Australian microhylid frogs (*Cophixalus* and *Austrochaperina*): phylogeny, taxonomy, calls, distributions and breeding biology

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Abstract

Despite a considerable surge in herpetological research in Australia over the last couple of decades the Australian microhylid frogs (*Cophixalus* and *Austrochaperina*) remain relatively poorly known. Herein I present the results of extensive fieldwork and molecular, morphological and call analysis with the aim of resolving taxonomy, call variation and distributions, and increasing our understanding of breeding biology. Analysis of 943 base pairs of mitochondrial 16S rRNA and 12S rRNA provides a well supported phylogeny that is largely consistent with current taxonomy. Levels of divergence between species are substantial and significant phylogeographic structuring is evident in *C. ornatus*, *C. neglectus* and *C. aenigma*, sp. nov. The description of *C. concinnus* was based on a mixed collection of two species from Thornton Peak and a new species is described to resolve this. *C. aenigma*, sp. nov., is described from high-elevation (>750 m) rainforest across the Carbine, Thornton, Finnigan and Bakers Blue Mountain uplands, north-east Queensland. *C. concinnus* is redescribed as a highly distinct species restricted to rainforest and boulder fields at the summit of Thornton Peak (>1100 m). Despite protection in Daintree National Park in the Wet Tropics World Heritage Area, predictions of the impact of global warming suggest *C. concinnus* to be of very high conservation concern (Critically Endangered, IUCN criteria). The mating call of two species (*C. mcdonaldi* and *C. exiguus*) is described for the first time and high levels of call variation within *C. ornatus*, *C. neglectus*, *C. hosmeri*, *C. aenigma* and *Austrochaperina fryi* are presented. Such variation is often attributable to genetically divergent lineages, altitudinal variation and courtship; however, in some instances (particularly within *C. hosmeri*) the source or function of highly distinct calls at a site remains obscure. Molecular, morphological and call analyses allow the clarification of species distributions, especially in the northern mountains of the Wet Tropics. Notes are presented on the breeding biology of *C. aenigma*, *C. bombiens*, *C. concinnus*, *C. exiguus*, *C. infacetus*, *C. mcdonaldi*, *C. monticola*, *C. neglectus*, *C. ornatus* and *C. saxatilis*, which are largely consistent with previous accounts: small terrestrial clutches usually attended by a male. Courtship behaviour in *C. ornatus* is described and the first records of multiple clutching in Australian microhylids are presented (for *C. ornatus* and *C. infacetus*).

Introduction

The diverse frog family Microhylidae has a global distribution centred on the tropics (Duellman and Trueb 1994). In Australia this family comprises a limited component of the frog fauna, representing just 9% of the species diversity and being restricted to northern Queensland and the very northern tip of the Northern Territory. In the rainforest of the Wet Tropics of north-east Queensland, however, microhylids dominate frog richness, accounting for 54% of the rainforest-restricted species and the group has been prominent in studies of biogeography and conservation prioritisation (Moritz *et al*. 2001, in press; Williams and Hero 2001). The family Microhylidae is represented in Australia by two genera in the subfamily Genyophryninae (Zweifel 1985): *Cophixalus*, 14 species, of which 11 are endemic to the Wet Tropics and three have restricted distributions on northern Cape York, and *Austrochaperina*, five species, of which three are endemic to the Wet Tropics, one is restricted to the northern tip of the Northern Territory and one is shared between northern Cape York and south-western Papua New Guinea.

Knowledge on the Australian *Cophixalus* and *Austrochaperina* has lagged behind that of most other Australian frog genera. This is primarily due to their restriction to remote areas in the far north into which access is limited during the wet season when males are calling. Additionally, the species are generally very small, morphologically conservative and lead cryptic lifestyles. Much of what is known of Australian microhylids can be attributed to the comprehensive work of Zweifel (1985). Through an analysis of museum specimens and calls his revision took the number of recognised species from 9 (5 *Cophixalus* and 4 *Sphenophryne*) to 16 (11 *Cophixalus* and 5 *Sphenophryne*). Zweifel (1985) also used external morphology to construct a tree of relationships; however, this was based on few characters for which the polarity could be determined and was described by the author as an arrangement that was 'tenuous at best'. The Australian *Austrochaperina* species were formerly included in *Sphenophryne* (Parker 1934; Zweifel 1965, 1985) but were recently referred back to *Austrochaperina*, a genus distributed through northern Australia and New Guinea (Zweifel 2000).

With the exception of the description of two new species – *C. monticola* from Mt Lewis (Richards *et al*. 1994) and *C. zweifeli* from Cape Melville (Davies and McDonald 1998) – and an assessment of distributions and conservation status (McDonald 1992), little has been added to our understanding of Australian microhylid frogs over the last two decades. Importantly, the interspecific relationships presented by Zweifel (1985) have not been tested, the calls of several species have remained undescribed, there has been limited assessment of call variation within species, distributional limits of several species have remained poorly known, and very little has been added with respect to the reproductive biology of the species. The most important effect of the absence of such information has been a level of confusion over the number of species in total and at particular localities, and speculation that several species remain undescribed. In particular, this has been the case in the northern Wet Tropics from where there have been regular suggestions of undescribed species based on unusual calls and uncertainty over the identity of *C. concinnus*. Zweifel (1985) recognised considerable variation in *C. concinnus* and questioned whether two species were included. As presented herein, *C. concinnus* was described from a type series consisting of two species.

This paper represents the culmination of seven years of fieldwork, molecular analysis, and assessment of museum specimens, and resolves the taxonomic confusion that has persisted over the last two decades. I present an mtDNA phylogeny, a description of a new species, a species redescription, new calls for two species, an assessment of call variation within species, and new data on species distributions and reproductive biology.

Methods

Morphometrics

Specimens examined are held in the Queensland Museum (QMJ codes) or will soon be deposited there by myself (N codes). Methods of measurement for the following characters follow Zweifel (1985): snout to vent length (SVL), tibia length (TL), head width (HW), eye diameter (ED), eye to naris distance (EN), distance between the nares (IN), third finger disc width (3DW), fourth toe disc width (4DW). SVL and ED are equivalent to the terminology SV and EYE used by Zweifel (1985). Additional measurements are: head length (HL) (jaw angle to tip of snout), body width (BW) (measured at armpits), third finger width (3FW) (width of penultimate phalange measured at right angle to the digital axis), third finger length (3FL) (length from split with second finger to tip of disc), fourth toe width (4TW) (width of penultimate phalange measured at right angle to the digital axis), fourth toe length (4TL) (length from split with third toe to tip of disc). All measurements were taken by myself using Mitutoyo electronic callipers to the nearest 0.01 mm. Finer measurements (ED, EN, IN, 3DW, 3FW, 3FL, 4DW, 4TW and 4TL) were performed under a dissecting

microscope. Field measurements of calling males were taken using Mitutoyo vernier callipers and were not included in morphological analyses. Morphological analysis was conducted using the software SPSS ver. 11.5.0.

Molecular systematics

Liver samples and toe clips were extracted using Chelex (Singer-Sam *et al*. 1989) or phenol–chloroform (Maniatus *et al*. 1982). Portions of the mitochondrial 16S rRNA and 12S rRNA were amplified using primers 16Sar and 16Sbr (Cunningham *et al*. 1992), and 12Sa and 12Sb (Kocher *et al*. 1989). All amplifications followed standard PCR conditions (Palumbi 1996) and products were gel-purified and both strands were sequenced manually or on an ABI 377 automated sequencer following standard dye-termination sequencing protocols. Sequences were aligned using Clustal X (Thompson *et al*. 1997) and by eye. The final dataset consisted of 943 base pairs (bp) (527 bp 16S and 416 bp 12S) of aligned mtDNA sequences for all Australian species of *Cophixalus* (except *C. peninsularis*) and *Austrochaperina* (except *A. adelphe*).

For phylogenetic analyses, the *Austrochaperina* spp. were used as an outgroup to the *Cophixalus* spp. Two methods were used – maximum likelihood using Paup* ver. 4.0b5 (Swofford 2000) and Markov-Chain Monte Carlo (MCMC)–Bayesian techniques implemented in MrBayes 2.0 (Huelsenbeck and Ronquist 2001). The Modelltest procedure (Posada and Crandall 2001) was used to choose a General Time Reversible model of nucleotide substitution with gamma-distributed rate variation among nucleotide sites for the combined 16S and 12S data. Four separate Markov-Chain Monte Carlo chains (one cold and three heated) were run for 1.0×10^6 generations and sampled every 100 generations to give a sample of 10 000 trees. The log-likelihood scores of sample points were plotted against generation time to assess the time taken for stationarity in scores to be achieved (Huelsenbeck and Ronquist 2001). The first 1000 sample points were excluded and the remaining 9000 trees (of 240 different topologies) were utilised to derive a 50% majority-rule consensus tree with posterior probabilities of the clades. Bootstrap analyses were conducted in Paup* ver. 4.0b5 using the same model with fixed parameters as determined in Modelltest, with 1000 heuristic tree searches using the tree-bisection-reconnection (TBR) branch-swapping algorithm. We used the likelihood-based Shimodaira–Hasegawa test to assess our preferred tree toplogy against alternative phylogenetic hypotheses (Shimodaira and Hasegawa 1999).

Call recording and analysis

A Sony Professional DAT recorder (TCD-D100) and a Sennheiser (K6 ME-66) directional microphone were used for most call recordings made by myself. Additionally, I used a Sanyo (M-5645) microcassette recorder for several recordings. Recordings were made at ~30 cm from the frog with gain controlled manually. Air temperature was taken to within 0.1°C and male SVL, TL, HW, 3DW and weight were measured. Calls were sampled at 44 100 Hz on a Macintosh G4, and were analysed using the software Canary ver. 1.2.1. The definition of call characteristics follow those outlined in Zweifel (1985). The following were measured: dominant frequency (the frequency at which the call is of greatest intensity), duration (beginning of the first pulse to the end of the last pulse), number of notes (measured for *Austrochaperina*, couplets were considered to consist of two notes), number of pulses (measured for *Cophixalus*), and note or pulse rate (number of notes or pulses divided by call duration). Frequency modulation refers to a change in dominant frequency over the duration of a call. Zweifel (1985) avoided using the term 'trill' due to possible confusion with musical terminology in which a trill may have modulations that alternate. I use the term herein simply to describe a call that is more finely pulsed than a tap but not as finely pulsed as a buzz.

The spectrograms presented display duration (*x*-axis), frequency (*y*-axis) and intensity (degree of shading) of a single representative call. Five replicate calls per individual and multiple individuals for most species (generally more than 4 and up to 40 for *C. ornatus*) were analysed to determine a representative call for each species or call 'type' within species. It was not possible to analyse the calls of multiple individuals for all species – the calls of only one individual were available for *A. gracilipes*, *C. crepitans* and *C. saxatilis*. Therefore the representative calls and call characteristics presented serve to illustrate the fundamental differences between species and significant call types within species, and do not account for minor variation within species or lineages resulting from such factors as male size and ambient air temperature (Duellman and Trueb 1994; Hoskin, unpublished data). As much as was possible I used calls recorded at similar temperatures across the species; however, recording temperatures were not available for several recordings made by other researchers.

Phylogeny

The phylogeny presented in Fig. 1 is the best estimate of relationships among the Australian *Austrochaperina* and *Cophixalus*. Parsimony analyses with various weighting schemes and Neighbour-Joining analyses using various models of sequence divergence resulted in trees
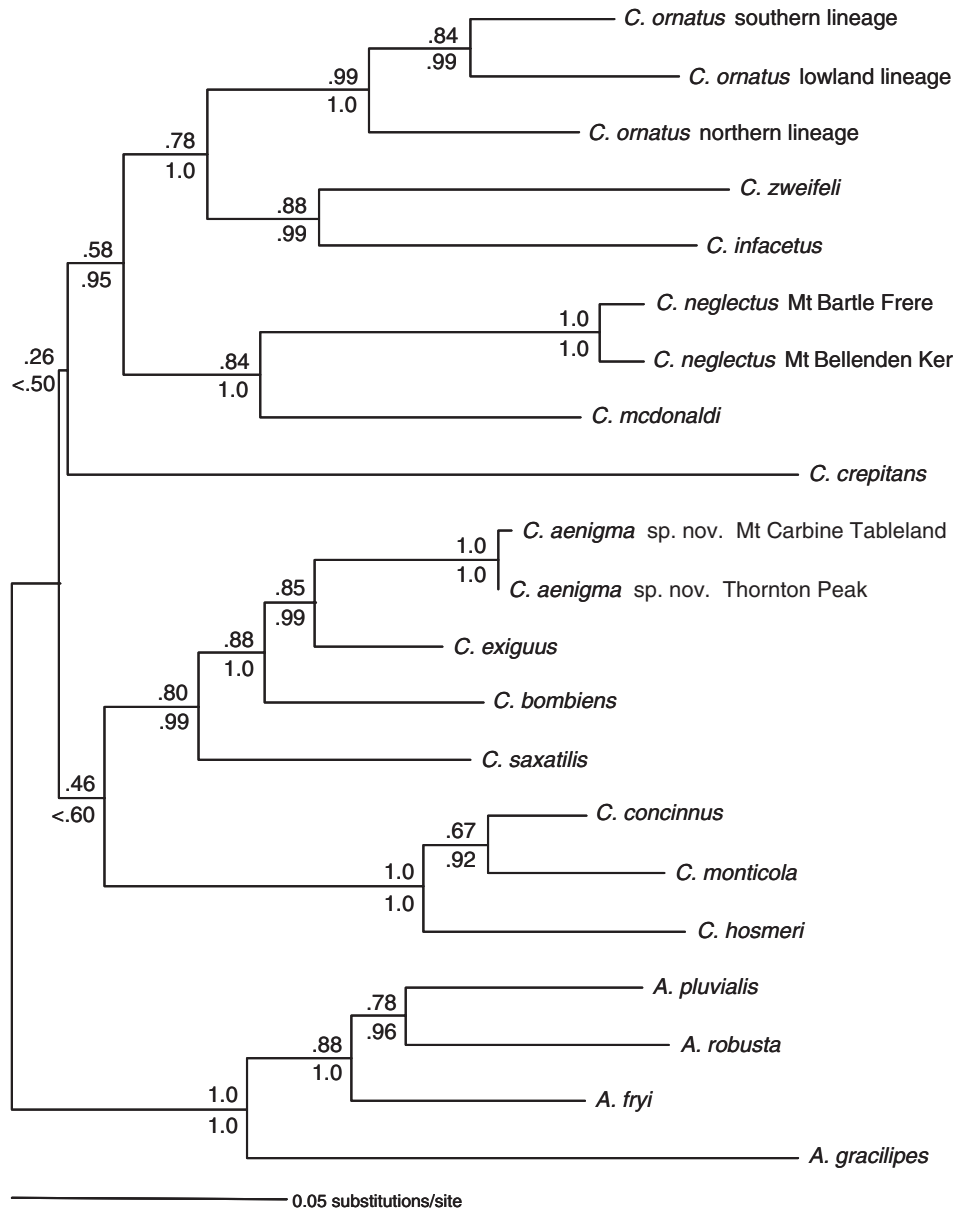

Fig. 1. Maximum-likelihood phylogeny of Australian microhylid frogs (*Cophixalus* and *Austrochaperina*) based on analysis of 943 bp of mitochondrial 16S rRNA and 12S rRNA genes. Bayesian posterior probabilities are presented below the branches and heuristic bootstrap proportions above the branches. For details on localities and number of individuals sequenced for each species see Appendix.

of similar topology. For simplicity, only one individual of each species or lineage is presented. See the Appendix for details on localities and the number of individuals sequenced for each species. In preliminary analyses incorporating several New Guinean species of *Cophixalus*, the Australian *Cophixalus* form a monophyletic clade (Hoskin and Bickford, unpublished data).

There is high posterior probability and bootstrap support for the following clades: 1. (*C. ornatus*, (*C. infacetus*, *C. zweifeli*)), (*C. neglectus*, *C. mcdonaldi*); 2. *C. crepitans*; 3. *C. saxatilis*, (*C. bombiens*, (*C. aenigma*, *C. exiguus*)); 4. *C. hosmeri*, (*C. concinnus*, *C. monticola*); and 5. *A. gracilipes*, (*A. fryi*, (*A. robusta*, *A. pluvialis*)). The relationship between the four major *Cophixalus* clades remains ambiguous. Average sequence divergence between species is very high, averaging 18% across *Cophixalus* and 13% across *Austrochaperina*. Divergence between sister species is substantial: *Cophixalus*, minimum 5%, mean = 11%, and *Austrochaperina*, minimum 9%, mean = 11.5%. There is also significant structuring within *C. ornatus* and between subpopulations in *C. neglectus* and *C. aenigma* (Hoskin *et al.*, unpublished).

The molecular phylogeny supports the current taxonomy with the exception of *C. aenigma* and *C. concinnus*, which are dealt with herein. Tissue samples for *C. peninsularis* and *A. adelphe* could not be obtained. This tree differs dramatically from that based on external morphological characters presented by Zweifel (1985). Attempts to construct a tree based on morphology were described as 'unsatisfying' and resulting in 'many similarly unparsimonious arrangements' (Zweifel 1985). Until the polarity of such characters can be established with some degree of confidence, trees of interspecific relationships based on external morphology will remain inaccurate.

Systematics

The following presents a resolution to the confusion surrounding *Cophixalus concinnus*. The original type series and all subsequent collections consist of two species. *C. concinnus* is redescribed based on the holotype, 2 paratypes and all 14 specimens of this species in the Queensland Museum collections. *C. aenigma*, sp. nov., is described from material in the original *C. concinnus* collection (including a paratype attributed to that species) and is assigned to *Cophixalus* on the basis of external morphological characters and molecular data. No internal morphology was assessed in this study.

Cophixalus aenigma, sp. nov. (tapping nursery-frog)

(Fig. 2)

Holotype

QMJ79446, male, summit of Thornton Peak (16°10′S, 145°22′20″E), north-east Queensland, 1300 m elevation, C. Hoskin, 25 November 1996.

Holotype data

QMJ79446, male (calling when captured), SVL 19.68 mm, TL 7.97 mm, HW 1.68 mm, HL 4.52 mm, BW 7.75 mm, ED 2.51 mm, EN 1.68 mm, IN 1.74 mm, 3DW 0.60 mm, 3FW 0.35 mm, 3FL 2.50 mm, 4DW 0.60 mm, 4TW 0.34 mm, 4TL 4.61 mm, TL/SVL 0.41, HW/SVL 0.34, HL/SVL 0.23, BW/SVL 0.39, ED/SVL 0.13, ED/SVL 0.13, EN/IN 0.97, 3DW/SVL 0.030, 3FL/SVL 0.13 mm, 4DW/SVL 0.030, 4TL/SVL 0.23 mm, 3DW/4DW 1.00.
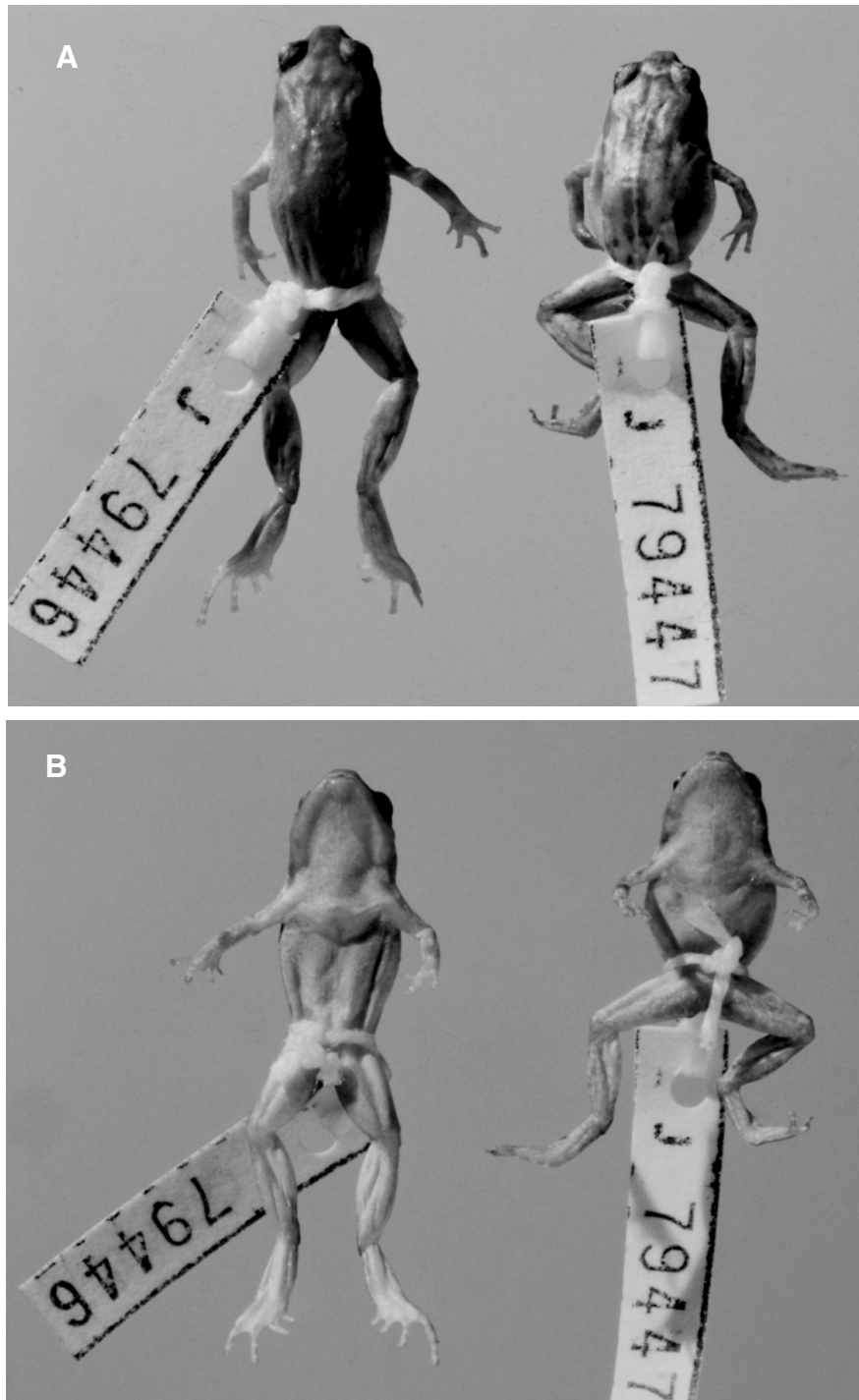
Fig. 2.   *Cophixalus aenigma*, sp. nov. (holotype, QMJ79446 and paratype, QMJ79447), dorsal (*A*) and ventral (*B*) view, Thornton Peak, north-east Queensland (photographs: Jeff Wright).

Paratypes

QMJ40565, QMJ40570, QMJ40572, QMJ40576, Mt Finnigan (15°49′30″S, 145°16′30″E); QMJ51923, QMJ60954, 1050 m, Mt Finnigan, via Helenvale (15°49′30″S, 145°16′30″E); QMJ62923, 1060 m, Mt Finnigan (15°49′30″S, 145°16′30″E); QMJ79447, male (calling when captured), 1300 m, Thornton Peak (16°10′S, 145°22′20″E); QMJ30746, male (calling when captured), 1250 m, Thornton Peak (16°10′S, 145°22′20″E); QMJ39889, QMJ39901, QMJ42246–7, QMJ42249–50, Thornton Peak (16°10′S, 145°22′20″E); QMJ67124, 1225 m, Mt Spurgeon (16°22′S, 145°13′E); QMJ66966, Black Mountain, 4.5 km N of Mt Spurgeon (16°24′S, 145°12′E); QMJ53915, Mt Spurgeon (16°26′S, 145°12′E); QMJ48715, Mossman Bluff, 10 km W of Mossman (16°27′S, 145°17′E); QMJ41690, 1000 m, The Bluff, 11 km W of Mossman (16°28′S, 145°16′E); QMJ67122–3, 1000 m, Mossman Bluff track, 9 km W of Mossman (16°28′S, 145°17′E); QMJ29603, QMJ53852, QMJ53858, QMJ53861, QMJ53871, QMJ53879, QMJ53901–2, QMJ53904, Mt Lewis (16°35′S, 145°17′E); QMJ39899, 900 m, Bakers Blue Mountain, 17 km W of Mt Molloy (16°42′S, 145°10′E).

Diagnosis

Cophixalus aenigma can be distinguished from Australian congeners by a combination of the following characters: moderate size (SVL 16.8–22.6 mm), eye to naris distance less than distance between the nares (EN/IN < 1), short hind legs (TL/SVL 0.36–0.44), tip of first finger disclike though not expanded, and call a slow to medium-paced tapping.

Description

Variation across type series (*n* = 33, all adult), range followed by mean in parentheses: *Measurements* (mm): SVL 15.72–22.58 (19.33), TL 6.47–8.66 (7.62), HW 6.01–8.74 (7.14), HL3.67–5.55 (4.64), BW 6.21–9.90 (7.26), ED 1.98–2.67 (2.28), EN 1.22–1.81 (1.50), IN 1.46–2.12 (1.72), 3DW 0.45–0.81 (0.61), 3FW 0.23–0.49 (0.38), 3FL 2.09–3.27 (2.57), 4DW 0.54–0.88 (0.68), 4TW 0.32–0.60 (0.46), 4TL 3.79–5.12 (4.44). *Proportions*: TL/SVL 0.36–0.44 (0.40), HW/SVL 0.33–0.42 (0.37), HL/SVL 0.22–0.27 (0.24), BW/SVL 0.34–0.46 (0.38), ED/SVL 0.10–0.13 (0.12), EN/IN 0.76–0.97 (0.87), 3DW/SVL 0.023–0.039 (0.032), 3FL/SVL 0.12–0.16 (0.13), 4DW/SVL 0.024–0.046 (0.035), 4TL/SVL 0.20–0.26 (0.23), 3DW/4DW 0.61–1.17 (0.91).

Variation in measurements between sexes could not be assessed as, although most of the type series were no doubt collected as calling males, for many such collection details were not recorded. As is the case for most Australian microhylids, no external sexual dimorphism is evident.

Head: slightly narrower than body; snout bluntly rounded in dorsal view and slightly projecting in profile, canthus rostralis rounded, loreal region steep, nostrils much closer to tip of snout than to eye, nostrils directed laterally; eye diameter greater than eye to naris distance; internarial distance greater than distance from eye to naris; tympanum small and indistinct beneath overlying skin. *Body:* urostyle prominent. *Limbs:* hindlimbs relatively short; fingers and toes unwebbed; fingers short, relative length 3 > 4 > 2 > 1, grooved, rounded finger discs obviously expanded from penultimate phalanx (3DW/3FW 1.22–2.13, mean = 1.61), first finger short with disc at most only marginally expanded, no tubercles on palm, metacarpal and subarticular tubercles low and indistinct; relative length of toes 4 > 3 > 5 > 2 > 1, grooved, rounded toe discs expanded from penultimate phalanx (4DW/4TW 1.05–1.82, mean = 1.49), disc on first toe not (or only marginally) expanded;

no tubercles on sole, metatarsal and subarticular tubercles low and indistinct; discs on longest fingers smaller to slightly larger than discs on longest toes (3DW/4DW 0.61–1.17, mean = 0.91). *Skin:* ventral surface smooth, dorsal surface of body, head and limbs smooth or with scattered low tubercles in some specimens; faint to distinct postorbital skin fold extending along dorso-lateral surface to mid-body.

Pattern and colour

In preservative (Fig. 2): Dorsal pattern and colour highly variable, ranging from even brown (*n* = 15) to uneven brown and heavily mottled with black (*n* = 17) and sometimes with a thin pale vertebral line (*n* = 1). Top of snout, canthal region and eyelids often darker and commonly a dark postorbital streak passing over ear and following the underside of the postorbital dorso-lateral skin fold. Occasionally, individuals are marked with a distinctly pale 'cap' between eyes and nares and pale elbows and ankles. Pale lumbar ocelli range from indistinct (*n* = 10) to moderately or highly distinct (*n* = 23). Ventrally evenly pale (*n* = 28), evenly grey (*n* = 3) or with fine dark speckling on a pale background (*n* = 2). Diffuse transition between dorsal and ventral colouration. *In life* (see '*C. concinnus*' photographs in McDonald 1991, 2000; Tyler 1992; Barker *et al.* 1995; Cogger 2000): Dorsal pattern and colour highly variable, ranging from even grey, brown or sand, to mottled brown or orange, to dark brown or pale with dark flecking, to grey or dark with a gold 'cap' and golden ankles and elbows. Some individuals have a thin pale vertebral stripe while others have a broad dark mid-dorsal area and paler flanks. Pale lumbar ocelli usually highly visible. Ventral surfaces evenly pale, grey or flushed with orange, especially in the axilla and groin. Last digit of fingers and toes pale and discs often orange or red. Pupil bordered by a thin red line. Iris dark but heavily flecked with grey or lime green in the lower and, particularly, upper sections.

Variation between subpopulations

Variation in morphology and pattern across the type series was assessed with respect to the four major subpopulations: Carbine Tableland (*n* = 16), Thornton Uplands (*n* = 9), Finnigan Uplands (*n* = 7) and Bakers Blue Mountain (*n* = 1). The subpopulations show a very high degree of morphological similarity for all characters and ratios measured. The only differences are in the relative widths of the discs of the third finger and fourth toe, which are slightly smaller in the frogs from Carbine Tableland and marginally larger in those from Mt Finnigan. With respect to pattern the only difference is in the presence of pale lumbar ocelli, which are rare in the frogs from Mt Finnigan (14%), moderately common in individuals from Thornton Peak (67%) and present in all frogs from Carbine Tableland and Bakers Blue Mountain.

Comparison

Cophixalus aenigma co-occurs with *C. monticola*, *C. hosmeri* and *C. ornatus* in the Carbine Uplands and with *C. concinnus* in the Thornton Uplands (Fig. 3). *C. aenigma* is not currently known to be in sympatry with *C. exiguus* or *C. bombiens* but the three species occur in close proximity in the vicinity of Mt Finnigan (Fig. 3). The section '*C. aenigma*, *C. concinnus* and *C. monticola*' (below) provides a detailed comparison of these three species. The relatively large adult body size of *C. aenigma* (rarely less than 17 mm) distinguishes it from *C. hosmeri* and *C. bombiens* (maximum adult size 17 mm) and from most *C. exiguus* (generally less than 17 mm) (Zweifel 1985). The first finger of *C. aenigma* is tipped with a grooved disc (though not expanded) as opposed to the discless first fingers
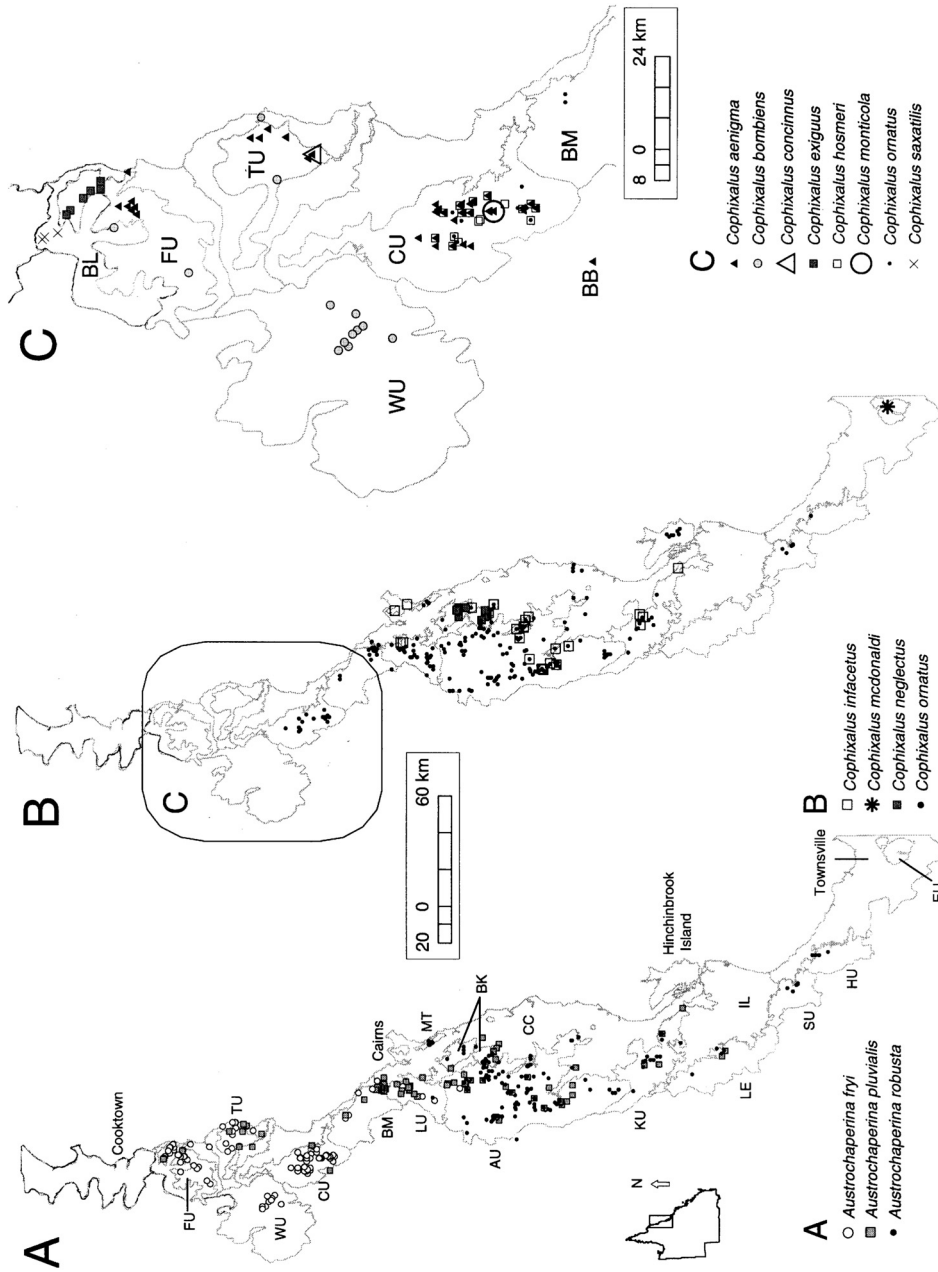
Fig. 3. Microhylid distributions in the Wet Tropics, north-east Queensland. Subregions are defined following Williams *et al.* (1996): BL, Bloomfield–Helenvale Lowlands; FU, Mt Finnigan Uplands; TU, Thornton Uplands; WU, Windsor Uplands; CU, Carbine Uplands; BB, Bakers Blue Mountain; BM, Black Mountain Corridor; LU, Lamb Uplands; MT, Malbon–Thompson Uplands; BK, Bellenden Ker/Bartle Frere; AU, Atherton Uplands; CC, Cairns–Cardwell Lowlands; KU, Kirrama Uplands; LE, Lee Uplands; IL, Ingham Lowlands; SU, Spec Uplands; HU, Halifax Uplands; EU, Elliot Uplands.
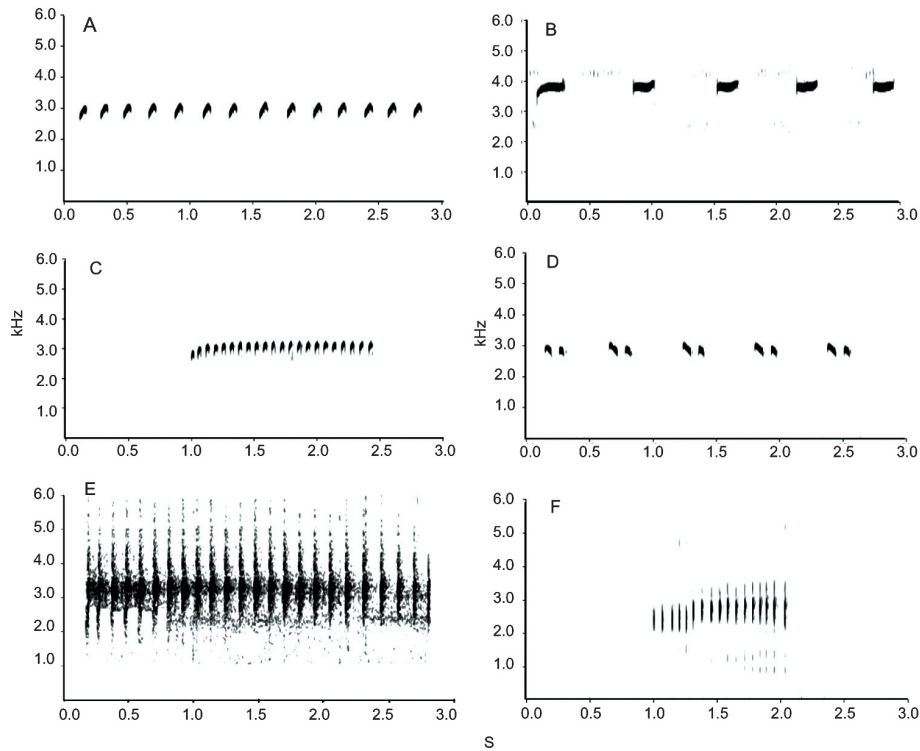
Fig. 4. Spectrograms of the advertisement calls of Australian *Austrochaperina* and *Cophixalus* (recording temp. °C). *A*: *A. fryi* (22); *B*: *A. gracilipes* (24); *C*: *A. pluvialis* (22); *D*: *A. robusta* (22); *E*: *C. aenigma* (Thornton, Carbine); *F*: *C. aenigma* (Mt Finnigan) (20); *G*: *C. bombiens*; *H*: *C. concinnus*; *I*: *C. crepitans* (24); *J*: *C. exiguus*, *K*: *C. hosmeri* (20); *L*: *C. infacetus* (21); *M*: *C. mcdonaldi* (22); *N*: *C. monticola* (20); *O*: *C. neglectus* (18); *P*: *C. ornatus* (21); *Q*: *C. saxatilis* (26). Additional recordings provided by Jean-Marc Hero (*E*, *H*), David Stewart (*B*, *G*, *J*) and Keith McDonald (*I*, *Q*). All calls shown to equal scale. All spectrograms represent one complete call except for *A. gracilipes* and *C. saxatilis* in which the call extends beyond the displayed duration. For details of call characteristics, snout to vent lengths and localities, see Table 1.

of *C. bombiens* and *C. hosmeri* (Zweifel 1985). The hind legs of *C. aenigma* are relatively short (TL/SVL 0.36–0.44, mean = 0.40) compared with those of *C. exiguus* (TL/SVL 0.40–0.49, mean = 0.45: Zweifel 1985), and the EN/IN ratio of *C. aenigma* is relatively high (0.76–0.97, mean = 0.87) compared with that in *C. hosmeri* (0.70–0.85, mean = 0.76: Zweifel 1985) and *C. bombiens* (0.69–0.83, mean = 0.75: Zweifel 1985). There is, however, considerable overlap in these measures. The relatively small, rounded finger discs of *C. aenigma* readily distinguish it from the large, nearly truncate finger discs of *C. ornatus*. The slow to medium-paced tapping call of *C. aenigma* differs obviously from the rapidly pulsed tapping calls of *C. hosmeri*, the buzz of *C. bombiens* and the very rapidly pulsed bleat of *C. ornatus* (Fig. 4; Table 1). The call of *C. aenigma* on the Carbine and Thornton Uplands is a much slower tapping than the medium-paced tapping of *C. exiguus* (Fig. 4; Table 1). The population of *C. aenigma* on Mt Finnigan utters a medium-paced tapping similar to the call of *C. exiguus* but it is ~1 KHz lower in dominant frequency (Fig. 4; Table 1).
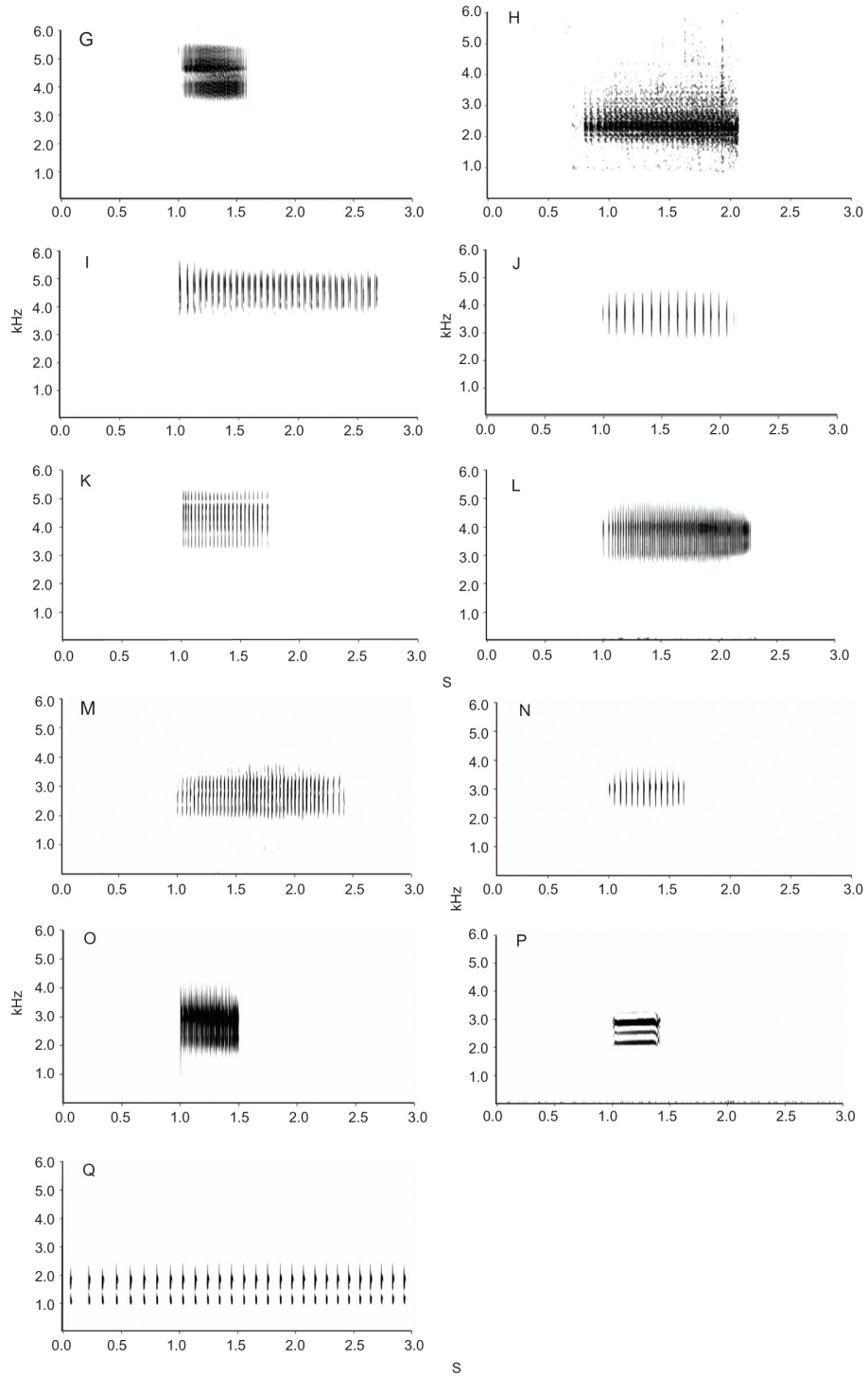
Fig. 4. (*Continued*).

Table 1.   Characteristics of representative calls of Australian microhylids with intraspecific variation noted

Note: calls of *Austrochaperina adelphe*, *Cophixalus peninsularis* and *C. zweifeli*. SVL = snout to vent length, T°C = recording temperature (n.a. = not available). See Appendix for locality coordinates, except for Lake Barrine (17°15′S, 145°38′E) and Mt Diamantina (18°25′S, 146°17′E)

Species	Call 'type'	Notes or pulses per call[A]	Duration (s)	Dominant frequency (kHz)	Notes or pulses per second[B]	SVL (mm)	Temp. (°C)	Locality
A. fryi		14	2.72	2.95	5.15	28.8	21.5	Lake Barrine
A. fryi	Unusual (hybrid?)	17	2.85	2.92	5.97	29.3	21.5	Lake Barrine
A. gracilipes		26	15.92	3.78	1.63	19.5	24.0	McIlwraith Range
A. pluvialis		22	1.43	3.10	15.38	23.5	21.5	Kuranda
A. robusta		10	2.41	2.86	4.15	23.0	22.0	Paluma Range
C. aenigma	Carbine Uplands	24	2.40	3.14	10.00	18.9	19.9	Mt Lewis
C. aenigma	Thornton Uplands	24	2.75	3.35	8.73	19.4	20.0	Thornton Peak
C. aenigma	Mt Finnigan	17	1.12	2.76	15.18	18.5	20.0	Mt Finnigan
C. aenigma	Unusual (Mt Finnigan)	40	1.19	3.17	33.61	18.5	20.0	Mt Finnigan
C. bombiens		68	0.59	4.67	114.88	13.5	n.a.	Windsor Tableland
C. concinnus		31	1.27	2.30	24.42	22.5	n.a.	Thornton Peak
C. crepitans		64	1.66	4.78	38.62	14.0	24.0	McIlwraith Range
C. exiguus		16	1.06	3.67	15.13	14.8	n.a.	Big Tableland
C. hosmeri	Buzz	75	0.70	5.15	106.94	12.1	19.8	Mt Lewis
C. hosmeri	Medium tap	14	1.00	5.10	14.00	14.0	19.9	Mt Lewis
C. hosmeri	Fast tap	23	0.71	4.70	32.47	13.3	19.8	Mt Lewis
C. infacetus		80	1.27	4.00	63.12	15.0	21.0	Palmerston
C. mcdonaldi		43	1.42	2.66	30.28	17.5	22.0	Mt Elliot
C. monticola		14	0.61	3.10	22.88	18.3	19.8	Mt Lewis
C. neglectus	Mt Bartle Frere	62	0.62	2.93	100.70	22.0	18.0	Mt Bartle Frere
C. neglectus	Mt Bellenden Ker	78	0.49	2.91	158.05	22.0	18.0	Mt Bellenden Ker
C. ornatus		168	0.42	2.90	399.62	23.0	20.5	Lamb Range
C. ornatus	Lowland	103	0.21	3.50	487.40	19.3	26.2	Mission Beach
C. ornatus	Hinchinbrook Is.	136	0.36	3.04	373.91	19.7	20.0	Mt Diamantina
C. ornatus	Unusual (hybrid?)	278	0.41	1.79	683.89	36.7	19.5	Mt Bartle Frere
C. ornatus	Leading	211	0.49	2.92	429.43	24.9	20.3	Lamb Range
C. ornatus	At nest	88	0.35	2.80	251.43	23.5	19.5	Lamb Range
C. saxatilis		42	4.03	1.85	10.43	32.0	26.0	Black Trevethan Range

[A]Note: calls of species of *Austrochaperina* are measured as notes per call, those of species of *Cophixalus* as pulses per call.
[B]Note: calls of species of *Austrochaperina* are measured as notes per second, those of species of *Cophixalus* as pulses per second.

Etymology

From the Latin *aenigma* = a riddle, what is obscure or a mystery; referring to the inclusion of this species among the type series and subsequent collections of *C. concinnus* and the confusion this has created.

Genetics

Average sequence divergence between *C. aenigma* and all other Australian *Cophixalus* is 16% (12S and 16S rRNA, Fig. 1). *C. aenigma* and *C. exiguus* are closely related sister-species (5.6% sequence divergence) nested in a strongly supported clade with *C. bombiens* and *C. saxatilis*. This group represents a clade of geographically adjacent sister-species (Hoskin *et al.*, unpublished). With respect to structuring within *C. aenigma*, less than 0.5% sequence divergence separates the subpopulations on the Thornton ($n = 4$) and Carbine Uplands ($n = 8$), whereas divergence between these subpopulations and the one on Mt Finnigan ($n = 3$) is considerably greater (1.5% 550 bp 16S rRNA: Hoskin, unpublished data). The Bakers Blue Mountain population was not sampled.

Call

A slow to medium-paced tapping reminiscent of a marble dropping on a tile (Figs 4*E*, *F*, 5; Table 1). Males of the Carbine and Thornton Upland subpopulations make a similar slow tapping call of the following mean characteristics: dominant frequency 3.24 kHz, duration 2.58 s, pulses per call 24 and pulse rate 9.36 pulses/s; recorded at ~20°C (Fig. 4*E*; Table 1). The call on Mt Finnigan is shorter and has a higher pulse rate and lower dominant frequency (dominant frequency 2.76 kHz, duration 1.12 s, pulses per call 17, and pulse rate 15.18 pulses/s; recorded at 20°C) (Fig. 4*E*; Table 1). Call variation within sites has been observed in *C. aenigma* and is presented in the section 'Call variation within species' (below). The call of the Bakers Blue Mountain population has not been recorded. The calls presented as *C. concinnus* in Zweifel (1985), Richards *et al.* (1994), Hero (1995) and Stewart (1998) are *C. aenigma*.

Distribution

Restricted to higher altitudes (generally >750 m) of the Mt Carbine Tableland, Thornton Uplands (Thornton Peak, Mt Pieter Botte, Mt Hemmant, Mt Halcyon), Finnigan Uplands (Mt Finnigan, Mt Finlay) and Bakers Blue Mountain, north-east Queensland (Fig. 3). These four regions (and possibly also several of those listed within the Thornton and Finnigan Uplands) represent isolated subpopulations separated by areas well below the minimum recorded altitude for *C. aenigma*. The Bakers Blue record is represented by one specimen (QMJ39899) that is morphologically consistent with *C. aenigma*. The specimen (QMJ27263) from Mt Finlay (15°48′S, 145°21′E) is of interest as the summit of this mountain (586 m) is of considerably lower altitude than all other records for this species.

Habitat and habits

Cophixalus aenigma occurs in montane vegetation mapped as simple microphyll vine-fern forest and simple microphyll vine-fern thicket (Tracey and Webb 1975). Males generally call from concealed sites among leaf litter, exposed roots, rocks and fallen debris on the forest floor. Occasionally, males call from slightly elevated sites (<0.3 m) on logs, rocks and low vegetation. The only information on clutch size comes from the dissection of a gravid female *C. aenigma* (N72131) collected on Mt Lewis on 22 January 1996, which contained 12 eggs. *C. aenigma* is sympatric with *C. hosmeri*, *C. monticola*, *C. ornatus* and *A. fryi* on
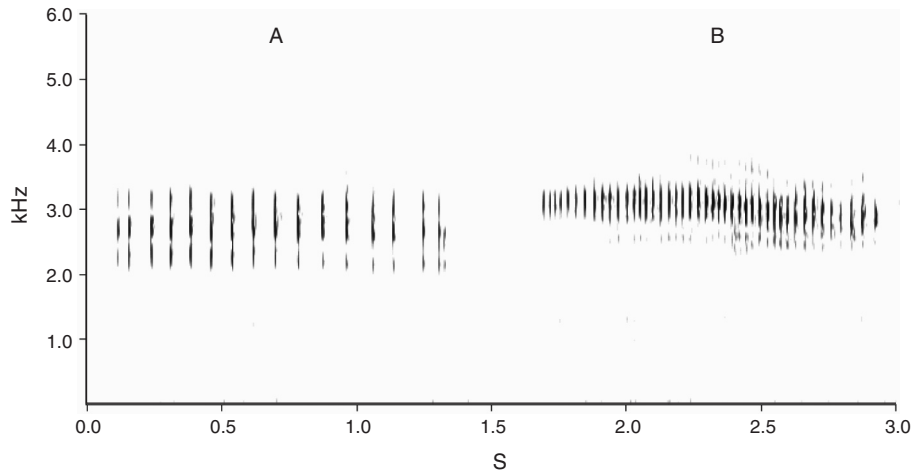
Fig. 5. Spectrogram of call variation in *Cophixalus aenigma* on Mt Finnigan. *A*: 'normal' call; *B*: unusual call (both recorded at 21°C).

the Mount Carbine Tableland, with *C. concinnus*, *A. fryi* and *A. pluvialis* in the Thornton Uplands, and with *A. fryi* and *A. pluvialis* in the Finnigan Uplands (Fig. 3).

Comments

This species was first collected on Mt Spurgeon in 1932 and included in *Sphenophryne polysticta* (a New Guinean species now recognised as *Austrochaperina polysticta*) along with several other Australian species of *Cophixalus* and *Sphenophryne* (Zweifel 1985). This collection was subsequently assessed by Zweifel (1962) and recognised as a distinct species to be described when more material became available. Subsequent collections were made on Mt Spurgeon, Mt Lewis, Mt Finnigan and Thornton Peak. However, the resulting description by Tyler (1979) was based on a series consisting of two species from Thornton Peak, and *C. aenigma* was included as a paratype (QMJ30746) of *C. concinnus*. *C. concinnus* is restricted to the summit of Thornton Peak and has rarely been collected since, with most of the collections representing the relatively widely distributed (geographically and altitudinally) *C. aenigma*.

The common name 'tapping nursery-frog' (Stewart 1998; McDonald 2000) was formerly associated with *C. concinnus* but is much more suitable for this species. Males of *C. aenigma* have a relatively slow tapping call whereas the call of *C. concinnus* is a rapidly pulsed trill.

Cophixalus concinnus Tyler, 1979 (beautiful nursery-frog)

(Fig. 6)

Material examined

QMJ30743 (holotype), female, 1250 m, Thornton Peak (16°10′S, 145°22′20″E), north-east Queensland; QMJ30744–5 (paratypes), males (calling when captured), location as for holotype; QMJ79448, male (calling when captured), QMJ79449, female, 1300 m, Thornton Peak (16°10′S, 145°22′20″E); QMJ43917, QMJ48729 (subadult), 1200 m, Thornton Peak (16°10′S, 145°22′20″E); QMJ42263, QMJ46009, 1100–1200 m, Thornton
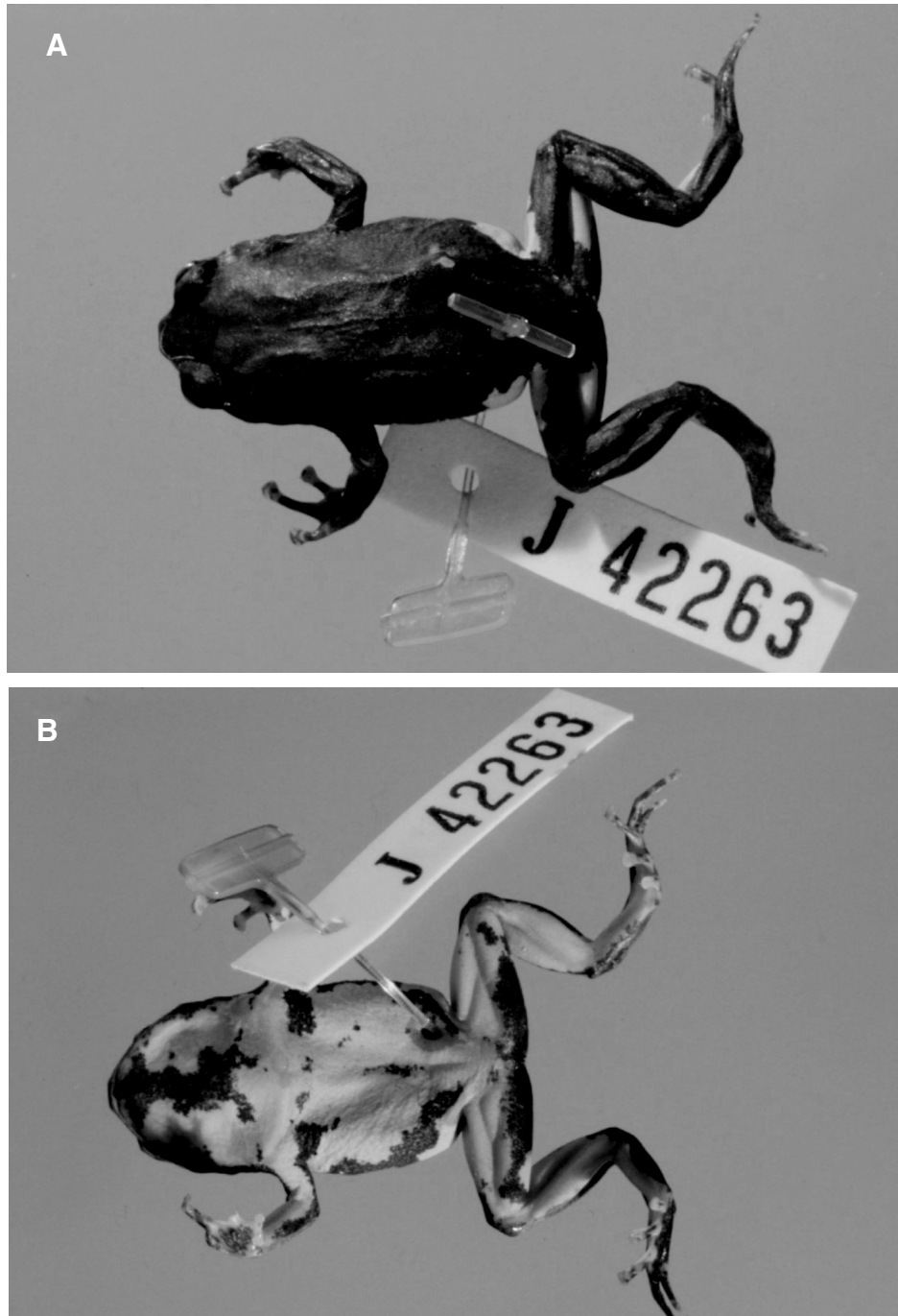
Fig. 6. *Cophixalus concinnus* (QMJ42263), dorsal (*A*) and ventral (B) view, Thornton Peak, north-east Queensland (photographs: Jeff Wright).

Peak (16°10′S, 145°22′20″E); QMJ39909, QMJ43885, QMJ43899, QMJ43908, 1100–1300 m, Thornton Peak (16°10′S, 145°22′20″E); QMJ43886–7, QMJ43889, unlabelled QM specimen, Thornton Peak (16°10′S, 145°22′20″E).

Diagnosis

Cophixalus concinnus has a unique ventral pattern and colouration of dark blotching on a red and white background. *C. concinnus* and *C. zweifeli* are the only Australian *Cophixalus* in which the distance between the eye and naris is greater than that between the nares (EN/IN > 1). Confusion between *C. concinnus* and *C. zweifeli* is unlikely as the latter is a very large, long-legged species restricted to boulder fields on Cape Melville. Additionally, *C. concinnus* can be separated from its Australian congeners by a combination of the following characters: large size (SVL 17.9–26.5 mm), short hind legs (TL/SVL 0.34–0.44), large finger discs (3DW/SVL 0.039–0.053), third finger disc slightly larger to twice the size of the fourth toe disc, and call a short trill.

Description

Details for the holotype (Tyler 1979) are correct but the remainder of the original description is based on a mix of two species (*C. concinnus* and *C. aenigma*). The following presents a redescription based on the above-listed specimens.

Measurements and proportions (*n* = 16, all adult; subadult QMJ48729 not included), range followed by mean in brackets: *Measurements* (mm): SVL 17.90–26.48 (20.94), TL 7.05–9.84 (8.12), HW 7.34–11.11 (8.60), HL 4.40–6.77 (5.24), BW 7.25–12.95 (9.39), ED 2.36–3.50 (2.70), EN 1.29–2.22 (1.69), IN 1.10–2.10 (1.45), 3DW 0.77–1.24 (0.95), 3FW 0.31–0.64 (0.43), 3FL 2.31–4.35 (3.26), 4DW 0.57–0.86 (0.70), 4TW 0.37–0.74 (0.50), 4TL 3.99–5.97 (4.82). *Proportions*: TL/SVL 0.34–0.44 (0.39), HW/SVL 0.37–0.45 (0.41), HL/SVL 0.22–0.26 (0.25), BW/SVL 0.40–0.49 (0.45), ED/SVL 0.12–0.15 (0.13), EN/IN 1.04–1.37 (1.17), 3DW/SVL 0.039–0.053 (0.045), 3FL/SVL 0.11–0.18 (0.16), 4DW/SVL 0.022–0.042 (0.034), 4TL/SVL 0.21–0.27 (0.23), 3DW/4DW 1.15–2.18 (1.38).

The two specimens known definitely to be females (gravid on capture) are considerably larger (QMJ30743, SVL 26.30 mm; QMJ79449, SVL 26.48 mm) than all the other specimens (range = 17.90–23.05, mean = 20.17, *n* = 14). However, variation in measurements between sexes could not be assessed rigorously as most of the specimens were not lodged with details on whether they were calling on capture.

Head: broad and flattened, slightly narrower than body; snout truncate in dorsal view and distinctly projecting in profile, canthus rostralis slightly angular, loreal region oblique, nostrils much closer to tip of snout than to eye, nostrils directed laterally (visible from above); eye large, diameter greater than eye to naris distance; internarial distance less than distance from eye to naris, resulting in a distinctly 'snub-nosed' appearance; tympanum small and indistinct beneath overlying skin. *Body*: broad. *Hindlimbs*: relatively short; fingers and toes unwebbed; fingers long, relative length 3 > 4 > 2 > 1, large, grooved finger discs obviously expanded from penultimate phalanx (3DW/3FW 1.77–2.57, mean = 2.26), finger discs rounded to slightly truncate, first finger short with disc moderately expanded, no tubercles on palm, metacarpal and subarticular tubercles low and indistinct; relative length of toes 4 > 3 > 5 > 2 > 1, grooved, rounded toe discs expanded from toes (4DW/4TW 1.16–1.95, mean = 1.44), disc on first toe marginally expanded, no tubercles on sole,

metatarsal and subarticular tubercles low and indistinct; discs on longest fingers distinctly larger than discs on longest toes (3DW/4DW 1.15–2.18, mean = 1.38). *Skin*: dorsal and ventral surfaces of body, head and limbs smooth; distinct postorbital skin fold extending to forelimbs.

Pattern and colour

In preservative (Fig. 6; also holotype, Fig. 1, Tyler 1979): Dorsal surface of head, body and limbs uniformly dark (*n* = 9) or dull brown (*n* = 8). This dark or brown appearance is due to very heavy stippling. Usually lacking pale lumbar ocelli (6%), faint when present. In dorsal view often white in the groin and an immaculate white bar on the posterior thigh (*n* = 13). Very distinct ventral patterning consisting of black blotching on a pale background. Always heavily blotched (*n* = 13) or stippled (*n* = 4) on throat and in armpits and often heavy blotching on ventro-lateral surface and lower stomach. Immaculate on underside of forearms and across chest between forearms. Groin and underside of hindlimbs usually pale. Joints of toes and discs of toes and fingers pale. Usually a sharp transition between dorsal and ventral colouration. Both specimens known to be female are noticeably paler in preservative than the other specimens. *In life*: Males are uniformly dark dorsally (often appearing black) with a ventral colouration consisting of a pattern of black blotching and areas of red/orange on a white background. The red markings are particularly bright on the vocal sac. The classic ventral patterning and colouration I have seen in males consists of an irregular, unbroken dark area extending from the chin across the central portion of the throat. The area surrounding this is bright orange to red. A pair of dark blotches are present in the armpits and on the lower stomach. The remainder of the ventral surfaces consist of small stippled areas, white background and orange concentrated laterally. The female I found (QMJ79449) was distinctive in her very pale dorsal colouration, almost appearing white. Ventrally, she was of the colouration described for the male except that the black dendritic markings and areas of orange were relatively subdued. The iris of both sexes is dark, often heavily speckled with grey in the upper half.

Comparison

Cophixalus concinnus is known to co-occur only with *C. aenigma*, from which it is readily separated by the characters outlined in the 'Diagnosis' and in detail in the following section '*C. aenigma*, *C. concinnus* and *C. monticola*'.

Genetics

Average sequence divergence between *C. concinnus* and all other Australian *Cophixalus* is 16.5% (Fig. 1). *C. concinnus* and *C. monticola* are closely related sister-species (5% sequence divergence) nested within a strongly supported clade with *C. hosmeri*. The relationship between this clade and the other major *Cophixalus* lineages is unclear. The phylogeny presented provides weak support for grouping these three species with the other clade containing species with narrow distributions in the northern Wet Tropics (*C. saxatilis*, (*C. bombiens*, (*C. exiguus*, *C. aenigma*))).

Call

A short trill with the following mean characteristics: dominant frequency 2.30 kHz, duration 1.27 s, pulses per call 31, and pulse rate 24.43 pulses/s; recorded at 20°C (Fig. 4*H*; Table 1). The call of *C. concinnus* is similar to that of *C. monticola* but differs in being of lower dominant frequency and longer duration (Fig. 4*N*; Table 1). The calls presented for

C. concinnus in Zweifel (1985), Richards *et al.* (1994), Hero (1995) and Stewart (1998) are actually of *C. aenigma*.

Distribution

Restricted to a very small high-altitude area (>1100 m elevation) around the summit of Thornton Peak (16°10′S, 145°22′20″E), north-east Queensland (Fig. 3). The area above 1100 m on Thornton Peak is 718 ha.

Habitat and habits

Found in simple microphyll vine-fern forest and simple microphyll vine-fern thicket (Tracey and Webb 1975) growing among boulders, and in exposed boulder fields around the summit of Thornton Peak. Males call from elevated locations (0.5–3 m) such as holes in tree trunks, rock crevices, fallen vegetation caught in branches, and especially from among vegetation such as orchids and *Rhododendron* growing on the vertical surfaces of large boulders. I have also heard males calling from deep in the exposed boulder fields at the very summit of Thornton Peak. The large finger discs (overlapping the range seen in *C. ornatus*, *C. saxatilis* and *C. zweifeli*: Zweifel 1985; Davies and McDonald 1998) indicate the scansorial habits of this species. The two females were both found at night ~1 m above the ground among low vegetation. *C. concinnus* is sympatric with *Austrochaperina fryi* and *C. aenigma* (Fig. 3) but males of both these species call from the ground or from only slightly elevated positions (<0.3 m).

Males call at the entrance of a small sheltered site and the large brightly patterned red, black and white vocal sac is highly visible. Limited data on female size (see 'Description') and colouration (see 'Pattern and colour') suggest that, unlike most other Australian microhylids (Zweifel 1985), there may be considerable external sexual dimorphism in this species. An adult *C. concinnus* (QMJ42263) of undetermined sex was collected in November 1983 attending 17 eggs beneath a rock at ~1150 m elevation near the summit of Thornton Peak. The eggs of the preserved clutch are joined in a string by a strong mucilaginous cord (Fig. 7).

Comments

The original type series in the Queensland Museum collections includes two species. The holotype (QMJ30743) and paratypes QMJ30745 and QMJ30744 are *C. concinnus* whereas the paratype QMJ30746 is *C. aenigma*. The remainder of the paratypes, which are in the South Australian Museum (R16375–76), were not examined. The inclusion of two species under the name *C. concinnus* is the source of the 'puzzling geographic variation' noted by Zweifel (1985) and the two call types and calling positions described by the collector Dr J. Winter (Tyler 1979; Zweifel 1985; QM registration notes). Dr J. Winter noted the males of the type series uttering 'a short rattle' from elevated positions 1–2 m above the ground except one male found under a leaf on the ground whose call was a 'high pitched long di-di-da-di' (Zweifel 1985). The *C. aenigma* male in the type series (QMJ30746) would have been the one uttering the long call from the ground while the *C. concinnus* were those rattling from elevated positions.

The common name 'beautiful nursery-frog' refers to the elegant form, dark dorsum and spectacular red, black and white ventral colouration. *C. concinnus* was formerly called the 'tapping nursery-frog' (Stewart 1998; McDonald 2000) or 'slow-rattling frog' (McDonald 1991) but the call of this species is a trill rather than a tapping sound. These common names were applied to this species through confusion with individuals now described as *C. aenigma*.

Fig. 7. *Cophixalus concinnus* (QMJ42263) collected in attendance of a clutch of 17 eggs joined by a strong mucilaginous cord, Thornton Peak, north-east Queensland (photograph Jeff Wright).

Cophixalus concinnus is without doubt one of the most restricted amphibian species in Australia, with a total distribution of ~718 ha (7.18 km^2). This area is completely protected in Daintree National Park within the Wet Tropics World Heritage Area and the species is currently at high density (Hoskin, personal observation). However, bioclimatic modelling of the effect of climate change on this species is startling (Williams *et al*. 2003). Predictive models encompassing a range of temperature-increase scenarios suggest that even the most conservative estimate of a 1°C increase in global temperature (a rise seen as inevitable over the next few decades) will result in the total loss of core environment and possible extinction of *C. concinnus* (Williams *et al*. 2003). The bioclimatic modelling predicts this species to be the first Wet Tropics vertebrate to go extinct due to climate change.

Cophixalus concinnus warrants a 'Critically Endangered' listing under IUCN criteria (IUCN Species Survival Commission 2001) as it has an 'extent of occurrence' considerably less than 100 km^2 and an 'area of occupancy' less than 10 km^2, coupled with the fact that it is known from a single mountain-top and the modelling predicts a serious decline in extent of occurrence, area of occupancy, quality of habitat, number of locations and number of mature individuals. *C. concinnus* (along with *C. neglectus*, *C. monticola* and *C. mcdonaldi*) should be seen as a priority species for monitoring to assess the impact of global climate change.

Comparison of *C. aenigma, C. concinnus* and *C. monticola*

It is necessary to define the differences between *C. aenigma*, *C. concinnus* and *C. monticola* for the following reasons: *C. concinnus* and *C. aenigma* were formerly in the same collection, *C. aenigma* and *C. monticola* co-occur and are regularly misidentified due to their morphological similarity, and *C. concinnus* and *C. monticola* are sister species on

neighbouring mountain-tops that share similar morphology and calls. Table 2 provides a summary of morphological and call characters of these three species. The material examined for *C. aenigma* (*n* = 33) and *C. concinnus* (*n* = 17) are listed in the species description and redescription above. The entire QM collection of *C. monticola* (*n* = 15) was examined: QMJ58727–33, QMJ58854–57, QMJ58871–74, Mt Lewis, Carbine Tableland (16°30′S, 145°16′E). The specimen from Mt Spurgeon (QMJ67125) was excluded as it is a misidentified *A. fryi*.

    Cophixalus concinnus and *C. monticola* do not co-occur but both species coexist with *C. aenigma* (Fig. 3). The slow tapping call of *C. aenigma* is easily distinguished from the short trill of *C. concinnus* and *C. monticola* (Fig. 4). Males of these two species almost always call from elevated sites whereas male *C. aenigma* call from the ground or very close to it. The calls of *C. concinnus* and *C. monticola* are similar; however, the trill of *C. concinnus* is of longer duration and lower frequency (Table 1; Fig. 4). In the field the black, white and red ventral colouration of male *C. concinnus* is distinctive, particularly in the throat region, which consistently has some degree of central dark marking surrounded by orange or red. Dark blotches in the armpits also appear to be a distinctive feature of *C. concinnus* (Fig. 6). *C. aenigma* and *C. monticola* cannot be separated in the field on the basis of colour or pattern.

    Principal Component Analysis of the ratios derived from the morphological measurements clearly separates *C. concinnus* from the other two species and provides moderate discrimination between *C. monticola* and *C. aenigma*. The ratios listed in Table 2 are the important characters for discrimination but are unfortunately also the hardest to measure in the field. The high EN/IN ratio (>1.0) and large finger discs (3DW/SVL, 3DW/4DW) separate *C. concinnus* from the other two species (Table 2). *C. aenigma* and *C. monticola* are harder to separate, the best characters being the larger toe discs (4DW/SVL) and body width (BW/SVL) of *C. monticola* (Table 2). However, there is considerable overlap in the range of these measurements and the obvious difference in call between these two species is the most reliable character.

Previously undescribed calls

Cophixalus mcdonaldi

Despite being collected in 1972 and described in 1985 (Zweifel 1985), *C. mcdonaldi* has remained poorly known. On 1 October 1999 I recorded *C. mcdonaldi* for the first time. During the day individuals were found sheltering in fallen palm fronds and beneath rocks along Alligator Ck at ~1000 m elevation on Mt Elliot (19°29′S, 146°58′E). At ~16:00 hours calling commenced and continued until sunrise. Heavy rain began at ~01:00 hours and continued throughout the night. Males were concentrated around the rocky margins of the main creek and tributaries and were observed calling from fallen palm fronds, leaf-litter among boulders and from within rock cracks and scree. All males were observed calling from ground level or close to it.

    The mating call of *C. mcdonaldi* is a short trill (Fig. 4*M*; Table 1). A male (17.5 mm SVL) was recorded uttering a call with the following mean characteristics: dominant frequency 2.66 kHz, duration 1.42 s, pulses per call 43, and pulse rate 30.28 pulses/s. Another male (19.5 mm SVL) produced a call with the following mean characteristics: dominant frequency 3.20 kHz, duration 1.12 s, pulses per call 32, and pulse rate 28.52 pulses/s. Both calls were recorded at ~22°C and the males were collected (N73634 and N73642 respectively) and sequenced. The mating call of *C. mcdonaldi* differs from all other

Table 2. Comparison of *Cophixalus aenigma*, *C. concinnus* and *C. monticola*: distributions, call characteristics (mean values) and diagnostic morphological traits
Sample sizes for morphology: *C. aenigma* (33), *C. concinnus* (16) and *C. monticola* (15). Localities: FU, Mt Finnigan Uplands; TU, Thornton Uplands; CU, Carbine Uplands; BB, Bakers Blue Mountain. See Table 1 for details of call characteristics

	Cophixalus aenigma	*Cophixalus concinnus*	*Cophixalus monticola*
Distribution	CU, TU, FU, BB	TU	CU
Altitudinal range (m)	>750	>1100	>1100
Call description	Slow to medium-paced tapping	Short trill	Short trill
Call duration (s)	2.4 (CU), 2.7 (TU), 1.1 (FU)	1.27	0.6
Call: dominant frequency (kHz)	3.14 (CU), 3.35 (TU), 2.76 (FU)	2.3	3.1
Call: pulses/s	10 (CU), 9.1 (TU), 15.2 (FU)	24.42	22.9
Call site	Terrestrial or slightly elevated (<30 cm)	Elevated (0.5–3 m)	Elevated (0.2–1.4 m)
Dorsal colouration (live)	Variable: even to mottled; grey, yellow, brown or dark	Evenly black or brown; white bar on posterior thigh	Variable: tan, yellow, brown, dark; usually with dark mottling
Ventral pattern/colour (live)	Evenly pale, rarely grey or stippled; often orange in groin and axilla	Blotched black on red and white; black and red vocal sac	Evenly pale, occasionally grey, orange, brown, speckled or smudged
Pale lumbar ocelli	Usually obvious (CU, TU, BB) or uncommon (FU)	Rare	Usually obvious
SVL (mm)	Range = 16.8–22.6 (mean = 19.45)	Range = 17.9–26.5 (mean = 21.0)	Range = 16.5–20.2 (mean = 18.3)
BW / SVL	Range = 0.34–0.46 (mean = 0.38)	Range = 0.40–0.49 (mean = 0.45)	Range = 0.37–0.49 (mean = 0.43)
3DW / SVL	Range = 0.023–0.039 (mean = 0.032)	Range = 0.039–0.053 (mean = 0.045)	Range = 0.035–0.044 (mean = 0.039)
3DW / 4DW	Range = 0.61–1.17 (mean = 0.91)	Range = 1.15–2.18 (mean = 1.38)	Range = 0.89–1.09 (mean = 0.98)
4DW / SVL	Range = 0.024–0.046 (mean = 0.035)	Range = 0.022–0.042 (mean = 0.034)	Range = 0.036–0.045 (mean = 0.040)
EN / IN	Range = 0.76–0.97 (mean = 0.87)	Range = 1.04–1.37 (mean = 1.17)	Range = 0.83–1.00 (mean = 0.90)

Australian *Cophixalus* and is obviously different from the buzz produced by its sister species *C. neglectus* (Fig. 4*O*; Table 1).

Cophixalus exiguus

The mating call of *C. exiguus* was recorded by Stewart (1998) and is a medium-paced tapping of the following mean characteristics: dominant frequency 3.67 kHz, duration 1.06 s, pulses per call 16, and pulse rate 15.13 pulses/s (Fig. 4; Table 2). Temperature and male body size were not measured. I recently recorded two males on Big Tableland (15°44′S, 145°17′E, 800 m elevation, 22.7°C) that had calls of the following mean characteristics: male 1 (14.5 mm SVL), dominant frequency 3.95 kHz, duration 0.79 s, pulses per call 15, and pulse rate 18.99 pulses/s; male 2 (16.1 mm), dominant frequency 4.10 kHz, duration 0.93 s, pulses per call 24, and pulse rate 25.81 pulses/s. The call of *C. exiguus* is similar to that of the Mt Finnigan population of *C. aenigma* but has a dominant frequency ~1 kHz higher (Fig. 4*F*; Table 1). I have observed male *C. exiguus* calling at ground level among leaf-litter, beneath rocks, and from a fallen epiphyte.

Call variation within species

The 'representative' calls presented in Fig. 4 and Table 1 are an advertisement call of average structure and dominant frequency for each of the lineages as determined through analysis of multiple calls or by ear. The calls of *C. peninsularis* and *C. zweifeli* have not been recorded and that of *A. adelphe* was not available (but see Zweifel 1985 for *A. adelphe*). Considerable call variation has been detected in several species and this has led to persistent suggestion that more species remain to be described. Here I present data on call variation for individuals that have been allocated to species via mtDNA sequencing. In some cases the different calls can be attributed to distinct lineages or subpopulations (*C. ornatus*, *C. neglectus*, *C. aenigma*), but in some species considerable variation of unknown function occurs between individuals at a given site (*C. hosmeri*, *C. aenigma* and *A. fryi*).

Cophixalus ornatus displays considerable call variation with the most noticeable deviations from the 'normal' call (Fig. 8*A*; Table 1) being: (i) a very short call of high dominant frequency and pulse rate in the lowland populations in the vicinity of Mission Beach, Tully Gorge, Palmerston and lower Mt Bartle Frere (Fig. 8*B*; Table 1); (ii) a short call of high dominant frequency at all altitudes on Hinchinbrook Island (Fig. 8*D*; Table 1); (iii) an obviously frequency-modulated call of very low dominant frequency and very high pulse rate in the Mt Bartle Frere area, possibly a result of hybridisation between historically isolated lineages (Hoskin and Moritz, unpublished) (Fig. 8*E*; Table 1); (iv) a longer call of higher pulse rate uttered when males are leading females to a nest (Fig. 9*A*; Table 1); and (v) a short call of very low pulse rate recorded on one instance when a male and female were in contact in the nest (Figs 8*F*, 9*B*; Table 1). The leading and nest-associated calls were also observed to be considerably softer and of higher note rate than the surrounding advertisement calls. Analysis of the structure and significance of variation in the advertisement call of *C. ornatus* across altitude and at contact zones between historically isolated lineages is currently being investigated (Hoskin and Moritz, unpublished).

Approximately 1.6% sequence divergence separates the isolated populations of *C. neglectus* on the summits of Mt Bellenden Ker and Mt Bartle Frere (Figs 1, 3). There are slight morphological differences between the two populations and minor differences in call have been reported (Zweifel 1985). The calls are noticeably different to the human ear and analysis of a limited number of calls from the two peaks reveals the call on Mt Bartle Frere
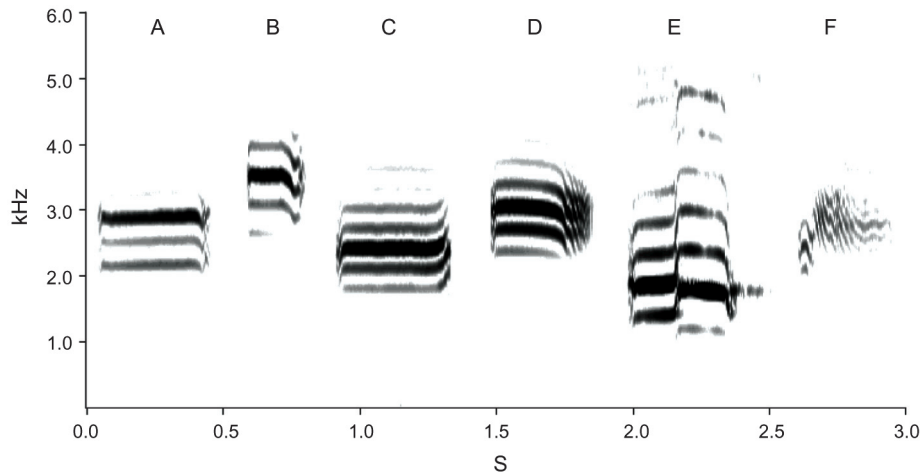
Fig. 8. Spectrogram of call variation in *Cophixalus ornatus* (recording temp. °C). *A*: 'normal' (21); *B*: lowland (26); *C*: upland (20); *D*: Hinchinbrook I. (20); *E*: unusual, Mt Bartle Frere (20); *F*: call at nest (20).
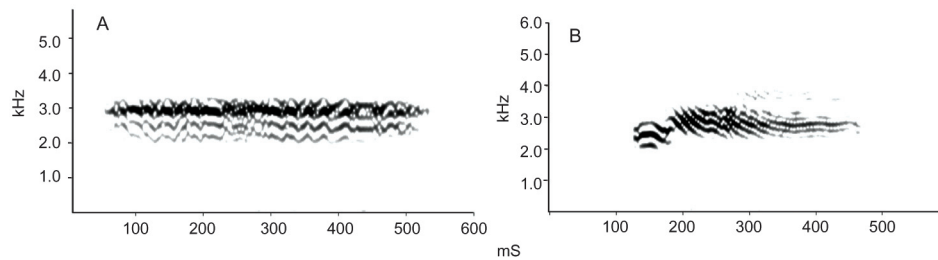

Fig. 9. Spectrogram of *Cophixalus ornatus* call when leading a female (*A*) and when in nest with female (*B*) (both recorded at 20°C).

to be of longer duration and noticeably lower pulse rate than that on Mt Bellenden Ker (Fig. 10; Table 1). Such differences do not appear to be attributable to male body size or temperature, although this has not been assessed in detail.

As already reported, the Mt Finnigan population of *C. aenigma* is ~1.5% divergent from, and has a noticeably different call to, the populations in the Thornton and Carbine uplands. Additionally, variation is evident within sites, the most noticeable being calls of greatly increased pulse rate. Fig. 5*B* displays the call of a male *C. aenigma* recorded on the summit of Mt Finnigan. The call was of similar duration, note rate and volume but of considerably higher pulse rate and dominant frequency than that of the surrounding males (Fig. 5*A*; Table 1). The male was morphologically and genetically indistinguishable from the surrounding males. The call was deemed to represent an advertisement call as it was uttered throughout the evening and the male was not in attendance of a nest or accompanied by a female. I have also encountered such a call occasionally on Mt Lewis.

The greatest within-site variation in call is displayed by *C. hosmeri*. On Mt Lewis morphologically and genetically indistinguishable males produce calls ranging from medium- and fast-paced taps to a buzz. Variation in calls is due primarily to dramatic differences in pulse rate whereas dominant frequency, call duration and note rate differ
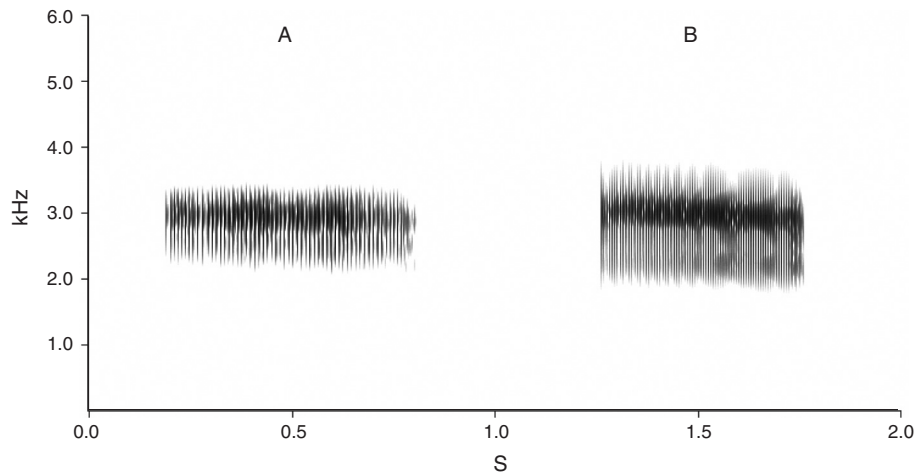
Fig. 10.   Spectrogram of advertisement call variation in *Cophixalus neglectus*. *A*: Mt Bartle Frere; *B*: Mt Bellenden Ker (both recorded at 18°C).

little. Individual males consistently utter a particular call type through a night and males uttering different call types do not appear to display different call site selection or occupy different microhabitats. All the call types appear to represent advertisement calls and no courtship has been witnessed. Three males of similar size recorded at 20°C on Mt Lewis made calls covering the full range of variation (Fig. 11; Table 1): (A) a male of 14.0 mm SVL producing a medium-paced tap, (B) a male of 13.3 mm SVL producing a fast tap, and (C) a male of 12.1 mm SVL producing a buzz. All three males were calling from among leaf litter on embankments and were morphologically and genetically indistinguishable.

Despite broad variation in call characteristics, the calls of *C. hosmeri* differ from those of other Australian *Cophixalus*. The buzz is similar to the call of *C. bombiens*, the fast tap is similar to the calls of *C. monticola* and *C. concinnus* and the medium-paced tap is similar to the calls of *C. exiguus* and *C. aenigma* (Mt Finnigan). However, in all these instances the call of *C. hosmeri* is of considerably higher frequency (Fig. 4*A*; Table 1).

Austrochaperina fryi and *A. robusta* are morphologically indistinguishable parapatric species with calls of different structure (Zweifel 1985). Both calls have a dominant frequency of ~3 kHz, with that of *A. fryi* consisting of a series of whistles and that of *A. robusta* a series of chirps arranged in couplets (Fig. 4*A, D*). The two species are in contact in the Lamb Range (Zweifel 1985), whereas to the east on the Atherton Tablelands clearing over the last century has largely isolated populations of the two species from one another. For example, *A. fryi* occupies the rainforest isolate surrounding Lake Barrine whereas it has never been recorded in the nearby fragment surrounding Lake Eacham, where *A. robusta* is common. The dynamics of the contact between these two species is not known, and here I report a possible hybrid call. A male recorded among a chorus of *A. fryi* at Lake Barrine displays a call of intermediate structure. Each call consisted of a string of whistle-like notes and chirped couplets (Fig. 12; Table 1). The number and order of single notes and couplets varies from call to call and the average call characteristics are presented in Table 1. The male was of similar size (29.3 mm SVL) to those calling around him. Genetic analysis is required to determine whether this individual is of hybrid origin.
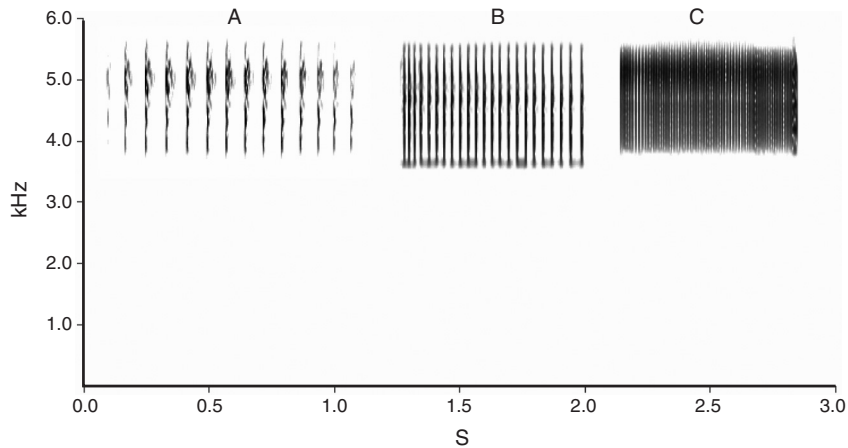
Fig. 11. Spectrogram of call variation in *Cophixalus hosmeri* on Mt Lewis. *A*: medium tap; *B*: fast tap; *C*: buzz (all recorded at 20°C).
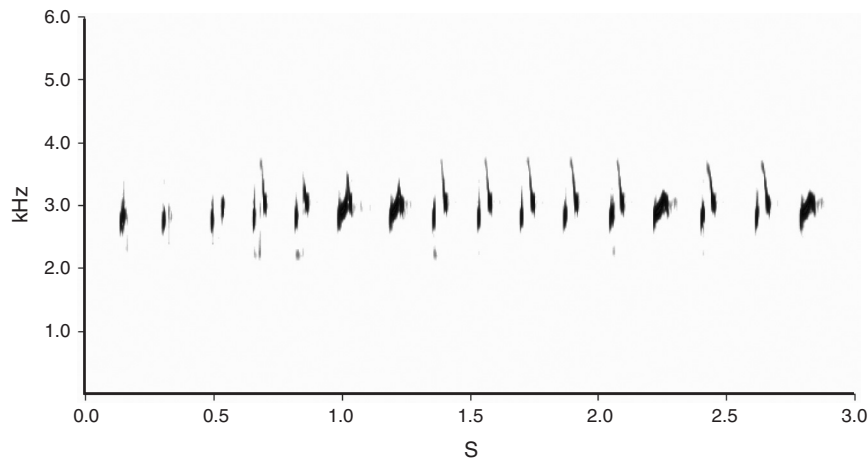

Fig. 12. Spectrogram of an unusual call in *Austrochaperina fryi*, Lake Barrine, recorded at 22°C.

Clarification of distributions

Clarification is required with respect to currently recognised species distributions. The distributions of microhylids outside of the Wet Tropics area (*A. adelphe*, north Northern Territory; *A. gracilipes*, north Cape York and south-west Papua New Guinea; *C. crepitans* and *C. peninsularis*, McIlwraith Range; and *C. zweifeli*, Cape Melville) remain as depicted in Zweifel (1985) and Davies and McDonald (1998). Fig. 3 shows the distribution of the species in the Wet Tropics as supported by my analysis of Queensland Museum specimens, genetic data, field measurements and calls. The distributions of *C. mcdonaldi*, *C. monticola*, *C. neglectus*, *C. ornatus* and *C. saxatilis* remain as widely accepted (Zweifel 1985; McDonald 1991, 1992, 2000; Richards *et al*. 1994).

Zweifel (1985) tentatively reported the presence of *A. fryi* at Lake Barrine (17°14′42″S, 145°38′22″E) and this is now confirmed through genetic and call analysis as the most southerly extent of the distribution of this species. *A. robusta* is absent around Lake Barrine but is present immediately to the south at Lake Eacham (17°16′58″S, 145°37′53″E). A

corridor being planted between these two lakes will bring these two species back into contact (as they are to the north-west in the vicinity of Mt Haig, Lamb Range, and to the east in Gadgarra State Forest). Zweifel (1985) reported the presence of *A. fryi* on the Malbon Thompson Range from morphological analysis of two specimens. All subsequent Queensland Museum collections from Malbon Thompson Range have been *A. robusta*, which I have confirmed through molecular and call analysis. Increased explorations have revealed the patchily distributed *A. pluvialis* to be more widespread than previously thought (Zweifel 1985), including records from the Seaview Range (18°37′S, 145°50′E) as far north as Big Tableland (15°42′S, 145°16′E) and Mt Finlay (15°48′S, 145°18′E).

Cophixalus bombiens was formerly recognised as the only vertebrate endemic to Windsor Tableland (Zweifel 1985; McDonald 1991, 1992); however, it is more widespread than this. I have sequenced individuals from the Kreb Track, Thornton Peak (QM60747–8, 16°06′S, 145°20′E), and it has been collected at Shiptons Flat (QMJ65691–6, 15°47′S, 145°14′E; QMJ27152–3, 15°49′S, 145°13′E), Mt Boolbun South (QMJ61115, QMJ61117, 15°56′S, 145°09′E), and recently at Cape Tribulation (to be lodged at QM, 16°04′15″S, 145°27′41″E, 20 m elevation). Persistent reports of the presence of *C. bombiens* on the Carbine Tableland have yet to be verified, but all suspect individuals that I have encountered or that have been forwarded to me have been genetically and morphologically consistent with *C. hosmeri*, which displays considerable call variation, including very rapidly pulsed calls similar to those produced by *C. bombiens* (Figs 4*K*, *G*, 11). These calls are of lower dominant frequency and pulse rate than those produced by *C. bombiens* (Table 1), and the individuals producing them display the morphological characteristics and genetic haplotype of neighbouring *C. hosmeri*. It would appear that *C. bombiens* is quite widely distributed through the lower and mid elevations in the Windsor–Thornton–Finnigan region but it does not appear to be present among the diverse array of *Cophixalus* at higher altitudes on the Carbine Tableland.

Cophixalus concinnus is now seen as a high-elevation (>1100 m) Thornton Peak endemic and *C. monticola* is a high-elevation (>1100 m) Carbine Tableland endemic (QMJ67125 from Mt Spurgeon is the only QM specimen not from Mt Lewis and is a misidentified *A. fryi*). *C. aenigma* has a disjunct distribution ranging across mid to high elevations (generally >750 m) on Thornton Peak, the Mt Carbine Tableland, Mt Finnigan, Mt Finlay, Mt Hemmant, Mt Pieter Botte, Mt Halcyon and Bakers Blue Mountain. The Bakers Blue Mountain record is of interest as this locality currently has limited areas of rainforest (<1000 ha, >900 m: Nix 1991) and is a western outlier to the rainforest of the northern Wet Tropics. The specimen (QMJ39899) is subadult and is not lodged with any call information. According to multivariate morphological analysis, this specimen is consistent in body proportions with *C. aenigma* from other localities. A recent survey of the rainforest at the summit of Bakers Blue Mountain in wet conditions, by Anthony Backer and myself, failed to locate any microhylid frogs. The only Wet Tropics–endemic amphibian or reptile located in this survey was the skink *Lampropholis coggeri*. Further surveys and collections are required from this locality, along with call recordings and genetic analysis, to confirm the presence of *C. aenigma* on Bakers Blue Mountain.

Cophixalus exiguus does not appear to be present on Mt Finnigan, despite reports in McDonald (1991, 1992, 2000), with such confusion probably arising from the similarity in calls between the *C. aenigma* population on Mt Finnigan and the call of *C. exiguus* (Fig. 4*F*, *J*; Table 1). *C. exiguus* appears to be restricted to Big Tableland (15°42′S,

145°16′E), Mt Hartley (15°46′S, 145°20′E) and the vicinity of Gap Creek (15°47′S, 145°18′E). Two 1975 records of *C. exiguus* (QMJ27152 and QMJ27153) from Little Forks, near Shiptons Flat (15°49′S, 145°13′E), are the result of misidentification of *C. bombiens*, which has subsequently been located at several low-elevation sites in this region. Further collecting is required in the Mt Hartley–Mt Finlay–Mt Finnigan area to determine the limits of the ranges of *C. exiguus*, *C. aenigma* and *C. bombiens*.

Cophixalus hosmeri is restricted to the Carbine Tableland and all specimens in the Queensland Museum collections outside this area are misidentifications. Zweifel (1985) described *C. infacetus* from a series collected at Palmerston and reported its probable occurrence further to the north in the vicinity of Crystal Cascades (16°57′50″S, 145°40′43″E). Further collecting now reveals this species to be patchily distributed along the eastern escarpment of the Atherton Tableland and Kirrama Range (McDonald 1992), often associated with areas of rocky substrate. Zweifel (1985) and McDonald (1992) reported the lower altitudinal range of *C. neglectus* to be 900 m, whereas, during extensive altitudinal surveys on Mt Bartle Frere through 2000 and 2001, I did not record the species below 1150 m.

Breeding notes

The breeding biology of Australian microhylid frogs remains poorly known. Table 3 presents a summary of breeding observations for two species of *Austrochaperina* and 11 species of *Cophixalus*. Like other genyophrynine microhylids, all breeding records of Australian *Austrochaperina* and *Cophixalus* involve clutches of large eggs laid in terrestrial situations which undergo direct development. Clutch size across species is consistently small, ranging from 6–22 eggs and averaging ~12. Eggs are coiled or clumped and at least partially joined by a strong mucilaginous cord (Fig. 7). There is a general trend of an adult frog (male in 86% of the observations in which sex was determined) in close proximity, if not straddling, the eggs (Table 3). Observations were made by myself of male attendance in a captive pair of *C. ornatus*. Egg laying was not witnessed but shortly thereafter the male was straddling the clutch of 15 eggs. Over the following two days he consumed several of the eggs and moved approximately half of the remaining clutch a short distance (approx. 4 cm) from plastic substrate to leaf litter. The relocated eggs were subsequently straddled through to hatching while the remainder were neglected and did not hatch. The function of male guarding is not known in Australian microhylids although Bickford (2001) attributed it to egg rehydration and protection from predators in New Guinean congeners. The limited dissection of *Cophixalus* gut contents I have performed has revealed predominately large ants, highlighting the potential for male attendance to be of importance for egg guarding. The records of multiple clutching by male *C. infacetus* and *C. ornatus* are the first published for Australian microhylid frogs. In both these instances the male was calling while in attendance of several clutches of obviously different developmental stage (Table 3).

Zweifel (1985) reports an observation of courtship behaviour in *C. ornatus* in which a male uttering a call of typical dominant frequency but unusually high note rate, increased note duration and low pulse rate, was seen leading a gravid female towards a hole in an embankment. I have observed such a scenario on several occasions. Typically, the male was encountered leading a gravid female through low vegetation or along the ground in a series of small jumps between which he called softly and waited for the female to follow. The 'lead call' uttered while this was occurring (Fig. 9*A*; Table 1) had the characteristics described above for Zweifel's account with the exception of the pulse rate, which was higher than that

Table 3. Breeding records for Australian microhylid frogs (*Austrochaperina* and *Cophixalus*)

Source: 1 = the author, 2 = Zweifel (1985), 3 = Yvette Williams (personal communication), 4 = Richards *et al.* (1994), 5 = Keith McDonald (personal communication), 6 = Rob Morgan and Mark Sanders (personal communication). See Appendix for locality coordinates, except for Hinchinbrook Is (18°21'S, 146°16'E)

Species	Date	Locality	Size	Clutch Development	Sex of attendant	Placement	Source
A. fryi	8 Nov. 1975	Thornton Peak	12	Well developed eggs	Male	Under debris	2
A. fryi	20 Jul. 1976	Thornton Peak	9	7 well developed eggs & 2 hatchlings	Male	Not recorded	2
A. fryi	Not recorded	Mt Lewis	11	Eggs	Female?	Under rock	2
A. robusta	18 Nov. 1996	Millaa Millaa	12	Well developed eggs	Not determined	Under log	1
C. aenigma	22 Jan. 1996	Mt Lewis	12	Unpigmented eggs[A]	Not determined		1
C. aenigma	18 Nov. 1999	Mt Lewis	21	Well developed eggs	Male (calling)	Hole in bank	3
C. bombiens	19 Jan. 2002	Windsor Tableland	7	Unpigmented eggs	Not determined	Under log	3
C. bombiens	21 Jan. 2002	Windsor Tableland	6	Well developed eggs	Not determined	Under log	3
C. concinnus	1 Nov. 1983	Thornton Peak	17	Early stage eggs	Not determined	Under rock	1
C. exiguus	9 Jan. 1996	Big Tableland	11	Unpigmented eggs	Male	Under epiphyte	1
C. exiguus	9 Jan. 1996	Big Tableland	7	Unpigmented eggs[A]			1
C. hosmeri	22 Jan. 1996	Mt Lewis	7	Hatchlings	Male (calling)	Under leaf litter	1
C. infacetus	July 19??	Palmerston	8	Unpigmented eggs	Not determined	Under epiphyte	2
C. infacetus	October 19??	Palmerston	10 & 11	Well developed eggs	Male & female	Not recorded	2
C. infacetus	2 Jan. 1996	Palmerston	14	Well developed eggs	Male (calling)[B]	Under leaf litter	1
			8	Hatchlings	Male (calling)[B]		
C. infacetus	25 Jan. 2003	Palmerston	8	Well developed eggs	Male (calling)	In palm axil	3
C. mcdonaldi	1 Oct. 1999	Mt Elliot	17	Unpigmented eggs[A]			1
C. monticola	17 Feb. 2000	Mt Lewis	8	Unpigmented eggs	Male (calling)	In palm axil	3
C. monticola	Not recorded	Mt Lewis	13	Unpigmented eggs	Unattended	In palm axil	4
C. neglectus	20 Jan. 1981	Mt Bellenden Ker	14	Unpigmented eggs	Male	Under branch on log	2
C. neglectus	10 Feb. 2001	Mt Bartle Frere	14	Unpigmented eggs	Male	Under palm frond on rock	1
C. neglectus	22 Jan. 2002	Mt Bellenden Ker	10	Mid development	Female	Under rock	5
C. neglectus	21 Jan. 2003	Mt Bellenden Ker	19	Early-stage eggs	Male (calling)	Under leaves in dirt chamber	3
C. ornatus	6 Oct. 1980	Not recorded	22	Unpigmented eggs	Male	Under moss	2

C. ornatus	26 Nov. 2000	Mt Bartle Frere	15	Unpigmented aggs	Male	Under leaf litter in tree hole	1
C. ornatus	14 Dec. 2000	Hinchinbrook I.	10	Unpigmented eggs	Male (calling)[B]		1
			15	Mid development	Male (calling)[B]		
			2	hatchlings	Male (calling)[B]		
C. ornatus	14 Dec. 2000	Hinchinbrook I.	3 & 4	Unpigmented eggs	3 adults of undetermined sex	Under slab of exfoliating rock	1
			5 & 7	Mid development			
C. ornatus	14 Dec. 2000	Hinchinbrook I.	7 & 15	Unpigmented eggs	4 adults of undetermined sex	Under slab of exfoliating rock	1
			5 & 6	Mid development			
C. saxatilis	15 Nov. 2001	Black Trevethan Range	13	Unpigmented eggs	Male	Rock crevice	6

[A] Clutch obtained by dissection of gravid female.   [B] Male multiple clutching.

of the surrounding 'advertisement calls' in all instances that I witnessed. Male leading ended with the gravid female following the male into a small earth hole beneath a rock ($n = 1$), a hole in a rotten log ($n = 2$), and a crevice among rocks ($n = 2$). In one of the instances the male call changed from the lead call to a very soft 'squelching' call (Figs 8*F*, 9*B*; Table 1) when he was joined by the female in a rock crevice.

Discussion

Several fundamental gaps remain in our knowledge of the Australian microhylid fauna. The genetic relationship between *A. adelphe* and the Australian and New Guinean populations of *A. gracilipes* is of considerable interest. *A. adelphe* is probably the sister taxon to *A. gracilipes* (Zweifel 1985) but this requires confirmation. No new data have been added on *C. peninsularis* since its description (Zweifel 1985) despite several visits by herpetologists in the vicinity of the type locality in the McIlwraith Range. Sympatric *C. crepitans* have been regularly encountered during this period. *C. peninsularis* was described as distinct from *C. crepitans* on the basis of its greater size (SVL >17 mm), longer hindlimbs and a description of call differences by the collectors. However, I have sequenced a specimen of *C. crepitans* of 17.8 mm SVL (QMJ74069), which is larger than the smaller of the two specimens of *C. peninsularis*. Additionally, the call difference, 'similar to *C. crepitans* but deeper in tone' (Zweifel 1985), could be attributed to the greater SVL of the *C. peninsularis* males in the original collection (a negative correlation between male size and dominant frequency is regularly reported in anurans: Duellman and Trueb 1994). The difference in relative hindlimb length (which held for the 17.8 mm SVL specimen of *C. crepitans* I sequenced) is great but then so too is the range within other narrowly distributed species such as *C. hosmeri* and *C. neglectus* (Zweifel 1985). Clearly, fieldwork in the McIlwraith Range is required to obtain specimens, call recordings and genetic material such that the identity of *C. peninsularis* can be resolved.

The call of *C. zweifeli* has yet to be recorded. Despite being distantly related, *C. zweifeli* and *C. saxatilis* share a highly distinct morphology that contrasts dramatically with that seen across the remainder of their morphologically conservative congeners in Australia (Davies and McDonald 1998). Their large size and other novel characteristics can be attributed to convergence in isolated boulder piles (Hoskin *et al.*, unpublished). Whether *C. zweifeli* shows a greater similarity in call to *C. saxatilis* or its sister species *C. infacetus* will illustrate the degree to which interspecific call differences are coupled with morphological change or phylogeny.

The level of call variation in several of the Australian *Cophixalus*, particularly *C. hosmeri*, is of considerable interest. Research is required to assess the degree to which the differences in call are discrete or spread along a continuum. Whether the different calls represent male–male aggression or male–female lead calls requires testing. Should there prove to be discrete call types that cannot be attributed to aggression or leading then more detailed genetic analysis and mate-choice trials should be performed to test for reproductive isolation. For now, the fact that males making the full range of call types are genetically and morphologically indistinguishable gives me little reason to suspect they represent different species.

Taxonomic resolution of the Australian microhylid frogs allows a clear understanding of diversity and distributions. This is of great importance as, for example, diversity and local endemism of *Cophixalus* have weighed heavily on models of biogeography and conservation planning in the Wet Tropics (Williams *et al*. 1996, 2003; Moritz *et al*. 2001, in press). Furthermore, the identification of narrowly distributed montane endemics

highlights species in need of conservation attention and further research, particularly in light of the recent dire predictions of the impacts of global warming on the moutain-top fauna of the Wet Tropics (Williams *et al*. 2003).

References

Barker, J., Grigg, G. C., and Tyler, M. J. (1995). 'A Field Guide to Australian Frogs.' (Surrey Beatty: Sydney.)

Bickford, D. (2001). The ecology and evolution of parental care in the microhylid frogs of New Guinea. Ph.D. Thesis, University of Miami.

Cogger, H. G. (2000). 'Reptiles and Amphibians of Australia.' 6th Edn. (Reed New Holland: Sydney.)

Cunningham, C., Blackstone, N., and Buss, L. (1992). Evolution of king crabs from hermit crab ancestors. *Nature* **355**, 539–542. doi:10.1038/355539A0

Davies, M., and McDonald, K. R. (1998). A new species of frog (Anura: Microhylidae) from Cape Melville, Queensland. *Transactions of the Royal Society of South Australia* **122**, 159–165.

Duellman, W. E., and Trueb, L. (1994). 'Biology of Amphibians.' (John Hopkins University Press: Baltimore.)

Hero, J.-M. (1995). 'Audio: Frog Calls of North-east Queensland.' (James Cook University: Townsville.)

Huelsenbeck, J. P., and Ronquist, F. (2001). MRBAYES: Bayesian inference of phylogenetic trees. *Bioinformatics* **17**, 754–755. doi:10.1093/BIOINFORMATICS/17.8.754

IUCN Species Survival Commission (2001). 'IUCN Red List Categories, Version 3.1.' (IUCN Council: Gland, Switzerland.)

Kocher, T. D., Thomas, W. K., Meyer, A., Edwards, S. V., Paabo, S., Villablanca, F. X., and Wilson, A. C. (1989). Dynamics of mtDNA evolution in animals: amplification and sequencing with conserved primers. *Proceedings of the National Academy of Sciences of the USA* **86**, 6196–6200.

Maniatus, T., Frisch, E. F., and Sambrook, J. (1982). 'Molecular Cloning: a Laboratory Manual.' (Cold Spring Harbour Laboratory Publications: New York.)

McDonald, K. (1991). Frogs. In 'Rainforest Animals: Atlas of Vertebrates Endemic to Australia's Wet Tropics'. (Eds H. A. Nix and M. A. Switzer.) pp. 83–103. (ANPWS: Canberra.)

McDonald, K. (1992). 'Distribution Patterns and Conservation Status of North Queensland Rainforest Frogs.' (Queensland Department of Environment and Heritage & Wet Tropics Management Agency: Cairns.)

McDonald, K. (2000). Frogs. In 'Wildlife of Tropical North Queensland'. (Eds M. Ryan and C. Burwell.) pp. 190–194. (Queensland Museum: Brisbane.)

Moritz, C., Richardson, K. S., Ferrier, S., Monteith, G. B., Stanisic, J., Williams, S. E., and Whiffin, T. (2001). Biogeographic concordance and efficiency of taxon indicators for establishing conservation

priority in a tropical rainforest biota. *Proceedings of the Royal Society of London. Series B. Biological Sciences* **268**, 1875–1881. doi:10.1098/RSPB.2001.1713

Moritz, C., Hoskin, C. J., Hugall, A. F., and Graham, C. H. (In press). Historical biogeography, diversity and conservation of Australian tropical rainforest herpetofauna. In 'Phylogeny and Conservation'. (Ed. A. Purvis) (Zoological Society: London.)

Nix, H. A. (1991). Biogeography: pattern and process. In 'Rainforest Animals: Atlas of Vertebrates Endemic to Australia's Wet Tropics'. (Eds H. A. Nix and M. A. Switzer.) pp. 83–103. (ANPWS: Canberra.)

Palumbi, S. R. (1996). Nucleic acids II: the polymerase chain reaction. In 'Molecular Systematics'. (Eds D. M. Hillis, C. Moritz and B. K. Mable.) pp. 205–247. (Sinauer Associates Inc.: Sunderland, MA.)

Parker, H. W. (1934). 'A Monograph of the Frogs of the Family Microhylidae.' (British Museum of Natural History: London.)

Posada, D., and Crandall, K. A. (2001). Selecting the best-fit model of nucleotide substitution. *Systematic Biology* **50**, 580–601. doi:10.1080/106351501750435121

Richards, S. J., Dennis, A. J., Trenerry, M. P., and Werren, G. L. (1994). A new species of *Cophixalus* (Anura: Microhylidae) from northern Queensland. *Memoirs of the Queensland Museum* **37**, 307–310.

Shimodaira, H., and Hasegawa, M. (1999). Multiple comparisons of log-likelihoods with applications to phylogenetic inference. *Molecular Biology and Evolution* **16**, 1114–1116.

Singer-Sam, J., Tanguay, R. C., and Riggs, A. D. (1989). Use of chelex to improve the PCR signal from a small number of cells. *Amplifications* **3**, 11.

Stewart, D. (1998). 'Audio: Australian Frog Calls: Tropical North-east.' (Nature Sound: Mullumbimby, NSW.)

Swofford, D. L. (2000). 'PAUP*: Phylogenetic Analysis Using Parsimony. Version 4.0b5.' (Sinauer: Sunderland, MA).

Thompson, J. D., Gibson, T. J., Plewniak, F., Jeanmougin, F., and Higgins, D. G. (1997). The CLUSTAL X windows interface: flexible strategies for multiple sequence alignment aided by quality analysis tools. *Nucleic Acids Research* **25**, 4876–4882. doi:10.1093/NAR/25.24.4876

Tracey, J. G., and Webb, L. J. (1975). 'Maps of the vegetation of the humid tropical region of north Queensland.' (CSIRO Division of Plant Industry: Indooroopilly, Qld.)

Tyler, M. J. (1979). A new species of *Cophixalus* (Anura: Microhylidae) from Queensland, Australia. *Copeia* **1979**, 118–121.

Tyler, M. J. (1992). 'Encyclopedia of Australian Animals: Frogs.' (Ed. R. Strahan.) pp. 93–101. (Angus and Roberston: Sydney.)

Williams, S. E., and Hero, J.-M. (2001). Multiple determinants of Australian tropical frog biodiversity. *Biological Conservation* **98**, 1–10. doi:10.1016/S0006-3207(99)00093-2

Williams, S. E., Pearson, R. G., and Walsh, P. J. (1996). Distributions and biodiversity of the terrestrial vertebrates of Australia's Wet Tropics: a review of current knowledge. *Pacific Conservation Biology* **2**, 327–362.

Williams, S. E., Bolitho, E. E., and Fox, S. (2003). Climate change in Australian tropical rainforests: an impending environmental catastrophe. *Proceedings of the Royal Society of London. Series B. Biological Sciences* **270**, 1887–1892. doi:10.1098/RSPB.2003.2464

Zweifel, R. G. (1962). A systematic review of the microhylid frogs of Australia. *American Museum Novitates* **2113**, 1–40.

Zweifel, R. G. (1965). Revisionary notes on Australian microhylid frogs of the genus *Sphenophryne*. *American Museum Novitates* **2214**, 1–9.

Zweifel, R. G. (1985). Australian frogs of the family Microhylidae. *Bulletin of the American Museum of Natural History* **182**, 265–388.

Zweifel, R. G. (2000). Partition of the Australopapuan microhylid frog genus *Sphenophryne* with descriptions of new species. *Bulletin of the American Museum of Natural History* **253**, 1–10. doi:10.1206/0003-0090(2000)2532.0.CO;2

Appendix.   Localities and number of individuals sequenced for each species of *Austrochaperina* and
Cophixalus

A. fryi.   Mt Finnigan, 15°49′S, 145°17′E, $n = 1$; Windsor Tableland, 16°14′S, 145°01′E, $n = 2$; Mt Lewis, 16°34′S, 145°16′E, $n = 2$.

A. gracilipes.   McIlwraith Range, 13°44′S, 143°21′E, $n = 3$.

A. pluvialis.   Gadgarra SF, 17°16′S, 145°40′E, $n = 2$.

A. robusta.   Lake Eacham, 17°17′S, 145°38′E, $n = 1$; Mt Bartle Frere, 17°23′S, 145°46′E, $n = 1$; Mt Baldy, 17°18′S, 145°26′E, $n = 2$; Millaa Millaa, 17°30′S, 145°37′E, $n = 1$; Paluma, 19°00′S, 146°12′E, $n = 2$.

C. aenigma.   Mt Finnigan, 15°49′S, 145°17′E, $n = 3$; Thornton Peak, 16°10′S, 145°22′E, $n = 4$; Mt Lewis, 16°34′S, 145°16′E, $n = 8$; Mt Spurgeon, 16°26′S, 145°12′E, $n = 1$.

C. bombiens.   Windsor Tableland, 16°14′S, 145°01′E, $n = 5$; Thornton Peak, 16°06′S, 145°20′E, $n = 2$.

C. concinnus.   Thornton Peak, 16°10′S, 145°22′E, $n = 5$.

C. crepitans.   McIlwraith Range, 13°44′S, 143°21′E, $n = 5$.

C. exiguus.   Big Tableland, 15°42′S, 145°16′E, $n = 6$; Gap Creek, 15°47′S, 145°18′E, $n = 1$.

C. hosmeri.   Mt Lewis, 16°34′S, 145°16′E, $n = 8$.

C. infacetus.   Palmerston, 17°36′S, 145°45′E, $n = 2$; Tully Gorge, 17°46′S, 145°38′E, $n = 3$.

C. mcdonaldi.   Mt Elliot, 19°30′S, 146°58′E, $n = 4$.

C. monticola.   Mt Lewis, 16°34′S, 145°16′E, $n = 4$.

C. neglectus.   Mt Bellenden Ker, 17°16′S, 145°51′E, $n = 4$; Mt Bartle Frere, 17°25′S, 145°49′E, $n = 4$.

C. ornatus.   Mt Lewis, 16°34′S, 145°16′E, $n = 3$; Kuranda, 16°49′S, 145°38′E, $n = 4$; Lamb Range, 17°06′S, 145°35′E, $n = 4$; Mt Bartle Frere, 17°23′S, 145°46′E, $n = 4$; Butcher's Creek, 17°18′S, 145°41′E, $n = 4$; Lake Eacham, 17°17′S, 145°38′E, $n = 2$; Topaz area, 17°27′S, 145°43′E, $n = 6$; Tully Gorge, 17°46′S, 145°38′E, $n = 4$; Tully Falls, 17°46′S, 145°33′E, $n = 2$; Mission Beach, 17°55′S, 146°04′E, $n = 3$; Palmerston, 17°36′S, 145°45′E, $n = 2$; Millaa Millaa, 17°30′S, 145°37′E, $n = 2$; Mt Hypipamee, 17°26′S, 145°29′E, $n = 2$; Kirrama Range, 18°13′S, 145°48′E, $n = 5$; Paluma, 19°00′S, 146°12′E, $n = 4$.

C. saxatilis.   Black Trevethan Range, 15°40′S, 145°16′E, $n = 3$.

C. zweifeli.   Cape Melville, 14°15′S, 144°28′E, $n = 2$.