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Skinks currently assigned to *Carlia aerata* (Scincidae : Lygosominae) of north-eastern Queensland: a preliminary study of cryptic diversity and two new species

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Abstract. A preliminary investigation of genetic diversity in *Carlia aerata*, by sequencing the mitochondrial ND4 gene, revealed the presence of two cryptic species, described herein. The sequence data was added to an existing phylogeny to discern molecular relationships. Interestingly, genetic affinities lie not with *C. aerata,* the species to which they key. Instead, one has affinities with *C. tanneri*, the other with *C. foliorum.* This casts doubt on the validity of morphological characters alone to infer relationships within this genus. Despite low levels of genetic divergence from sister taxa, the new species can be diagnosed from these by morphological characters that exhibit little or no intraspecific variation. The addition of these new species to the gene tree did not enhance resolution of the phylogenetic relationships at the deeper nodes of the *Carlia* tree. The discovery of these two new cryptic species provides further support for a previously suggested rapid mid-Miocene diversification of *Carlia* that may have resulted from the successful expansion of a rainforest-dwelling ancestor into the expanding woodlands associated with Miocene climate fluctuations.

Introduction

Australia's reptiles are a diverse group with more than 830 described species; many others are recognised but still await description (Wilson and Swan 2003; Couper and Hoskin, unpublished data; Sadlier, personal communication). Molecular techniques provide a means of recognising faunal diversity that can remain undetected using traditional morphological criteria. Over the last decade, genetic evidence has become increasingly important in clarifying species boundaries and identifying cryptic elements in the fauna, which often represent highly divergent lineages (Mather 1990; Couper and Gregson 1994; James *et al*. 2001; Donnellan *et al*. 2002). The extent of cryptic speciation within Australian reptiles remains unknown, but given the small proportion of taxa examined (at least 24 of 141 genera have had at least one species group examined: S. Donnellan, personal communication) and the number of cryptic species already detected (25 published and other studies identifying species complexes within existing taxa), it could be considerable. Indeed, Australian *Cryptoblepharus*, currently under review, are now known to consist of 23 species where only six were previously recognised (Horner 2003). Attempts to describe cryptic species identified by molecular data are often thwarted by a lack of diagnosable morphological characters (Moritz *et al*. 1993; Schneider *et al*. 1999). Hence faunal diversity is often recognised only in a phylogenetic context, without being placed in a taxonomic framework. Land-management authorities can therefore overlook these genetic lineages in a system where fauna-conservation priorities are linked to name-based lists.

The genus *Carlia* (rainbow skinks) occurs widely in northern and eastern Australia (and also New Guinea), where it currently comprises 30 species and shows extreme morphological conservatism relative to many other congeneric lizard species (Storr 1974; Ingram and Covacevich 1988, 1989; Couper 1993; Couper *et al*. 1994). Recent studies on *Carlia* members indicate that cryptic speciation may predominate in this genus (Schneider *et al*. 1999; Stuart-Fox *et al*. 2002). Highly divergent lineages have been shown to exist within *C. rubrigularis* (Schneider *et al*. 1999) and *C. amax*, *C. gracilis*, *C. jarnoldae*, *C. schmeltzii* and *C. vivax* (Stuart-Fox *et al*. 2002). This study aims to further elucidate the extent of diversity within *Carlia* by investigating observed colour pattern differences in populations of *C. aerata* from north-eastern Queensland. This species occurs as two distinct colour forms: individuals are either dorsally dark brown with dark tails or medium brown with reddish hind limbs and tails. Examination of specimens in the Queensland Museum's herpetological collection showed that both occur sympatrically at four localities (Palmer River, Shipton's Flat, Isabella Falls and Laura). The most recent description of this small, litter-dwelling species was by

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Ingram and Covacevich (1988). These authors, recognising the existence of sexual dichromatism in *Carlia* species, regarded the red-tailed form as breeding males. We do not concur with this conclusion. The occurrence of red-tailed females and juveniles argues for a distinct species, not sexual dimorphism. Molecular data (mitochondrial protein coding ND4 gene) offered a means to test our hypothesis that the observed colour pattern differences in '*C. aerata*' actually represent distinct species.

Materials and Methods

Genetics

Samples, PCR and Sequencing

Tissues were obtained from seven specimens initially identified as *C. aerata* collected at three different localities in Queensland (Table 1). This sample includes the two sympatric colour forms of '*C. aerata*' recorded at Shipton's Flat (15°48′S, 145°16′E), via Cooktown. Tissues were available for analysis from another two Queensland *Carlia* species: *C. sesbrauna* and *C. tanneri*. The latter species was also analysed by Stuart-Fox *et al*. (2002), but was assigned to the wrong species in 'material examined' (see Results). Total genomic DNA was extracted from all tissues using a standard kit (DNeasy Tissue Kit, Qiagen). In order to discern the phylogenetic relationships of these new *Carlia* samples, we targeted the same region of the mitochondrial ND4 gene used by Stuart-Fox *et al*. (2002) to generate their recent molecular phylogeny of the *Carlia* group. Furthermore, we were able to access and download from GenBank all the other ND4 sequences generated by Stuart-Fox *et al*. (2002) for *Carlia* species (accession numbers AJ290504–53). While the same outgroup species used by Stuart-Fox *et al*. (2002) were unavailable, ND4 sequences were obtained from two other species also belonging to the *Pseudemoia* group of lygosomine skinks: *Morethia butleri* (accession number AY169647) and *Eugongylus rufescens* (accession number AY169642).

Using the primer pairs listed in Stuart-Fox *et al*. (2002), the same 726-bp region of the mitochondrial ND4 gene was amplified and sequenced. However, PCR conditions and amplification parameters varied from that paper. Each 25-μL reaction contained to a final concentration 1 × Taq polymerase buffer, 0.4 μM each primer; 0.8 mM dNTPS, 2.0 mM $MgCl_2$ and 0.75 U of Taq polymerase. The use of the hot start polymerase AmpliTaq Gold (Applied Biosystems) required an initial denaturation at 95°C for 10 min before the commencement of the remaining cycle parameters; then followed 35 cycles of 95°C for 30 s, 50°C for 45 s, 72°C for 45 s and a final extension 72°C for 5 min, 22°C for 30 s.

PCR products were gel purified and sequencing reactions carried out according to standard ABI PRISM dye-deoxy terminator sequencing protocols using Big Dye Terminator ver. 1.1. Sequences from the new specimens have been deposited in GenBank nucleotide sequence database (accession numbers AY533654–62).

Phylogenetic analysis

Chromatographs were checked and all sequences were aligned using Se-Al v2.0a10 (Rambaut 1996). Maximum parsimony analyses, identical to those performed by Stuart-Fox *et al*. (2002) were conducted using PAUP* v4.b10 (Swofford 2002). Trees were derived without bootstrapping using heuristic searches with tree bisection reconnection branch swapping and 1000 random stepwise sequence additions. A bootstrap tree was generated in the same manner using only 10 stepwise sequence additions with 1000 bootstrap pseudoreplications.

Bayesian analyses were carried out using MrBayes v2.01 (Huelsenbeck and Ronquist 2001) and posterior probabilities were calculated using a Marko chain, Monte Carlo sampling approach. These analyses used the TVM (transversion model) + Γ (gamma distribution of rates) and I (proportion of invariant sites) model of sequence evolution, as was suggested by Modelltest (Posada and Crandall, 1998). Starting trees were random and four simultaneous Markov chains were run for 1 000 000 generations with trees sampled every 100 generations. To generate the consensus tree, burnin values were set at 50 000 generations based on empirical values of stabilising likelihoods.

Morphometrics

All body measurements were taken using Mitutoyo electronic callipers. Supraciliaries, supralabials, infralabials and subdigital lamellae on the fourth toe were counted on the left side only. Both left and right counts are given for type specimens. The supraciliaries represent the scale row starting behind the prefrontal that has full contact with the supraoculars along its upper edge. Infralabials are the series fully contained between the mental and the posterior margin of the last supralabial. Subdigital lamellae were counted between the claw and the 3rd/4th toe junction. The total number of enlarged nuchals is given. Only original tails were included in the morphometric analysis (largely assessed by eye; X-rayed for *C. malleolus*, sp. nov.). Abbreviations for body measurements are as follows: snout–vent length (SVL); forelimb (axilla to tip of longest digit, L1); hind limb (groin to tip of longest digit, L2); axilla to groin (AG); tail length (original tail, posterior margin of preanal scales to tip, TL); head length (tip of snout to mid-anterior edge of ear opening, HL); head width (level with posterior margin of parietal shields, HW). Configuration of the preocular/presubocular scales is discussed and illustrated in Appendix 1. Colour pattern descriptions include detail that is visible only with magnification.

Table 1. Species samples and localities for molecular analysis
Museum registration codes are as follows: QMJ, Queensland Museum; USNM-Field Herp, Smithsonian Institution, National Museum of Natural History, USA

Initial species identification	Locality	Museum registration no.	Final species identification[A]
Carlia aerata	Donkey Springs, Bulleringa NP, Qld	QMJ74495	*Carlia abscondita* 1
Carlia aerata	Donkey Springs, Bulleringa NP, Qld	QMJ74496	*Carlia abscondita* 2
Carlia aerata	Donkey Springs, Bulleringa NP, Qld	QMJ74498	*Carlia abscondita* 3
Carlia cf. *aerata*	Shipton's Flat, Cooktown, Qld	QMJ78404	*Carlia malleolus*
Carlia aerata	Shipton's Flat, Cooktown, Qld	QMJ78405	*Carlia aerata* 1
Carlia aerata	Shipton's Flat, Cooktown, Qld	QMJ78378	*Carlia aerata* 2
Carlia aerata	Hann River, Cape York, Qld	QMJ78381	*Carlia aerata* 3
Carlia sesbrauna	Klondyke, Cape York, Qld	USNM-Field Herp 36306	*Carlia sesbrauna* 2
Carlia tanneri	McIvor River Crossing, Qld	QMJ62424	*Carlia tanneri* 2

[A]Numbers refer to how the samples appear in the phylogeny (Fig. 1).

In 'Comparison with other species', the new taxa are separated from other *Carlia* species (and the *koshlandae/sadlieri/timlowi* subgroup of *Menetia*) by published descriptions (Ingram and Covacevich 1988, 1989; Greer 1991; Couper 1993; Cogger 2000) and the examination of museum specimens (Appendix 2).

Scale counts and measurements were compared between samples using ANOVAs and unpaired two-tailed *t*-tests. In most cases the results were uninformative, largely due to the small sizes of the Bulleringa and Mt Mulligan samples.

Authorships for the new taxa do not follow that of the paper as a whole.

Results

Phylogeny of Carlia

The addition of the new species sequences failed to enhance the resolution of the phylogenetic relationships at deeper nodes of the *Carlia* tree. Our results are essentially the same as those reported by Stuart-Fox *et al*. (2002), with both maximum-parsimony trees (consensus and bootstrap) and the trees generated by Bayesian inference (consensus) showing little support for any major resolution among lineages within *Carlia* (Fig. 1). The same sister-species groupings at shallower nodes of the tree reported in that study are in general also found here (Fig. 1).

Two errors appear in the appendix of Stuart-Fox *et al*. (2002). These, however, do not affect their published phylogeny. First, the registration number provided for the *C. macfarlani* sample should be corrected to NTMR23034 (listed as NTMR20234). The number given belongs to a specimen of *Litoria caerulea.* Second, specimen QMJ62425, listed as *C. zuma*, is a topotypic specimen of *C. tanneri*, which groups with the new *C. tanneri* sequence in our gene tree (QMJ62424; our specimen was collected at the same time and place as that used by Stuart-Fox *et al*. (2002). The *C. zuma* tissues used in the study of Stuart-Fox *et al*. (2002) came from the material listed as *C. tanneri*, SAMR32519. This specimen, unavailable for examination, was collected at Mt Spec, Queenland. *C. tanneri* does not occur this far south, being narrowly restricted to riverine rainforests and monsoon forests in the Cooktown region (Ingram and Covacevich 1988). *C. zuma* is morphologically similar to *C. tanneri*: both species have moveable lower eyelids, seven supralabials, 27 or fewer midbody scale rows and flat ear lobules (Ingram and Covacevich 1988; Couper 1993). *C. zuma*-like specimens are known to occur at Mt Spec and are represented in the Queensland Museum's herpetological holdings. We note that the affinities of this population remain uncertain. *C. zuma* was described from specimens collected from the Mackay district. Between Mackay (Central Mackay Coast Zoogeographic Region) and Mt Spec (Wet Tropics Zoogeographic Region) lies an expanse of dry woodland known as the 'Burdekin Gap', which has separated the faunas of these regions for an 'evolutionarily long period' (Joseph *et al*. 1993).

Despite the lack of resolution at the deeper nodes of the *Carlia* tree, both maximum parsimony and Bayesian analyses identified three distinct and strongly supported clades among the '*Carlia aerata*' samples, providing support for the recognition of two new *Carlia* species (Fig. 1). *C. aerata sensu stricto* (see Systematics of *Carlia aerata* below) forms a monophyletic clade that comprises only three of the seven '*aerata*' individuals in the phylogeny (two from Shipton's Flat, 15°48′S, 145°16′E, and one from Hann River, 15°11′21″S, 143°52′25″E). The red-tailed '*aerata*' from Shipton's Flat is the sister species of *Carlia tanneri* (100% bootstrap support) and is here described as *Carlia malleolus*, sp. nov. The three specimens from Bulleringa National Park (17°35′12″S, 143°48′46″E) also form a distinct group whose phylogenetic affinities lie with neither *C. aerata* nor *C. malleolus*, sp. nov., but rather with *C. foliorum* (bootstrap value 100).

The placement of the Bulleringa specimens results in the *C. foliorum* branch of the phylogeny becoming paraphyletic. The Queensland *C. foliorum* specimen (Mt Aberdeen) is more closely allied to the Bulleringa specimens (4.36% average sequence divergence, 68% bootstrap support) than it is to its New South Wales counterpart (Denman Tip, 6.47% sequence divergence). Reanalysis of the morphology of the Bulleringa specimens and their comparison with 50 *C. foliorum* specimens, including north Queensland individuals ($n = 26$, Appendix 2), found that they could be reliably separated from *C. foliorum* in all instances. It is therefore unlikely that the Bulleringa population merely represents a range extension of *C. foliorum*. The diagnostic character, a moveable lower eyelid (versus preablepharine condition), is taxonomically significant. There is no known intraspecific variation in this character in any scincid lizard (A. Greer, personal communication). This, coupled with their apparent geographic isolation, was pivotal to our decision to describe the Bulleringa specimens as *C. abscondita*, sp. nov. Despite some authors' confusion in distinguishing between a moveable lower eyelid and a preablepharine condition (Ingram and Covacevich 1988), we could find no ambiguity in this character. All *C. foliorum* specimens, including those used in the genetic analysis, were found to possess the preablepharine state and a free interparietal, characters that separate *C. foliorum* from all other *Carlia* species.

Sequence-divergence estimates between *C. malleolus*, sp. nov., and *C. abscondita*, sp. nov., with *C. aerata* differ by an average 14.47% and 13.87% respectively. In contrast, *C. malleolus*, sp. nov., differs from its sister taxon, *C. tanneri*, by only an average of 6.68% and *C. abscondita*, sp. nov., from its sister taxon, *C. foliorum*, by an average of 5.05%.

Systematics of Carlia aerata

Lygosoma aeratum Garman, 1901 was described from a single specimen collected from 'Cooktown'. In the same paper, Garman recognised a second species, *Ablepharus heteropus*, from 'the Great Barrier Reef'. Subsequent

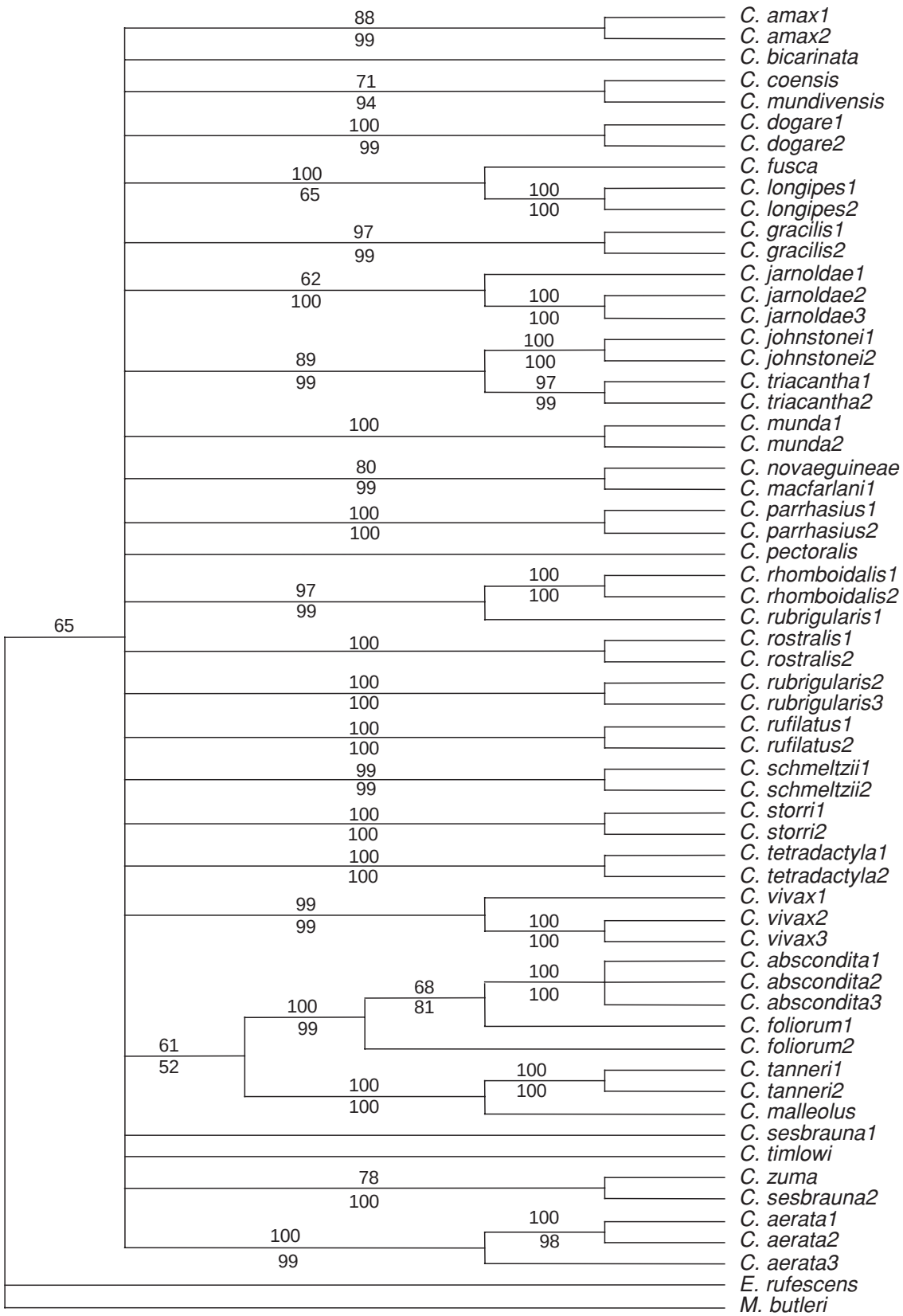

Fig. 1. Strict consensus tree. Numbers above branches represent bootstrap values obtained from maximum parsimony analysis (1000 replicates), numbers below branches represent frequency of observed bipartitions from MrBayes consensus tree (1 000 000 generations).

authors (Cogger *et al*. 1983; Ingram and Covacevich 1988) have regarded these taxa as conspecific and Ingram and Covacevich (1988) chose *aerata* as the available name, on the basis of page priority. These authors assigned *aerata* to the genus *Lygisaurus*, which they resurrected from synonymy with *Carlia*. Recent molecular studies (Stuart-Fox *et al*. 2002) have assessed the phylogenetic relationships of *Carlia* and *Lygisaurus* by examining 29 species (23 *Carlia*, 6 *Lygisaurus*). The resulting phylogeny showed that most *Lygisaurus* form a single clade nested within *Carlia*. The clade also includes *Carlia parrhasius*, which possesses characters that assign it to *Carlia sensu stricto* (number of supradigital scales on 4th toe, size and scale carinations: see Couper *et al*. in press). Stuart-Fox *et al*. (2002) resynonymised *Lygisaurus* with *Carlia* on the strength of this evidence, coupled with the paucity of external morphological characters separating the two genera (Ingram and Covacevich 1988, 1989; Couper *et al*. in press). The nomenclature in this paper follows Stuart-Fox *et al*. (2002) in treating *Lygisaurus* de Vis, 1884 and *Carlia* Gray, 1845 as congeneric.

Herein, we describe the two new species, redescribe *C. aerata* and highlight a morphologically distinct population from Mt Mulligan (16°52′S, 144°52′E), which we tentatively refer to *C. abscondita*, sp. nov. The types of *Lygosoma aeratum* Garman, 1901 and *Ablepharus heteropus* Garman, 1901 were examined and enhanced descriptions are provided.

The new species are assigned to *Carlia* (as defined by Stuart-Fox *et al*. 2002) by the following external character states (polarity follows Greer 1979, and outgroup comparison follows Hutchinson *et al*. 1990): fore limbs tetradactyl, hind limbs pentadactyl (digital formula 4/5, derived); supraocular scales transversely oriented (primitive); ear opening surrounded by sharp lobules (derived); prefrontal scales present (primitive); frontoparietals fused to form a single shield (derived) and lower eyelid moveable, with transparent disc (primitive) (Ingram and Covacevich 1988, 1989; Greer 1991; Cogger 2000; Couper *et al*. in press). The only other Australian scincid genera containing species with a 4/5 digital formula are: *Eroticoscincus*, *Menetia* (as defined by Greer 1991) and *Saproscincus*. *Eroticoscincus* lacks prefrontal scales (present in *Carlia*). Six species of *Menetia* (*M. alanae*, *M. amaura*, *M. concinna*, *M. greyii*, *M. maini* and *M. surda*) have obliquely oriented supraoculars. The remaining three species (*M. timlowi*, *M. koshlandae* and *M. sadlieri*) have transversely oriented supraoculars like *Carlia* but lack lobules on the margins of the ear. *Saproscincus* has paired frontoparietal shields. Our genetic analysis clearly places *timlowi* as a member of the *Carlia* group. The relationship of *timlowi* to *koshlandae* and *sadlieri*, and the generic placement of these species is yet to be assessed using molecular techniques.

Carlia malleolus Roberts, Couper, Worthington Wilmer, Amey & Zug, sp. nov.

(Figs 2, 3)

Lygisaurus aeratus (in part) Ingram & Covacevich, 1988: 341.

Material examined

Holotype. QMJ42740, Shipton's Flat, via Cooktown (15°48′S, 145°16′E).

Paratypes. QMJ17818, Isabella Falls, 32 km NW Cooktown (15°17′S, 145°02′E), 4.x.1969; QMJ74221–22, Coal Seam Ck, S of Laura (15°37′S, 144°29′E), 28.x.2000; QMJ78379, QMJ78404, Shipton's Flat, via Cooktown (15°48′S, 145°14′E), 15.x.2002; QMJ40975–76, Shipton's Flat, via Cooktown (15°48′S, 145°16′E), July–September 1982; QMJ42738–39, QMJ42741–42, Shipton's Flat, via Cooktown (15°48′S, 145°16′E), July 1984; QMJ62404, Palmer R. (16°09′S, 144°08′E), 10.vii.1996; QMJ38755, Mt Windsor Tableland (16°19′S, 145°01′E), 20–21.xii.1980; QMJ45571–73, Granite Gorge, via Mareeba (17°01′S, 145°21′E), 14.iv.1985; QMJ26691, Atherton Tableland, Walkamin (17°08′S, 145°26′E), 5.x.1974.

Diagnosis

Carlia malleolus, sp. nov., is distinguished from all other Australian *Carlia* species by the following characters combined: small size (maximum SVL 32.2 mm); medium brown body; hind limbs and tail reddish orange; venter unpatterned, body scales smooth, lower eyelid moveable (containing large palpebral disc), six supraciliaries, seven supralabials; ear round (horizontal axis sometimes slightly longer) with sharp lobules on margins.

Description

SVL (mm) 19.1–32.2. Proportions as %SVL: TL 152–172 (160 ± 6 (mean ± s.d.), n = 3); AG 46.1–56.1 (51.2 ± 2.4, n = 17); L1 24.2–32.6 (28.5 ± 2.2, n = 18); L2 34.6–42.9 (38.6 ± 2.5, n = 18); HL 18.6–23.2 (21.1 ± 1.0, n = 18). Body robust. Head barely distinct from neck. HW 63.8–76.3% HL (70.3 ± 3.4, n = 18). Limbs moderate. L1 66.3–83.3% L2 (73.8 ± 3.8, n = 18).

Scalation. Rostral in broad contact with frontonasal. Prefrontals large, narrowly to widely separated. Supraoculars 4, 1 and 2 in contact with frontal, 2, 3 and 4 in contact with frontoparietal. Frontoparietals fused, forming a single shield. Interparietal distinct. Enlarged nuchal scales 2–3 (mode = 2, 78%, n = 18). Snout rounded in profile. Loreals 2. Preoculars 2. Presubocular single (see Appendix 1). Supraciliaries 5–7 (mode = 6, 89%, n = 18). Lower eyelid moveable with clear window; palpebral disc large, occupying more than half of lower eyelid. Ear aperture much smaller than palpebral disc; round, or with slightly longer horizontal axis, with sharp lobules on margins. Supralabials 7 (n = 18), with the fifth below the eye. Infralabials 5–6 (mode = 6, 83%, n = 18). Midbody scale rows 22–26 (mode = 24, 50%, n = 18). Paravertebral scale rows 41–48 (mode = 43, 33%, n = 15). Lamellae beneath 4th toe 18–23 (mode = 21, 43%, n = 14).

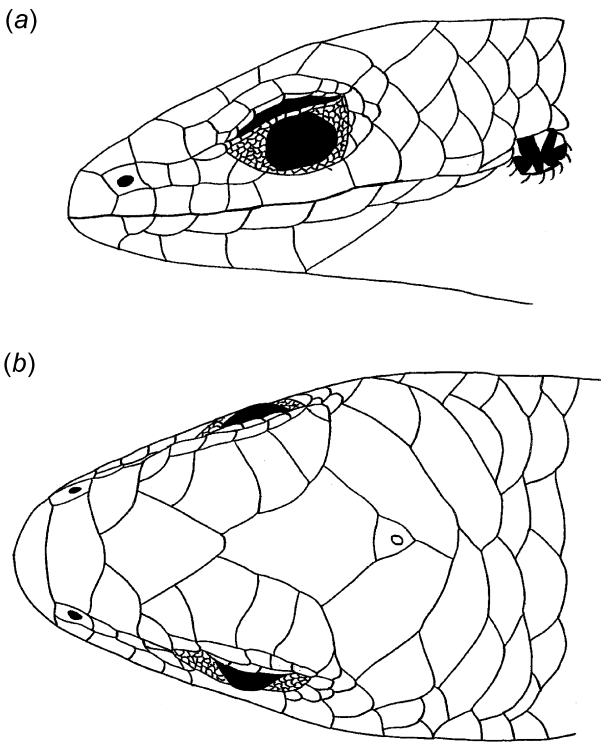

Fig. 2. *Carlia malleolus*, paratype QMJ40976, head in lateral (*a*) and dorsal (*b*) views.

Skeletal. Presacral vertebrae 26–27 (mode = 27, 89%, *n* = 18); caudal vertebrae 37–41 (mode = 41, 66%, *n* = 3).

Colour pattern in preservative (alcohol)

Medium brown above. Dorsal and lateral scales finely marked with 2–3 dark longitudinal streaks. White to cream below. Head shields stippled with black (not visible to naked eye). A dark streak in front of eye, encompassing a portion of the prefrontal, first and second supraciliaries, loreals, preoculars and presubocular; continuing as a fine line along dorsal edge of fifth supralabial. Labials heavily barred. Several dark, broken lines running from angle of mouth to forelimb. Upper surfaces of tail and hind limbs with greatly reduced ground colour; reddish orange (in all size classes examined, irrespective of season). Forelimbs also orange, but heavily speckled with brown. Belly immaculate, but sometimes with dark edging to outer scales. Faint speckling (not visible to naked eye) beneath tail and hind limbs.

Fig. 3. *Carlia malleolus* in life, paratype QMJ78404 from Shipton's Flat, via Cooktown (photograph by G. Cranitch).

Measurements and scale counts for the holotype

SVL 29.3 mm, T regrown, AG 14.3 mm, L1 8.36 mm, L2 10.9 mm, HL 6.2 mm, HW 4.3 mm, midbody scale rows 24, paravertebral scale rows 44, supraciliaries 6/6, supralabials 7/7, infralabials 6/6, scales between nasal and presubocular 3/3, subdigital lamellae beneath 4th toe 20/21, nuchals 2.

Comparison with other species

Within *Carlia*, *C. malleolus* can only be confused with the species formerly assigned to *Lygisaurus* (i.e. small size, coupled with striate body scales: Ingram and Covacevich 1988) or *Menetia* (*timlowi, sadlieri* and *koshlandae*: Greer, 1991). Morphologically, it is most like *C. aerata*, to which it would key in Cogger (2000) and Ingram and Covacevich (1988), from which it is readily distinguished by body colour pattern (hind limbs and tail reddish orange *v.* brown) and ventral colouration (tail, hind limbs and groin not patterned or very faintly speckled *v.* strongly speckled). It is further distinguished from this species by the number of supralabial scales (7 *v*. 6, rarely 7) and the shape of its ear aperture (round to slightly horizontally elongate *v.* horizontally elongate, upper and lower edges often in close proximity). Its genetic affinities clearly lie with *C. tanneri*, which is identified as its sister taxon with 100% bootstrap support. *C. malleolus* is readily separated from *C. tanneri* by the size of its palpebral disc (large *v.* small) and the shape of its ear lobules (sharp *v.* low and flat). It is also separated from *C. laevis*, *C. macfarlani*, and *C. sesbrauna* by the size of the palpebral disc (large *v.* small) and from *C. rococo* by the shape of its ear lobules (sharp *v*. low and flat). *C. malleolus* differs from *C. foliorum* and the '*timlowi* group' by the state of its lower eyelid (moveable *v*. fused).

Distribution

Coastal and subcoastal areas of north-eastern Queensland (Fig. 4) from slightly north of Cooktown (Isabella Falls, 15°17′S, 145°16′E) to just south of Cairns (Walkamin, 17°08′S, 145°26′E). All known localities lie east of 144°00′E. In addition to localities for which voucher specimens exist (see material examined), *C. malleolus* has also been recorded at the following localities (field examinations by LR, voucher specimens not taken): McIvor River (15°07′S, 145°00′E), Bald Hills (15°18′S, 145°02′E), Mount Rose (15°23′S, 145°02′E), Hazelmere Station (15°23′S, 145°03′E), Crocodile Station (15°43′S, 144°40′E), Lakeland

Downs (15°53′S, 144°47′E), Fairlight Station (15°47′S, 144°03′E), West Normanby River (15°53′S, 144°57′E), Bonnyglen Station (15°57′S, 144°47′E), Palmerville (16°00′S, 144° 04’ E), Mt Mulgrave, 5 km E, (16°23′S, 144E°01′E), Cyclone Creek (16°23′S, 144°35′E) and Campbell Creek (16°28′S, 144°58′E).

Habits and habitat

Carlia malleolus occurs in sparsely grassed open eucalypt woodlands on poor soils. It is found in leaf-litter, particularly around rocky outcrops, logs and grass tussocks. The dominant trees in these communities are *Melaleuca viridiflora*, *Erythrophleum chlorostachys* (Cooktown Ironwood) and eucalypt species, including *Corymbia clarksoniana*, *C. nesophila*, *C. tessellaris*, *Eucalyptus chlorophylla*, *E. crebra*, *E. cullenii*, *E. leptophleba*, *E. persistens* and *E. platyphylla*.

Etymology

Latin, fire-dart (Handford and Herberg 1966). ‘The term malleolus denoted a hammer, the transverse head of which was formed for holding pitch and tow; which, having been set on fire, was projected slowly, so that it might not be extinguished during its flight, upon houses and other buildings in order to set them on fire; and which was therefore commonly used in sieges together with torches and falaricae (Liv. xxxviii.6; Non. Marcellus, p556, ed. Lips.; Festus, s.v.; Cic. pro Mil. 24; Veget. de Re Mil. iv.18; Vitruv. x.16.9 ed. Schneider).’ We propose the name in reference to this Roman usage for a fire-dart and in our context for a fast-moving, small, red-tailed skink.

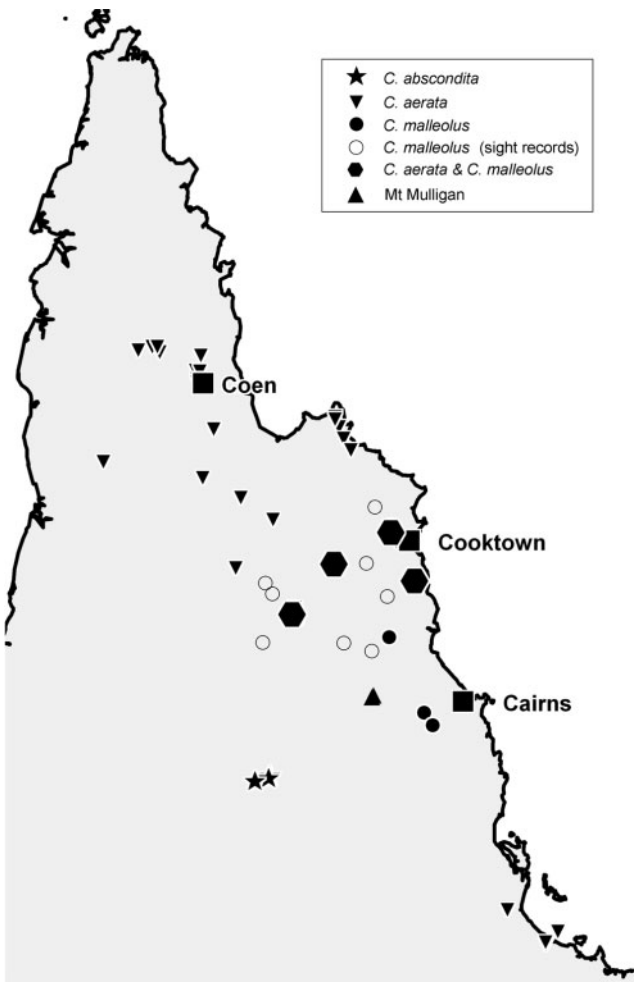

Fig. 4. Distribution of *Carlia abscondita*, *C. aerata* and *C. malleolus.*

Carlia abscondita Worthington Wilmer, Couper, Amey, Zug & Roberts, sp. nov.

(Figs 5, 6)

Material examined

Holotype. QMJ74496, Donkey Springs (near), Bulleringa NP (17°35′12″S, 143°48′46″E).

Paratypes. QMJ74495, Donkey Springs (near), Bulleringa NP (17°35′12″S, 143°48′46″E); QMJ74498, Donkey Springs, N, Bulleringa NP (17°36′14″S, 143°48′38″E); QMJ74234–35, Bulleringa NP via Mt Surprise (17°39′S, 143°44′E); QMJ80043, Donkey Spring Gorge, Bulleringa NP (17°35′12″S, 143°48′51″E).

Diagnosis

Carlia abscondita is distinguished from all other Australian *Carlia* species by the following characters combined: small size (maximum SVL 30.0 mm); dark olive brown body; hind limbs and tail lighter than body, but retaining dark pigment; faint dark speckles visible on underside of tail and limbs; body scales smooth; lower eyelid moveable (containing large palpebral disc) with a clearly defined row of upper ciliaries; six supraciliaries; seven supralabials; ear round with sharp lobules on margins.

Description

SVL (mm) 26.4–30.0. Proportions as %SVL: TL 121.8–154.2 (138.7 ± 14.4 (mean ± s.d.), n = 4); AG 49.2–54.0 (51.6 ± 2.2, n = 5); L1 23.2–31.6 (28.7 ± 3.4, n = 5); L2 32.1–43.6 (40.2 ± 4.6, n = 5); HL 20.3–22.1 (21.2 ± 0. 77, n = 5). Body robust. Head barely distinct from neck. HW 63.8–69.3% HL (65.8 ± 2.1, n = 5). Limbs moderate. L1 64.9–74.1% L2 (71.4 ± 3.68, n = 5).

Scalation. Rostral in broad contact with frontonasal. Prefrontals large, moderately separated. Supraoculars 4, 1 and 2 in contact with frontal, 2, 3 and 4 in contact with frontoparietal. Frontoparietals fused, forming a single shield. Interparietal distinct. Enlarged nuchal scales 2. Snout rounded in profile. Loreals 2. Preoculars 2. Presubocular single (see Appendix 1). Supraciliaries 6. Lower eyelid movable with clear window; palpebral disc large, occupying more than half of lower eyelid; upper ciliaries present. Ear aperture much smaller than palpebral disc; round, or with slightly longer horizontal axis, with sharp lobules on margins.

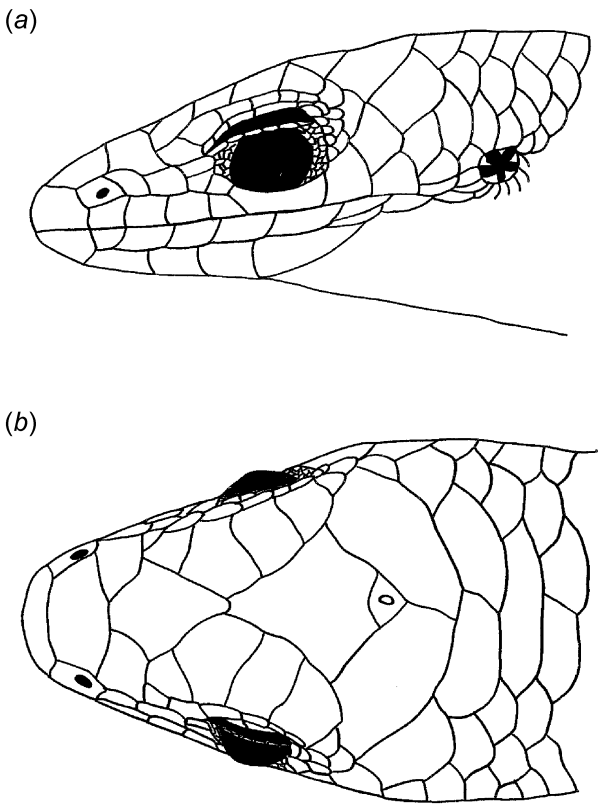

Fig. 5. *Carlia abscondita*, paratype QMJ74234, head in lateral (*a*) and dorsal (*b*) views.

Supralabials 7, with the fifth below the eye. Infralabials 6. Midbody scale rows 24–26 (mode = 24, 80%, *n* = 5). Paravertebral scale rows 42–44 (mode = 43, 40%, *n* = 5). Lamellae beneath 4th toe 21–25 (mode = 25, 50%, *n* = 4).

Colour pattern in preservative (alcohol)

Dark olive brown above. Dorsal and lateral scales finely marked with 2–3 dark, longitudinal streaks. White to silvery grey below. Head shields stippled with black (not visible to naked eye). A dark streak in front of eye, encompassing a portion of the prefrontal, first and second supraciliaries, loreals, preoculars and presubocular; continuing as a fine line along dorsal edge of fifth supralabial. Labials heavily barred with black. Several dark, broken lines running from angle of mouth to forelimb. Upper surfaces of tail and hind limbs paler than body though still heavily etched with darker pigment. Belly immaculate, sometimes with dark edging to outer scales. Faint speckling beneath the tail and hind limbs (visible to naked eye).

Fig. 6. *Carlia abscondita* in life, QMJ80043, Donkey Spring Gorge, Bulleringa NP, 17°35′12″S, 143°50′35″E (photograph by Colin Dollery, QEPA).

Measurements and scale counts for the holotype

SVL 27.4 mm, TL 42.3, AG 14.8 mm, L1 8.7 mm, L2 12.0 mm, HL 6.1 mm, HW 3.9 mm, midbody scale rows 24, paravertebral scale rows 42, supraciliaries 6/6, supralabials 7/7, infralabials 6/6, scales between nasal and presubocular 3/3, subdigital lamellae beneath 4th toe 25/25, nuchals 2.

Comparison with other species

The diagnosis will separate *C. abscondita* from all other Australian *Carlia* species. However, difficulty may arise in morphologically distinguishing it from *C. malleolus*, to which it is similar in all aspects of scalation. These species do, however, exhibit subtle differences in colour pattern. While both species are medium-dark brown above, *C. malleolus* has a greater degree of pigment loss from the tail and hind limbs, which are reddish orange in all size classes, irrespective of season. This species also shows some loss of pigment in the forelimbs. In *C. abscondita,* the tail and hind limbs are generally paler than the dorsal ground colour, but remain heavily etched with darker pigment. There is no loss of pigment from the forelimbs of this species. *C. malleolus* and *C. abscondita* also differ in the intensity of spotting on the underside of the tail and hind limbs. In the former, these markings are so diffuse that they are not visible to the naked eye. In the latter, these markings can be seen without magnification. The genetic affinities of *C. abscondita* clearly lie with *C. foliorum*, which is identified as its sister taxon with 100% bootstrap support. The two species are readily distinguished. *C. abscondita* has a moveable lower eyelid with a clearly defined series of upper ciliaries (*v.* eyelid immoveable, upper ciliaries absent). Further, *C. abscondita* always has a presubocular scale (*v.* rarely present in *C. foliorum*, only one of 26 specimens examined from north Queensland). The configuration of the preocular/presubocular scales in *C. foliorum* is variable and is discussed further in Appendix 1.

Distribution

Carlia abscondita is currently known from a single population in Bulleringa NP (17°39′S, 143°44′E), via Mt Surprise, north-eastern Queensland (Fig. 4).

Habits and habitat

Carlia abscondita inhabits open woodlands dominated by *Eucalyptus* and *Corymbia* species with a sparse to medium/dense grass cover. The Donkey Springs specimens were found in leaf-litter among exfoliated sandstone slabs. The type locality is a narrow creek line, fed by a perennial spring. This dissects an area of sand sheets and cuts deeply into the underlying sandstone, forming a small gorge system. The foot slopes and creek bed contain sandy patches as well as silt and colluvium deposits. There are also areas of exposed rock with larger boulders present above the creek line.

Notes

In our assessment of *C. abscondita* we examined a series of specimens from the Mt Mulligan area (16°52′S, 144°52′E, see Appendix 2). These specimens are, in most respects, morphometrically indistinguishable from this species. However, the Mt Mulligan specimens have a statistically higher paravertebral count than *C. abscondita* (46–48 *v.* 42–44; unpaired two-tailed *t*-test $t = 7.60777$, d.f. = 10, $P < 0.0001$). In the absence of biochemical data to support these differences between specimens of *C. abscondita* from Bulleringa NP and those from Mt Mulligan, 130 km to the north-east, we are reluctant to comment further on the status of this population.

Etymology

Latin, concealed, hidden (Handford and Herberg 1966). The name alludes to the species' close similarity to *C. malleolus* and its initial detection using molecular techniques.

Redescription of *Carlia aerata*

Carlia aerata (Garman)

(Figs 7, 8)

Lygosoma aeratum Garman, 1901: 7. Holotype MCZ6476, Cooktown, Queensland.

Ablepharus heteropus Garman, 1901: 9. Holotype MCZ6484, Great Barrier Reef, Queensland.

Material examined

QMJ80023, Mungan-Kaanju NP; QMJ58224, QMJ58231, Rokeby NP; QMJ23442, Rokeby Hsd, QMJ37489, Peach Ck, 12 km NE Mt Croll; QMJ37527, Coen Airport, 23 km NNW Coen; QMJ77438, Coen, 20 km N, QMJ26272 Coen, 3 km N; QMJ26263–65, Coen, 2 km up Lankelly Ck; QMJ20517, Melville Ra.; QMJ64614–15, QMJ64617–18, Cape Melville NP; QMJ78393–95, Musgrave–Coen Rd; QMJ20485, Cape Melville, Wakooka Outstation; QMJ63493, Altanmoui Range, Cape Melville NP; QMJ57984, Meton Yard, Strathgordon Holding; QMJ38029–30, Glen Garland Stn, 24 km N, via Musgrave; QMJ78383–86, Windmill Ck, Artemis Stn; QMJ78381–82, QMJ78396, Hann River Crossing; QMJ42770, Isabella Falls, 32 km NW Cooktown; QMJ27089, McIvor Rd, 20.8 km W Cooktown; QMJ78397, Laura; QMJ74218, Peninsula Developmental Road, ~8 km S Laura; QMJ57781, Pinnacles Dam; QMJ78378, QMJ78405, QMJ40977–82, Shipton's Flat, via Cooktown (15°48′S, 145°16′E); QMJ57785, Sandy Ck, Maytown; QMJ62400, Palmer R.; QMJ26611–13, QMJ26615–17, Ingham, 19.9 km S, on Bruce Hwy; QMJ70114, Rattlesnake I., 20 km NE of Townsville; QMJ65224, Clemant SF, 5 km SE Rollingstone; QMJ67487, Clemant SF, 40 km N Townsville.

Description

SVL (mm) 15.0–30.1. Proportions as %SVL: TL 129.8–153.9 (140.0 ± 7.7 (mean ± s.d.), $n = 13$); AG 45.4–55.9 (51.8 ± 2.5, $n = 49$); L1 24.5–31.7 (27.7 ± 1.8, $n = 49$); L2 30.6–41.0 (36.5 ± 2.3, $n = 49$); HL 19.1–24.3 (21.7 ± 1.1, $n = 50$). Body robust. Head barely distinct from neck. HW 53.1–75.8% HL (69.9 ± 4.0, $n = 50$). Limbs moderate. L1 69.2–97.0% L2 (75.9 ± 5.5, $n = 49$).

Scalation. Rostral in broad contact with frontonasal. Prefrontals large, narrowly to widely separated. Supraoculars 4, 1 and 2 in contact with frontal, 2, 3 and 4 in contact with frontoparietal ($n = 54$) or 3 with 1 in contact with frontal, 1, 2 and 3 in contact with frontoparietal ($n = 2$). Frontoparietals fused, forming a single shield. Interparietal distinct. Enlarged nuchal scales 2–4 (mode = 3, 41%, $n = 54$). Snout rounded in profile. Loreals 2. Preoculars 2. Presubocular single (see Appendix 1). Supraciliaries 5–6 (mode = 6, 96%, $n = 55$). Lower eyelid movable with clear window; palpebral disc large, occupying more than half of lower eyelid. Ear aperture much smaller than palpebral disc; horizontally elongate, with sharp lobules on margins. Supralabials 6–7 (mode = 6, 87%, $n = 55$, rarely 5 as in one

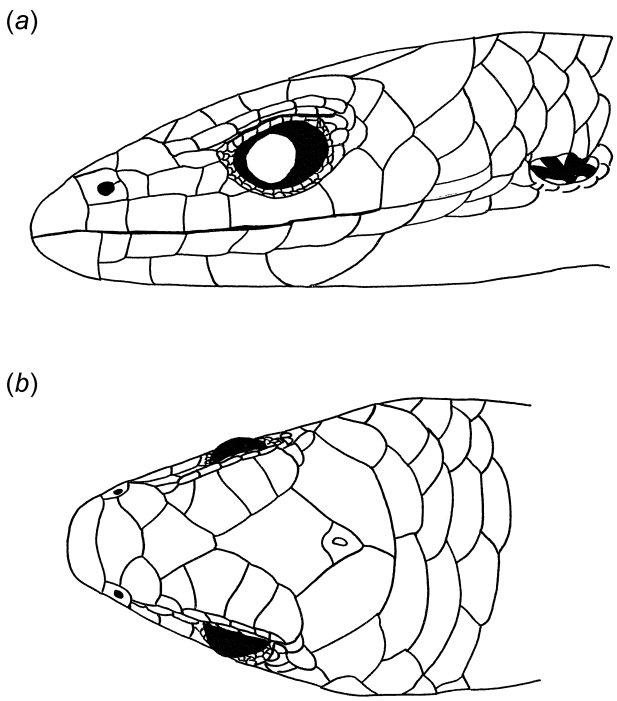

Fig. 7. *Carlia aerata*, QMJ78378, head in lateral (*a*) and dorsal (*b*) views.

side of holotype MCZR6476), usually 4th below eye. Infralabials 5–6 (mode = 6, 95%, *n* = 55). Midbody scale rows 22–25 (mode = 22, 51%, *n* = 47). Paravertebral scale rows 42–48 (mode = 44, 43%, *n* = 49). Lamellae beneath 4th toe 16–23 (mode = 21, 35%, *n* = 44).

Colour pattern in preservative (alcohol)

Medium-dark olive brown above. Flanks with or without white speckling. A broad, dark vertebral streak, encompassing both paravertebral scale rows is evident in many specimens. Dorsal and lateral scales finely marked with 2–3 dark, longitudinal streaks. White to silvery grey below. Head shields stippled with black (not visible to naked eye). A dark streak in front of eye, encompassing a portion of the prefrontal, 1st and 2nd supraciliaries, loreals, preoculars and presubocular; continuing as a fine line along dorsal edge of 5th supralabial (not always obvious in darker specimens). Labials heavily barred with black. Several dark, broken lines running from angle of mouth to forelimb. Upper surfaces of tail sometimes paler than body but lacking reddish orange flush; sometimes marked with small white specks. Belly usually immaculate but sometimes boldly spotted; darker edging often present on outer scales. Speckling beneath the tail and hind limbs generally bold.

Comparison with other species

Carlia aerata is separated from all other *Carlia* species formerly assigned to *Lygisaurus* by the following suite of characters: 6 supralabial scales; lower eyelid moveable, with large palpebral disc; ear aperture horizontally elongate, surrounded by sharp lobules. On rare occasions where *C. aerata* has 7 supralabial scales, it superficially resembles *C. foliorum, C. malleolus* and *C. abscondita.* It is readily distinguished from *C. foliorum* by the state of its lower eyelid (moveable *v.* fused above forming a fixed spectacle over the eye). It is separated from both *C. malleolus* and *C. abscondita* by the shape of the ear aperture (horizontally elongate *v.* round to slightly elongate) and the intensity of the speckling beneath the tail and hind limbs (bold *v.* diffuse).

Fig. 8. *Carlia aerata* in life, QMJ78405, Shipton's Flat, via Cooktown (photograph by G. Cranitch).

Distribution

Coastal and subcoastal areas of north-eastern Queensland (Fig. 4) from the Rokeby Station area (Mungan-Kaanju NP, 13°36′40″S, 142°47′24″E) to just north of Townsville (Clemant SF, 19°08′11″S, 146°27′42″E). All known localities lie east of 142°00′E.

Habits and habitat

Commonly found in sympatry with *C. malleolus* (see account of *C. malleolus*).

Notes

Ingram and Covacevich (1988) comment on the difficulty in distinguishing *C. aerata* from *C. foliorum* in preservative because it is not always easy to determine whether the eyelid is fused above. Such confusion occurs when the lower eyelid begins to separate along the suture on its upper edge. Any attempt to examine this condition closely usually results in tearing and makes interpretation of this character more difficult. Interpreting the state of the lower eyelid in these species, however, is relatively straightforward. In *C. aerata*, a series of upper ciliaries indicates the moveable eyelid condition (these lie immediately below the supraoculars). *C. foliorum* has no upper ciliaries.

Re-examination of Garman types

Lygosoma aeratum Garman

Lygosoma aeratum Garman, 1901: 7.

Material examined

Holotype. MCZR6476, Cooktown, Queensland.

Description

SVL (mm) 27.8. Proportions as %SVL: TL broken; AG 49.6; L1 25.2; L2 38.5; HL 21.1. Body robust. Head barely distinct from neck. HW 62.7% HL. Limbs moderate. L1 65.4% L2.

Scalation. Rostral in broad contact with frontonasal. Prefrontals large, moderately separated. Supraoculars 4, 1 and 2 in contact with frontal. Frontoparietals fused, forming a single shield. Interparietal distinct. Enlarged nuchal scales 2. Snout rounded in profile. Loreals 2. Preoculars 2. Presubocular single. Supraciliaries 6. Lower eyelid moveable with clear window; palpebral disc large, occupying more than half of lower eyelid. Ear aperture smaller than palpebral disc; horizontally elongate, with sharp lobules on margins. Supralabials 6/5, with 3rd or 4th beneath eye. Infralabials 6. Two scales between nasal and presubocular scale. Midbody scale rows 24. Paravertebral scale rows 46. Lamellae beneath 4th toe 16–17.

Colour pattern in preservative (alcohol)

Not informative because of age and original manner of preservation. Medium to dark brown dorsally and laterally; light brown to tan ventrally.

Measurements and scale counts for the holotype

SVL 27.8 mm, T broken, AG 13.8 mm, L1 7.0 mm, L2 10.7 mm, HL 5.9 mm, HW 3.7 mm.

Ablepharus heteropus Garman

Ablepharus heteropus Garman, 1901: 9.

Material examined

Holotype. MCZR6484 (mature female), Great Barrier Reef, Queensland.

Description

SVL (mm) 25.3. Proportions as %SVL: TL 94.8; AG 51.4; L1 24.9; L2 30.0; HL 19.0. Body robust. Head barely distinct from neck. HW 79.2% HL. Limbs moderate. L1 82.9% L2.

Scalation. Rostral in broad contact with frontonasal. Prefrontals large, moderately separated. Supraoculars 4, 1 and 2 in contact with frontal. Frontoparietals fused, forming a single shield. Interparietal distinct. Enlarged nuchal scales 2. Snout rounded in profile. Loreals 2. Preoculars 2. Presubocular single. Supraciliaries 6. Lower eyelid moveable with clear window; palpebral disc large, occupying more than half of lower eyelid. Ear aperture much smaller than palpebral disc; nearly circular, largely hidden by sharp lobules around margin. Supralabials 6, with fourth beneath eye. Infralabials 6. Three scales between nasal and presubocular scale. Midbody scale rows 24. Paravertebral scale rows 45. Lamellae beneath 4th toe 17–19.

Colour pattern in preservative (alcohol)

Not informative because of age and original manner of preservation. Medium to dark brown dorsally and laterally; light brown to tan ventrally.

Measurements and scale counts for the holotype

SVL 25.3 mm, T 24 mm, AG 13.0 mm, L1 6.3 mm, L2 7.6 mm, HL 4.8 mm, HW 3.8 mm.

Notes

Our examination of the Garman types (GZ) concurs with the findings of Ingram and Covacevich (1988); both taxa are clearly conspecific. They also exhibit characters that show they are not referrable to *C. malleolus* or *C. abscondita*, both of which have seven supralabials (*v.* 6/5 MCZR6476 and 6/6 MCZR6484). The subdigital lamellae counts for these specimens (MCZR6484 17–19, MCZR6476 16–17) are more consistent with the lower end of the range for *C. aerata* (16–23) than for *C. malleolus* (18–23) or *C. abscondita* (21–25). Unfortunately, the condition of the Garman types did not allow colour pattern comparisons with the new taxa.

Discussion

Carlia abscondita and *C. malleolus* are truly cryptic species, both keying to *C. aerata* and separated from one another by subtle pattern differences. This, while problematic for field identification, in no way diminishes their validity as species. Skinks can be highly visually oriented and subtle pattern differences can play important roles in mate recognition. The significance of ultraviolet reflectance in males of the congeneric *C. pectoralis* has been demonstrated (Blomberg *et al*. 2001).

Both *C. abscondita* and *C. malleolus* represent discrete lineages in the phylogeny of *Carlia* (Fig. 1). In considering the appropriate criteria for species recognition in *Batrachoseps* (slender salamanders), Jockusch *et al*. (2001) justified their recognition of *B. minor* from its close congeners *B. incognitus* and *B. luciae* because of its isolation from both, and it was regarded as being 'on its own unique evolutionary trajectory'. We believe the same to be true of *C. abscondita*. This species falls apart from its morphologically closest congeners, *C. malleolus* and *C. aerata*, on the phylogenetic tree, its genetic affinities clearly lying with *C. foliorum*. There is no doubt that *C. abscondita* and *C. foliorum* are distinct, their separation supported by a character state that exhibits no intraspecific variation. Further, on the basis of existing collections, C. *abscondita* is geographically isolated from *C. malleolus*, *C. aerata* and *C. foliorum*.

Carlia shows remarkable morphological conservatism for such an ecologically diverse assemblage (Storr 1974; Stuart-Fox *et al*. 2002). Character states used to diagnose species include differences in palpebral disc size, ear and ear lobule shape, scale shape and degree of keeling. Some species are so close morphologically that they have been diagnosed from what are presumed to be their closest relatives by colour pattern differences alone (for example, *C. rhomboidalis* from *C. rubrigularis*, and *C. rostralis* from *C. longipes*). Hence, the presence of new taxa, particularly within the smaller, less conspicuous forms, is not surprising.

The placement of the new taxa within our phylogeny of *Carlia* is of particular interest. Both *C. malleolus* and *C. abscondita* are morphologically consistent with the diagnosis of *C. aerata* (as *Lygisaurus aeratus*) provided by Ingram and Covacevich (1988). All three taxa are small (max SVL <33 mm) with smooth body scales, have a moveable lower eyelid containing a large palpebral disc and an ear aperture surrounded by sharp lobules. These combined characters separate them from all other *Carlia* species. That *C. malleolus* and *C. abscondita* form strongly supported sister-species groupings with *C. tanneri* (a species with a small palpebral disc and flat ear lobules) and *C. foliorum* (fused lower eyelid) respectively, suggests that the morphological characters used to delineate species boundaries do

not necessarily point to close phylogenetic relationships. The placement of *C. longipes* and *C. rostralis* in the molecular phylogeny (Stuart-Fox *et al*. 2002, present study) further illustrates this point. These species, separated from one another on colour pattern differences, were both assigned to the '*C. fusca*' complex (Ingram and Covacevich 1989). The consensus tree clearly shows that *C. rostralis* has molecular affinities with *C. dogare* and *C. vivax* while *C. longipes* is placed with *C. fusca* (from New Guinea: Zug 2004). A similar disparity between molecular and morphological 'relatedness' is seen in the scincid genera *Cryptoblepharus*, *Ctenotus* (both morphologically conservative) and *Egernia*. Australian *Cryptoblepharus* show a disparity between morphological and genetic data: 'In some cases genotypes were divergent but phenotypes indistinguishable or, conversely, phenotypes divergent but genotypes were shared' (Horner 2003). Within *Ctenotus*, colour pattern is often paramount in species delineation and Storr (1981) created species groups, largely pattern based, as an aid to identification. These groups were later expanded by Wilson and Knowles (1988). A preliminary molecular study shows that the validity of these species-groups as monophyletic assemblages is questionable (Pianka, personal communication 1996, http://utexas.edu/~varanus/ctenotus.html). The placement of any *Ctenotus* species within the existing scheme remains largely subjective (Couper *et al*. 2002). A recent study on *Egernia* showed that '… species groups appear to be paraphyletic and the morphological characters on which they are based may represent instances of convergence to a particular environment …' (Chapple 2003). The validity of morphological criteria alone for defining species is questioned by Donnellan *et al*. (1993). These authors show that this approach is often inadequate and give case studies: *Mixophyes* (Mahony *et al.*, unpublished data), *Sphenodon* (Daugherty *et al*. 1990), *Pseudemoia* (Donnellan and Hutchinson 1990; Hutchinson and Donnellan 1992) and *Thamnophis* (Lawson and Dessauer 1979), in which morphologically defined species have later, under genetic scrutiny, been shown to contain several taxa.

A further assessment of *C. aerata*, with genetic sampling across the species' range is likely to reveal additional new taxa. Our examination of *C. aerata* also revealed colour pattern differences between adult-sized individuals. These differences were considered to be sexual differences initially, with darker specimens having spotted sides being adult males in breeding condition. Less ornate specimens were believed to be adult females. Examination of gonads showed that this was not the case. The dark, spotted specimens were of both sexes (QMJ78738, J78382, J78384 ♀; J78393, J78396 ♂, the latter in peak reproductive condition), as were the paler, inornate specimens (QMJ37527 ♀ gravid; J58224 ♂). Without genetic sampling to assess divergence, the taxonomic significance of these characters remains problematic.

The intraspecific genetic distances between populations of some *Carlia* species (*C. amax* 21%; *C. vivax* 20%; *C. rubrigularis* 22%: Stuart-Fox *et al*. 2002; *C. sesbrauna* 11%: this study) are in the order of 2–4 times those separating *C. malleolus* and *C. abscondita* from their sister taxa, *C. tanneri* (6.68%) and *C. foliorum* (5.05%). Such large distances, combined with paraphyletic relationships among individuals of at least two other species (*C. rubrigularis* and *C. sesbrauna*), suggest that these 'units' may represent more than just divergent populations of a single species. Recognition and description of cryptic species is fundamental to conserving biodiversity (Donnellan *et al*. 1993), and available data clearly point to *Carlia* as a group warranting further investigation.

Most of Australia's *Carlia* species inhabit open forests and woodland communities. Indeed, only six of the 30 described species could be termed rainforest dwellers, and even these thrive in edge habitats. North-eastern Queensland is especially rich in *Carlia* species and could be termed a diversity hotspot for the genus (19 species occur in this region and 15 of these are largely restricted to latitudes north of 20°S).

An overall lack of phylogenetic resolution among *Carlia* species led Stuart-Fox *et al*. (2002) to propose a scenario for a relatively rapid speciation within this group. However, they did not attempt to speculate on the underlying forces that may have driven this process. Their molecular divergence estimates loosely date this diversification as occurring sometime in the Miocene. This is consistent with other phylogeographic studies of rainforest vertebrates in this region, which have indicated that most recognised species are of Miocene or Pliocene age (Joseph and Moritz 1993; Moritz *et al*. 1997; Schneider *et al*. 1998). However, we acknowledge the weaknesses of biogeographical discussions in the absence of strong supporting evidence (Greer 1989). Yet, assuming that the timing of Stuart-Fox *et al.* (2002) is correct, we suggest that the rapid-speciation scenario is congruent with current theories on Miocene climate and habitat changes (mid-Miocene onwards). It is widely accepted that a drop in temperature combined with an expansion of the Antarctic ice sheet led to increasing aridity over the Australian continent with a reduction of widespread rainforests in favour of xerophytic woodlands (Galloway and Kemp 1981). Such environmental shifts may have provided new opportunities for ancestral *Carlia*, allowing them to diversify in the expanding open woodland habitats. If ancestral *Carlia* had the same edge-dwelling propensities as modern rainforest forms, this may have conferred advantages for the colonisation of drier woodland habitats. The recognition (in this study) of two new taxa, coupled with molecular evidence suggesting considerable cryptic speciation, indicates that this radiation event may be more dramatic than previously thought.

Acknowledgments

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Appendix 1. Configuration of preocular/presubocular scales

The character, 'number of scales between the second presubocular and the nasal scale', has been used to diagnose *Lygisaurus* species and remains a significant character in separating *C. aerata* and *C. foliorum* (Ingram and Covacevich 1988): the former species usually has three scales, while the latter usually has two. This character, however, can be confusing. Some *C. foliorum* specimens (3 of 26 examined) exhibit a downward rotation of the upper preocular scale, so that it contacts an upper labial along its anterior margin. When this occurs, the scale count between the second presubocular and the nasal increases from two to three, without any change in the number of scales present. The normal configuration is illustrated in Fig. 9*a*. Fig 9*b* illustrates the reconfigured state. It is less confusing to consider the scales by name (i.e. preocular and presubocular) and then score presence or absence. In *C. foliorum*, the normal condition is two preoculars, no presuboculars, with only 8% of the sample possessing a presubocular scale. A presubocular is always present in *C. abscondita* but the preoculars are often fused. We define preoculars as the scales that are situated immediately anterior to the orbit. These are upper and lower (but may be fused) and are in broad medial contact. The presubocular contacts the posteroventral margin of the lower preocular. Our lower preocular and presubocular scales were regarded as two presuboculars by Ingram and Covacevich (1988).

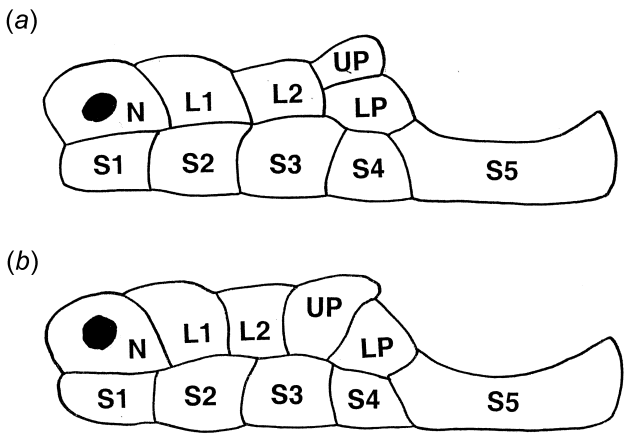

Fig. 9. Configuration of preocular scales in *Carlia foliorum*. (*a*) Normal configuration – upper preocular not contacting supralabials. (*b*) Rotation of upper preocular, excluding lower preocular from second loreal. N = nasal, L1–L2 = 1st and 2nd loreal, UP = upper preocular, LP = lower preocular, S1–S5 = supralabials 1st–5th supralabial.

Appendix 2. Additional material examined

All material is from Queensland unless otherwise stated.

Carlia cf. aerata (Mount Mulligan population)

QMJ45385–87, QMJ45404–07, QMJ64429, Mount Mulligan; QMJ45359, Mt Mulligan summit, 2.5 km SW Mt Mulligan township.

Carlia foliorum

QMJ11891, Tinaroo Dam, 8 km N; QMJ75430–31, Kennedy Hwy, W Ravenshoe; QMJ59749, 40 Mile Scrub NP; QMJ31054, 40 Mile Scrub; QMJ74275, Princess Hills NP; QMJ42461–63, Peak Ra; QMJ70401–02, Conjuboy Holdings; QMJ57284, Eight Mile Ck; QMJ26614, Ingham, 19.9 km S; QMJ58072, QMJ58134, QMJ58136, Hidden Valley, 22 km W Paluma; QMJ58690, Forty Mile Scrub NP; QMJ26625, Moongobulla, 1 km W; QMJ27691–92, QMJ32567–8, Hencamp Ck., 5 km N; QMJ26338, Magnetic I.; QMJ76644–45, Arcadia, Magnetic I.; QMJ77454, Blackbraes NP; QMJ62701, Mt Aberdeen. South Australian Museum R33733, Denham Tip, NSW.

Carlia macfarlani

Northern Territory Museum R23021, R23031, R23034, Maxwell Ck., Melville I., NT; QMJ78355, Coen; QMJ78392, Coen, 2 km S.

Carlia sesbrauna

QMJ78356, QMJ78387–91, USNM Field Herp 036306–7 Klondyke Mine, Station Ck, McIlwraith Ra.

Carlia tanneri

Holotype. QMJ32352, Morgan R Crossing.

Paratypes. QMJ32358–59, Hopevale Mission, 33 km N; QMJ20609–11, QMJ32362–64, McIvor R Crossing; QMJ22380, Tanner Farm; QMJ42771–2, Endeavour R.; QMJ27093–96, Cooktown, 13 km W; QMJ24117–18, Endeavour R., 15 km W Cooktown; QMJ22789, Cedar Scrub, via Cooktown.