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Article



Two new frog species (Microhylidae: *Cophixalus*) from the Australian Wet Tropics region, and redescription of *Cophixalus ornatus*

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Abstract

In Australia the frog family Microhylidae is largely restricted to tropical rainforests of the Wet Tropics region in the northeast of the country, but in that region the family is diverse. Only one species, Cophixalus ornatus, is widespread in the Wet Tropics but there has been suspicion that it may comprise multiple species. A recent study (Hoskin et al. 2011) assessed genetic and phenotypic variation across the range of C. ornatus, finding three deeply divergent genetic lineages that differ in mating call and some aspects of morphology. Two of these lineages abutt in the central Wet Tropics and in that area hybridization was found to be very limited despite sympatry at high densities. Based on multiple lines of data, Hoskin et al. (2011) concluded that the three genetic lineages represent biological species. The taxonomy of these three lineages is resolved here. I describe two new species, Cophixalus australis sp. nov. and Cophixalus hinchinbrookensis sp. nov., and redescribe C. ornatus. The three species are not distinguishable based on any single morphological or call trait and are best identified by genetics or locality. The distributions of the three species are largely allopatric. Cophixalus ornatus is found in rainforest in the northern Wet Tropics, C. australis sp. nov. occurs in rainforest and adjacent wet sclerophyll forests in the central and southern Wet Tropics, and C. hinchinbrookensis sp. nov. inhabits rainforest and montane heath on Hinchinbrook Island. All three species are common. Cophixalus australis sp. nov. contains three genetic subgroups that are considered a single species based on phenotypic similarity and high levels of hybridization at contact zones. The description of Cophixalus australis sp. nov. and Cophixalus hinchinbrookensis sp. nov. brings the number of Australian Cophixalus species to 18, 15 of which are restricted to the Wet Tropics region.

Key words: Cophixalus australis, Cophixalus hinchinbrookensis, rainforest, heath, Australia

Introduction

The family Microhylidae is represented in Australia by 21 species — 16 *Cophixalus* Boettger, 1892 and 5 *Austrochaperina* Fry, 1912. The centre for microhylid diversity in Australia is the Wet Tropics bioregion, an area of mountainous rainforest between Townsville and Cooktown in north-east Queensland. Fourteen species occur in this area, representing two-thirds of Australia's microhylid species (Hoskin 2004; Hoskin & Aland 2011). Since the major revision of the Australian microhylids by Zweifel (1985), only two new microhylid species have been described for the Wet Tropics — *Cophixalus monticola* Richards, Dennis, Trenerry & Werren, 1994 and *C. aenigma* Hoskin, 2004. The other three species described in the last 25 years have come from boulder-fields in remote areas of Cape York to the north of the Wet Tropics: *C. zweifeli* Davies & McDonald, 1998, *C. kulakula* Hoskin & Aland, 2011, and *C. pakayakulangun* Hoskin & Aland, 2011. Most Australian *Cophixalus* have very small distributions, generally being restricted to a single or several neighbouring mountain-tops or boulder-fields (Zweifel 1985; Hoskin 2004; Hoskin & Aland 2011). The major exception is *C. ornatus*, which is distributed through much of the Wet Tropics region. Previous studies of Australian microhylids have revealed the presence of divergent genetic lineages within *C. ornatus* (Hoskin 2004) and phenotypic differences between lowland and upland populations (Zweifel 1985; Hoskin 2004).

Hoskin *et al.* (2011) investigated genetic and phenotypic diversity across the range of *C. ornatus*. This revealed three highly divergent genetic lineages — the 'northern' lineage in the north of the Wet Tropics, the 'central'

lineage in the central and southern Wet Tropics, and the 'Hinchinbrook' lineage restricted to Hinchinbrook Island (Hoskin *et al.* 2011; Fig. 1). These three lineages are monophyletic for mtDNA and multiple nDNA loci, and are highly divergent from each other. Sequence divergences between the three lineages for both mtDNA and nuclear genes are greater than between some Australian *Cophixalus* species (e.g. *C. concinnus* and *C. aenigma*; *C. aenigma* and *C. exiguus*; Hoskin *et al.* unpub. data), and are of sufficient magnitude to suggest the potential for at least partial postmating isolation (Hoskin *et al.* 2011). All three lineages differ significantly from each other in morphology and, particularly, in mating call in multivariate analyses (Hoskin *et al.* 2011). Calls of the three major lineages of *C. ornatus* differ significantly in key traits for mate choice and species recognition in frogs (Gerhardt and Huber 2002; Hoskin *et al.* 2011), suggesting strong potential for premating isolation among the lineages. Based on the genetic and phenotypic data, Hoskin *et al.* (2011) concluded that there is likely substantial reproductive isolation between the lineages where they are currently in contact, or should they come into contact in future.

This was supported by analyses of the contact zone between two of these lineages, northern and central (Hoskin *et al.* 2011). These two lineages overlap at high abundance in a secondary contact zone on the western side of Mt Bartle Frere (Fig. 1). This contact zone is very narrow (< 1 km in width) and there is very little hybridisation, despite ample opportunity for this to occur (Hoskin *et al.* 2011). Intensive sampling of the contact zone revealed evidence of admixture in just one individual (Hoskin *et al.* 2011). The Hinchinbrook lineage is isolated on an island so does not overlap with the other two lineages. However, it is similarly divergent at mtDNA and nDNA loci and there is greater morphological and call divergence between this lineage and the other two lineages than there is between the northern and central lineages (Hoskin et al 2011). Therefore, it is reasonable to assume that there would also be very limited, if any, hybridisation between this lineage and the other two lineages if they were to come into contact in future. Based on these lines of evidence — genetic divergence, morphological and call divergence and analysis of secondary contact zones — Hoskin *et al.* (2011) concluded that the three lineages represent species. This was based on a 'substantial reproductive isolation' interpretation of the Biological Species Concept (Coyne & Orr 2004), in which complete or near-complete reproductive isolation is concluded from multiple lines of evidence (Hoskin 2007).

The taxonomy of the three lineages is resolved here, with two new species being described and *C. ornatus* being redescribed. It is important first to resolve which lineage the holotype of *C. ornatus* represents. The type specimen is listed as coming from "25 miles [40 km] inland from Cairns" and was collected in 1888 by E. J. Cairn and R. Grant (Fry 1912). This is rather vague, particularly use of the term 'inland'. If this is taken to mean 25 miles straight-line west of Cairns, then the site falls in unsuitably dry open woodland habitat in the vicinity of Mareeba, where *C. ornatus* does not occur. If 25 miles inland referred to a distance via road or rail west of Cairns (Zweifel 1985), then it would refer to one of the following areas: the Black Mtn/Macalister Ra. area, the Kuranda/Speewah region, or the northern Lamb Range. If this were the case then the type specimen would represent the northern lineage. It is also possible that 'inland' referred to a straight line or road/track distance SW of Cairns, in the southern Lamb Range/northern Atherton Tablelands area. This is a distinct possibility because Cairn and Grant collected extensively in this area, particularly in the vicinity of Boar Pocket (Tinaroo area), around that time (Longmore 1991). This would also make the holotype a northern lineage individual. A 40 km western arc from Cairns, drawn from NW round to SW (i.e. what could conceivably be termed 'inland'), falls comfortably within the northern lineage.

Methods

Morphometrics: Specimens examined are held in the Queensland Museum (QMJ codes) and the Australian Museum (AM R). The following characters were measured: snout to vent length (SVL), from snout to urostyle; tibia length (TL), from knee to heel; forearm length (FL), from elbow to 'heel' of the palm; head width (HW), measured at the tympana (i.e. at widest point of the head); head length (HL), from anterior edge of tympanum to snout; head depth (HD), at the crown between the eyes; eye diameter (ED); eye to naris distance (EN); distance between the nares (IN); third finger length (3FL), from split with second finger to tip of disc; third finger disc width (3DW); fourth toe length (4TL), from split with third toe to tip of disc; fourth toe disc width (4DW). All measurements were taken using Mitutoyo electronic callipers and rounded to the nearest 0.1 mm. A large number

of field measurements were collected and analysed by Hoskin *et al.* (2011), and a summary of these is presented here for each species. Field measurements of SVL, TL, HW, 3DW and weight (WT) were taken using Mitutoyo vernier callipers and a spring-loaded Pezola, respectively.

Call data: For details of call recording and analysis see Hoskin *et al.* (2011). A summary of the call data is presented here for each species. The following call traits are presented: 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 of a call), number of pulses, pulse rate (number of pulses divided by call duration), and call rate (time between last pulse of a call) to first call of the next call). The representative calls for each species presented in Figure 3 were selected because they are from similar altitudes and temperatures, and because they fall near the group centroid of variation within each species from analyses in Hoskin *et al.* (2011).

Genetic data: The genetic data referred to in this paper is presented in Hoskin *et al.* (2011), a detailed analysis of mtDNA and four nDNA loci across the range of '*C. ornatus*'. For identification purposes I have included a table herein listing some of the single nucleotide polymorphisms (SNPs) in the 16S mtDNA data that are diagnostic among the three species. The primer pair for amplifying a 513 bp section of 16S mtDNA in these species is: 16SarC, 5'-CGCCTGTTTATCAAAAACATC-3' and 16S2R, 5'-GCTACTAAAGGTTCGTTTGTTCAAC-3' (Hoskin *et al.* 2011). SNP position is labelled by base number from the first base of the forward primer (16SarC). Given that sequence reads are often 'messy' near the beginning, for reference, positions 48–67 (a 20 bp conserved section early in the sequence) are: GCCTGCCCAGTGATAAACTT.

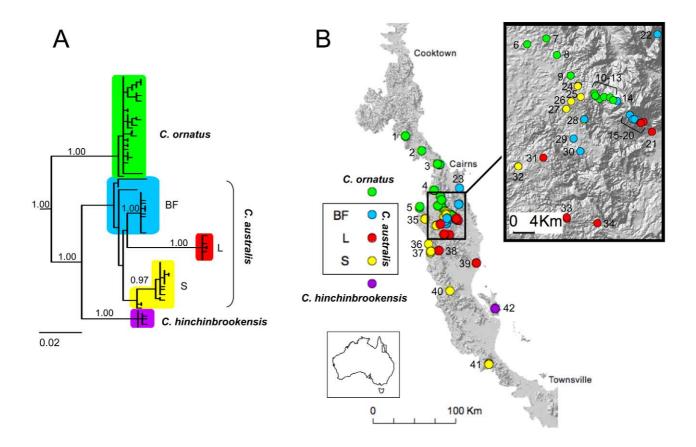


FIGURE 1. Phylogeny (A) and distributions (B) of *C. australis* **sp. nov.**, *C. hinchinbrookensis* **sp. nov.** and *C. ornatus*. (A) Maximum likelihood tree constructed from 513 bp 16S mtDNA. The phylogeny shows the relationship between *C. ornatus*, *C. australis* **sp. nov.** and *C. hinchinbrookensis* **sp. nov.** The tree also shows the three subgroups within *C. australis* **sp. nov.** Mt Bartle Frere region (BF), Lowland (L) and Southern (S). Numbers at major nodes are Bayesian posterior probabilities. (B) Map of the Wet Tropics region of north-east Australia and an enlargement of the Atherton Tablelands-Mt Bartle Frere region. The coloured dots show the most common mtDNA lineage at each site, with dot colour matching the phylogeny. The site numbers match the locality details in Table 1. This figure is modified from Figs 3 and C1 in Hoskin *et al.* (2011).

Systematics

The two new species are clearly assignable to *Cophixalus* based on genetic data (Hoskin 2004; Hoskin *et al.* 2011). Morphological diagnosis of Australo-Papuan microhylid genera is based on characters of internal morphology (Zweifel 1985, 2000). *Cophixalus ornatus*, the sister lineage to the two species described here, has previously been assigned to *Cophixalus* based on these characters (Zweifel 1985).

Cophixalus australis sp. nov.

Southern Ornate Nursery-frog (Figs 2A, 2B)

Material examined. Holotype: QMJ43655, male, Mt Spec, Paluma Ra. (18°57'S, 146°11'E), north-east Queensland, C. Corben, 11 January 1976. **Paratypes:** QMJ39923, North Bell Peak, Malbon Thompson Ra. (17°05'S, 145°53'E); QMJ50700, Douglas Ck Rd, Kirrama Ra. (18°12'S, 145°45'E, elevation 800 m); QMJ61251, Mid Macks, Kirrama Ra. (18°02'30"S, 145°36'30"E); QMJ65377, Kirrama Ra. (18°01'30"S, 145°35'30"E, elevation approx. 900 m); QMJ70701, Lacey Ck, Mission Beach (17°51'05"S, 146°04'50"E, elevation 40 m); QMJ70710, QMJ70711, Loop track at picnic ground, Paluma township (19°00'30"S, 146°12'30"E, elevation 900 m); QMJ70782, The Crater/Mt Hypipamee National Park (17°25'54"S, 145°29'08"E, elevation 980 m). Additional material: An additional 296 individuals were measured in the field, and mating calls were measured from 141 of these (Table 2).

Diagnosis. Cophixalus australis **sp. nov.** can be identified from similar congeners, except *C. ornatus* and *C. hinchinbrookensis* **sp. nov.**, by the presence of large, truncated finger pads and by call, which is a 'beep' rather than a call with obvious pulses or notes. Cophixalus australis **sp. nov.** can be reliably identified from *C. ornatus* and *C. hinchinbrookensis* **sp. nov.** genetically, using the loci outlined in Hoskin *et al.* (2011). For 16S mtDNA, diagnostic SNPs are presented in Table 3. It can also be readily identified based on distribution. Cophixalus australis **sp. nov.** does not co-occur with *C. hinchinbrookensis* **sp. nov.** and only narrowly abuts the range of *C. ornatus* (Fig. 1). Cophixalus australis **sp. nov.** differs from *C. ornatus* and *C. hinchinbrookensis* **sp. nov.** in multivariate analyses of mating call and some aspects of morphology (Hoskin *et al.* 2011), but these three species cannot be distinguished on any known single trait. Regarding colour pattern, the groin and posterior thigh generally lack a yellow wash in *C. australis* **sp. nov.** (vs. typically present in *C. ornatus*; Fig. 2F).

Etymology. From the Latin *australis* for 'southern', in reference to the fact that this species occurs in the southern half of the Wet Tropics region. The epithet is to be treated as a noun in apposition.

Description of holotype (Fig. 2A). QMJ43655; male. Measurements (mm): SVL 22.2; TL 8.2; FL 5.5; HW 7.7; HL 5.4; ED 2.2; EN 1.6; IN 1.3; 3FL 3.1; 3DW 1.1; 4TL 4.6; 4DW 1.0. Head: Narrower than body, triangular in dorsal view; snout moderately truncated at the nares, projecting in profile; canthus rostralis rounded, loreal region steep; nares much closer to tip of snout than to eye, nares anterolateral on tip of snout; eyes large; eye diameter greater than eye to naris distance; internarial distance about equal to distance from eye to naris; tympanum small (less than half diameter of eye) and indistinct beneath overlying skin, bordered dorsally by supratympanic fold. Body: Rotund. Limbs: Hindlimbs short, forearms relatively long; fingers and toes unwebbed; relative finger length 3>2>4>1; fingers 2, 3 and 4 long and slender with large and truncated discs, first finger short with barely expanded small round disc; low, rounded inner and outer palmar tubercles; subarticular tubercles low, moderately prominent; relative length of toes 4>3>5>2>1, toe 4 very long and slender; large, truncated discs on toes 2, 3 and 4, discs smaller and more rounded on toes 1 and 5; low, rounded inner and outer metatarsal tubercles; subarticular tubercles low and rounded; discs on longest fingers larger than discs on longest toes. Skin: Ventral surface generally smooth, finely granular on belly; dorsal surfaces smooth with just a few low tubercles; distinct supra-tympanic fold. Colour pattern in preservative: Dorsal surfaces uneven brown, darker towards the head, with dark smudging on the lateral surface above the axilla and a dark band on the wrist of each forearm; pale lumbar ocelli bordered posteriorly by a dark bar; dark cloacal region. Loreal region dark, and a dark line along tympanic fold. Tympanum pale brown. White patches at the base of the finger and toe discs. Dark brown dorsal colouration merges to lighter brown on flanks. Ventral surface of head and body creamy-brown with fine light brown stippling, particularly under throat. Ventral surfaces of limbs brown; discs brown, tubercles white.

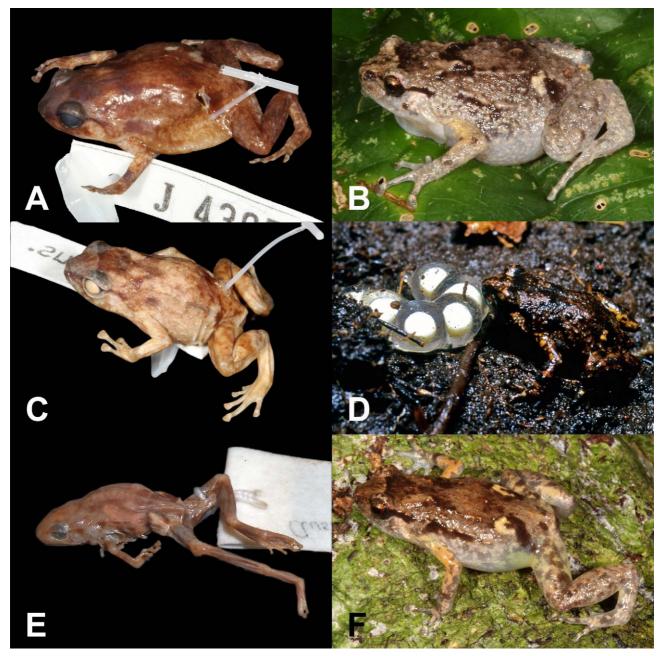


FIGURE 2. Photos of: (A) the holotype of *C. australis* **sp. nov.** (QMJ43655); (B) *C. australis* **sp. nov.** in life, Mt Hypipamee (photo: Conrad Hoskin); (C) the holotype of *C. hinchinbrookensis* **sp. nov.** (QMJ44166); (D) *C. hinchinbrookensis* **sp. nov.** in life, Hinchinbrook Island (photo: Alex Anderson); (E) the holotype of *C. ornatus* (R222); (F) *C. ornatus* in life, Kuranda (photo: Conrad Hoskin).

Description of type series (N = 9). Data presented as range followed by mean in brackets. Adult measurements (mm): SVL 18.3–24.3 (21.0); TL 7.4–9.8 (8.7); FL 4.3–5.8 (5.1); HW 6.5–8.0 (7.3); HL 4.9–5.9 (5.3); ED 1.6–2.2 (2.0); EN 1.3–1.7 (1.5); IN 1.2–1.5 (1.3); 3FL 2.8–3.7 (3.2); 3DW 0.9–1.4 (1.2); 4TL 3.9–5.4 (4.6); 4DW 0.7–1.0 (0.8). Adult proportions: TL/SVL 0.37–0.45 (0.42); FL/SVL 0.22–0.27 (0.24); FL/TL 0.53–0.67 (0.59); HW/SVL 0.29–0.39 (0.35); HL/SVL 0.23–0.29 (0.25); HW/HL 1.20–1.53 (1.38); ED/SVL 0.08–0.11 (0.10); EN/HL 0.25–0.33 (0.29); EN/IN 1.01–1.34 (1.16); EN/ED 0.62–0.94 (0.77); 3FL/SVL 0.13–0.18 (0.15); 3DW/SVL 0.045–0.069 (0.056); 4TL/SVL 0.19–0.24 (0.22); 4DW/SVL 0.031–0.045 (0.040); 3DW/4DW 1.13–1.63 (1.39). Comparison of sexes: Based on field measurements (Table 2), females are generally larger (e.g. average SVL 25.5 *vs.* 22.7), have proportionally larger finger discs, and are bulkier (i.e. heavier relative to SVL). Colour pattern in preservative: Generally as for holotype (N = 5) – light brown background with areas of darker brown smudging and mottling. Several individuals (N = 3) have pale body with broad creamy yellow vertebral

band edged with dark brown band. Consistent features on all specimens are: grey/brown triangle on snout, grey on eyelids, dark W-shaped mark on shoulders; pale lumbar ocelli marked behind by dark patch, irregular dark blotch above axilla on lateral surfaces, sometimes with associated dark blotches along the flanks, dark band from snout through eye and along supratympanic fold; generally a dark band on wrist, pale dots at base of finger and toe pads, often dark mottling on hindlimbs. Ventral surfaces variable: evenly pale (N = 6) or mottled grey (N = 2) or brown with white spotting (N = 1). Undersides of limbs generally brown, tubercles and pads generally pale.

Measurements of live individuals. Table 2 presents measurements for 288 males and 8 females in the field.

Colour pattern in life. Dorsal pattern highly variable. There are three broad morphs: (1) 'mottled'— irregular dark markings on an uneven pale, orange or brown background; consistent dark markings being a dark W-shaped mark in the scapular region, an irregular dark bar across the top of the head between the eyes and a dark mark associated with pale lumbar ocelli, (2) 'broad band'—a broad cream or yellow vertebral band bordered with black on a brown or dark background, and (3) 'vertebral line'—a very thin cream or yellow vertebral line on an uneven brown or dark background, usually with accompanying thin line along hindlimbs. The first morph (mottled) is the most common but individuals with vertebral bands are present in most populations. Dorsal markings found on all morphs include pale or yellow lumbar ocelli and a paler triangle on the snout. Dorsal surfaces of limbs mottled with grey, brown or black. Forelimbs usually irregularly marked with orange or yellow, with similar colouration sometimes also present on ankles often similarily tinged. Dorsal colouration merges to white, cream or grey on flanks. Consistent lateral markings include an irregular dark line from nare through eye and along supra-tympanic fold, and a dark irregular bar above the axilla. Groin and posterior thigh similar pale or grey colouration to flanks and with grey mottling. Ventral surfaces usually evenly white, cream, grey or light brown, but sometimes flecked or mottled with darker markings. Iris heavily flecked with gold and pupil often bordered with a red or copper line. No sexual dimorphism in colour pattern evident.

Call. A finely pulsed 'beep' (Fig. 3A) of the characteristics outlined in Table 2.

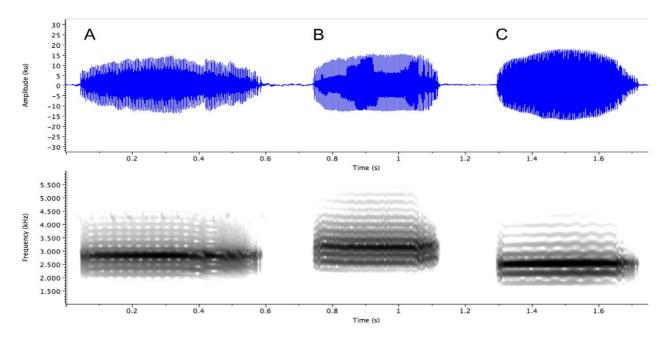


FIGURE 3. A single representative call of: (A) *C. australis* **sp. nov.**, Tully Falls, 750 m a.s.l., 18° C; (B) *C. hinchinbrookensis* **sp. nov.**, Mt Diamantina, Hinchinbrook Island, 770 m a.s.l., 19° C; (C) *Cophixalus ornatus*, Butchers Ck, 715 m a.s.l., 18.5° C. These calls were selected because they are from similar altitudes and temperatures, and because they fall near the group centroid of variation within each species from analyses in Hoskin *et al.* (2011). Waveforms display amplitude (*y*-axis) against time (*x*-axis, seconds); Spectrograms display call frequency (*y*-axis) and intensity (degree of shading) against time (*x*-axis, seconds).

Comparison. Only likely to be confused with other rainforest microhylids. *Cophixalus australis* **sp. nov.** can be distinguished from these species (except *C. ornatus* and *C. hinchinbrookensis* **sp. nov.**) by the presence of large, truncated finger pads and by the mating call, which is a finely-pulsed 'beep' rather than a call with obvious pulses or notes. *Cophixalus australis* **sp. nov.** is phenotypically similar to *C. ornatus* and *C. hinchinbrookensis* **sp. nov.**. There are multivariate differences in mating call and morphology between these three species (Hoskin *et al.* 2011)

but they cannot be identified based on any single known phenotypic trait in the field (Table 2). Colouration and pattern are highly variable within each of these three species. The only difference detected so far is that *C. ornatus* typically has a yellow wash to the groin and posterior thigh (Fig. 2F), which is generally absent in the other two species. The three species can be reliably identified by genetics, representing divergent monophyletic lineages for both mtDNA and nDNA loci (Hoskin *et al.* 2011). For 16S mtDNA, the SNPs presented in Table 3 and the GenBank sequences listed below can be used for identification. The three species can be identified in the field based on locality, except at sites within the narrow contact zone between *C. australis* **sp. nov.** and *C. ornatus* in the central Wet Tropics (Fig. 1; Table 1).

Genetics. *Cophixalus australis* **sp. nov.** is the 'Central' lineage referred to in Hoskin *et al.* (2011). A representative 16S mtDNA sequence for this species from near the type locality is JF743720 (GenBank accession number). Other 16S sequences for *C. australis* **sp. nov.** are: JF743692, JF743693, JF743695-97, JF7436999, JF743706, JF743710, JF743714-18, JF743722, JF743726, JF743728, JF743729, JF743731-34, JF743738, JF743740, JF743744, JF743745, JF743747-49, JF743751, JF743753, JF743754, JF743757, JF743761 (Hoskin *et al.* 2011). *Cophixalus australis* **sp. nov.** consists of three genetic subgroups: (1) the 'Mt Bartle Frere' subgroup (BF), found on the Bellenden Ker Range, south-eastern Atherton Tablelands and Malbon Thompson Range, (2) the 'Southern' subgroup (S), found from the southern Atherton Tablelands down to the Paluma Range; and (3) the 'Lowland' subgroup (L), found in the lowlands around south-eastern Mt Bartle Frere, the Palmerston Valley area, Tully Gorge and Mission Beach (Hoskin *et al.* 2011; Fig. 1). The taxonomic status of these subgroups is covered in the Discussion.

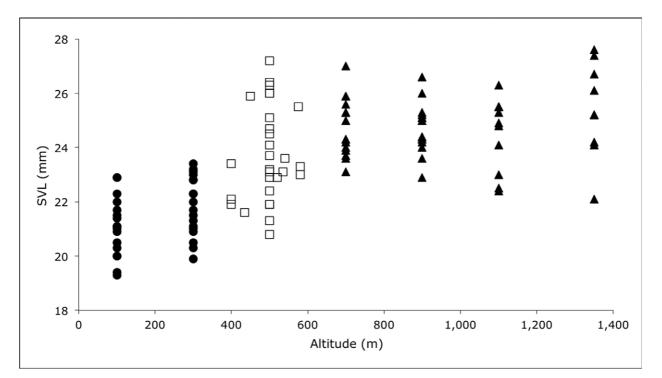


FIGURE 4. The snout to vent length (SVL) of male *C. australis* **sp. nov.** on an altitudinal transect up the eastern slope of Mt Bartle Frere. Symbols represent the Mt Bartle Frere region (BF) genetic subgroup (closed triangles) and the Lowland (L) subgroup (closed circles). These two lineages are sympatric at sites between 400–600 m a.s.l. All individuals at these sites are here treated as potential hybrids (open squares) because genetic analyses have revealed extensive introgression at these sites and because the status of all individuals could not be determined with certainty based on the loci used (low power to detect back-crosses).

Distribution. Found in the central and southern Wet Tropics: Malbon Thompson Ra, Mt Bellenden Ker, summit of Mt Bartle Frere and eastern and southern slopes, southern Atherton Tablelands, lowlands of the Innisfail/Mission Beach/Tully Gorge area, Kirrama Ra and Paluma Ra (south to Mt Halifax) (Fig. 1; Table 1; Hoskin *et al.* 2011). The northern extent of the distribution on the Atherton Tablelands is approximately a line between Herberton and Topaz, with *C. australis* **sp. nov.** known to occur at sites at least as far north as Mt Hypipamee, Millaa Millaa Falls, Topaz and Lamins Hill (Fig 1; Table 1; Hoskin *et al.* 2011). *Cophixalus australis*

sp. nov. is common throughout mid and high elevations (up to 1500 m) but lowland populations (< 400 m a.s.l.) are localised and only known from scattered sites in the central Wet Tropics: south-eastern slope of Mt Bartle Frere, Palmerston, Tully Gorge, Mission Beach and Innisfail area.

Habitat and habits. *Cophixalus australis* **sp. nov.** inhabits rainforest. It also occurs in montane heath and boulder fields where these occur among rainforest, and in some areas it occurs in wet sclerophyll forest adjacent to rainforest. Males call during and following wet weather. Males call from elevated postions (0.3–3 m above the ground) such as on stems and trunks, among foliage and dead vegetation caught amongst foliage, palm axils, tree hollows and among rocks. The most common calling position is facing head upwards on a vertical stem approximately 0.5–1.5 m off the ground. Females are rarely encountered at night. When a female approaches a calling male, he changes his call to a courtship call (a shorter, higher pitched call) and leads the female to a nest chamber in the earth, under a rock, or in a hollow in a rotten log or stem (Zweifel 1985; Hoskin 2004; Felton *et al.* 2006). Similar behaviour has been observed in *Cophixalus kulakula* (Hoskin & Aland 2011). Mate choice in *C. australis* **sp. nov.** is believed to involve multiple steps: male call, male leading and nest quality (Felton *et al.* 2006). As for other Australian microhylids (Zweifel 1985; Hoskin 2004), *C. australis* **sp. nov.** is a terrestrial breeder, with small clutches of large eggs. A clutch of 15 unpigmented eggs has been found under leaf litter in a tree hole, and was attended by a male (Hoskin 2004). *Cophixalus australis* **sp. nov.** is an abundant frog throughout its range.

TABLE 1. List of localities shown in Fig. 1, and species present at each. Modified from Tables A1 and C1 in Hoskin et al.
(2011).

Site	Locality	Dec. Lat/Long	Species
1	Mt Lewis, Carbine Tableland	-16.5108, 145.2695	C. ornatus
2	Harris Peak, Macalister Range	-16.6728, 145.4527	C. ornatus
3	Kuranda	-16.8267, 145.6544	C. ornatus
4	Lamb Range	-17.1063, 145.5913	C. ornatus
5	Mt Baldy	-17.2769, 145.4472	C. ornatus
6	Lake Eacham	-17.2827, 145.6314	C. ornatus
7	Gillies Hwy, top of the range	-17.2158, 145.6738	C. ornatus
8	Red Cedar, Gadgarra Forest Reserve	-17.2725, 145.6666	C. ornatus
9	Butchers Creek area	-17.3383, 145.7109	C. ornatus
10	Gourka Rd (end)	-17.3794, 145.7628	C. ornatus
11	Mt Bartle Frere, W access, 700 m	-17.3761, 145.7719	C. ornatus
12	Mt Bartle Frere, W access, 900 m	-17.3770, 145.7829	C. ornatus
13	Mt Bartle Frere, W access, 1100 m	-17.3820, 145.7881	C. ornatus, C. australis
14	Mt Bartle Frere, W access, 1350 m	-17.3838, 145.7957	C. australis
15	Mt Bartle Frere, E access, 1350 m	-17.4081, 145.8186	C. australis
16	Mt Bartle Frere, E access, 1100 m	-17.4158, 145.8238	C. australis
17	Mt Bartle Frere, E access, 900 m	-17.4155, 145.8272	C. australis
18	Mt Bartle Frere, E access, 700 m	-17.4171, 145.8329	C. australis
19	Mt Bartle Frere, E access, 500 m	-17.4212, 145.8381	C. australis
20	Mt Bartle Frere, E access, 300 m	-17.4203, 145.8438	C. australis
21	Mt Bartle Frere, E access, 100 m	-17.4378, 145.8590	C. australis
22	Mt Bellenden Ker	-17.2677, 145.8691	C. australis
23	Malbon Thompson Range	-17.0863, 145.8796	C. australis
24	Lamins Hill	-17.3560, 145.7242	C. australis
25	Gourka Rd (halfway)	-17.3759, 145.7290	C. australis
26	Old Boonjie Rd (start), Topaz area	-17.3837, 145.7115	C. australis
27	Mausdale, Topaz area	-17.3967, 145.7022	C. australis

continued next page

TABLE 1. (continued)

Site	Locality	Dec. Lat/Long	Species
28	Old Boonjie Rd (end), Topaz area	-17.4151, 145.7351	C. australis
29	Towalla, Topaz area	-17.4487, 145.7153	C. australis
30	The Early Diggings, Topaz area	-17.4712, 145.7277	C. australis
31	Zillie Falls	-17.4820, 145.6596	C. australis
32	Millaa Millaa Falls	-17.4973, 145.6136	C. australis
33	Beatrice R, Palmerston Hwy	-17.5878, 145.7020	C. australis
34	Henrietta Ck, Palmerston Hwy	-17.5981, 145.7576	C. australis
35	Mt Hypipamee	-17.4250, 145.4850	C. australis
36	Tully Falls	-17.7752, 145.5499	C. australis
37	Koombooloomba Dam	-17.7916, 145.5454	C. australis
38	Tully Gorge	-17.7681, 145.6415	C. australis
39	Mission Beach	-17.9100, 146.0684	C. australis
40	Kirrama Range	-18.2072, 145.7636	C. australis
41	Paluma Range	-19.0089, 146.2054	C. australis
42	Hinchinbrook Island	-18.3533, 146.2658	C. hinchinbrookensis

TABLE 2. Morphology and call data collected from live individuals in the field. Morphology codes are: SVL: snout to vent length, TL: tibia length, HW: head width, 3DW: third finger disc width, WT: weight, N: sample size.

		C. ornatus		C. australis sp. nov.			C. hinchinbrookensis sp. nov.			
Trait	Sex	av.	range	Ν	av.	range	Ν	av.	range	Ν
SVL (mm)	М	23.6	18.9–28.6	153	22.7	16.9–27.6	288	19.9	17.2–24.1	83
SVL (mm)	F	25.5	20.2-29.1	5	25.5	20.3-29.1	8	22.6	20.8-25.9	5
TL (mm)	М	9.7	8.5-11.7	153	9.5	7.4–11.3	288	8.2	7.0–9.7	83
TL (mm)	F	10.3	8.5-11.4	5	10.5	8.7-11.8	8	9.3	8.1–10.4	5
HW (mm)	М	7.1	6.0-8.2	153	6.9	5.4-8.2	288	6.3	5.2–7.3	83
HW (mm)	F	7.7	6.4-8.5	5	7.6	5.9-8.6	8	7.2	6.6–7.5	5
3DW (mm)	М	1.3	0.8–2.0	153	1.3	0.7–2.2	288	1.0	0.7–1.3	83
3DW (mm)	F	1.6	1.2-2.0	5	1.6	0.9–1.9	8	1.1	0.9–1.4	5
WT (g)	М	1.0	0.7-1.7	153	0.9	0.4–1.5	288	0.7	0.4–1.3	83
WT (g)	F	1.3	0.7–1.9	5	1.3	0.6–1.8	8	1.0	0.7-1.2	5
TL/SVL	М	0.41	0.37-0.45	153	0.42	0.37-0.48	288	0.41	0.38-0.50	83
TL/SVL	F	0.41	0.39-0.42	5	0.41	0.40-0.43	8	0.41	0.39-0.44	5
HW/SVL	М	0.30	0.27-0.33	153	0.30	0.27-0.34	288	0.32	0.26-0.35	83
HW/SVL	F	0.30	0.29-0.32	5	0.30	0.29-0.32	8	0.32	0.29-0.33	5
3DW/SVL	М	.056	.042074	153	.058	.039–.084	288	.049	.041068	83
3DW/SVL	F	.062	.057–.069	5	.062	.044–.074	8	.050	.043054	5
WT/SVL	М	.043	.033–.066	153	.040	.024–.055	288	.033	.020059	83
WT/SVL	F	.049	.035–.064	5	.048	.030–.062	8	.042	.034–.052	5
Call dom. freq. (kHz)	М	2.73	2.37-3.04	45	2.95	2.2-3.83	141	3.16	2.84-3.43	14
Call duration (ms)	М	418	281-517	45	380	211-599	141	373	337–404	14
Call # pulses	М	392	228-520	45	342	232-571	141	297	243-374	14
Call pulses/s	М	955	624–1786	45	987	477–2331	141	801	603-1028	14
Call rate (s)	М	4.4	2.9–9.7	45	5.4	3.2–10.8	141	4.1	2.8-6.5	14

Species \ Position	84	124	157	190	254	257	266	277	284
C. australis	С	С	С	С	Т	С	С	Т	С
C. hinchinbrookensis	А	С	С	Т	Т	С	С	Т	С
C. ornatus	Т	А	А	Т	С	А	Т	С	Т
Species \ Position	373	382	383	395	416	466	473	476	518
C. australis	С	G	Т	Т	С	С	Т	А	А
C. hinchinbrookensis	Т	А	С	Т	Т	Т	Т	С	G
C. ornatus	С	G	С	С	С	Т	С	А	А

TABLE 3. Some SNPs on the 16S mtDNA gene that are diagnostic among *C. australis* **sp. nov.**, *C. hinchinbrookensis* **sp. nov.** and *C. ornatus*. Position is base position, numbered from the first base of the forward primer (see Methods).

Cophixalus hinchinbrookensis sp. nov.

Hinchinbrook Island Nursery-frog (Figs 2C, 2D)

Material examined. Holotype: QMJ44166, male, upper Gayundah Ck, Hinchinbrook Island (18°22'S, 146°15'E, elevation 850 m), north-east Queensland, G. B. Monteith and D. J. Cook, 11 November 1984. **Paratypes:** QMJ44163, QMJ44164, QMJ44231, upper Gayundah Ck, Hinchinbrook Island (18°22'S, 146°15'E, elevation 850 m); QMJ76065, near Mt Diamantina, Hinchinbrook Island (18°25'34S, 146°17'23"E, elevation 750 m); QMJ76066, summit Mt Bowen, Hinchinbrook Island (18°21'31"S, 146°15'55"E, elevation 1100 m); QMJ76067, near Mt Diamantina, Hinchinbrook Island (18°24'48"S, 146°16'55"E, elevation 740 m). **Additional material:** An additional 88 individuals were measured in the field, and mating calls were measured from 14 of these (Table 1).

Diagnosis. Cophixalus hinchinbrookensis **sp. nov.** can be identified from similar congeners, except *C. australis* **sp. nov.** and *C. ornatus*, by the presence of large, truncated finger pads and by call, which is a 'beep' rather than a call with obvious pulses or notes. Cophixalus hinchinbrookensis **sp. nov.** can be reliably identified from *C. australis* **sp. nov.** and *C. ornatus* genetically, using the loci outlined in Hoskin *et al.* (2011). For 16S mtDNA, diagnostic SNPs are presented in Table 3. It can also be readily identified based on distribution, as it does not co-occur with the other two species and is restricted to Hinchinbrook Island. Cophixalus hinchinbrookensis **sp. nov.** differs from *C. australis* **sp. nov.** and *C. ornatus* in multivariate analyses of mating call and some aspects of morphology (Hoskin *et al.* 2011), but these three species cannot be distinguished on any known single trait. Regarding colour pattern, the groin and posterior thigh generally lack a yellow wash in *C. hinchinbrookensis* **sp. nov.** (*vs.* typically present in *C. ornatus*).

Etymology. The name is derived from the fact that this species occurs only on Hinchinbrook Island, with the *ensis* extension being latin for 'belonging to'. The epithet is to be treated as a noun in apposition.

Description of holotype (Fig. 2C). QMJ44166; male. **Measurements** (mm): SVL 19.0; TL 7.7; FL 4.4; HW 7.6; HL 5.2; ED 1.7; EN 1.5; IN 1.3; 3FL 2.8; 3DW 1.1; 4TL 3.9; 4DW 0.9. *Head:* About same width as body, snout triangular in dorsal view and moderately truncated at the nares, rounded in profile; canthus rostralis rounded, loreal region steep; nares much closer to tip of snout than to eye, nares anterolateral on tip of snout; eyes large; eye diameter greater than eye to naris distance; internarial distance about equal to distance from eye to naris; tympanum small (less than half diameter of eye) and indistinct beneath overlying skin, bordered dorsally by indistinct supra-tympanic fold. *Body:* Rotund. *Limbs:* Hindlimbs short, forearms relatively long; fingers and toes unwebbed; relative finger length 3>2>4>1; fingers 2, 3 and 4 long and slender with large and truncated discs, first finger short with small round disc; low, rounded outer palmar tubercle and smaller rounded inner palmar tubercle; subarticular tubercles low, moderately prominent; relative length of toes 4>3>5>2>1, toe 4 very long and slender; large, truncated discs on toes 2, 3 and 4, discs smaller and more rounded on toes 1 and 5; low, ovoid inner metatarsal tubercle, no outer metatarsal tubercle; subarticular tubercles low and rounded; discs on longest fingers larger than discs on longest toes. *Skin:* Ventral surfaces generally smooth, finely granular on belly; dorsal surfaces smooth with scattered low tubercles; indistinct supra-tympanic fold. **Colour pattern in preservative:** Dorsal surfaces pale brown with darker blotching and mottling, particularly on shoulders and between eyes; grey triangle

on head, grey eyelids; dark smudging on the lateral surface above the axilla; pale lumbar ocelli bordered posteriorly by a dark blotch; dark cloacal region; indistinct dark bar from nare to eye and along tympanic fold. Tympanum pale brown. White patches at the base of the finger and toe discs. Dark brown dorsal colouration merges to lighter brown on flanks. Ventral surface of head and body creamy-brown with fine pale spotting, particularly under throat. Ventral surfaces of limbs creamy-brown; discs and tubercles pale.

Description of type series (N = 7). Data presented as range followed by mean in brackets. Adult measurements (mm): SVL 17.1-23.8 (20.4); TL 7.5-9.8 (8.6); FL 3.8-5.7 (4.7); HW 6.5-8.5 (7.6); HL 4.3-6.0 (5.3); ED 1.7-2.6 (2.0); EN 1.3-1.9 (1.6); IN 1.2-1.7 (1.4); 3FL 2.4-3.3 (2.9); 3DW 0.8-1.3 (1.0); 4TL 3.8-4.7 (4.3); 4DW 0.7-0.9 (0.8). Adult proportions: TL/SVL 0.40-0.44 (0.42); FL/SVL 0.20-0.25 (0.23); FL/TL 0.51-0.58 (0.55); HW/SVL 0.35-0.40 (0.37); HL/SVL 0.23-0.27 (0.26); HW/HL 1.39-1.55 (1.45); ED/SVL 0.09-0.11 (0.10); EN/HL 0.29-0.32 (0.30); EN/IN 1.08-1.27 (1.15); EN/ED 0.66-0.90 (0.79); 3FL/SVL 0.13-0.15 (0.14); 3DW/SVL 0.042-0.060 (0.051); 4TL/SVL 0.18-0.22 (0.21); 4DW/SVL 0.034-0.047 (0.039); 3DW/4DW 1.14–1.44 (1.33). Comparison of sexes: Based on field measurements (Table 2), females are generally larger (e.g. average SVL 22.6 vs. 19.9), have proportionally larger finger discs, and are bulkier (i.e. heavier relative to SVL). **Colour pattern in preservative:** Generally as for holotype – light brown background with areas of darker brown smudging and mottling. Other specimens are dark brown with darker mottling or smudged areas. Consistent features on most specimens are: grey/brown triangle on snout, grey on eyelids, dark W-shaped mark or shoulders; pale lumbar ocelli marked behind by dark patch, dark irregular band/s above axilla on lateral surfaces, dark band from snout through eye and along supratympanic fold; generally dark band on wrist, pale dots at base of finger and toe pads, dark mottling on hindlimbs and lateral surfaces. Ventral surfaces variable: evenly pale cream (N = 3), brown with white flecking (N = 3) or grey brown (N = 1). Undersides of limbs pale to dark brown with white mottling, tubercles and pads generally pale.

Measurements of live individuals. Table 2 presents measurements for 83 males and 5 females in the field.

Colour pattern in life. As for *C. australis* sp. nov.

Call. A finely pulsed 'beep' (Fig. 3B) of the characteristics outlined in Table 2.

Comparison. Only likely to be confused with other rainforest microhylids. *Cophixalus hinchinbrookensis* **sp. nov.** can be distinguished from these species (except *C. australis* and *C. hinchinbrookensis* **sp. nov.**) by the presence of large, truncated finger pads and by the mating call, which is a finely-pulsed 'beep' rather than a call with obvious pulses or notes. *Cophixalus hinchinbrookensis* **sp. nov.** is phenotypically similar to *C. australis* and *C. hinchinbrookensis* **sp. nov.**. There are multivariate differences in mating call and morphology between these three species (Hoskin *et al.* 2011) but they cannot be identified based on any single known phenotypic trait in the field (Table 2). Calls of *C. hinchinbrookensis* **sp. nov.** are of relatively high pitch, short duration, low pulse number and slow pulse rate (Table 2; Fig. 3; Hoskin *et al.* 2011). Males and females of *C. hinchinbrookensis* **sp. nov.** are generally smaller and less bulky (i.e. lighter relative to SVL) frogs and have proportionally smaller finger discs (Table 2; Hoskin *et al.* 2011). *Cophixalus hinchinbrookensis* **sp. nov.** can be reliably identified by genetics, representing a divergent monophyletic lineage for both mtDNA and nDNA loci (Hoskin *et al.* 2011). For 16S mtDNA, the SNPs presented in Table 3 and the GenBank sequences listed below can be used for identification. *Cophixalus hinchinbrookensis* **sp. nov.** can be readily identified to Hinchinbrook Island (Fig. 1), where it is the only *Cophixalus*.

Genetics. *Cophixalus hinchinbrookensis* **sp. nov.** is the 'Hinchinbrook Island' lineage referred to in Hoskin *et al.* (2011). Two representative 16S mtDNA sequences for this species from near the type locality are JF743704 and JF743756 (GenBank accession numbers).

Distribution. *Cophixalus hinchinbrookensis* **sp. nov.** is restricted to Hinchinbrook Island, a large island off the coast of north-east Queensland (Fig. 1). The species has been recorded around Mt Diamantina and Mt Bowen, from 300 m elevation to the highest point on the island, the summit of Mt Bowen (1120 m).

Habitat and habits. Cophixalus hinchinbrookensis sp. nov. inhabits rainforest, montane heath and rocky areas. The mid and high elevations of Hinchinbrook Island consist of a mosaic of low, dense heath in exposed areas, rainforest in the sheltered gullies, and exposed rock. Cophixalus hinchinbrookensis sp. nov. is abundant throughout these habitats. The species has not been recorded from the extensive areas of lowland rainforest on the island. The only other frog species recorded during surveys in the higher elevations of Hinchinbrook Island were Litoria serrata and a species of stoney creek frog for which species identity was not determined with certainty (Litoria jungguy or L. wilcoxii). Cophixalus hinchinbrookensis sp. nov. males call during and following wet

weather. Males call from ground-level to about 2 m above the ground. Calling sites include rocks, tree trunks, stems of saplings and vines, thick tangles of ferns or other low vegetation, and dead leaf litter caught amongst low vegetation. The most common calling position is facing head upwards on a vertical stem approximately 50 cm off the ground. Females are rarely encountered at night. A gravid female was observed following a male uttering a lead call in amongst rocks to a probable nest site. Adults of both sexes, sub-adults and egg clutches were readily found under granite rock slabs. As for all Australian microhylids (Zweifel 1985; Hoskin 2004), the species is a terrestrial breeder, with small clutches of large eggs (Fig. 2D). Recorded clutch sizes range from 3–15 eggs (average = 8 eggs, N = 10). A male was usually found in close proximity to each clutch (e.g. Fig 2D), sometimes straddling it. In a number of instances a single male appeared to be attending two clutches of different developmental stage. In one case, multiple clutching appeared to involve 3 clutches. A male was found calling beside a hollow in a small tree stem approximately 1.5 m above the ground. Inside the hollow was a clutch of 10 unpigmented early-stage eggs, a clutch of 15 eggs of mid development, and 2 metamorphs. During the day the male was found sheltering inside the hollow with the egg clutches.

Cophixalus ornatus (Fry, 1912) Northern Ornate Nursery-frog

(Figs 2E, 2F)

Austrochaperina ornata Fry, 1912, p. 91. Phrynixalus reginae Andersson, 1916, p. 4. Synonymy that of Cogger *et al.* (1983). Sphenophryne variabilis (non Boulenger, 1896), Procter, 1923, p. 1071. (fide Parker, 1934, p. 1071). Sphenophryne ornata Nieden, 1926, p. 48 (new combination). Cophixalus ornatus Parker, 1934, p. 173 (new combination). Phrynomantis ornata Loveridge, 1935, p. 55 (new combination).

Comment on *Phrynixalus reginae* **Andersson, 1916.** The series for this description consisted of 10 specimens from Malanda (collected February 1913) and one from Cedar Creek (collected April 1913). The type locality is taken to be Malanda (Parker 1934). Cogger *et al.* (1983) synonymised *Phrynixalus reginae* in *Cophixalus ornatus.* This synonymy remains because individuals sequenced from Malanda fell within the 'northern' genetic lineage of the *C. ornatus* species complex (Hoskin, unpub. data), as did individuals from sites in close proximity to Malanda (Lake Eacham, Butchers Ck) (Hoskin *et al.* 2011).

Type locality for *Cophixalus ornatus*. The type locality is stated by Fry (1912) as "25 miles [40 km] inland from Cairns". No further information is available to determine where exactly this refers to. However, as covered in the Introduction, under all conceivable interpretations of "25 miles inland from Cairns", the type locality falls within the distribution of the 'northern' genetic lineage of the *C. ornatus* species complex (Hoskin *et al.* 2011).

Comment on paratype. One paratype (R30833) was included in the original description of *C. ornatus*, with the collection locality listed as Russell River (Fry, 1912). This locality does not fall within the range of *C. ornatus* but rather falls in the range of *C. australis* **sp. nov.**, so this specimen belongs to the latter species.

Material examined. AM R222, **holotype**, male, 25 miles inland from Cairns, E. J. Cairn and R. Grant, 1888; QMJ40620, Black Mountain, 17 km ESE of Julatten (16°39'S, 145°29'E); QMJ53656, Mt Spurgeon (16°26'S, 145°12'E); QMJ53723, Mt Lewis (16°35'S, 145°17'E); QMJ55476, Streets Ck, 3 km E of Kuranda (16°51'S, 145°40'E); QMJ55517, Mt Lewis (16°35'S, 145°17'E); QMJ56514, Mt Lewis, summit (16°35'S, 145°17'E); QMJ61976, Mt Lewis (16°33'30"S, 145°16'30"E, elevation 1000 m); QMJ70724, Lake Eacham NP (17°17'30"S, 145°36'30"E, elevation 1000 m); Additional material: An additional 158 individuals were measured in the field, and mating calls were measured from 45 of these (Table 2).

Diagnosis. Cophixalus ornatus can be identified from similar congeners, except *C. australis* **sp. nov.** and *C. hinchinbrookensis* **sp. nov.**, by the presence of large, truncated finger pads and by call, which is a 'beep' rather than a call with obvious pulses or notes. Cophixalus ornatus can be reliably identified from *C. australis* **sp. nov.** and *C. hinchinbrookensis* **sp. nov.** genetically, using the loci outlined in Hoskin *et al.* (2011). For 16S mtDNA, diagnostic SNPs are presented in Table 3. It can also be readily identified based on distribution. Cophixalus ornatus does not co-occur with *C. hinchinbrookensis* **sp. nov.** and only narrowly abuts the range of *C. australis* **sp. nov.** (Fig. 1). Cophixalus ornatus differs from *C. australis* **sp. nov.** and *C. hinchinbrookensis* **sp. nov.** in multivariate analyses of

mating call and some aspects of morphology (Hoskin *et al.* 2011), but these three species cannot be distinguished on any known single trait. Regarding colour pattern, the groin and posterior thigh are typically pale yellow in *C. ornatus* (*vs.* no yellow wash in *C. australis* **sp. nov.** and *C. hinchinbrookensis* **sp. nov.**).

Description of holotype (Fig. 2E). AM R222; male. Measurements (mm): SVL 20.5; TL 9.2; FL 4.8; HW 6.7; HL 5.4; ED 1.8; EN 1.7; IN 1.4; 3FL 3.1; 3DW 0.8; 4TL and 4DW could not be measured due to damage to the toes. *Head:* Narrower than body, triangular in dorsal view; snout moderately truncated to rounded at the nares, projecting slightly in profile; canthus rostralis rounded, loreal region steep; nares much closer to tip of snout than to eye, nares anterolateral on tip of snout; eyes large; eye diameter greater than eye to naris distance; internarial distance less than distance from eye to naris; tympanum small (less than half diameter of eye) and moderately distinct beneath overlying skin, bordered dorsally by indistinct supra-tympanic fold. **Body:** Even width, not rotund. *Limbs:* Hindlimbs short, forearms relatively long; fingers and toes unwebbed; relative finger length 3>2>4>1; fingers 2, 3 and 4 long and slender with large and truncated discs, first finger short with barely expanded small round disc; low, rounded inner and outer palmar tubercles; subarticular tubercles low, moderately prominent; toe length and disc traits could not be assessed due to damage to the specimen; low, rounded outer metatarsal tubercle; subarticular tubercles low and rounded. Skin: Ventral and dorsal surfaces generally smooth; indistinct supratympanic fold. Colour pattern in preservative: Dorsal surfaces uneven cream-brown, with brown markings on the lateral surface above the axilla and a brown band on the wrist of each forearm; indistinct pale lumbar ocelli bordered posteriorly by a brown marking. Head and loreal region pale, with a faint brown line along tympanic fold. Tympanum pale. White patches at the base of the finger discs. Pale brown colouration on flanks. Ventral surface of head and body cream-brown with light brown smudging, particularly under throat. Ventral surfaces of limbs greybrown; discs brown.

Description of series (N = 9): Data presented as range followed by mean in brackets. Adult measurements (mm): SVL 20.4-24.7 (22.3); TL 8.6-10.1 (9.5); FL 4.7-5.9 (5.3); HW 7.2-8.6 (7.8); HL 5.1-5.8 (5.4); ED 1.8-2.4 (2.1); EN 1.5-1.9 (1.7); IN 1.3-1.8 (1.5); 3FL 3.2-4.2 (3.7); 3DW 1.2-1.8 (1.4); 4TL 4.0-5.6 (5.1); 4DW 0.7–1.2 (1.1). Adult proportions: TL/SVL 0.39–0.45 (0.42); FL/SVL 0.22–0.26 (0.24); FL/TL 0.54–0.59 (0.56); HW/SVL 0.32-0.38 (0.35); HL/SVL 0.23-0.25 (0.24); HW/HL 1.37-1.48 (1.44); ED/SVL 0.09-0.10 (0.09); EN/ HL 0.28-0.34 (0.31); EN/IN 1.00-1.26 (1.14); EN/ED 0.74-0.87 (0.81); 3FL/SVL 0.15-0.18 (0.17); 3DW/SVL 0.053-0.073 (0.064); 4TL/SVL 0.19-0.25 (0.23); 4DW/SVL 0.032-0.053 (0.047); 3DW/4DW 1.14-1.64 (1.38). Comparison of sexes: Based on field measurements (Table 2), females are generally larger (e.g. average SVL 25.5 vs. 23.6), have proportionally larger finger discs, and are bulkier (i.e. heavier relative to SVL). Colour pattern in preservative: Generally (N = 7) light brown background with areas of darker markings like blotches, smudges and bands. One specimen has a broad pale vertebral band with dark bands along edge. One specimen has a thin yellow vertebral stripe, with the strip also being present along the hindlimbs. Consistent features on most specimens are: grey/brown triangle on snout, grey on eyelids, indistinct to distinct dark W-shaped mark on shoulders; pale lumbar ocelli marked behind by dark patch, dark band on lateral surfaces above axilla, dark band from snout through eye and along supratympanic fold; generally a dark band on wrist, pale dots at base of finger and toe pads, some individuals have dark mottling on hindlimbs and lateral surfaces. Some individuals have pale areas evident in the groin and hidden areas of the posterior thigh. Ventral surfaces variable: generally evenly pale cream, grey or light brown (N = 6), dark brown (N = 1), pale with darker mottling (N = 1) or brown with white flecking (N = 1). Undersides of limbs generally light brown white, tubercles and pads generally pale.

Measurements of live individuals. Table 2 presents measurements for 153 males and 5 females in the field.

Colour pattern in life. As for *C. australis* **sp. nov.**, except that the groin and posterior thigh are generally pale yellow in *C. ornatus*.

Call. A finely pulsed 'beep' (Fig. 3C) of the characteristics outlined in Table 2.

Comparison. See the 'Comparison' section for *C. australis* sp. nov..

Genetics. *Cophixalus ornatus* is the 'Northern' lineage referred to in Hoskin *et al.* (2011). 16S mtDNA sequences for *C. ornatus* are (GenBank accession numbers): JF743694, JF743698, JF743700-703, JF743705, JF743707-709, JF743711-713, JF743719, JF743721, JF743723-725, JF743727, JF743730, JF743735-737, JF743739, JF743741-743, JF743746, JF743750, JF743752, JF743755, JF743758-760 (Hoskin *et al.* 2011).

Distribution. Found in the northern Wet Tropics: Carbine Tableland (north to Mt Spurgeon), Macalister Range, Kuranda area, Lamb Range, northern Atherton Tablelands and western slope of Mt Bartle Frere (Fig. 1; Table 1; Hoskin *et al.* 2011). The southern extent of the distribution on the Atherton Tablelands is approximately a

line between Mt Baldy (near Atherton) and Butchers Ck, with *C. ornatus* known to occur at sites at least as far south as: Mt Baldy, Lake Eacham, Gadgarra Forest Reserve, Malanda, Butchers Ck, Gourka Road and the western slope of Mt Bartle Frere (Fig. 1; Table 1; Hoskin *et al.* 2011). Records of *C. ornatus* come from 330–1100 m elevation. *Cophixalus ornatus* is absent from the lowlands, with considerable survey effort failing to find it at sites < 300 m a.s.l.

Habitat and habits. Similar to *C. australis* **sp. nov.** and *C. hinchinbrookensis* **sp. nov.** Inhabits rainforest and adjacent wet slerophyll forest in some areas. Common at many sites throughout range but generally more localised and less abundant at sites than the other two species. Males call during and following wet weather from elevated sites (approximately 0.5–2 m above the ground) such as tree trunks, vines, foliage, dead leaves, and rocks. Breeding behaviour appears similar to that of the other two species, with the male leading the female to a nest using a courtship call. *Cophixalus ornatus* is a terrestrial breeder, with small clutches of large eggs (Zweifel 1985; Hoskin 2004; Hoskin & Hero 2008).

Discussion

The description of C. australis sp. nov. and C. hinchinbrookensis sp. nov. brings the number of Australian Cophixalus species to 18. Fifteen of these species (72%) are restricted to the Wet Tropics region. The two species described here add to the list of Wet Tropics endemic vertebrates described in the last decade or so: Phyllurus amnicola Hoskin, Couper, Schneider & Covacevich, 2000 (in Couper et al. 2000); Phyllurus gulbaru Hoskin, Couper & Schneider, 2003; Glaphyromorphus clandestinus Hoskin & Couper, 2004; Cophixalus aenigma Hoskin, 2004; Mixophyes coggeri Mahony, Donnellan, Richards & McDonald, 2006; Mixophyes carbinensis Mahony, Donnellan, Richards & McDonald, 2006; Litoria myola Hoskin 2007. This shows that despite a long history of scientific exploration, the Wet Tropics region still yields exciting species discoveries. Cophixalus hinchinbrookensis sp. nov. is of note in being the only vertebrate species known to be endemic to Hinchinbrook Island. This large, mountainous island is separated from the mainland by a narrow, shallow sea channel that was exposed during historical periods of lower sea-level (e.g. the last glacial maxima) (Nix 1991). The fact that C. hinchinbrookensis sp. nov. has not been found in areas of suitable habitat on the adjacent mainland, despite surveys in these areas, suggests that C. hinchinbrookensis sp. nov. was isolated on Hinchinbrook Island even when the strait was exposed. A combination of contraction of suitable moist habitat to high elevation pockets (Hoskin et al. 2011) and domination of the strait by unsuitable dry forest types (Nix 1991) mean the strait probably operated as a barrier even during these periods.

Cophixalus australis sp. nov. contains substantial genetic diversity, structured as three subgroups: (1) the 'Mt Bartle Frere region' subgroup, found on the Bellenden Ker Range, south-eastern Atherton Tablelands and Malbon Thompson Range; (2) the 'Southern' subgroup, found from the southern Atherton Tablelands down to the Paluma Range; and (3) the 'Lowland' subgroup, found in the lowlands around south-eastern Mt Bartle Frere, the Palmerston Valley area, Tully Gorge and Mission Beach (Hoskin et al. 2011; Fig. 1). Zweifel (1985) and Hoskin (2004, 2008) have commented on the noticeably smaller body size and the shorter, higher-pitched calls of frogs representing the Lowland subgroup. To some extent, these differences can be attributed to altitude—across the C. ornatus species complex in general, frogs at lower altitudes are smaller and have shorter, higher-pitched calls (Hoskin et al. 2011). Previous comparisons between upland and lowland populations (e.g. Zweifel 1985) have suggested discrete differences in traits that in fact exhibit more continuous variation when assessed in detail along altitudinal transects. Transects between the lowland subgroup and the other two subgroups (BF and S) reveal that altitude explains a component of phenotypic variation between the subgroups, but not all the variation in traits (Hoskin, unpublished data; e.g., see Fig. 4 for SVL vs altitude). Further investigation is required to resolve the phenotypic differences between the three genetic subgroups of C. australis sp. nov. In contrast to the abrupt parapatric boundary between C. australis sp. nov. and C. ornatus, there is considerable admixture and introgression at hybrid zones between the subgroups of C. australis sp. nov. (Hoskin et al. 2011). Therefore the subgroups of C. australis sp. nov. are considered a single species, pending further investigation of the hybrid zones.

Acknowledgments

I particularly thank the primary co-authors of the *C. ornatus* evolutionary research: Craig Moritz, Maria Tonione and Megan Higgie. For assistance in the field I thank Jacque Milton, Megan Higgie, Keith McDonald, Steve Williams and Alex Anderson. For assistance at the Queensland Museum I thank Patrick Couper and Andrew Amey, and at the Australian Museum I thank Ross Sadlier. Maria Tonione made components of Figure 1 and Megan Higgie assisted with Figure 2. I thank Alex Anderson for use of his photo (Fig. 2D) and I thank Stephen Zozaya, Robert Puschendorf, Stewart McDonald and Angus McNab for providing other photos for consideration. This work was funded by the Australian Biological Resources Study, the Australian Research Council, the National Science Foundation, James Cook University, The University of Queensland, and The Australian National University.

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