
	Marlo, VIC (27/09/1981)	3	17 (16.4–7.6)	108.5 (105.6–112.1)	2.25 (2.14–2.36)	24.3 (22–26)	225 (202–241)	-	
	Jervis Bay, ACT (17/01/1963)	2	15.5 (-)	84.5 (83.1–85.9)	2.06 (2.03–2.09)	22 (18–26)	259 (208–311)	-	

Embryos and tadpoles. Embryos and tadpoles were staged using Gosner (1960). A pair of *U. mahonyi* sp. nov. in amplexus was collected at the type locality on 4 March, 2013 and transported to the University of Newcastle, where they laid fertile eggs in an artificial enclosure. Embryos were allowed to develop in pond water collected from the type locality and a sample was preserved in 10% buffered formalin at stages 7–8 and at hatching (stages 20–22).

Tadpoles at stages 38–41 were collected on 26 March, 2009 and tadpoles at stages 25–29 plus a single embryo which later hatched, were collected on 31 October, 2010 at the type locality. Some were raised to metamorphosis in 40 cm plastic containers (opaque sides) holding water to a depth of 15 cm over a substrate of sand, leaf litter from the collection site, and rocks. They were fed pieces of crushed *Spirulina* algae discs. Water temperature was not controlled. Metamorphosis was complete from 28 December, 2010. Samples were photographed then preserved at various stages (Table 3). Morphometric measurements of anaesthetised and preserved specimens were obtained with the aid of Vernier callipers and a micrometer eye-piece attached to a stereoscopic microscope. Voucher specimens were preserved in 4% buffered formalin (Tyler 1962) and some in 70% ethanol. The drawing of the oral disc was prepared with the aid of a drawing tube attached to the microscope. Tadpoles were staged according to Gosner (1960). Methods of measurement and abbreviations of morphometric measurements of tadpoles are shown in (Table 1) and follow Anstis (2013). Measurements are of random samples at different stages, and not the same individuals measured through growth stages.

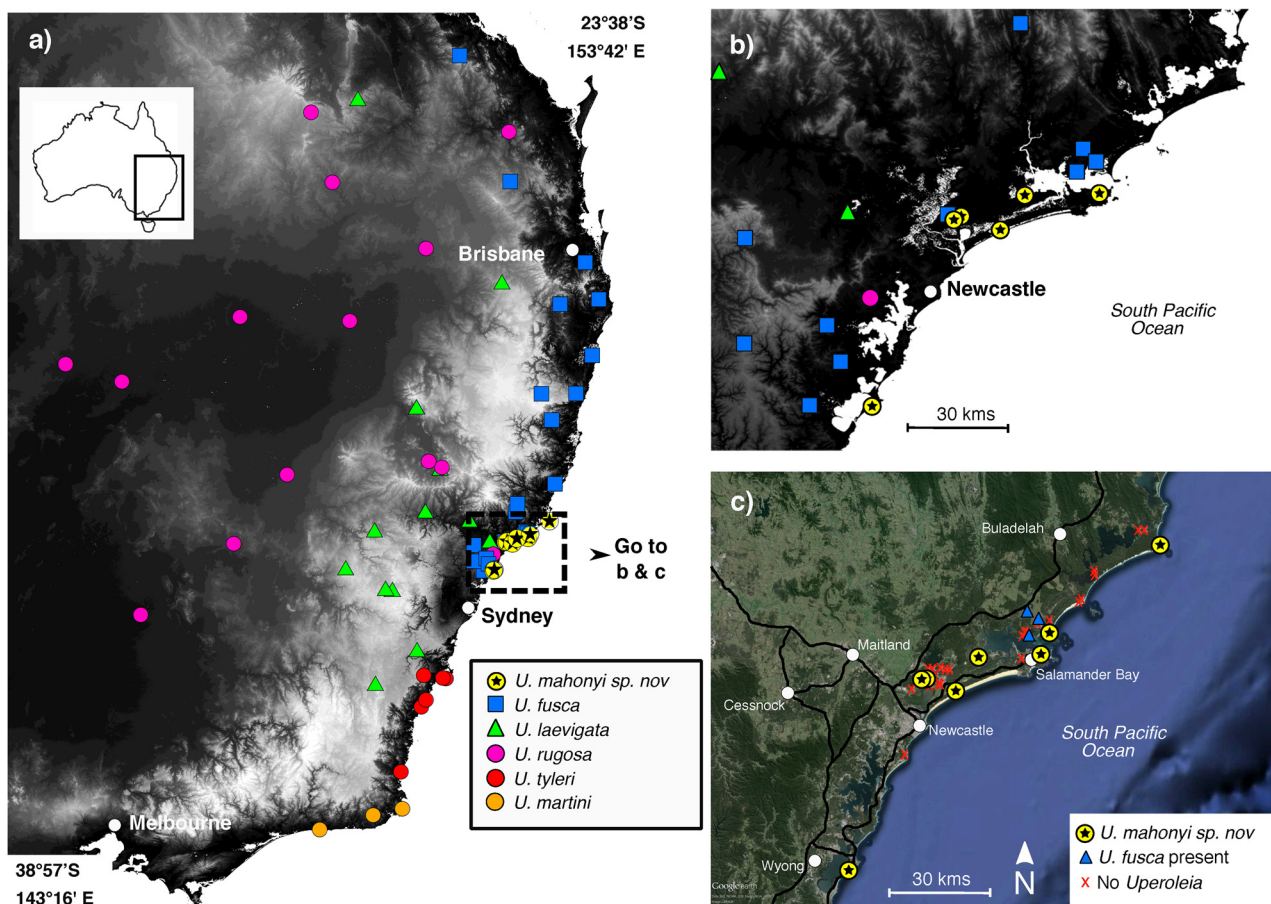


FIGURE 1. Distribution of eastern *Uperoleia* sampled for this study. (A) distribution of eastern *Uperoleia* species across southern Queensland, New South Wales and Victoria as determined through phylogenetic evidence; (B) zoomed in image of the distribution of *Uperoleia mahonyi* sp. nov. phylogenetic samples, including records of other sympatric *Uperoleia* spp.; (C) the results of the targeted surveys, including sites surveyed where no *Uperoleia* were detected. Black lines in (C) represent major roads.

Distribution and habitat. Potentially suitable sites for the species were identified using topographic maps and satellite images of an area of the mid-north coast of NSW, approximately 70km to the north and south of the type locality (Fig. 1). The survey area encompassed the coastal sandbed systems of the Central Coast to the south (lying to the north of the Sydney Basin, approximately -33.3670, 151.4434) to the top of the Myall Lakes sandbed system

to the north (around Seal Rocks, approximately -32.4164, 152.5418). A variety of water body types known to form potential habitat for other species of *Uperoleia* were selected as survey sites and included swamps; ditches, dams and swales (both naturally occurring and man-made); and areas subjected to inundation. Water bodies selected also ranged from permanent to ephemeral. A total of 45 survey sites were chosen haphazardly from all those identified from maps and images (Fig. 1C). In addition to the formal surveys, communications were made with other known amphibian biologists and enthusiasts that had previously worked in, or had surveyed in the area. In these cases, photographs of any *Uperoleia* that they had identified were requested and used to identify the species present, along with details of habitat and location.

All sites were inspected in the day to record basic notes on the type of waterbody present, and to assess their suitability for survey. Any species of frog observed during diurnal inspections were recorded. Sites were then surveyed at night to locate frog species by aural detection and habitat searches. In most cases where a *U. mahonyi* sp. nov. was found, a call recording was taken to build a library of calls across its range. All other species of frogs observed at each site were also recorded.

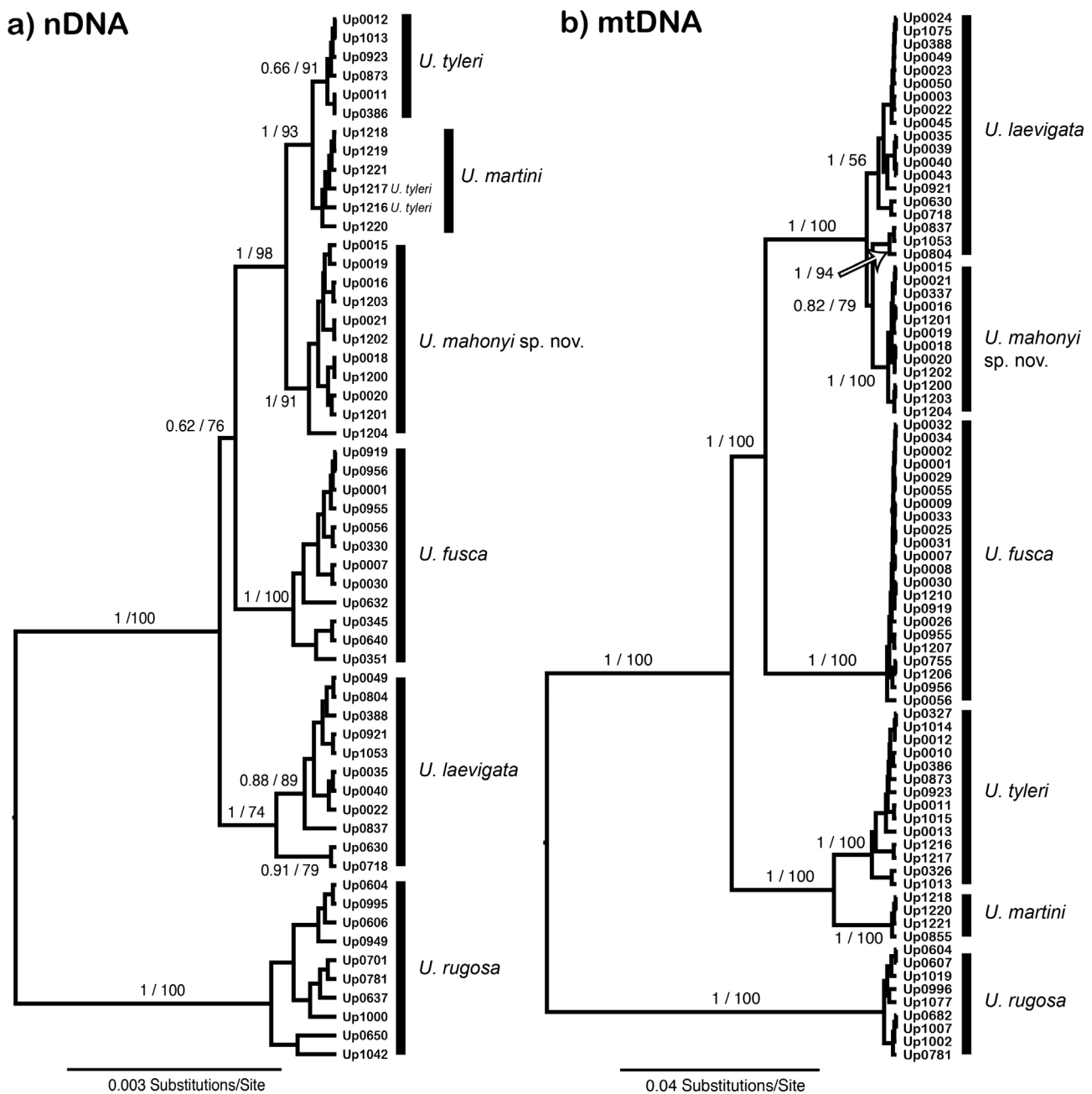


FIGURE 2. Differing nuclear (A) and mitochondrial (B) phylogenies of eastern *Uperoleia* including *Uperoleia mahonyi* sp. nov. See text for details.

Results

Phylogenetic analysis. The nuclear alignment comprised 2,961 base pairs, and no individual was missing more than a single locus in the nuclear alignment. The mitochondrial alignment comprised 1,946 base pairs, and was 98.75% complete for mtDNA gene 16S, and 97.5% complete for ND2 (Appendix 2: Genbank Accession Numbers).

The concatenated Beast analysis of the nuclear DNA (Fig. 2A) recovered five well-supported clades. Clade 1 consisted of individuals from *U. tyleri* and *U. martini*. Although the close relationship of these two species was strongly supported (Bayesian Posterior Probability (BPP) = 1), our nuclear dataset was unable to distinguish between them. Clade 2, sister to clade 1 (BPP = 1), comprises all individuals from *U. mahonyi* **sp. nov.** (BPP = 1). Clades 3 (representing *U. fusca*) and 4 (representing *U. laevigata*) each form well supported monophyletic clades (BPP = 1), however, the placement of *U. fusca* and *U. laevigata* in relation to the *U. tyleri/U. martini/U. mahonyi* **sp. nov.** clade is not well supported. *Uperoleia rugosa*, a NSW species that forms part of another major radiation of *Uperoleia* (Catullo & Keogh 2014), forms a well-supported outgroup to all other NSW species (BPP = 1).

The concatenated Beast analysis of the mitochondrial DNA (Fig. 2B) found a substantially different topology from the nuclear DNA, but also recovered strong support (BPP = 1) for the *U. tyleri*, *U. martini*, *U. fusca*, and *U. rugosa* species. The clade consisting of all *U. mahonyi* **sp. nov.** individuals formed a well-supported monophyletic group (BPP = 1), however, this clade is placed within the broader *U. laevigata* clade (BPP = 1). The maximum likelihood analyses recovered the same topologies, with generally strong support.

Systematics

The new species is clearly assignable to *Uperoleia* based on genetic data and external characters, including small body size, squat body, rough skin, short limbs, the distinct femoral colour patch, well developed glands that cover the tympana, unwebbed hands, lack of vomerine teeth, horizontal pupil and call.

Genus *Uperoleia* Gray, 1841

Uperoleia Gray, 1841, Ann. Mag. Nat. Hist., Ser. 1, 7: 90.

Hyperoleia Agassiz, 1846, Nomencl. Zool., Fasc. 12: 384. Unjustified emendation.

Glauertia Loveridge, 1933, Occas. Pap. Boston Soc. Nat. Hist., 8: 89. Type species: *Glauertia russelli* Loveridge, 1933, by monotypy. Synonymy by Tyler *et al.* 1981, Aust. J. Zool., Suppl. Ser., 29 (79): 9.

Hosmeria Wells & Wellington, 1985, Aust. J. Herpetol., Suppl. Ser., 1: 2. Type species: *Uperoleia marmorata laevigata* Keferstein, 1867, by original designation. Synonymy by Catullo *et al.* 2011, Zootaxa, 2902; 1–43.

Prohartia Wells & Wellington, 1985, Aust. J. Herpetol., Suppl. Ser., 1: 3. Type species: *Pseudophryne fimbrianus* Parker, 1926, by original designation. Synonymy by Catullo *et al.* 2011, Zootaxa, 2902; 1–43.

Type species. *U. marmorata* Gray, 1841, by monotypy.

Uperoleia mahonyi **sp. nov.**

Mahony's Toadlet

Figs. 3 & 4

Holotype. SAMA R66193 (male), collected in an ephemeral swale on sand at Oyster Cove, NSW (-32.7394, 151.9557) by S. Clulow on 12 February, 2008.

Paratypes. SAMA R66187, SAMA R66188, SAMA R66189, SAMA R66190, SAMA R66191, AMS R185691 and AMS R185692 (adult males), collected at type locality, NSW (-32.7394, 151.9557) on 4 October 2007; SAMA R66192 (adult female), collected at type locality, NSW on 31 March 2007; SAMA R66194 (adult male), collected at the same locality and date as the holotype; AMS R185695 (adult male), collected at type locality, NSW on 12 October 2009; AMS R185701 (adult female), collected at type locality, NSW on 1 March 2013; SAMA R66186 and SAMA R66195 (sex not determined), collected at type locality, date not recorded; AMS R185693 (adult male), collected in an artificial dam on sand at Nelson Bay Golf Course, NSW (-32.7294,

152.1511) on 5 October 2009; AMS R185697 and AMS R185698 (adult males), collected in a sand dune swale behind Stockton Beach, NSW (-32.8293, 151.8825) on 1 November 2009; AMS R185696 (adult male), collected in an ephemeral swale on the Tomago sandbed, NSW (-32.7939, 151.7880) on 22 October 2009; AMS R185694 (adult male), collected in a Melaleuca swamp off Masonite Road, Tomago, NSW (-32.8026, 151.7646); AMS R185699 and AMS R185700 (adult females), collected in pit traps on a sand dune at Wyrabalong National Park ~400 m from a coastal hind dune swamp (-33.2970, 151.5503) on 28 May 2012.

Diagnosis. Distinguished as a *Uperoleia* by a combination of small body size (males 20–30 mm), large parotoid glands covering tympanum, unwebbed fingers, vomerine teeth vestigial or absent, inguinal colouration present, and presence of inner and outer metatarsal tubercles. Distinguished from all other *Uperoleia* by a combination of ventral pigment (ventral surface completely covered with black and white marbling), presence of maxillary teeth, toes unwebbed, lack of colour patch below the knee, and a “squelch” as a call.

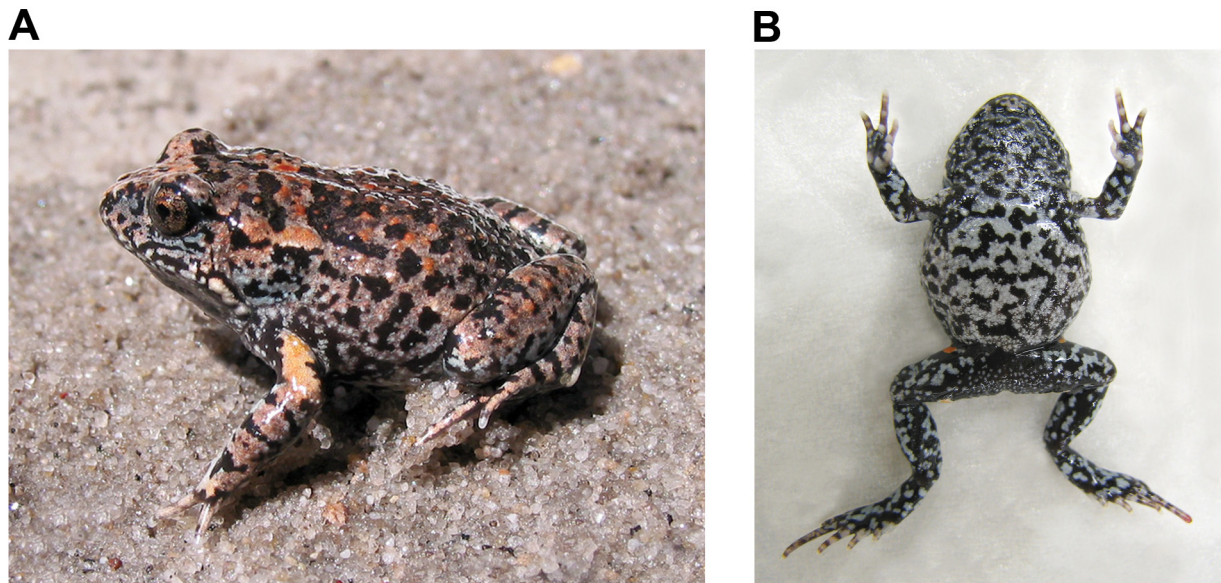


FIGURE 3. Dorsolateral (A) and ventral (B) photographs of holotype of *Uperoleia mahonyi* sp. nov. (SAMA R66193) in life. Photographs S. Clulow.

Holotype measurements. Measurements (in mm): SVL—22.2; TibL—9.3; HW—9.0, E—2.6; E-N—1.9; IN—1.7; T—3.3; CP—1.9; CP-K—1.4; CP-V—3.4.

Measurements of series. Mean ± standard deviation in mm. Adult males (n = 11): SVL—25.2±3.1; TibL—10.0±0.4; HW—9.9±1.1, E—3.1±0.6; E-N—2.1±0.3; IN—1.7±0.2; CP—3.2±0.9; CP-K—1.5±0.3; CP-V—3.7±0.4. Adult females (n = 3): SVL—29.3±2.5; TibL—11.1±1.2; HW—10.7±1.5, E—3.1±0.4; E-N—2.3±1.8; IN—1.8±0.2; CP—3.9 (n = 1); CP-K—1.0 (n = 1); CP-V—5.1 (n = 1).

Description of species. Body is robust and moderately large for a *Uperoleia*, with males up to 30mm SVL and females up to 32 mm SVL. Head is short, snout rounded from above and in profile. Canthus rostralis well defined and slightly protruding; loreal region slopes steeply to jaw and is very slightly concave. There is a moderately sharp medial projection (synthesis of mentomeckelian bones) of the lower jaw that matches notch on upper jaw. Nostrils directed upward and outward; nares with slight rim. Tongue oval and elongate. Maxillary teeth present; vomerine teeth absent. E-N larger than IN (E-N/IN = 1.2 for males and 1.3 for females). Tympana hidden; covered by skin and parotoid glands. Eyes with horizontal iris. Vocal sac unilobular.

Arms and hands slightly built. Fingers long, slender, slightly fringed and unwebbed. Finger length $3 > 2 \geq 4 > 1$. Tubercles under fingers well developed; one on first and second, two on third and fourth. Well-developed, prominent outer palmar tubercle on distal portion of wrist; well-developed inner palmer tubercle on medial portion of wrist.

Legs relatively short (TL/SVL = 0.4 for both males and females) and moderately built. Toes slender, unwebbed and fringed. Toe length $4 > 3 > 5 > 2 > 1$. Tubercles under toes well developed and slightly conical in shape; one on first and second, two on third and fifth, and three on fourth toe. Inner metatarsal tubercle long and conical, aligned along the first toe. Outer metatarsal tubercle spade-shaped and prominent, oriented in the direction of the fifth toe.

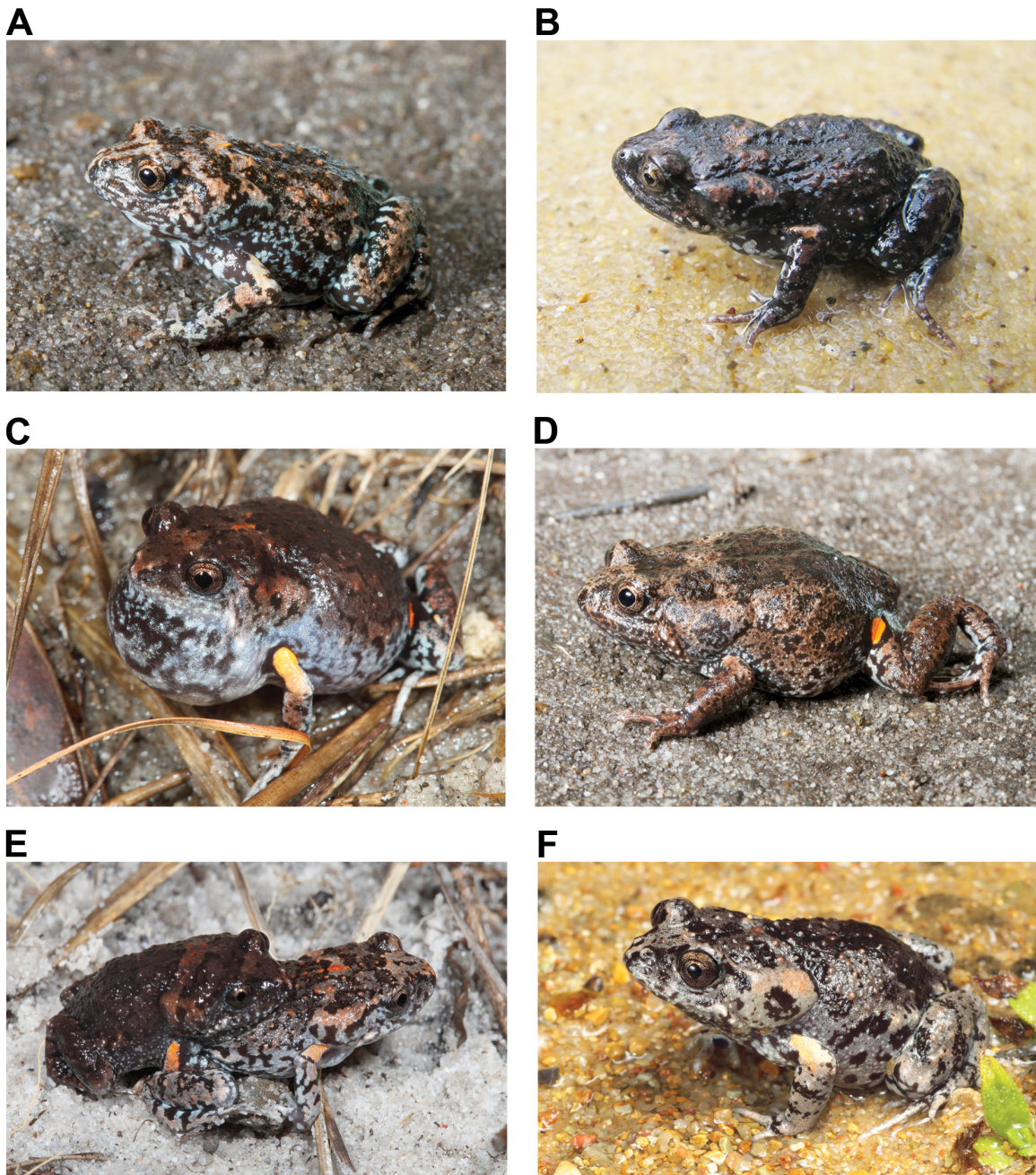


FIGURE 4. *Uperoleia mahonyi* sp. nov. demonstrating the range of variation in dorsal colour and patterning observed in life. (A) female AMS R185700, Wyrrabalong National Park NSW, and (B) same specimen in dark phase (photographs S. Clulow); (C) calling male with vocal sac extended, specimen not collected, type locality (photograph S. Mahony); (D) female AMS R185700 showing groin colour patch, Wyrrabalong National Park NSW (photograph S. Clulow); (E) male and female in amplexus, specimens not collected, type locality (photograph S. Mahony); (F) male, specimen not collected, Norah Head NSW (photograph J. Mulder).

Dorsum smooth to moderately rugose, with scattered fine tubercles on back, head and limbs. Ventral surface weakly granular. Cloacal flap present and fimbriated. Parotoid glands large and prominent, appearing hypertrophied and usually wider than high. Inguinal glands occasionally discernible but not well-developed and rarely obvious. Coccygeal glands indistinct. Mandibular gland moderately developed but small in most, present at corner of the jaw.

Colouration. In life, dorsum patterned with irregular patches of pale, tan, chocolate or dark brown (verging on black) and occasionally greys throughout. In some darker specimens the colour can appear almost uniform. The dorsal colouration usually merges into patterns of bluish grey and dark brown onto the lower flanks. Dorsal

tubercles often (but not always) tipped with a pale yellow-orange to rust-orange, which can also occur on the parotoid glands. Many individuals have a lighter brown triangular patch on head from between the eyes to tip of snout, although this can also contain small patterns or flecks of darker brown. Ventral surface entirely pigmented, black with suffusions of irregular patches of small off-white/bluish-white dots. The patches of white dots appear as solid patches to the naked eye, especially on the legs. The patterns of black and white patches appear marbled, more similar to the bellies of *Pseudophryne* spp. rather than simply stippled as commonly observed in *Uperoleia* spp. (see Figs 3 & 5). Inguinal and femoral colour patches orange in all specimens observed. Femoral colour patch irregular in shape and large and always closer to knee than vent. Throats of calling males may have dark anterior margin, sometimes covering most of the chin.

TABLE 3. Morphometric measurements of preserved larval *Uperoleia mahonyi* sp. nov. from the type locality. Values in mm, mean \pm STD with range shown beneath. Developmental stages follow Gosner (1960). Abbreviations for measurements are explained in Table 1.

N	2	4	1	2	1	1	1	3	1
STAGE	25	26	27	29	30	33	34	35	37
TL	14, 14.5	21.4 \pm 2.1; 19.5–24.0	24.5	24.0, 24.0	24.0	26.0	26.6	26.6 \pm 1.7; 25.3–28.5	29.2
BL	6.0, 6.1	9.5 \pm 1.2; 8.1– 10.9	11.3	10.6, 10.8	10.3	11.8	11.6	11.7 \pm 0.1; 11.6–11.8	13.1
BW	4.0, 4.2	6.5 \pm 0.9; 5.3– 7.4	7.9	7.4, 7.9	7.0	8.2	7.9	7.9 \pm 0.3; 7.6–8.1	8.7
BD	3.1, 3.5	5.9 \pm 1.2; 4.8– 7.4	6.9	6.1, 6.6	5.8	7.1	6.1	6.7 \pm 0.1; 6.6–6.8	7.6
EBW	3.2, 3.2	4.9 \pm 0.6 4.0–5.3	6.0	4.0, 5.3	5.3	6.1	5.8	5.7 \pm 0.3; 5.5–6.0	6.0
IO	1.0, 1.1	1.6 \pm 0.2; 1.3– 1.8	1.7	1.9, 2.1	1.9	2.3	1.9	2.2 \pm 0.4; 1.9–2.6	2.3
IN	0.5, 0.6	0.7 \pm 0.1; 0.8– 0.8	0.8	0.8, 1.0	0.8	1.0	1.0	0.9 \pm 0.1; 0.8–1.0	0.8
N	0.2, 0.2	0.4 \pm 0.1 0.2– 0.5	0.4	0.4, 0.5	0.4	0.5	0.4	0.5 \pm 0.1; 0.4–0.6	0.4
EN	0.5, 0.5	0.7 \pm 0.1; 0.6– 0.8	0.8	0.8, 0.8	0.8	0.8	0.8	0.8 \pm 0; 0.8–0.8	0.8
SS	4.7, 4.8	7.4 \pm 0.1; 6.1– 8.4	8.5	8.2, 8.9	7.9	9.2	9.0	9.0 \pm 0.5; 8.5–9.4	9.5
SN	0.6, 0.6	0.9 \pm 0.2; 0.8– 1.1	0.8	0.8, 1.0	0.8	1.0	1.1	1.0 \pm 0.2; 0.8–1.1	1.0
SE	1.1, 1.1	1.9 \pm 0.3; 1.5– 2.1	1.7	2.1, 2.3	2.1	2.1	2.3	2.2 \pm 0.2; 2.1–2.4	2.3
ED	0.6, 0.6	1.0 \pm 0.1; 0.8– 1.1	1.1	1.1, 1.1	1.0	1.3	1.3	1.3 \pm 0.1; 1.2–1.3	1.5
BTM	1.1, 1.1	1.7 \pm 0.2; 1.5– 1.9	2.3	1.8, 2.1	1.8	2.4	2.3	2.2 \pm 0.3; 1.9–2.4	2.3
TD	3.2, 3.4	4.6 \pm 0.4; 4.2– 5.0	5.6	5.2, 5.4	5.7	6.0	6.1	6.0 \pm 0.7; 5.3–6.6	5.8
DF	1.3, 1.5	2.0 \pm 0.3; 1.6– 2.2	2.6	2.3, 2.3	2.4	2.3	2.6	2.5 \pm 0.1; 2.4–2.6	2.4
TM	0.8, 1.0	1.2 \pm 0.1; 1.1– 1.3	1.6	1.3, 1.5	1.6	1.8	1.9	1.7 \pm 0.3; 1.5–2.1	1.6
VF	1.0, 1.1	1.4 \pm 0.1; 1.3– 1.5	1.5	1.6, 1.6	1.7	1.9	1.6	1.7 \pm 0.2; 1.5–1.9	1.8
ODW	1.2, 1.2	1.7 \pm 0.2; 1.4– 1.9	1.0	1.9, 2.0	1.8	2.0	2.1	1.9 \pm 0.3; 1.7–2.3	2.0

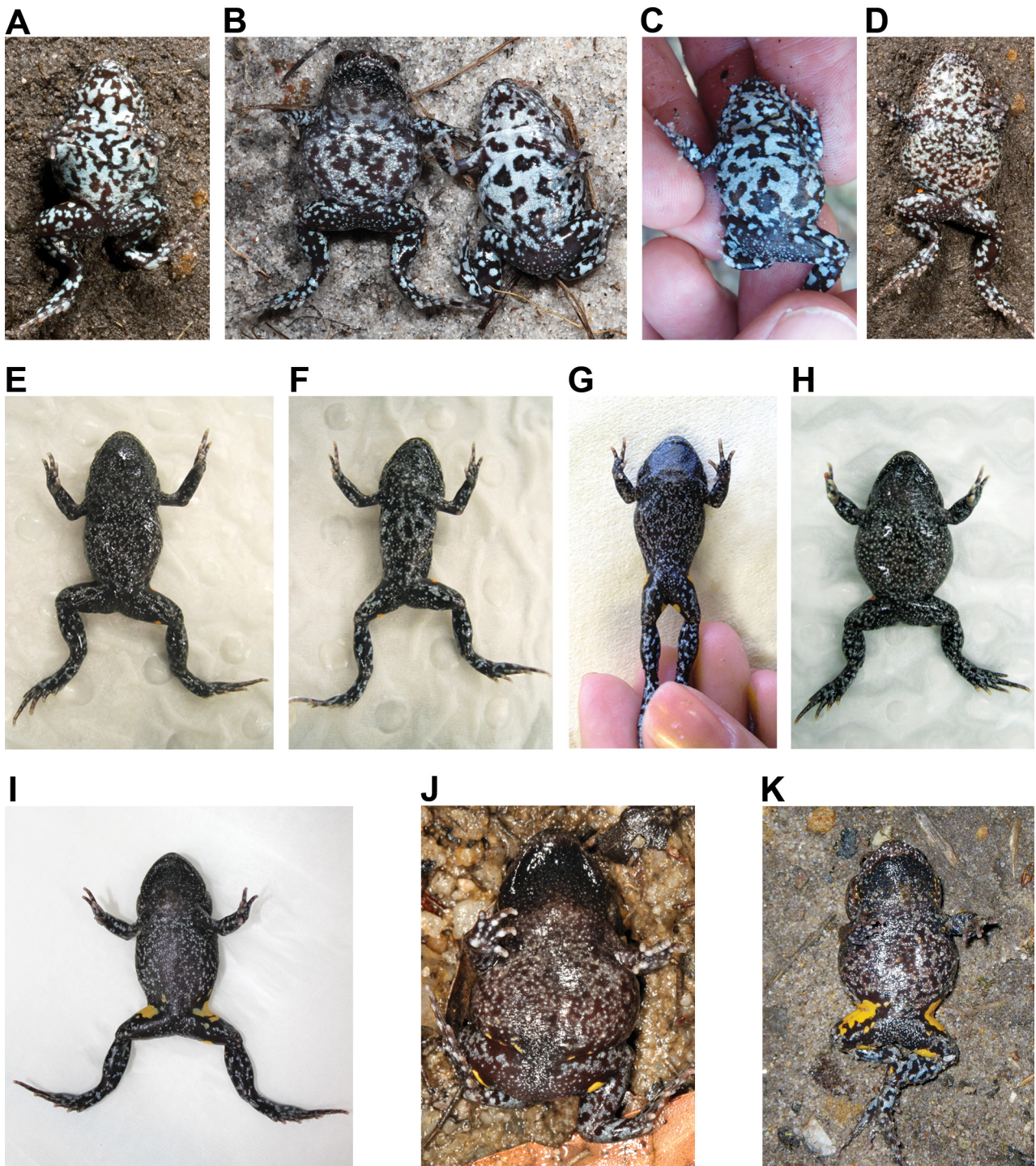


FIGURE 5. Photographs of the ventral surfaces of *Uperoleia mahonyi* sp. nov. (A–D), *U. tyleri* (E–H) and *U. martini* (I–K) showing the variation in colour and pattern. *Uperoleia mahonyi* sp. nov. (A) female AMS R185699, Wyrabalong National Park (photograph S. Clulow); (B) male (left) and female (right) (previously in amplexus), specimens not collected, type locality (photograph S. Mahony); (C) sex unknown, Wyrabalong National Park (photograph D. Beckers); (D) female AMS R185700, Wyrabalong National Park (photograph S. Clulow); *Uperoleia tyleri* (E) male SAMA R66200, Jervis Bay NSW (photograph S. Clulow); (F) sex unknown SAMA R66203, Jervis Bay NSW (photograph S. Clulow); (G) male RAC002, Kioloa NSW (photograph R. Catullo); (H) male SAMA R66205, Jervis Bay NSW (photograph S. Clulow); *Uperoleia martini* (I) male RAC0083, Nadgee Swamp Nature Reserve NSW, (photograph R. Catullo); (J) male not collected, Far East Gippsland Victoria (photograph M. Clancy); (K) male not collected, Marlo Victoria (photograph G. Webster).

Advertisement call. The advertisement call is a single audible ‘squelch’ sound of about one third of a second duration, repeated on average 25 times per minute (range observed is between 15 and 33 calls per minute from 9 individuals). This ‘squelch’ comprises 24 to 37 pulses, pulsed at 96 pulses per second on average. The mean dominant frequency is 2.37 kHz. Mean values of call characteristics from six individuals from the type locality (over two separate occasions) and one individual from each of three other localities are given in Table 2, along with the call properties of other eastern *Uperoleia* that are known or potentially occur in sympatry. A representative oscillogram and spectrogram of a single call of *Uperoleia mahonyi* **sp. nov.** is presented in Fig. 6.

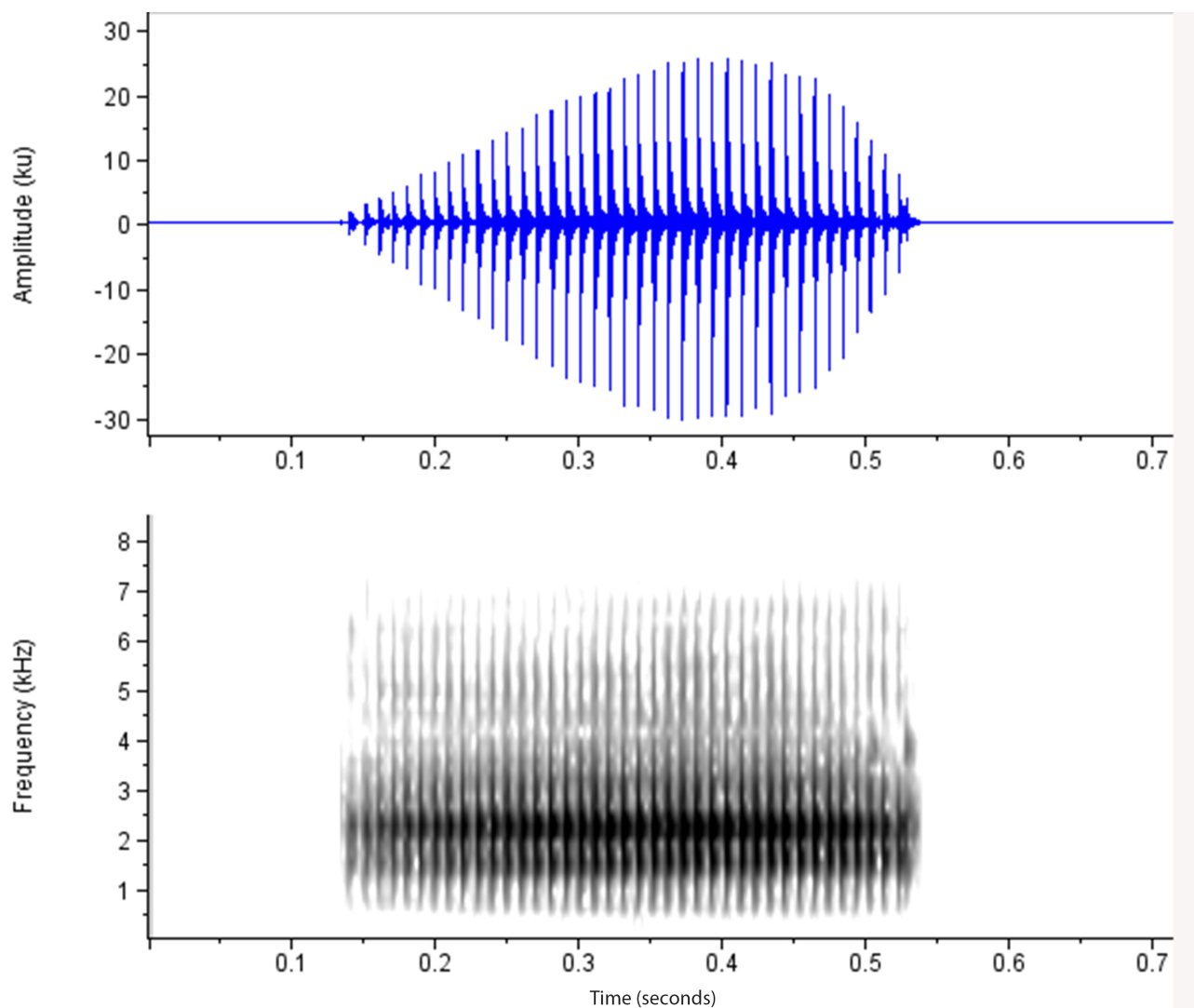


FIGURE 6. A representative oscillogram (above) and spectrogram (below) of the advertisement call of *Uperoleia mahonyi* **sp. nov.**, Oyster Cove, NSW. The x-axis is time in seconds.

Embryos and tadpoles. *Embryos.* Breeding is known to occur in autumn (March) and spring (October–November). The total number of eggs laid by one female is unknown. The eggs are laid singly and although only observed in the laboratory and not in the field, under natural conditions they are likely to be attached to thin strands of submerged vegetation and substrate such as leaf litter similar to all other members of this genus (Anstis, 2013). Eggs laid in the laboratory in autumn and preserved at stages 7–8 were slightly misshapen when examined in 2015, and the jelly had lost some rigidity, but the capsule is small with a single jelly layer and thin, adhesive outer coating, mean diameter 2.8 ± 0.18 (n=8). The top one-third of the animal pole is brown, vegetal pole white. Mean diameter 1.7 ± 0.06 (n=9).

Hatchlings. Hatching occurred 5–6 days after the eggs were laid. One preserved recent hatchling is at stage 20, with brown pigment over head, vertebral region and tail muscle and a white yolk sac, fins not arched. Preserved embryos at stage 22, seven days after eggs were laid, have clear, slightly arched fins, expanded operculum,

increased dorsal pigment and discernible, partly pigmented eyes. Mean TL of five hatchlings at stages 20–22 was 7.0 ± 0.48 , BL 2.8 ± 0.08 . One live embryo at about stage 24 examined about three days after hatching, measured TL 7.1, BL 4.5, Fig. 7C). The body wall is entirely transparent with an expanded operculum. In lateral view, dorsal one-third of body and tail muscle very dark, yolk white below this and remainder of tail muscle unpigmented. Dorsum and dorsal tail muscle very dark, dissected by a distinct transparent pale brown broad band down centre of body tapering onto tail muscle.

Tadpoles. Tadpoles were found in a large swale at the type locality where they were observed on a sandy substrate among leaf litter, often in the shallow verges of the water. Material from the type locality is listed in Appendix 1 and morphometric measurements in Table 3. Maximum length 35.0 mm, BL 12.4 mm (stage 41, Fig. 7B). Almost fully grown by stage 28. Figure 7 shows an embryo, tadpoles in life and the oral disc.

Body: Small, plump and oval to rounded, abdomen wider than deep. Snout narrowly rounded in dorsal view, rounded in profile. Eyes dorsolateral with anterodorsal tilt. Nares narrowly spaced, moderately large and cavernous with a narial flap; open dorsally, maximum diameter 0.5mm. Spiracle long, opens lateroposterally just above body axis about two-thirds along body (Fig. 7A). Vent tube dextral, very short, opens midway up from edge of ventral fin.

Dorsum of tadpoles at stage 26–30 golden brown to dark brown over almost black layer beneath which shows through in small patches. Lighter brown vertebral stripe bordered on both sides by very dark brown with transparent stripe on either side of this over head, and from between nares to tip of snout. Light brown stripe extends behind each eye. As tadpoles grow, the body is usually dense, dark mottled brown, with the lighter stripes mostly obscured. Iris golden mainly above and below pupil, with gold ring around pupil. Sides of body mostly transparent with numerous gold clusters. Venter transparent with numerous copper-gold clusters, increasing in density in later stages.

Tail: Dorsal fin begins from just onto base of body, arches slightly or moderately over midpoint of tail and tapers to a rounded tip. Ventral fin similarly shaped, but slightly less arched. Muscle moderate, tapers to a narrow point.

A specimen at stage 41 photographed soon after capture has large dark blotches scattered mainly along edges of both fins to tip, and finer melanophores between (especially on dorsal fin), increasing towards tail tip. The tail muscle has a mostly continuous, dark stripe along dorsal and ventral edges (non-pigmented stripe between), with scattered dark blotches. Specimens raised in captivity were similar, but the tail blotches were not as prominent.

Oral disc (Fig. 7G): Type 14, ventral (Anstis, 2013). No papillae around anterior margin. Very narrow posterior medial gap in single row of marginal papillae. Two upper and three lower tooth rows; A^2 has a distinct medial gap and P^1 has either a very narrow gap or is entire. P^3 is the shortest row (about one third length of P^2) and sits on edge of flexible ridge. Jaw sheaths slender; upper broadly arched with long sides. $LTRF = 2(2)/3(1)$.

Metamorphosis. Tadpoles collected at stage 41 in autumn metamorphosed six days later. Tadpoles collected at stages 26 and 27 in October and raised in captivity metamorphosed 58 days later in December. Larval life span in spring/summer is therefore likely to be about 3–4 months. One specimen a week after metamorphosis (Fig. 7E, F) has a dark brown dorsum with darker spots, a light brown crown on the head and light brown on some tubercles on upper back and on very small parotoid glands. A dark inverted triangular patch mirrors pale crown on head posterior to eyes. Upper arms lighter brown. Sides of body dark grey. Ventral surface of body and limbs whitish-grey with numerous black spots. Ventral surface of a specimen just metamorphosed at stage 46 is dark grey with a dense layer of very fine white spots which are more distinct and spread out on the darker chin and limbs. SVL, 10.1 mm (stage 45), and SVL of another two at stage 46, 10.2 and 13 mm.

Habitat. Current observations indicate the species is a habitat specialist, inhabiting coastal ephemeral and semi-permanent swamps and swales, and occasionally man made dams, in heath or wallum habitats almost exclusively on a substrate of white/leached sand. Commonly associated with acid paperbark swamps. Females have been caught in pit or funnel traps up to 400m away from these water bodies at several localities.

Water bodies containing calling males ranged from ca. 70m x 20m up to 300m x 500m in size, and from ca. 10–50 cm in depth. Water salinity recorded at two sites ranged up to 0.1 parts per thousand at two water bodies and dissolved oxygen between 4.53 and 6.24 mg/L.

Vegetation communities in which the frog has been found include wallum heath, swamp mahogany-paperbark swamp forest, heath shrubland and Sydney red gum woodland. Terrestrial vegetation associations include the tree species *Melaleuca quinquenervia*, *Eucalyptus robusta*, *Angophora costata*, *Acacia longifolia* and *Banksia* spp.

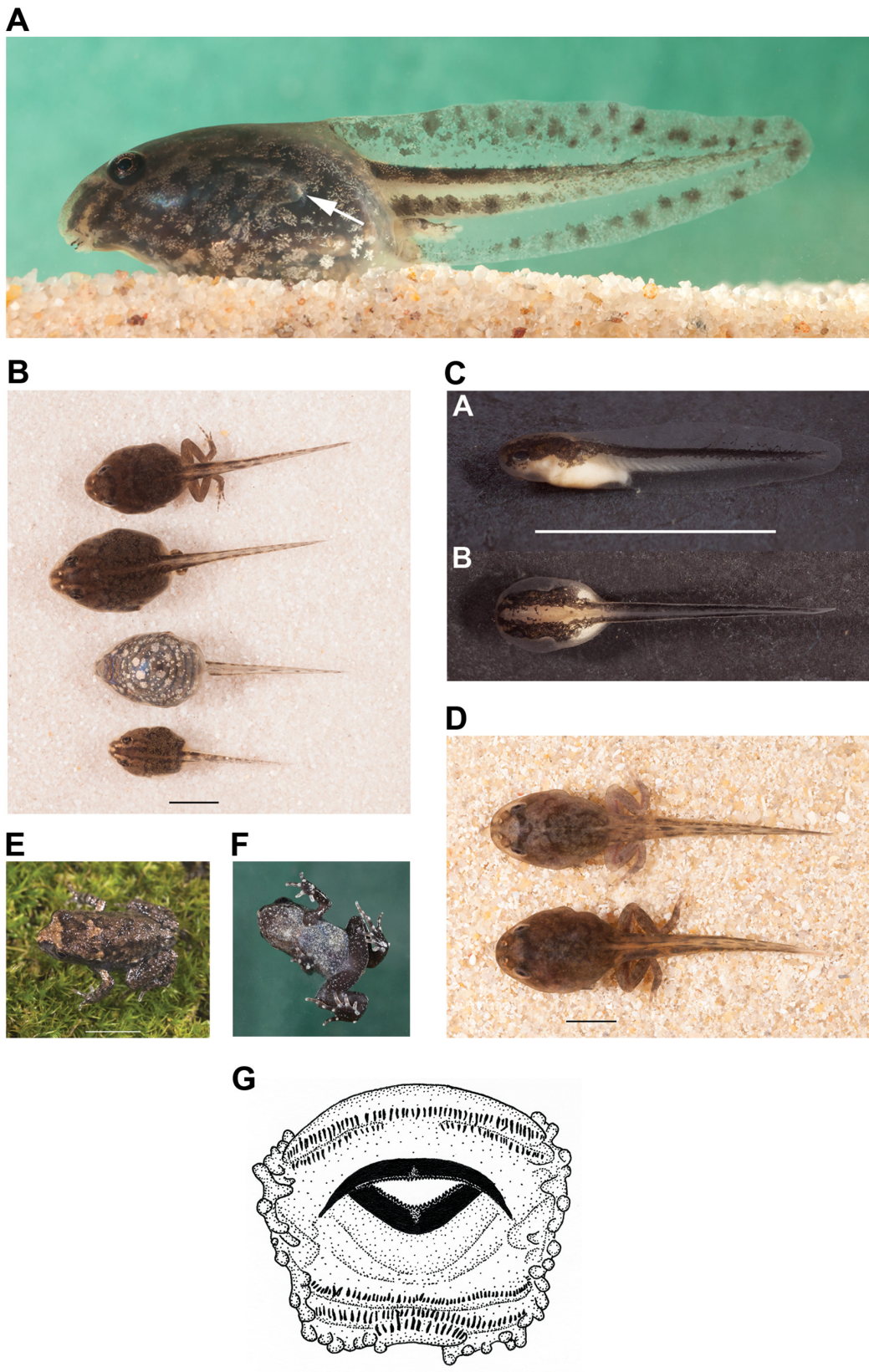


FIGURE 7. Development of tadpoles of *Uperoleia mahonyi* sp. nov. (A) fully grown tadpole stage 36 (lateral view), arrow indicates opening of spiracle; (B) (top to bottom) stages 41, 38 (dorsal view), stage 27 (ventral view) and stage 26 (dorsal view), bar represents 5 mm; (C) hatched embryo at stage 24, lateral (A) and dorsal (B) views, bar represents 5 mm; (D) tadpoles at stage 41 (dorsal view) after capture at type locality; (E, F) newly metamorphosed froglet at stage 46, dorsal and ventral views (ventral pattern not yet fully developed); (G) = oral disc of stage 28 tadpole, bar represents 1 mm.

(including *B. serrata* and *B. aemula*). Shrub and herb species include Geebung (*Persoonia lanceolata*), drumsticks (*Isopogon anemonifolius*), heathy parrot pea (*Dillwynia retorta*), bracken (*Pteridium esculentum*), mat rush (*Lomandra longifolia*), heathy *Platysace* (*Platysace lanceolata*), sweet scented wattle (*Acacia suaveolens*), blady grass (*Imperata cylindrical*), swamp water fern (*Blechnum indicum*), harsh ground fern (*Hypolepis muelleri*), zig-zag bog rush (*Schoenus brevifolius*), native rush (*Baloskion pallens*), *Leptocarpus tenax* and *Gahnia clarkei*. Aquatic vegetation associations include *Shoenopectus* spp., *Baumea* spp., *Typha orientalis* and *Lepironia articulata*.

Distribution and frog species associations. The species appears to have a highly restricted distribution, found to date only throughout the Port Stephens, Myall Lakes and northern Central Coast sand beds in a relatively small area of eastern coastal New South Wales (Fig. 1).

A total of 45 sites were surveyed throughout the Port Stephens and Myall Lakes sand bed systems. Six sites in the Port Stephens sand beds were found to contain *U. mahonyi* **sp. nov.** in addition to the sites already known at the type locality at Oyster Cove (Table 4; Figure 1c). *Uperoleia fusca* was observed calling in an ephemeral swale <100 m from an area of *Melaleuca* swamp where *U. mahonyi* **sp. nov.** was calling at one site. No sites surveyed in the Myall Lakes system were found to contain *U. mahonyi* **sp. nov.** during the formal surveys, although four sites contained *U. fusca* (Table 4; Figure 1c). There were, however, records of *U. mahonyi* **sp. nov.** identified from quality photographs obtained from local biologists and enthusiasts in Hawks Nest and Seal Rocks, located at the southern and northern ends of the Myall Lakes sand beds respectively (Fig. 1B). *Uperoleia mahonyi* **sp. nov.** was also identified from quality photographs at Wyrabalong National Park and Norah Head on the NSW Central Coast (later confirmed from voucher specimens collected; Fig. 1b).

At sites where *U. mahonyi* **sp. nov.** were located, calling activity was generally high, with estimates of calling males ranging from ca. 6 to >25. All water bodies occupied by *U. mahonyi* **sp. nov.** occurred on a substrate of leached (often white) sand.

Fourteen other non-*Uperoleia* species of frog were found throughout the formal surveys (Table 4). Eight of these species were found to co-exist in the same water bodies as *U. mahonyi* **sp. nov.**

Etymology. Named in recognition of Prof. Michael Mahony of the University of Newcastle, for his contributions to the study of Australian amphibians.

Comparisons with other species. Superficially, *U. mahonyi* **sp. nov.** most closely resembles the large, ventrally pigmented eastern *U. tyleri* and *U. martini*; although the ranges of both are geographically separated from *U. mahonyi* **sp. nov.** by several hundred kms. It can be distinguished from these and all other *Uperoleia* by the distinct black and white marbled pattern on the ventral surface of *U. mahonyi* **sp. nov.**, formed by relatively continuous patches of white dots on a black background. The ventral surfaces of other eastern *Uperoleia* including *U. fusca*, *U. tyleri* and *U. martini* all present a more even suffusion/stippling of white or off-white pigment on a dark background, which appears more speckled than marbled (refer to Fig. 5 for ventral images of *Uperoleia mahonyi* **sp. nov.**, *U. tyleri* and *U. martini*). *Uperoleia laevigata* and *U. rugosa* both lack ventral pigmentation in at least the groin region and arms (and sometimes much of the belly).

Uperoleia mahonyi **sp. nov.** can be further distinguished from *U. tyleri* by a longer call with more pulses and a higher dominant frequency, from *U. martini* by a shorter call (almost half the duration) with ca. 50% less pulses, and a higher dominant frequency, and from *U. fusca* by having more pulses per call (Table 2). *Uperoleia mahonyi* **sp. nov.** has orange colour in the inguinal and femoral patches in all specimens observed to date, while *U. martini* and *U. tyleri* usually have yellow coloured patches.

Tadpoles of all species of eastern *Uperoleia* can be distinguished from tadpoles of other myobatrachid genera of similar size by a combination of their characteristic blotched tail pigmentation, position of the spiracle, oral disc and larger nares. Tadpoles of *Uperoleia mahonyi* **sp. nov.** closely resemble those of other species of *Uperoleia* and no reliable means of separation of sympatric species was found. They do not appear to grow as large (to 35 mm) as those of other coastal species *U. tyleri*, *U. martini*, *U. fusca* and *U. laevigata*, all of which can reach a maximum of 42 mm in length and a body length of 15 mm (Anstis, 2013).

Discussion

The description of *U. mahonyi* brings the total number of *Uperoleia* to 28; by far the largest genus in the

Myobatrachidae. Despite a public perception that species discoveries of vertebrates in developed countries such as Australia are rare, vertebrate discoveries for some taxonomic groups—particularly the reptiles and amphibians—still occur at surprising rates. For example, more than 30 species of gecko have been described from a diversity of habitats across the Australian mainland over the past ten years alone (Cogger 2014; Doughty & Oliver 2013; Hoskin & Couper 2013; Pepper *et al.* 2013; Hutchinson *et al.* 2014; Oliver *et al.* 2014a,b; Oliver & Parkin 2014). Such species discoveries can be due to a number of reasons; amphibians and reptiles are generally smaller, less mobile and thus less conspicuous than their more mobile and conspicuous counterparts such as birds and mammals. In Australia, many species have adapted to inhabit remote, arid regions of the continent that are often inhospitable to mammals and birds and rarely visited by people (Doughty *et al.* 2007a; Doughty *et al.* 2007b). Cryptic behaviour and/or highly conserved morphology between related species can also make it difficult to recognise new species (Oliver *et al.*, 2014a). It is likely that several of these factors are at play for the *Uperoleia* genus, which has had five new species described in the past decade alone. *Uperoleia* often occur in remote locations, are small and cryptic in behaviour and congeneric morphology is highly conserved. It is thus likely that this will not be the last description of *Uperoleia* species, with more likely to be identified in coming years.

The genetic and morphological data clearly supports the species status of *U. mahonyi*. The nuclear DNA dataset places this species, located within 90 km to the north and south of Newcastle (Fig. 1), as sister to *U. tyleri* and *U. martini*. These two genetically divergent allopatric species, which superficially resemble *U. mahonyi* morphologically, are found substantially to the south of the Sydney Basin, a division of several hundred kilometres. This pattern of divergence has been found in numerous other organisms native to the NSW coastal region (Chapple *et al.* 2011; Pepper *et al.* 2014). Shared ancestry between these regions is often linked to the early-mid Pliocene (Chapple *et al.* 2011), prior to the development of extremely arid conditions in the centre of the continent. This drying may have caused repeated incidences of allopatric speciation, as species were restricted to the coastal plains and divided by the uplifted sandstones of the Sydney region (Byrne *et al.* 2011).

The mitochondrial DNA dataset suggests hybridization occurred between *U. laevigata* and *U. mahonyi* in the relatively recent past, resulting in the capture of the *U. laevigata* mitochondrial genome by *U. mahonyi*. However, *U. mahonyi* forms well-supported monophyletic group (BPP = 1, Fig. 2B) in the mitochondrial phylogeny as a result of novel mutations only found in the species, indicating *U. mahonyi* is currently reproductively isolated from *U. laevigata*. This pattern of mitochondrial capture followed by reproductive isolation is relatively common within *Uperoleia* (see Catullo & Keogh 2014), although the mechanisms are currently unknown.

Our study has highlighted also the usefulness of the degree and pattern of ventral pigment in providing diagnostic characters of eastern *Uperoleia* in the field. Due to the high level of conserved morphology between congeners, *Uperoleia* have always provided a challenge for field biologists to identify reliably using morphology. However, we have shown that by breaking down the group into those with completely pigmented ventral surfaces versus those without, and the pigmented species into groups by ventral pattern (marbled versus simple stippling), it breaks the eastern *Uperoleia* into groups of 2-3 species, which are then easily distinguished by secondary characters such as teeth and glands. In addition, we have provided a novel character not previously reported (colour patch that extends below the knee which occurs in only two species; *U. fusca* in 100% of cases and *U. laevigata* in ca. 50% of cases). Used in conjunction with their ventral pigmentation, this is another effective character to help identify the eastern *Uperoleia* in the field (*U. fusca* is completely pigmented on the ventral surface whereas *U. laevigata* is not).

Habitat use. The fact that *U. mahonyi* has only been detected in coastal sand beds, primarily in wallum and heath habitat on a substrate of leached sand, indicates that it is a habitat specialist. In this regard, its biology may make it more prone to threats from urban development and sand mining activities, both of which are common along the coastal zone of NSW. Several other species of frog in eastern Australia that are similarly dependent upon wallum habitat are currently listed as threatened, all of which face the same threatening processes of habitat loss, sand mining and tree plantations (Meyer *et al.* 2006). These frogs include a range of taxa from phylogenetically distant groups, all linked together by their habitat specialisation (species include *Litoria olongburensis*, *L. cooloolensis*, *L. freycineti* and *Crinia tinnula*). In fact, the threats that face this group are so ubiquitous that the NSW and QLD governments took the unusual step of creating a joint recovery plan for all of them together (Meyer *et al.* 2006). *Uperoleia mahonyi* might well be another, distant relation that could be added to that list. The detection of *U. mahonyi* in man-made water bodies, such as a golf course dam and a swale created by past sand mining activities, indicates that the species displays some ability to adapt to anthropogenic disturbance in at least

some cases, although it is unclear how abundant the species was in these areas prior to disturbance, and whether or not they are less abundant now. All of these human-modified habitats were created on a substrate of leached sand, however, and had at least regrowth vegetation surrounding them. Native vegetation is likely important for this species, which to date has not been found in non-vegetated habitats.

Recent work on habitat use in the closely related *U. tyleri* identified a number of characteristics (Westgate *et al.* 2012), which are likely shared by *U. mahonyi* and contribute to concern over conservation status. *Uperoleia tyleri* was often captured along high-relief locations away from the breeding aggregation, not along drainage lines where vegetation buffers are generally placed. Unlike non-*Uperoleia* species in the same area, *U. tyleri* consistently occupied habitat up to (and likely over) 200 metres from the breeding aggregation, and showed migratory behaviour toward breeding ponds during the spring (Westgate *et al.* 2012). Another close relative, *U. martini*, is now listed as Critically Endangered in the State of Victoria (Department of Sustainability and Environment 2013), and is now only found around waterbodies with extensive intact vegetation (Clemann 2015). These observations fit with our findings for *U. mahonyi*; it is primarily found in areas where the breeding ponds have extensive intact native vegetation surrounding the water body, and individuals have been located several hundred metres away from those water bodies (up to 400m or more at three separate sites). These data suggest this group of frogs likely spends extensive time in native forest and requires extensive vegetation buffers, larger than required for other sympatric species, in order for populations to persist. Currently in NSW, riparian vegetation buffers range from 10–40 m from the highest bank of a watercourse, depending upon the order of stream (Department of Primary Industries 2012), which is significantly less than the distance that these frogs have been observed from water bodies.

In addition to the above threats associated with high degrees of habitat specialisation, *U. mahonyi* has been found to date to be highly restricted in distribution. An intensive, targeted survey was carried out as part of this study with many sites turning up no record of the species. It is possible that, in the course of time, its known distribution will expand as more populations are discovered, although large range extensions are thought to be unlikely. Due to its habitat specialisation, it is unlikely to be found out of the coastal zone and there are few areas of Wallum habitat remaining in coastal NSW, all of which are generally heavily fragmented due to coastal developments.

Conservation status. Under the IUCN's criteria for species listings under the red list, restricted distribution is a key criterion (IUCN 2012). Given the current known distribution for *U. mahonyi*, it should be assessed for an Endangered or Critically Endangered status under the red list based upon the criterion of restricted distribution, dependent upon how the area currently occupied was determined. For such a listing to occur, two other sub-criteria from three would need to be met: either (i) the habitat could be shown to be severely fragmented, (ii) the extent of occurrence/occupancy, habitat quality or number of sub populations/mature individuals could be shown or inferred to be declining; and/or (iii) there were extreme fluctuations in those same metrics as in (ii) (IUCN 2012). Wallum habitat is already considered to be severely fragmented in eastern Australia, meeting criteria (i) (Meyer *et al.* 2006). Given that other wallum frogs have been shown to be declining or fluctuating (Meyer *et al.* 2006), it is possible that future studies will identify that one or both of the remaining two sub-criteria are met for *U. mahonyi*, thus warranting listing on the IUCN red list. Studies investigating population size and fluctuations, through either field or genetic methods, should be a priority for research in the near future.

Conclusion

The fact that this species was discovered in a populated region of Australia is significant. The region in which it occurs has been subject to coastal developments and sand mining for many decades, and has been subject to fauna surveys. In the state of NSW, development applications require fauna surveys to be undertaken in order to assess likely environmental impacts. Indeed, the type locality where the frog was initially discovered is a former sand mine rehabilitation area where an environmental assessment and associated fauna surveys would have been carried out, and individuals of *U. mahonyi* are highly likely to have been encountered. Although the species is superficially similar to other *Uperoleia* in the area, it is still morphologically distinct and any thorough inspection of the animal by an experienced amphibian ecologist should have identified it as novel. It is unlikely that the species has never been detected by ecologists working in the region before, but failure to identify it as an undescribed species during surveys highlights the problem of non-specialist ecologists conducting specialist surveys for development applications.

TABLE 4. List of all *Uperoleia* and non-*Uperoleia* frog species detected at water bodies during targeted surveys of mid-north coast NSW sand beds. SP = semi-permanent, Eph = ephemeral, Perm = permanent. L. nas = *Litoria nasuta*; Lit. per = *Litoria peronii*; L. lat = *Litoria latopalmata*; L. tyl = *Litoria tyleri*; L. rev = *Litoria revelata*; L. fal = *Litoria fallax*; L. frey = *Litoria freycineti*; Lim. per = *Limnodynastes peronii*; L. tas = *Limnodynastes tasmaniensis*; P. has = *Paracrinia haswelli*; C. sis = *Crinia signifera*; C. tin = *Crinia timula*; L. jerv = *Litoria jervisiensis*; P. cor = *Pseudophryne coriacea*.

Site	Latitude	Longitude	Waterbody Type	U. mahonyi	L. nas	L. lat	L. tyl	L. rev	L. fal	L. frey	L. jerv	P. has	C. sis	C. tin	L. jerv	P. cor
Port Stephens																
Tomago	-32.7951	151.7864	Inundated eph swamp/swale (<i>Melaleuca</i> regrowth)	x	x	x	x	x	x	x	x					
Tomago	-32.8019	151.7631	Eph swamp/ditch	x	x											
Grahamstown	-32.7686	151.7984	SP <i>Melaleuca</i> swamp					x								x
Medowie	-32.7672	151.8371	Perm dam					x								
Medowie	-32.7679	151.8386	Eph swamp													
Medowie	-32.7715	151.8549	Perm <i>Melaleuca</i> swamp													
Nelson Bay	-32.7294	152.1512	Perm dam on sand	x	x				x	x	x	x	x	x	x	
Oyster Cove	-32.7394	151.9557	Eph swale (<i>Melaleuca</i> regrowth)	x	x				x	x	x					x
Fingal Bay	-32.7381	152.1733	SP <i>Melaleuca</i> swamp	x	x				x	x	x					
Medowie	-32.7725	151.8659	SP <i>Melaleuca</i> swamp													
Tomago	-32.8221	151.7469	SP <i>Melaleuca</i> swamp													x
Tomago	-32.8136	151.8022	SP <i>Melaleuca</i> swamp													
Williamtown	-32.8103	151.8384	Perm <i>Melaleuca</i> swamp													
Tomago	-32.8025	151.7641	SP <i>Melaleuca</i> swamp	x	x				x	x	x					x
Tomago	-32.7947	151.7796	SP swamp (fringe of <i>Melaleuca</i>)	x					x							
Tomago	-32.7952	151.8	SP heath swamp					x								x
Tomago	-32.7995	151.8097	Inundated eph grass area													
Tomago	-32.801	151.816	Eph soak													
Tomago	-32.7704	151.8083	SP <i>Melaleuca</i> swamp													x
Tomago	-32.7682	151.813	SP <i>Melaleuca</i> swamp					x								
Tomago	-32.7965	151.7695	SP rehabilitated <i>Melaleuca</i> swamp		x	x			x	x	x					

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TABLE 4. (Continued)

Site	Latitude	Longitude	Waterbody Type	<i>U. makhoyi</i>	<i>L. fusca</i>	<i>L. nas</i>	<i>L. per</i>	<i>L. lat</i>	<i>L. tyl</i>	<i>L. rev</i>	<i>L. fal</i>	<i>L. frey</i>	<i>L. Lim.</i>	<i>L. per</i>	<i>L. tas</i>	<i>L. has</i>	<i>C. sig</i>	<i>C. tin</i>	<i>C. L.</i>	<i>L. jerv</i>	<i>P. cor</i>
Lake Macquarie																					
Awabakal NR	-32.9967	151.7245	Coastal lagoon		x				x						x						
Great Lakes																					
Tea Gardens	-32.6458	152.1428	SP <i>Melaleuca</i> swamp							x											x
Tea Gardens	-32.6439	152.1434	SP <i>Melaleuca</i> swamp																		x
Tea Gardens	-32.6199	152.1116	Large eph grassy soak	x																	
Tea Gardens	-32.6197	152.1127	Small eph grassy soak	x																	
Pindimar	-32.6724	152.1104	Eph <i>Melaleuca</i> swamp																		
Pindimar	-32.6723	152.1105	Eph road ditch																		
Pindimar	-32.6795	152.1085	Eph swamp/soak	x																	
Pindimar	-32.6739	152.1096	Perm pond	x																	
Bindibah	-32.6801	152.0965	Eph swamp/soak																		
Pindimar	-32.6686	152.1033	Eph swamp																		
Myall Lakes	-32.6409	152.1802	Perm <i>Melaleuca</i> swamp																		
Old Gibba	-32.509	152.3216	Perm <i>Melaleuca</i> swamp																		
Mungo Brush	-32.5204	152.3227	Perm <i>Melaleuca</i> swamp																		
Mungo Brush	-32.5852	152.2811	SP ditch																		
Mungo Brush	-32.591	152.2741	Perm dam																		
Hawkes Nest	-32.6654	152.1843	Perm dam																		
Hawkes Nest	-32.6676	152.1819	Perm dam																		
Smith's Lake	-32.399	152.4798	Perm swamp																		
Smith's Lake	-32.4002	152.4595	Perched swamp																		

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APPENDIX 1. Details of specimens examined for morphology, acoustics and DNA sequencing. M = male, F = female, st. = stage in "Sex/ life stage" column; V = visual inspection, M = morphometrics in "Morphology" column; mt = mtDNA, n = nDNA in "DNA" column.

<i>Uperoleia</i> Species	Genetic_ ID	Field/ museum ID	Location	Latitude	Longitude	Sex/ life stage	Date Collected	Morphology	Acoustics	DNA
<i>fusca</i>	Up0755	SAMA R39813	Junction of Washpool & Desert Creeks	-29.5652	153.2679	-	-	-	-	mt
<i>fusca</i>	Up0919	ABTC25047	Ourimbah State Forest	-33.2969	151.3786	-	-	-	-	mt + n
<i>fusca</i>	Up0955	ABTC25945	Richmond Range	-28.6767	152.7064	-	-	-	-	mt + n
<i>fusca</i>	Up0956	ABTC25953	Lamington NP	-30.6806	152.5639	-	-	-	-	mt + n
<i>fusca</i>	Up0640	ABTC84891	Mundoolan Connection Road, Canungra Creek Valley, Wonglepong	-27.9447	153.1439	-	-	-	-	n
<i>fusca</i>	Up0345	Up0345	Kroombit Tops	-24.3577	150.9627	-	-	-	-	n
<i>fusca</i>	Up0351	HBH201	Near Kingaroy, SEQ.	-26.5390	151.8404	-	-	-	-	n
<i>fusca</i>	Up0001	MM1120	Paxton	-32.8507	151.2084	-	15/02/2007	V	-	mt + n
<i>fusca</i>	Up0002	MM1121	Paxton	-32.8507	151.2084	-	15/02/2007	V	-	mt
<i>fusca</i>	-	MM1124	Stembeck's Pond	-33.1329	151.2061	M	14/03/2007	V	-	-
<i>fusca</i>	-	MM1126	Stembeck's Pond	-33.1329	151.2061	M	14/03/2007	V	-	-
<i>fusca</i>	-	MM1129	Stembeck's Pond	-33.1329	151.2061	M	14/03/2007	V	-	-
<i>fusca</i>	-	MM1130	Stembeck's Pond	-33.1329	151.2061	M	14/03/2007	V	-	-
<i>fusca</i>	-	MM1131	Stembeck's Pond	-33.1329	151.2061	M	14/03/2007	V	-	-
<i>fusca</i>	-	MM1133	Stembeck's Pond	-33.1329	151.2061	M	14/03/2007	V	-	-
<i>fusca</i>	-	MM1138	Stembeck's Pond	-33.1329	151.2061	M	14/03/2007	V	-	-
<i>fusca</i>	-	MM1140	Stembeck's Pond	-33.1329	151.2061	M	14/03/2007	V	-	-
<i>fusca</i>	-	MM1141	Stembeck's Pond	-33.1329	151.2061	M	14/03/2007	V	-	-
<i>fusca</i>	-	MM1142	Stembeck's Pond	-33.1329	151.2061	M	14/03/2007	V	-	-
<i>fusca</i>	-	MM1205	Heatherbrae	-32.7885	151.7436	M	3/10/2007	V	-	-
<i>fusca</i>	-	MM1206	Heatherbrae	-32.7885	151.7436	M	4/10/2007	V	-	-
<i>fusca</i>	Up0007	MM1207	Heatherbrae	-32.7885	151.7436	F	4/10/2007	V	-	mt + n
<i>fusca</i>	Up0008	MM1208	Heatherbrae	-32.7885	151.7436	M	4/10/2007	V	-	mt
<i>fusca</i>	Up0009	MM1209	Heatherbrae	-32.7885	151.7436	M	4/10/2007	V	-	mt
<i>fusca</i>	Up0025	MM1259	Gloucester	-32.2777	151.9379	-	27/11/2007	V	-	mt

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APPENDIX 1. (continued)

<i>Uperoleia</i> Species	Genetic_ ID	Field/ museum ID	Location	Latitude	Longitude	Sex/ life stage	Date Collected	Morphology	Acoustics	DNA
<i>fusca</i>	Up0026	MM1260	Gloucester	-32.2777	151.9379	-	27/11/2007	V	-	mt
<i>fusca</i>	-	MM1261	Gloucester	-32.2777	151.9379	-	27/11/2007	V	-	-
<i>fusca</i>	-	MM1262	Gloucester	-32.2777	151.9379	-	27/11/2007	V	-	-
<i>fusca</i>	Up0029	MM1263	Gloucester	-32.2777	151.9379	-	27/11/2007	V	-	mt
<i>fusca</i>	Up0030	MM1264	Stratford	-32.1407	151.9662	-	27/11/2007	V	-	mt + n
<i>fusca</i>	Up0031	MM1265	Stratford	-32.1407	151.9662	-	27/11/2007	V	-	mt
<i>fusca</i>	Up0032	MM1266	Stratford	-32.1407	151.9662	-	27/11/2007	V	-	mt
<i>fusca</i>	Up0033	MM1267	Stratford	-32.1407	151.9662	-	27/11/2007	V	-	mt
<i>fusca</i>	Up0034	MM1268	Stratford	-32.1407	151.9662	-	27/11/2007	V	-	mt
<i>fusca</i>	-	MM1299	Pindimar	-32.6754	152.0907	M	14/02/2008	V	-	-
<i>fusca</i>	Up0330	MM1300	Pindimar	-32.6754	152.0907	M	14/02/2008	V	-	n
<i>fusca</i>	-	MM1301	Pindimar	-32.6754	152.0907	M	14/02/2008	V	-	-
<i>fusca</i>	-	MM1302	Pindimar	-32.6754	152.0907	M	14/02/2008	V	-	-
<i>fusca</i>	Up0056	MM1325	Whian Whian	-28.5911	153.3816	M	16/01/2008	V	-	mt + n
<i>fusca</i>	-	MM1408	Coramba bottom pond	-30.2213	157.9868	M	1/11/2010	V	-	-
<i>fusca</i>	Up1206	MM1409	Coramba bottom pond	-30.2213	157.9868	-	1/11/2010	V	-	mt
<i>fusca</i>	Up1207	MM1410	Chaelundi	-30.2243	152.3803	-	1/11/2010	V	-	mt
<i>fusca</i>	-	MM1411	Chaelundi	-30.2243	152.3803	-	1/11/2010	V	-	-
<i>fusca</i>	Up1210	MM1413	Martinsville	-33.0849	151.4236	-	9/11/2010	V	-	mt
<i>fusca</i>	-	MM1414	Martinsville	-33.0849	151.4236	-	9/11/2010	V	-	-
<i>fusca</i>	-	MM1424	Coopermook S. F.	-	-	-	4/12/2010	V	-	-
<i>fusca</i>	-	MM1425	Coopermook S. F.	-	-	-	4/12/2010	V	-	-
<i>fusca</i>	-	MM1872	Boral Soak	-32.6199	152.1116	M	26/10/2009	V	-	-
<i>fusca</i>	-	MM1873	Boral Soak	-32.6199	152.1116	M	26/10/2009	V	-	-
<i>fusca</i>	-	MM4061092	Wyeec	-33.1771	151.4651	-	29/09/2006	V	-	-
<i>fusca</i>	-	MM4061093	Wyeec	-33.1771	151.4651	-	29/09/2006	V	-	-

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APPENDIX 1. (continued)

<i>Uperoleta</i> Species	Genetic_ ID	Field/ museum ID	Location	Latitude	Longitude	Sex/ life stage	Date Collected	Morphology	Acoustics	DNA
<i>fusca</i>	-	SC0040	Sternbeck's Pond	-33.1329	151.2061	-	1/03/2008	V	-	-
<i>fusca</i>	-	SC0049	Coopermook S. F.	-31.7930	152.6188	-	28/12/2009	V	-	-
<i>fusca</i>	-	SC0050	Coopermook S. F.	-31.7930	152.6188	-	28/12/2009	V	-	-
<i>laevigata</i>	Up0630	ABTC100564	Thane Creek, Durikoi State Forest, Warwick	-28.2881	151.6963	-	-	-	-	mt + n
<i>laevigata</i>	Up0804	SAMA R40851	Ik NE Penrose	-34.6667	150.2167	-	-	-	-	mt + n
<i>laevigata</i>	Up0837	SAMA R39216	5k E Bungendore	-35.2500	149.5000	-	-	-	-	mt + n
<i>laevigata</i>	Up0921	ABTC25149	Styx River camping area	-33.2485	148.9846	-	-	-	-	mt + n
<i>laevigata</i>	Up0718	ABTC99546	Ruined Castle - Reedy Creek Road, 5.4k E Mapala - Taroom Road, NW Taroom	-25.1039	149.1928	-	-	-	-	mt + n
<i>laevigata</i>	Up1053	AMS R167862	Mudgee, Protea Farm	-32.5931	149.4839	-	-	-	-	mt + n
<i>laevigata</i>	Up0003	MM1122	Paxton	-32.8507	151.2084	-	15/02/2007	V	-	mt
<i>laevigata</i>	-	MM1123	Sternbeck's Pond	-33.1329	151.2061	M	7/10/2006	V	-	-
<i>laevigata</i>	-	MM1125	Sternbeck's Pond	-33.1329	151.2061	M	14/03/2007	V	-	-
<i>laevigata</i>	-	MM1127	Sternbeck's Pond	-33.1329	151.2061	M	14/03/2007	V	-	-
<i>laevigata</i>	-	SAMA R66208	Sternbeck's Pond	-33.1329	151.2061	M	14/03/2007	V	-	-
<i>laevigata</i>	-	MM1132	Sternbeck's Pond	-33.1329	151.2061	M	14/03/2007	V	-	-
<i>laevigata</i>	-	MM1134	Sternbeck's Pond	-33.1329	151.2061	M	14/03/2007	V	-	-
<i>laevigata</i>	-	SAMA R66209	Sternbeck's Pond	-33.1329	151.2061	M	14/03/2007	V	-	-
<i>laevigata</i>	-	SAMA R66210	Sternbeck's Pond	-33.1329	151.2061	M	14/03/2007	V	-	-
<i>laevigata</i>	-	MM1137	Sternbeck's Pond	-33.1329	151.2061	M	14/03/2007	V	-	-
<i>laevigata</i>	-	SAMA R66211	Sternbeck's Pond	-33.1329	151.2061	M	14/03/2007	V	-	-
<i>laevigata</i>	Up0022	SAMA R66184	Mt Owen	-32.4147	151.1315	-	1/10/2007	V	-	mt + n
<i>laevigata</i>	Up0023	SAMA R66185	Mt Owen	-32.4147	151.1315	-	1/10/2007	V	-	mt
<i>laevigata</i>	Up0024	MM1228	Mt Owen	-32.4147	151.1315	-	1/10/2007	V	-	mt
<i>laevigata</i>	Up0035	SAMA R66180	Ebor Quarry	-30.4564	150.2092	-	17/12/2007	V	-	mt + n
<i>laevigata</i>	-	MM1277	Ebor Quarry	-30.4564	150.2092	-	17/12/2007	V	-	-

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APPENDIX 1. (continued)

<i>Uperoleia</i> Species	Genetic_ ID	Field/ museum ID	Location	Latitude	Longitude	Sex/ life stage	Date Collected	Morphology	Acoustics	DNA
<i>laevigata</i>	Up0040	MM1281	Ebor Quarry	-30.4564	150.2092	-	17/12/2007	V	-	mt + n
<i>laevigata</i>	-	MM1282	Ebor Quarry	-30.4564	150.2092	-	17/12/2007	V	-	-
<i>laevigata</i>	-	MM1283	Ebor Quarry	-30.4564	150.2092	-	17/12/2007	V	-	-
<i>laevigata</i>	Up0043	SAMA R66181	Ebor Quarry	-30.4564	150.2092	-	17/12/2007	V	-	mt
<i>laevigata</i>	-	MM1285	Mt Owen - Southern Frog Zone	-32.4147	151.1314	-	1/12/2007	V	-	-
<i>laevigata</i>	Up0045	MM1288	Wentworth Swamp	-32.7784	151.4838	-	22/09/2007	V	-	mt
<i>laevigata</i>	-	SAMA R66182	Merriwa	-32.2587	150.3638	M	4/01/2008	V	-	-
<i>laevigata</i>	Up0049	SAMA R66183	Merriwa	-32.2587	150.3638	-	4/01/2008	V	-	mt + n
<i>laevigata</i>	Up0050	MM1318	Merriwa	-32.2587	150.3638	-	4/01/2008	V	-	mt
<i>laevigata</i>	-	MM1397	Mt Owen - Southern Frog Zone	-32.4147	151.1314	M	1/12/2007	V	-	-
<i>laevigata</i>	Up0388	RAC0003	Watagan SF	-33.1331	151.2062	-	-	-	-	mt + n
<i>laevigata</i>	Up1075	RAC0005	Farm dam on Warrah Ridge Rd	-31.5196	150.6206	-	-	-	-	mt
<i>laevigata</i>	-	SC0023	O'Connell Rd Dam	-33.6234	149.7904	M	3/11/2009	V	-	-
<i>laevigata</i>	-	SC0037	Campbells Rv Pond	-33.6064	149.6782	-	12/11/2009	V	-	-
<i>laevigata</i>	-	SC0038	Campbells Rv Pond	-33.6064	149.6782	-	12/11/2009	V	-	-
<i>laevigata</i>	-	SC0039	Campbells Rv Pond	-33.6064	149.6782	-	12/11/2009	V	-	-
<i>laevigata</i>	-	SC0041	Sternbeck's Pond	-33.1329	151.2061	-	1/03/2008	V	-	-
<i>laevigata</i>	-	SC0042	Sternbeck's Pond	-33.1329	151.2061	-	1/03/2008	V	-	-
<i>laevigata</i>	-	MM1316	Merriwa	-32.2587	150.3638	-	4/01/2008	V	-	-
<i>laevigata</i>	-	MM1397	Mt Owen - Southern Frog Zone	-32.4147	151.1314	-	30/12/2007	V	-	-
<i>mahonyi</i>	-	SAMA R66186	Oyster Cove	-32.7394	151.9557	-	-	V + M	-	-
<i>mahonyi</i>	Up0015	SAMA R66187	Oyster Cove	-32.7394	151.9557	M	4/10/2007	V + M	Yes	mt + n
<i>mahonyi</i>	Up0016	SAMA R66188	Oyster Cove	-32.7394	151.9557	M	4/10/2007	V + M	Yes	mt + n
<i>mahonyi</i>	-	AMS R185691	Oyster Cove	-32.7394	151.9557	M	4/10/2007	V + M	Yes	mt
<i>mahonyi</i>	Up0018	SAMA R66189	Oyster Cove	-32.7394	151.9557	M	4/10/2007	V + M	Yes	mt + n
<i>mahonyi</i>	Up0019	SAMA R66190	Oyster Cove	-32.7394	151.9557	M	4/10/2007	V + M	Yes	mt + n

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APPENDIX 1. (continued)

<i>Uporeoleia</i> Species	Genetic ID	Field/ museum ID	Location	Latitude	Longitude	Sex/ life stage	Date Collected	Morphology	Acoustics	DNA
<i>mahonyi</i>	-	SAMA R66193	Oyster Cove	-32.7394	151.9557	M	12/02/2008	V + M	Yes	-
<i>mahonyi</i>	-	SAMA R66194	Oyster Cove	-32.7394	151.9557	M	12/02/2008	V + M	Yes	-
<i>mahonyi</i>	Up0337	SAMA R66195	Oyster Cove	-32.7394	151.9557	M	-	V + M	-	mt + n
<i>mahonyi</i>	Up1200	AMS R185693	Nelson Bay Golf Course	-32.7294	152.1512	M	5/10/2009	-	Yes	mt + n
<i>mahonyi</i>	Up1201	AMS R185694	Tomago	-32.8025	151.7641	M	7/10/2009	-	Yes	mt + n
<i>mahonyi</i>	-	AMS R185695	Oyster Cove	-32.7394	151.9557	M	12/10/2009	-	Yes	-
<i>mahonyi</i>	Up1202	AMS R185696	Waterboard Easement	-32.7951	151.7864	M	22/10/2009	-	Yes	mt + n
<i>mahonyi</i>	Up1203	AMS R185697	Stockton Beach	-32.8293	151.8825	-	1/11/2009	-	-	mt + n
<i>mahonyi</i>	Up1204	AMS R185698	Stockton Beach	-32.8293	151.8825	-	1/11/2009	-	-	mt + n
<i>mahonyi</i>	-	AMS R185699	Wyrabalong	-33.2970	151.5503	F	28/05/2012	V + M	-	-
<i>mahonyi</i>	-	AMS R185700	Wyrabalong	-33.2970	151.5503	F	28/05/2012	V + M	-	-
<i>mahonyi</i>	-	AMS R185701	Oyster Cove	-32.7394	151.9557	F	1/03/2013	-	-	-
<i>mahonyi</i>	-	AMS R184083	Oyster Cove	-32.7394	151.9557	1 hatchling st. 24	7/11/2010	V + M	-	-
<i>mahonyi</i>	-	AMS R184076	Oyster Cove	-32.7394	151.9557	2 tadpoles st. 26; 1 st. 35; 1 st. 37	19/12/2010	V + M	-	-
<i>mahonyi</i>	-	AMS R184077	Oyster Cove	-32.7394	151.9557	4 tadpoles st. 25-27	31/10/2010	V + M	-	-
<i>mahonyi</i>	-	AMS R184078	Oyster Cove	-32.7394	151.9557	2 tadpoles st. 26, 29; 1 st. 35	15/12/2010	V + M	-	-
<i>mahonyi</i>	-	AMS R184080	Oyster Cove	-32.7394	151.9557	3 tadpoles st. 33, 34, 35	26/12/2010	V + M	-	-
<i>mahonyi</i>	-	AMS R184082	Oyster Cove	-32.7394	151.9557	1 tadpole st. 29; 1 stage 30	15/11/2010	V + M	-	-
<i>mahonyi</i>	-	AMS R184084	Oyster Cove	-32.7394	151.9557	2 metamorphs st. 46	3/01/2011	V + M	-	-
<i>mahonyi</i>	-	AMS R184085	Oyster Cove	-32.7394	151.9557	10 eggs st. 7-8	4/03/2013	V + M	-	-
<i>mahonyi</i>	-	AMS R184090	Oyster Cove	-32.7394	151.9557	5 recent hatchlings st. 20-22	13/03/2013	V + M	-	-
<i>martini</i>	Up0855	SAMA R40949	near Marlo	-37.8000	148.5333	-	-	-	-	mt

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APPENDIX 1. (continued)

<i>Uperoleia</i> Species	Genetic_ ID	Field/ museum ID	Location	Latitude	Longitude	Sex/ life stage	Date Collected	Morphology	Acoustics	DNA
<i>martini</i>	Up1221	RAC0086	Wingan Swamp, VIC	-37.5478	149.4580	-	-	-	-	mt + n
<i>rugosa</i>	Up1002	HH 1537	34 km N of Injune	-25.3434	148.3814	-	-	-	-	mt
<i>rugosa</i>	Up0604	SAMA R33514	Gunbar	-34.0667	145.4167	-	-	-	-	mt + n
<i>rugosa</i>	Up0606	SAMA R33516	Gunbar	-34.0667	145.4167	-	-	-	-	n
<i>rugosa</i>	Up0607	SAMA R33517	Gunbar	-34.0667	145.4167	-	-	-	-	mt
<i>rugosa</i>	Up0632	QM J86620	The Causeway, Eel Creek, Utopia, Browena	-25.6481	152.1093	-	-	-	-	n
<i>rugosa</i>	Up0781	ABTC12475	Ban Ban Springs	-25.6817	151.8153	-	-	-	-	mt + n
<i>rugosa</i>	Up0949	ABTC25848	Awaba	-33.0122	151.5428	-	-	-	-	n
<i>rugosa</i>	Up0637	ABTC84872	Mundoolan Connection Rd, Wonglepong	-27.9447	153.1439	-	-	-	-	n
<i>rugosa</i>	Up0650	ABTC84957	Northern edge of Moonie	-27.7122	-27.7122	-	-	-	-	n
<i>rugosa</i>	Up0682	ABTC99411	Culgoa Floodplain NP, Dirranbandi	-28.9028	147.1449	-	-	-	-	mt
<i>rugosa</i>	Up0701	ABTC99498	Dargal Road, c. 2.3k WNW intersection with Currey Street, Roma	-26.5611	148.7512	-	-	-	-	n
<i>rugosa</i>	Up1042	AMS R140825	Wanaaring, 5 km W - Tibbooburra	-29.7167	144.1167	-	-	-	-	n
<i>rugosa</i>	Up1007	AMS R153289	Mungindi, Mungindi Airstrip and Quarry	-28.9683	149.0556	-	-	-	-	mt
<i>rugosa</i>	Up1019	AMS R156781	Condoblin Area, Nyora Property	-32.8333	147.0333	-	-	-	-	mt
<i>rugosa</i>	Up0995	MM1843	Quirindi Reserve	-31.5133	150.6519	-	-	V	-	n
<i>rugosa</i>	Up0996	MM1844	Caroona	-31.4083	150.4175	-	-	V	-	mt
<i>rugosa</i>	Up1000	MM1848	15.3km NE of Warren	-31.6344	147.9625	-	-	V	-	n
<i>rugosa</i>	Up1077	MM1868	West of Bourke	-30.0207	145.0898	-	8/07/2009	V	-	mt
<i>tyleri</i>	Up0873	SAMA R43772	near Tianjara Falls	-35.1167	150.3333	-	-	-	-	mt + n
<i>tyleri</i>	Up0923	ABTC25149	South Durass	-35.6636	150.2939	-	-	-	-	mt + n
<i>tyleri</i>	Up1013	AMS R154137	Booderie National Park, Jervis Bay	-35.1736	150.7186	-	-	-	-	mt + n
<i>tyleri</i>	Up1014	AMS R154138	Booderie National Park, Jervis Bay	-35.1736	150.7186	-	-	-	-	mt
<i>tyleri</i>	Up1015	AMS R154139	Booderie National Park, Jervis Bay	-35.1736	150.7186	-	-	-	-	mt
<i>tyleri</i>	Up0010	SAMA R66196	Ryan's Swamp, Jervis Bay	-35.1607	150.6651	-	6/10/2007	V	-	mt

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APPENDIX 1. (continued)

<i>Uperoleia</i> Species	Genetic ID	Field/ museum ID	Location	Latitude	Longitude	Sex/ life stage	Date Collected	Morphology	Acoustics	DNA
<i>tyleri</i>	-	MM1214	Ryan's Swamp Jervis Bay	-35.1607	150.6651	-	6/10/2007	V	-	-
<i>tyleri</i>	-	MM1215	Ryan's Swamp Jervis Bay	-35.1607	150.6651	-	6/10/2007	V	-	-
<i>tyleri</i>	-	SAMA R66199	Ryan's Swamp Jervis Bay	-35.1607	150.6651	M	16/02/2008	V	-	-
<i>tyleri</i>	-	SAMA R66200	Ryan's Swamp Jervis Bay	-35.1607	150.6651	M	16/02/2008	V	-	-
<i>tyleri</i>	-	SAMA R66201	Ryan's Swamp Jervis Bay	-35.1607	150.6651	-	16/02/2008	V	-	-
<i>tyleri</i>	Up0326	SAMA R66202	Ryan's Swamp Jervis Bay	-35.1607	150.6651	-	16/02/2008	V	-	mt
<i>tyleri</i>	Up0327	SAMA R66203	Ryan's Swamp Jervis Bay	-35.1607	150.6651	-	16/02/2008	V	-	mt
<i>tyleri</i>	-	SAMA R66204	Ryan's Swamp Jervis Bay	-35.1607	150.6651	-	16/02/2008	V	-	-
<i>tyleri</i>	-	SAMA R66205	Ryan's Swamp Jervis Bay	-35.1607	150.6651	M	16/02/2008	V	-	-
<i>tyleri</i>	-	MM1308	Ryan's Swamp Jervis Bay	-35.1607	150.6651	-	5/04/2008	V	-	-
<i>tyleri</i>	-	MM1310	Ryan's Swamp Jervis Bay	-35.1607	150.6651	-	6/04/2008	V	-	-
<i>tyleri</i>	-	SAMA R66206	Ryan's Swamp Jervis Bay	-35.1607	150.6651	-	3/04/2008	V	-	-
<i>tyleri</i>	-	SAMA R66207	Ryan's Swamp Jervis Bay	-35.1607	150.6651	M	3/04/2008	V	-	-
<i>tyleri</i>	Up0386	RAC0001	Kioloa, NSW	-35.5422	150.3753	-	-	-	-	mt + n
<i>tyleri</i>	Up1216	RAC0080	Dingle Lagoon, Bournda National Park, NSW	-36.7950	149.9356	-	-	-	-	mt + n
<i>tyleri</i>	Up1217	RAC0081	Dingle Lagoon, Bournda National Park, NSW	-36.7950	149.9356	-	-	-	-	mt + n

APPENDIX 2. Genbank accession numbers for molecular data.

Genetic ID	16S	ND2	A2AB	BDNF	BMP2	NTF3	RAG1
Up0001	KJ874820	KX790245	KJ949751	KJ949852	KJ916094	KJ819724	KJ874546
Up0002	KX768493	KX790246	NA	NA	NA	NA	NA
Up0003	KX768494	KX790247	NA	NA	NA	NA	NA
Up0007	KJ874709	KX790248	KJ949776	KJ949923	KJ915960	KJ819782	KJ874469
Up0008	KX768495	KX790249	NA	NA	NA	NA	NA
Up0009	KX768496	KX790250	NA	NA	NA	NA	NA
Up0010	KJ874938	KX790251	NA	NA	NA	NA	NA
Up0011	JF263330	JF263217	KF659040	KF658831	KF659204	KF659103	KF659384
Up0012	KJ874737	KX790252	KJ949780	KJ949854	KJ916069	KJ819725	KJ874586
Up0013	KJ874871	KX790253	NA	NA	NA	NA	NA
Up0015	KX768497	KX790254	KX768436	KX768422	KX768451	KX768465	KX768479
Up0016	KX768498	KX790255	KX768437	KX768423	KX768452	KX768466	KX768480
Up0018	KX768499	KX790256	KX768438	KX768424	KX768453	KX768467	KX768481
Up0019	KX768500	KX790257	KX768439	KX768425	KX768454	KX768468	KX768482
Up0020	KX768501	KX790258	KX768440	KX768426	KX768455	KX768469	KX768483
Up0021	KX768502	KX790259	KX768441	KX768427	KX768456	KX768470	KX768484
Up0022	KJ874853	KX790260	KJ949779	KJ949914	KJ916095	KJ819656	KJ874584
Up0023	KX768503	KX790261	NA	NA	NA	NA	NA
Up0024	KX768504	KX790262	NA	NA	NA	NA	NA
Up0025	KX768505	KX790263	NA	NA	NA	NA	NA
Up0026	KX768506	KX790264	NA	NA	NA	NA	NA
Up0029	KX768507	KX790265	NA	NA	NA	NA	NA
Up0030	KJ874703	KX790266	KJ949709	KJ949872	KJ915995	KJ819735	KJ874481
Up0031	KX768508	KX790267	NA	NA	NA	NA	NA
Up0032	KX768509	KX790268	NA	NA	NA	NA	NA
Up0033	KX768510	KX790269	NA	NA	NA	NA	NA
Up0034	KX768511	KX790270	NA	NA	NA	NA	NA
Up0035	KJ874906	KX790271	KJ949824	KJ949996	KJ916049	KJ819776	KJ874447
Up0039	KX768512	KX790272	NA	NA	NA	NA	NA
Up0040	JF263331	JF263219	KF659066	KF658903	KF659298	KF659194	KF659443
Up0043	KX768513	KX790273	NA	NA	NA	NA	NA
Up0045	KX768514	KX790274	NA	NA	NA	NA	NA
Up0049	KJ874714	KX790275	KJ949838	KJ950005	KJ916075	KJ819720	KJ874515
Up0050	KX768515	KX790276	NA	NA	NA	NA	NA
Up0055	KX768516	KX790277	NA	NA	NA	NA	NA
Up0056	JF263332	JF263220	KF659026	KF658891	KF659224	KF659080	KF659364
Up0326	KJ874753	KX790278	NA	NA	NA	NA	NA
Up0327	KJ874674	KX790279	NA	NA	NA	NA	NA
Up0330	NA	NA	KJ949731	KJ949967	KJ915949	KJ819622	KJ874507
Up0337	KX768517	NA	NA	NA	NA	NA	NA
Up0345	NA	NA	KJ949848	KJ949937	KJ915956	KJ819774	KJ874567
Up0351	NA	NA	KJ949832	KJ949930	KJ916000	KJ819752	KJ874590

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APPENDIX 2. (Continued)

Genetic ID	16S	ND2	A2AB	BDNF	BMP2	NTF3	RAG1
Up0386	KJ874679	KX790280	KJ949739	KJ949920	KJ916102	KJ819709	KJ874479
Up0388	KJ874719	KX790281	KJ949703	KJ949904	KJ915953	KJ819736	KJ874616
Up0604	KJ874854	KX790282	KJ949772	KJ949865	KJ916019	KJ819745	KJ874529
Up0606	NA	NA	KF659008	KF658947	KF659243	KF659132	KF659403
Up0607	KX768518	KX790283	NA	NA	NA	NA	NA
Up0630	KJ874856	KX790284	KJ949802	KJ949953	KJ915996	KJ819788	KJ874563
Up0632	NA	NA	KJ949727	KJ949971	KJ916024	KJ819708	KJ874552
Up0637	NA	NA	KJ949842	KJ949983	KJ916098	KJ819760	KJ874611
Up0640	NA	NA	KJ949812	KJ950019	KJ916067	KJ819757	KJ874445
Up0650	NA	NA	NA	KX768428	KX768457	KX768471	KX768485
Up0682	KX768519	KX790285	NA	NA	NA	NA	NA
Up0701	NA	NA	KJ949758	KJ949982	KJ915998	KJ819769	KJ874522
Up0718	KJ874694	KX790286	KJ949820	KJ949972	KJ916003	KJ819716	KJ874486
Up0755	KJ874866	KX790287	NA	NA	NA	NA	NA
Up0781	KJ874752	KX790288	KJ949716	KJ949910	KJ916054	KJ819791	KJ874453
Up0804	KJ874878	KX790289	KJ949773	KJ950007	KJ916093	KJ819652	KJ874539
Up0837	KJ874797	KX790290	KX768442	KJ950013	KJ915972	KJ819726	KJ874558
Up0855	KJ874787	KX790291	NA	NA	NA	NA	NA
Up0873	KJ874944	KX790292	KJ949790	KJ949979	KJ916058	KJ819662	KJ874562
Up0919	KX768520	KX790293	KJ949831	KJ949876	KJ916001	KJ819639	KJ874521
Up0921	KX768521	KX790294	KX768443	KX768429	KX768458	KX768472	KX768486
Up0923	KX768522	KX790295	KX768444	KX768430	KX768459	KX768473	KX768487
Up0949	NA	NA	KJ949835	KJ949989	KJ915969	KJ819727	KJ874489
Up0955	KJ874901	KX790296	KJ949730	KJ949978	KJ915970	KJ819790	KJ874477
Up0956	KJ874727	KX790297	KJ949803	KJ949893	KJ916064	KJ819660	KJ874455
Up0995	NA	NA	KJ949818	KJ949966	KJ915971	KJ819632	KJ874454
Up0996	KX768523	KX790298	NA	NA	NA	NA	NA
Up1000	NA	NA	KJ949819	KJ950023	KJ916037	KJ819625	KJ874591
Up1002	KX768524	KX790299	NA	NA	NA	NA	NA
Up1007	KJ874810	KX790300	NA	NA	NA	NA	NA
Up1013	KJ874801	KX790301	KJ949827	KJ950008	KJ916066	KJ819618	KJ874496
Up1014	KJ874791	KX790302	NA	NA	NA	NA	NA
Up1015	KJ874665	KX790303	NA	NA	NA	NA	NA
Up1019	KX768525	KX790304	NA	NA	NA	NA	NA
Up1042	NA	NA	KJ949749	KJ949890	KJ916082	KJ819700	KJ874446
Up1053	KJ874679	KX790305	KJ949718	KJ949980	KJ916026	KJ819670	KJ874602
Up1075	KX768526	KX790306	NA	NA	NA	NA	NA
Up1077	KX768527	KX790307	NA	NA	NA	NA	NA
Up1200	KX768528	KX790308	KX768445	KX768431	KX768460	KX768474	KX768488
Up1201	NA	KX790309	KX768446	KX768432	KX768461	KX768475	KX768489
Up1202	KX768529	NA	KX768447	KX768433	KX768462	KX768476	KX768490
Up1203	KX768530	KX790310	KX768448	KX768434	KX768463	KX768477	KX768491

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APPENDIX 2. (Continued)

Genetic ID	16S	ND2	A2AB	BDNF	BMP2	NTF3	RAG1
Up1204	KX768531	KX790311	KX768449	KX768435	KX768464	KX768478	KX768492
Up1206	KX768532	KX790312	NA	NA	NA	NA	NA
Up1207	KX768533	KX790313	NA	NA	NA	NA	NA
Up1210	KX768534	KX790314	NA	NA	NA	NA	NA
Up1216	KJ874744	KX790315	KX768450	KJ949929	KJ915962	KJ819785	KJ874480
Up1217	KJ874685	KX790316	KJ949811	KJ949891	KJ916092	KJ819665	KJ874601
Up1218	KJ874859	KX790317	KJ949748	KJ949908	KJ916057	KJ819626	KJ874506
Up1219	NA	NA	KJ949794	KJ949917	KJ916081	KJ819767	KJ874607
Up1220	KJ874852	KX790318	KJ949682	KJ950015	KJ916023	KJ819691	KJ874594
Up1221	KJ874849	KX790319	KJ949762	KJ949901	KJ916053	KJ819738	KJ874599