AUSTRALIAN LEAF-TAILED GECKOS: PHYLOGENY, A NEW GENUS, TWO NEW SPECIES AND OTHER NEW DATA

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Phylogenetic analyses of the leaf-tailed geckos, based on DNA sequences from the mitochondrial cytochrome b gene, show that *Saltuarius*, as currently constituted, is paraphyletic. *Saltuarius cornutus*, *S. salebrosus*, *S. wyberba* and *S. swaini* form a well-supported monophyletic group which is the sister group to the apparently monophyletic *Phyllurus*. *'Saltuarius' occultus* is the sister group to the clade containing *Phyllurus* and all other *Saltuarius* spp. Thus, *'Saltuarius' occultus* represents a long, independent, evolutionary lineage within the leaf-tailed geckos and is recognised from both morphological and molecular data as distinct at the generic level (*Orraya* gen. nov.). *Orraya* gen. nov. can be distinguished from all other Australian padless carphodactylines by a combination of four apomorphies, the most obvious being greatly elongated cervical vertebrae. The phylogenetic analyses also revealed genetically distinct populations from Chaelundi State Forest, New South Wales and Oakview State Forest, southeast Queensland. These specimens are assigned to *S. wyberba* and *P. caudiannulatus* respectively, pending examination of more material. Description of *Phyllurus amnicola* sp. nov. and *P. championae* sp. nov. brings to 12 the number of leaf-tailed geckos from eastern Australia. The former, known only from Mt Elliot, NEQ, is separated from its congeners by a combination of characters (large size; very small, spinose body tubercules; a leaf-shaped tail with the anterior-most band broken, but spanning full tail width; and a partially-divided rostral with 5-6 scales along its dorsal margin). *Phyllurus championae* sp. nov. from only two localities (Cameron Ck and Blue Mtn, MEQ), is the only *Phyllurus* species with a leaf-shaped tail and a fully divided rostral scale. Large genetic distances between *P. amnicola* sp. nov., *P. championae* sp. nov. and previously recognised *Phyllurus* spp. further support the recognition of these species. They join a long list of rainforest reptile taxa known from only single localities or very narrow ranges. The distribution of 'leaf-tails' reflects the preservation of ancient taxa in relictual rainforest and elevated heath fragments in eastern Australia. Despite these narrow ranges, and because all collection localities for leaf-tails are in reserves, for conservation purposes under IUCN definitions, they should be classed 'Data Deficient'. ❐ *Reptilia, Gekkonidae, Phyllurus spp., Saltuarius spp., Orraya gen. nov.; phylogeny; eastern Australia.*

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Australia's rainforests and adjoining moist sclerophyll forests and heaths are well known for their high diversity and for many species confined to either single localities, or very narrow ranges. Leaf-tailed geckos from such forests well illustrate these characteristics. For nearly 200 years of discovery and description of Australia's reptiles, only two species of 'leaf-tails', *Phyllurus platurus* (Shaw, 1790) and *P. cornutus* (Ogilby, 1892) = *Saltuarius cornutus* (Ogilby,1892), were known. Morphological studies since 1975 have resulted in the recognition of many new species and the genus *Saltuarius* Couper, Covacevich & Moritz, 1993 — *P. caudiannulatus* Covacevich, 1975; *P. isis* Couper, Covacevich & Moritz, 1993; *P. nepthys* Couper, Covacevich & Moritz, 1993; *P. ossa* Couper, Covacevich & Moritz, 1993; *S. salebrosus* (Covacevich, 1975); *Saltuarius occultus* Couper, Covacevich & Moritz, 1993 and *S. swaini* (Wells & Wellington, 1985). Eight of the 12 presently known species have narrow distributions with four confined to single localities. Molecular analyses, which have both confirmed and refined previous morphologically-based taxonomic work on these padless Australian carphodactyline geckos, commenced in the mid-1990s. For the first time, a combination of both methods was used in the description of *S. wyberba* Couper, Schneider &

Covacevich, 1997. From joint morphological/molecular comparisons and field work in previously unexplored rainforests, we can now present a phylogeny (based on DNA sequences from the mitochondrial cytochrome *b* gene), erect a new genus to accommodate '*Saltuarius*' *occultus* and provide substantial new data (including descriptions of two new species) on *Phyllurus* spp.

METHODS

GENETICS. A 399 base pair fragment of the mitochondrial cytochrome *b* gene, corresponding to codons 1-133, was amplified and sequenced from at least two individuals from each species of leaf-tailed gecko (Appendix 1). Protocols for amplification and sequencing follow those outlined in Couper et al. (1997). Sequences were aligned by eye using the translated amino acid sequences. For phylogenetic analyses, each nucleotide position was treated as a single character with up to four unordered states. The most parsimonious tree was found using equal-weights parsimony (all characters equally weighted and unordered), as well as a variety of weighting schemes. Additionally, maximum likelihood analyses, with a variety of models of nucleotide substitution were performed. In all analyses, sequences from *Carphodactylus laevis* Günther, 1897 were used as an outgroup to root the tree. Bootstrap resampling and parsimony criteria were used to assess support for the recovered phylogeny. PAUP* 4.0b2 (Swofford, 1999) was used for all phylogenetic analyses.

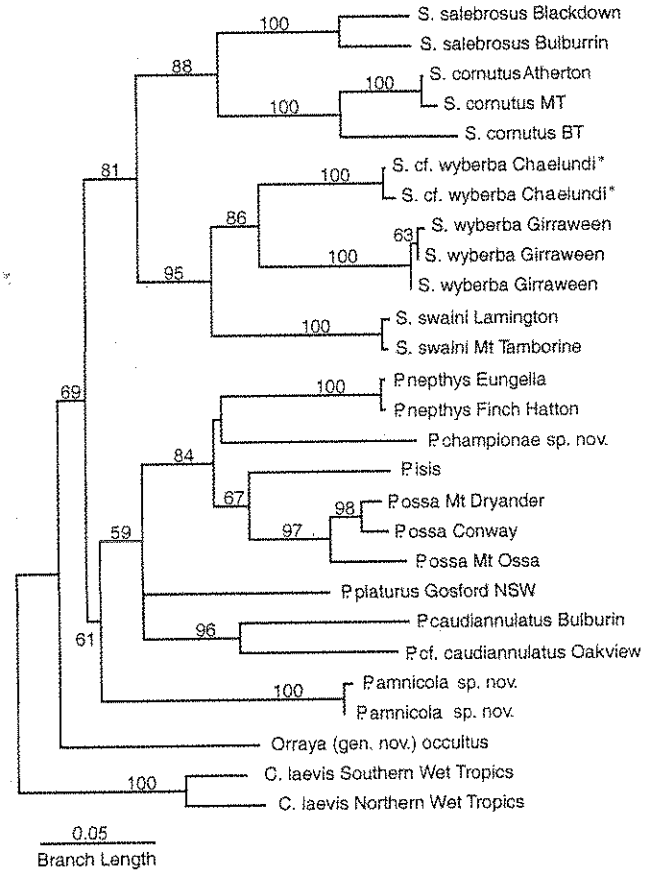

FIG. 1. Phylogeny of leaf-tailed geckos based on a 399 base pair fragment of MtDNA cytochrome *b* gene. Sequences from *Carphodactylus laevis* were used as an outgroup to root the tree and bootstraps >50% are presented (see Appendix 1 for specimen details). * Possible new species; here referred to *Saltuarius* cf. *wyberba*, pending collection of more specimens.

MORPHOMETRICS. All specimens examined are held in the Queensland Museum. Measurements were taken using Mitutoyo electronic callipers. Supralabials, infralabials and subdigital lamellae were counted on both sides of specimens examined. External morphological characters follow Covacevich (1975) and Couper et al. (1993). Skeletal definitions follow Bauer (1990). Abbreviations: SVL, snout to vent length; T, tail length, from posterior margin of cloaca to tip of tail; TT, attenuated tip of original tail; HL, head length; HW, head width; S, snout length; L1, length of front leg, axilla to tip of longest digit; L2, length of hind leg, groin to tip of longest digit; NL, neck length, axilla to posterior margin of ear.

PHYLOGENY. The mitochondrial cytochrome *b* DNA sequence data contained 183 parsimony-informative characters which provided good resolution of the phylogenetic relationships among species of leaf-tailed geckos. One hundred heuristic searches with random taxon addition and all characters unordered and equally weighted resulted in three equally parsimonious trees of 620 steps (C.I = 0.463). The strict consensus of these trees, which differed only in the placement of *P. platurus*, is shown in Fig. 1. Bootstrap support for the clade containing all

Saltuarius, except *'Saltuarius' occultus* (here recognised as generically distinct) is relatively high, while support for the monophyly of *Phyllurus* is somewhat weaker. Phylogenetic analyses and bootstrap resampling with various weighting schemes to account for differences among codon positions in rates of substitution and transition/transversion ratios resulted in the identical topology with similar bootstrap support to the equal weights bootstrap tree. Similarly, maximum likelihood analyses under a wide range of nucleotide substitution models (Jukes-Cantor, HKY85G, General time reversible) resulted in trees that did not differ from the equal weights parsimony tree. Species in the genus *Phyllurus*, exclusive of *P. amnicola*, are characterised by a derived karyotype as well as a number of morphological synapomorphies (see *Phyllurus* spp. nov.). The karyotype of *P. amnicola* is unknown but morphological synapomorphies are consistent with the DNA sequence data in supporting the inclusion of *P. amnicola* in the genus *Phyllurus*.

Authorships for three sections of this paper (*Orraya* gen. nov., *Phyllurus amnicola* sp. nov. and *Phyllurus championae* sp. nov.) do not follow that of the paper as a whole.

Orraya gen. nov.
Couper, Covacevich, Schneider & Hoskin
(Fig. 2)

Saltuarius occultus Couper, Covacevich & Moritz, 1993.

A parsimony analysis of morphological and karyotypic characters performed by Couper et al. (1993) resulted in the recognition of two monophyletic subgroups within the leaf-tailed geckos — *Phyllurus* Goldfuss, 1820 (*P. caudiannulatus*, *P. isis*, *P. nepthys*, *P. ossa* and *P. platurus*) and *Saltuarius* Couper, Covacevich & Moritz,1993 (*S. cornutus*, *S. occultus*, *S. salebrosus* and *S. swaini*). These clades were strongly supported in a bootstrap analysis present in 98% of pseudoreplicates. However, Couper et al. (1993) also observed '... evidence for grouping of *S. swaini*, *S. cornutus* and *S. salebrosus* to the exclusion of *S. occultus* ...' and that *Saltuarius occultus* has skeletal characters (elongation of the cervical vertebrae and 3 lumbar vertebrae) that are unique amongst its congeners. Derived characters, including elongate cervical vertebrae, along with DNA sequences from the mitochondrial cytochrome b gene (Fig. 1, Table 1), support the recognition of a new genus to accommodate *'Saltuarius' occultus*. In our phylogenetic analyses, this taxon is the sister group to the clade containing *Phyllurus spp* and *Saltuarius spp.*

TYPE SPECIES. *Orraya occultus* (Couper, Covacevich & Moritz, 1993).

ETYMOLOGY. 'Orraya' is the Morrobalama language word for 'older brother' (Gunnawarra, N. & Kullakulla, M., 1994) refering to the phylogenetic relationship between *occultus* and its *Phyllurus* and *Saltuarius* 'siblings'. Peach Ck, the type locality of *Orraya occultus* drains the McIlwraith Ra. the traditional land of the Morrobalama.

DIAGNOSIS. *Orraya* gen. nov. can be separated easily from all other Australian padless carphodactyline genera by the following combined apomorphies: cervical vertebrae greatly elongated; three lumbar vertebrae (defined as non-rib-bearing vertebrae, immediately anterior to sacrum); male preanal organs greatly enlarged; regrown tail with broad, spinose tubercules on margins. A detailed description of *Orraya occultus* (as *Saltuarius occultus*) was provided by Couper et al., 1993: 104-106. For details of original tail, see Lethbridge et al., 1994.

Phyllurus spp.

NEW SPECIES. The new species (from Mt Elliot, NEQ and Cameron Ck/Blue Mtn, MEQ) are assigned to *Phyllurus* by the following synapomorphies: anterior-most autotomy septum in fifth caudal vertebra; no enlarged postmental scales; tail finely- attenuated and terminating in a small knob; rostral scale partially, or totally divided; males without preanal pores (polarity determined by Bauer, 1990). This assignment is supported further by the following character states (after Couper et al., 1993): nostril not in contact with rostral scale; anterior margin of interclavicle with a distinct process; axilla invaginated; epipubic cartilage small to moderate and original tail simply flared.

Phyllurus amnicola sp. nov.
Hoskin, Couper, Schneider & Covacevich
(Fig. 3)

ETYMOLOGY. From the Latin 'dwelling by a river', a reference to the type locality.

MATERIAL. HOLOTYPE: QMJ64408 ♀, Alligator Ck, Mt Elliot, Bowling Green Bay NP (19°28'S, 146°59'E) NEQ, C. Hoskin & J. Gratten, 1 Feb 1998. PARATYPES: QMJ64406-07, J67852 as for holotype.

DIAGNOSIS. *P. amnicola* can be separated from its congeners by the following combined characters: large size (maximum SVL >110 mm);

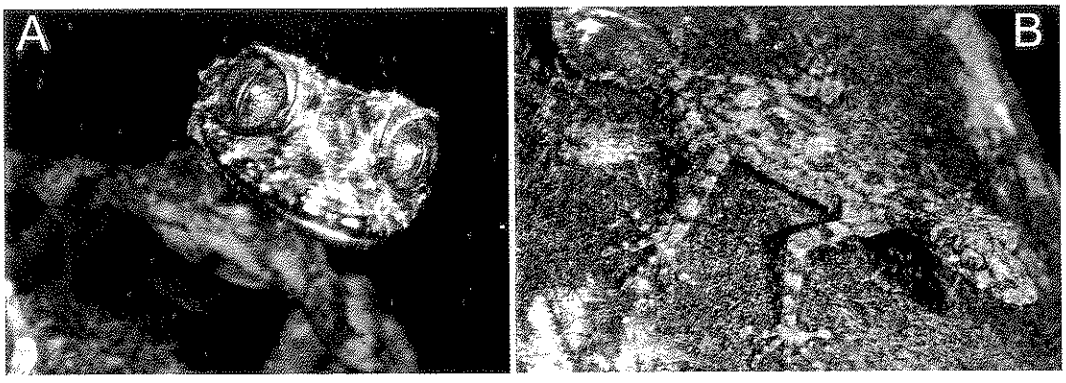

FIG. 2. *Orraya occultus* (QMJ62596), Peach Ck, McIlwraith Ra., Cape York Peninsula (13°45'S, 143°19'E) NEQ. (Jeff Wright)

spinose body tubercules very small; leaf-shaped tail with anterior-most band broken but spanning full tail width; rostral partially divided with 5-6 scales along its dorsal margin. (Note: SVL includes three specimens measured by one of us (CJH) in the field (2♂ 104mm, ♀113mm). These measurements have been included in the diagnosis but not in the morphometrics for the species description.)

DESCRIPTION. SVL (mm): 90.3-103 (n = 4, mean = 96.5). Proportions as % SVL: L1 43.9-45.1 (n = 4, mean = 44.6); L2 53.8-58.9 (n = 4, mean = 56.2); T 86.1 (n = 1); TT 36.9 (n = 1); HL 27.7-29.1 (n = 4, mean = 28.2); HW 20.7-21.4 (n = 4, mean = 21.1); S 12.4-13.2 (n = 4, mean = 12.7); NL 20.7-23.3 (n = 4, mean = 21.6).

Head large, depressed, triangular, distinct from neck; covered in small granules which are intermixed with larger conical tubercles; skin of head not co-ossified with skull; deep, vertical groove partially dividing rostral scale (n = 4); rostral excluded from nostril; 5-6 scales along the dorsal margin of rostral shield (n = 3); ear opening elliptical, vertical, much less than half as large as eye; supralabials 15-16 (n = 8, mean = 15.5); infralabials 13-15 (n = 8, mean = 13.9). Neck broad. Body depressed, covered in small granules; dorsal granules intermixed with larger conical tubercles; tubercles very small on back, flanks and sides of neck; basal scales surrounding flank tubercules not enlarged; no enlarged tubercules or granules on ventral surface of body. Preanal pores absent. Axilla moderately to deeply invaginated. Limbs long, covered in small pointed tubercles dorsally; lacking enlarged tubercules on ventral surface, except on upper forelimb; digits strong, strongly compressed distally; subdigital lamellae (fourth toe) 22-25 (n = 8, mean = 20.3). Original tail (n = 1) depressed, flared, contracted at base and attenuated at tip, terminating with a minute rounded knob; dorsal surface of flared portion with prominent enlarged spinose tubercules on basal 1/3rd and along margins; 6 rows of minute spines across basal portion of attenuated tail-tip; attenuated tip accounts for 42.9% of total tail length; ventral surface smooth with a slight depression along midline (excluding attenuated tip). Regenerated tail (n = 3) depressed, broad and strongly flared, contracted at base and attenuated at tip; covered with uniform granules, except on basal margin which has small spinose tubercules; ventral surface without groove along midline.

Pattern. In spirit, dorsal base colour beige with irregular dark brown blotches on head, body and limbs; blotches on body tend to be aligned transversely. Limbs banded; digits strongly banded; inner anterior digit with reduced pigment. Body and limbs ventrally off-white to cream (immaculate); labials off-white, mottled with brown. Original tail dorsally tan/grey, marked with irregular dark brown blotches; six cream bands on tail, only those on attenuated portion (4) extending to ventral surface; ventrally cream, peppered with brown specks. Regenerated tail lacking cream bands; dorsally tan/grey, mottled with dark brown blotches; ventral surface similar, but with reduced pigmentation.

Skeletal Features. Material examined: (radiographs) QMJ64406-08; (alizarin stained) QMJ67852. Supraocular portion of frontal grooved; anterior process of interclavicle pronounced; epipubic cartilage moderately expanded; presacral vertebrae 26; sacral vertebrae 2; lumbar vertebrae 2; first autotomy

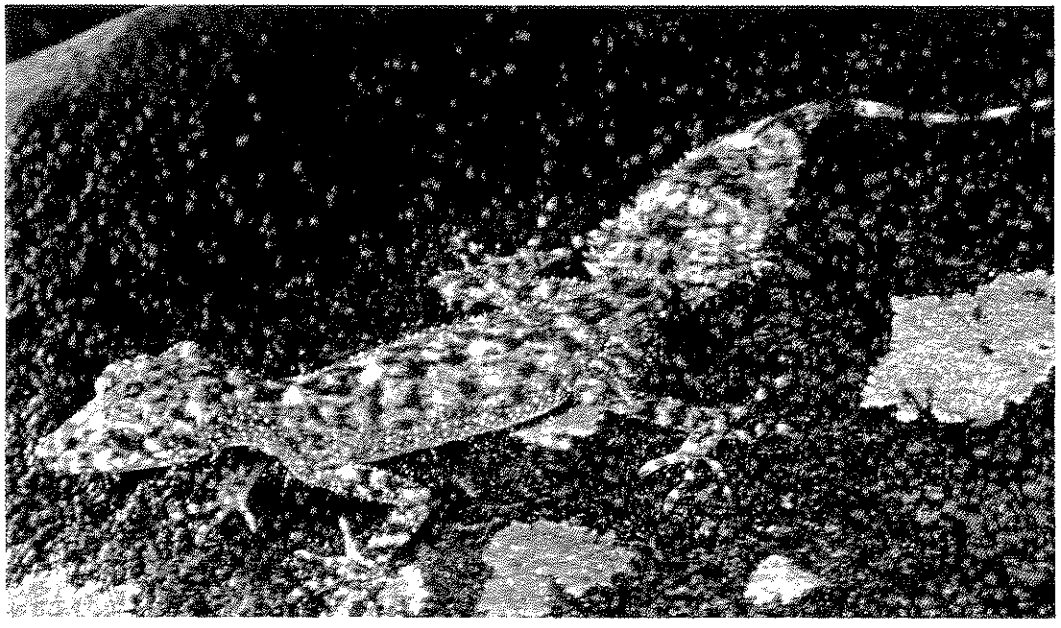

FIG. 3. *Phyllurus amnicola* sp. nov. (holotype, QMJ64408; QM photographic collection, image ref. NW982), Mt Elliot, NEQ. (Jeff wright)

septum on postsacral vertebra 5; abdominal vertebrae bearing reduced ribs 4; rib-free cervicals 3; sternal ribs 3; mesosternal ribs 2.

Holotype Data. QMJ64408, ♀; SVL 90.3mm; L1 40.6mm; L2 53.2mm; T 77.8mm; TT 33.4mm; HL 25.1mm; HW 18.8mm; S 11.3mm; NL 19.0mm; supralabials 15/16; infralabials 15/14; subdigital lamellae 22/22.

COMPARISON. *Phyllurus amnicola* can be confused with only its congeners. *P. amnicola* is distinguished from *P. caudiannulatus* by tail shape (flared vs cylindrical); from *P. platurus* by pattern of original tail (flared portion with distinct white bands vs without white bands); from *P. isis* by pattern of original tail (anterior-most band spanning full width of tail vs anterior band reduced, with two narrowly-spaced midline blotches); from *P. nepthys* by colour/pattern of ventral surface (immaculate vs peppered with brown specks); from *P. championae* by spinosity of original tail (enlarged spinose tubercules restricted to anterior third of tail and tail margins vs tail covered with spinose tubercules) and from *P. ossa* by the rostral groove/s (one groove partially dividing rostral vs 1-3 grooves, usually 3, only rarely 1 or 2, partially dividing rostral). *P. amnicola* is further distinguished from *P. isis* and *P. ossa* by the number of scales along dorsal margin of rostral shield (5-6 vs 9-11 and 8-11, respectively).

GENETICS. *Phyllurus amnicola* shows a 21-27% sequence divergence from all other *Phyllurus* spp. for the cytochrome *b* portion of mtDNA (Table 1, Fig. 1). The phylogenetic position of *P. amnicola* as the sister group to the remaining *Phyllurus* is not strongly supported by the cytochrome *b* data (Fig.1), but morphological characters support its placement in a monophyletic *Phyllurus*.

HABITAT & DISTRIBUTION. Mt Elliot, Bowling Green Bay NP, 30kms SE of Townsville (19°28'S, 146°59'E) NEQ (Fig. 4). Found amongst boulders at 450m, in a moist 'tongue' of forest along a creek running from the rainforested upper slopes of Mt Elliot (Fig. 5). Dense rainforest is the dominant vegetation above 750m. A recent survey (CJH and J. Gratten, Oct., 1999) showed *P. amnicola* to be relatively common between 400-1000m along a major drainage line. Surveys on the summit of Mt Elliot have failed to locate this species.

HABITS. Most specimens were found head down, on granite boulders close to permanent water. Several were foraging on rocks directly above flowing water and one was observed

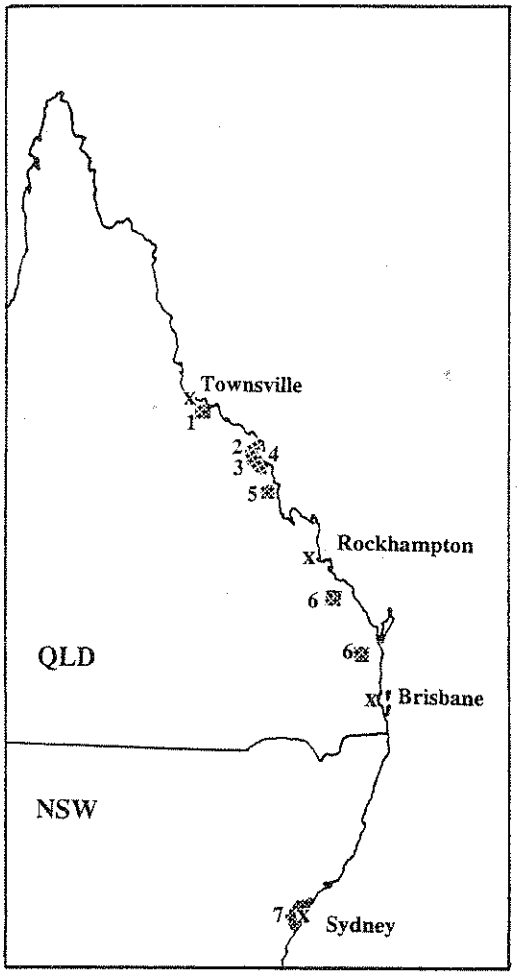

FIG. 4. Occurrence of *Phyllurus* spp. in eastern Australia; 1 = *P. amnicola*, 2 = *P. ossa*, 3 = *P. nepthys*, 4 = *P. isis*, 5 = *P. championae*, 6 = *P. caudiannulatus*, 7 = *P. platurus*.

foraging in a thin film of water in the splash zone of a cascade. All specimens, but one, have been found on rocks. The exception was on a thin tree trunk amongst boulders. Activity began soon after dark, even during persistent rain. Of 27 specimens (14♂'s, 11♀'s and 2 juveniles) encountered during two nights (Oct., 1999), 70% had regenerated tails. This proportion was similar in both sexes.

REPRODUCTION. One gravid female, captured and released (4 Feb., 1998), contained a single, shelled egg. A male (QMJ67852) that died in captivity (Dec., 1998) was sexually mature, with

FIG. 5. Alligator Ck, Mt Elliot, NEQ, the type locality for *P. amnicola* sp. nov. (Conrad Hoskin)

sperm present in its epididymis (inferred by opacity). Fourteen mature females were encountered on the first two nights of Oct., 1999. Eight of these carried well-developed, shelled eggs (3 with 1 egg, 4 with 2 eggs, 1 with 3 eggs).

CONSERVATION. *P. amnicola* is one of the most narrowly restricted reptile species in Queensland. However, it is well protected. The only known locality for this species is in Bowling Green Bay NP which is not subject to any known threatening processes. The potential effect of fire on pockets of riparian rainforest at and near the type locality is not known.

Phyllurus championae sp. nov.
Schneider, Couper, Hoskin & Covacevich
(Fig. 6)

ETYMOLOGY. Named for Irene Champion, a Resource Ranger with Queensland Parks and Wildlife Service, Mackay, MEQ, who focussed the attention of one of us (CJS) on Cameron Ck/Black Mtn, as a phytogeographically interesting area, possibly pointing to the presence of unusual fauna.

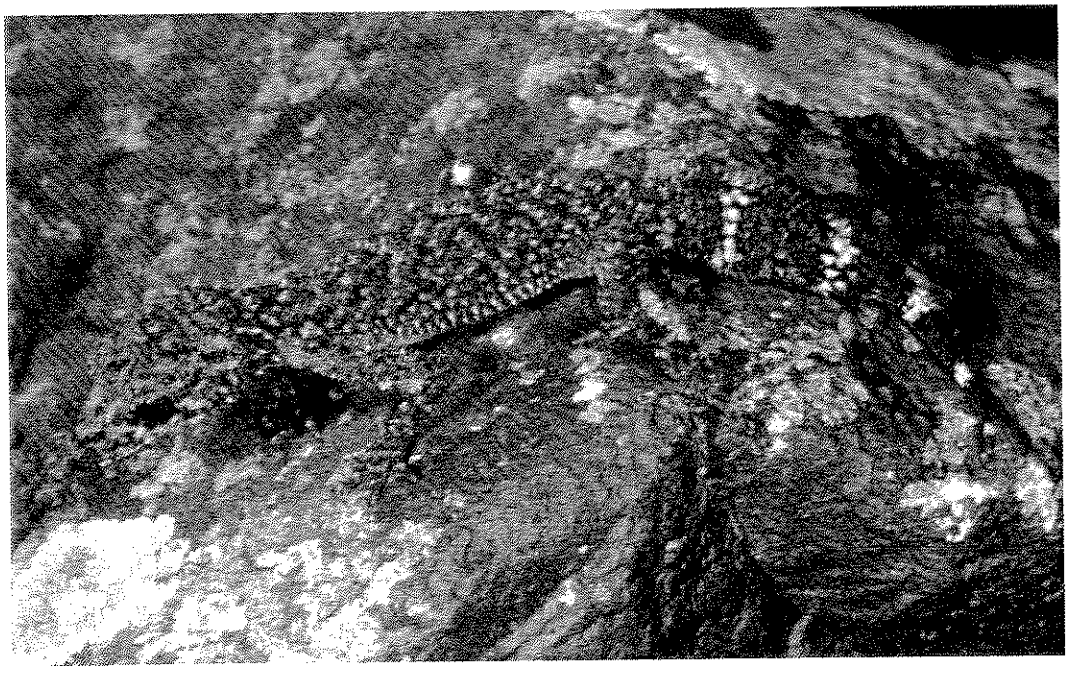

FIG. 6. *Phyllurus championae* sp. nov. (QM photographic collection, image ref. NX758) Cameron Ck, MEQ. (Jeff Wright)

MATERIAL. HOLOTYPE: QMJ64847 ♂, Cameron Ck, 6.5km WNW Koumala (21°34'24"S, 149°11'06"E) MEQ, P. Couper & C. Hoskin, 18 April 1998. PARATYPES: QMJ62757-58, J62766, J63907, J64845-46, J64848, locality as for holotype; J64854-64 Blue Mtn (21°36'S, 148°58'E) MEQ.

DIAGNOSIS. *P. championae* almost invariably (18/19) has a fully divided rostral scale. This feature, combined with a leaf-shaped tail, distinguish it from all other *Phyllurus* spp. A specimen of *P. championae* with an only partially divided rostral could be confused with some specimens of *P. ossa* which have a rostral partially divided by a single groove. (This is a rare state in *P. ossa* which usually has 2 or 3 partial grooves). From such specimens of *P. ossa*, 'partial single groove' specimens of *P. championae* can be distinguished readily by a straight groove vs a Y-shaped groove.

DESCRIPTION. SVL(mm): 33.3-80.6 (n = 19, mean = 61.5). Proportions as % SVL: L1 41.2-48.0 (n = 19, mean = 44.0); L2 52.5-60.5 (n = 19, mean = 56.50); T 64.2-81.7 (n = 8, mean = 75.7); TT 28.9-40.7 (n = 8, mean = 35.7); HL 28.9-31.8 (n = 19, mean = 30.1); HW 23.1-26.4 (n = 19, mean = 24.40); S 12.4-14.6 (n = 19, mean = 13.1): NL 18.8-23.6 (n = 19, mean = 20.6).

Head large, depressed, triangular, distinct from neck; covered in small granules which are intermixed with larger, conical tubercles, extremely prominent on snout; skin of head co-ossified with skull; deep, vertical groove totally dividing rostral scale (n=18) or (rarely) partially dividing rostral scale (n=1); rostral excluded from nostril; 5-8 scales along dorsal margin of rostral shield (n = 10); ear opening elliptical, vertical, much less than half as large as eye: supralabials 12-14 (n=38, mean=13.3, mode=14); infralabials 11-15 (n=38, mean=12.7, mode=13). Neck broad. Body depressed, covered in small granules; dorsal granules intermixed with larger, conical tubercles; tubercles small on back, pronounced on flanks, most prominent on sides of neck; basal scales surrounding flank tubercules only slightly enlarged; no enlarged tubercules or granules on ventral surface of body. Preanal pores absent. Axilla deeply invaginated. Limbs long, covered in large pointed tubercles dorsally; without enlarged tubercules on ventral surface, except on upper forelimb; digits strong, compressed distally; subdigital lamellae (fourth toe) 16-20 (n = 38, mean = 17.9, mode = 17). Original tail (n = 8) depressed, flared to carrot-shaped, contracted at base and attenuated at tip, terminating with a

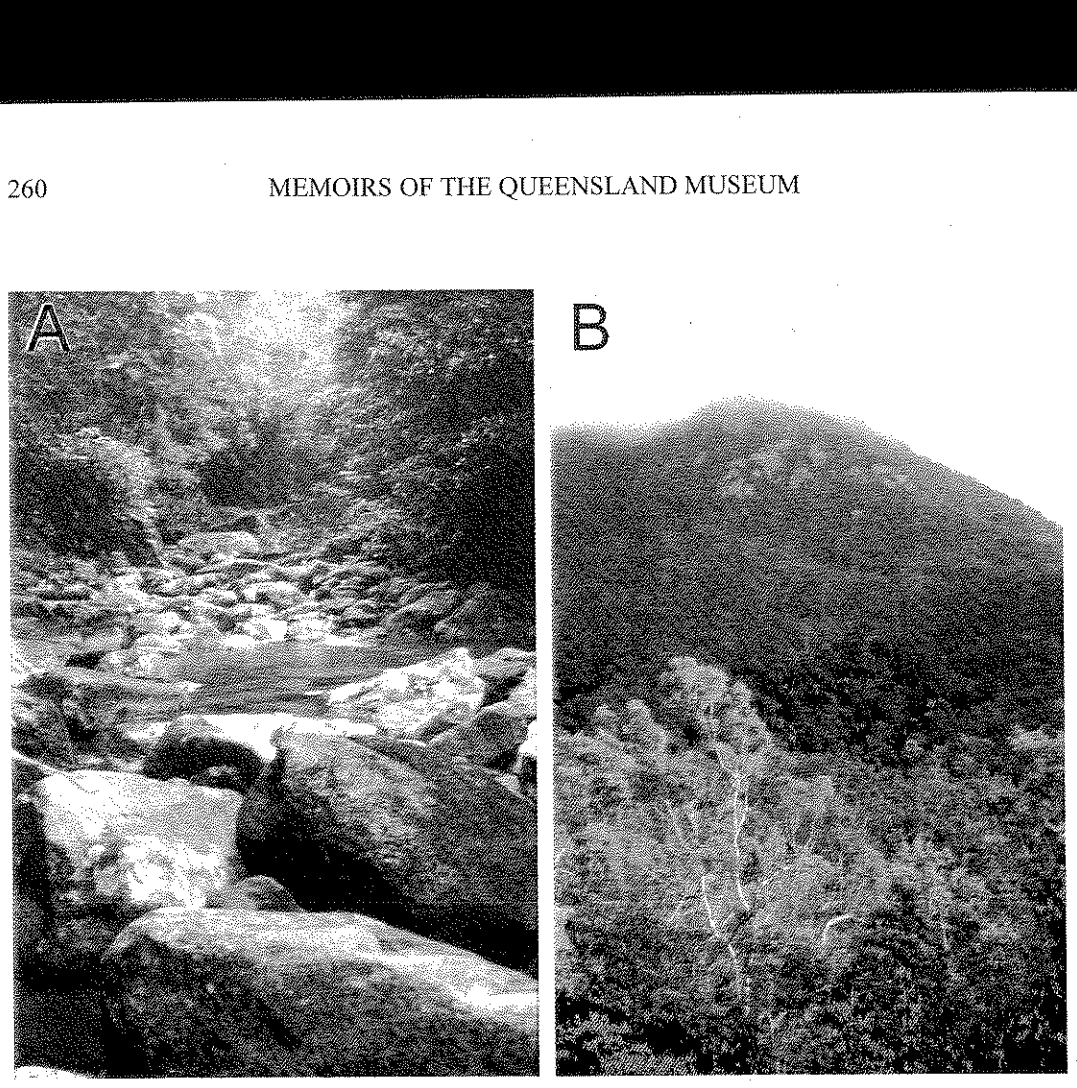

FIG. 7. A, Cameron Ck, MEQ, the type locality for *P. championae* sp. nov. B, dry rainforest below the summit of Blue Mtn, MEQ, the second known locality for *P. championae* sp. nov. (Conrad Hoskin)

minute rounded knob; covered dorsally with numerous moderate-sized, spinose tubercules which become smaller along the vertebral line; tubercles terminate approximately half-way along the attenuated tip which is long; 8 rows of enlarged spines across the basal portion of attenuated tail-tip; attenuated tip accounts for 38-52% of total tail length; ventral surface smooth, or with slight depression along midline. Regenerated tail: (n = 10) depressed, broad and strongly flared, contracted at base and attenuated at tip; with small, spinose tubercules which are most prominent around the edges; ventral surface without groove along midline. The Cameron Ck specimens are significantly smaller than those from Blue Mtn (max SVL = 69mm, n = 7, small juveniles excluded, mean = 61.9mm vs max SVL = 81mm, n = 9, small juveniles excluded, mean = 69.6mm; Student's T-Test, $t_{1,14}$ = 2.14, 0.05> P>0.025).

Pattern. In spirit, dorsal base colour mid brown with irregular, black blotches on head, body and limbs. Digits obscurely banded; inner anterior digit not significantly lighter than others. Body and limbs ventrally off-white to cream; labials off-white, mottled with brown. Original tail dorsally tan, heavily mottled with black (almost entirely black in hatchlings); five white bands on tail, only those (2-3) on attenuated portion extending to ventral surface; ventrally cream with grey mottling. Regenerated tail lacking cream bands; dorsally, tan/grey with black blotches; ventral surface similar, but with reduced pigmentation.

Skeletal Features. Material examined: (radiographs) QMJ63907, J64845-48, J64854-55, J64858-59, J64864; (alizarin stained) QMJ64863. Supraocular portion of frontal flat; anterior process of interclavicle pronounced; epipubic cartilage not expanded; presacral vertebrae 26; sacral vertebrae 2; lumbar vertebrae 2; first autotomy septum on postsacral vertebra 5; abdominal vertebrae bearing reduced ribs 4; rib-free cervicals 3; sternal ribs 2; mesosternal ribs 3.

TABLE 1. Kimura 2-parameter distance estimates (Kimura, 1980) between species and populations within species for 399bp cytochrome *b* sequence data. Species are numbered in the same order across the top of the data matrix. See Appendix 1 for specimen details.

		1	2	3	4	5	6	7	8	9	10	11	12	13	14
1	S. salebrosus Blackdown	-													
2	S. salebrosus Bulburrin	0.0625	-												
3	S. cornutus Atherton	0.1833	0.1760	-											
4	S. cornutus MalbonThompso	0.1872	0.1722	0.0076	-										
5	S. cornutus BigTableland	0.2039	0.1785	0.0894	0.0960	-									
6	S. cf. wyberba Chaelundi	0.1987	0.2119	0.2677	0.2726	0.2733	-								
7	S. cf. wyberba Chaelundi	0.1987	0.2119	0.2677	0.2726	0.2733	0.0054	-							
8	S. wyberba Girraween	0.2280	0.2376	0.2640	0.2687	0.2921	0.1321	0.1321	-						
9	S. wyberba Girraween	0.2244	0.2384	0.2602	0.2648	0.2878	0.1288	0.1288	0.0025	-					
10	S. wyberba Girraween	0.2208	0.2347	0.2563	0.2610	0.2835	0.1255	0.1255	0.0050	0.0025	-				
11	S. swaini Lamington	0.2251	0.2087	0.2296	0.2383	0.2627	0.1520	0.1600	0.1733	0.1700	0.1668	-			
12	S. swaini MtTamborine	0.2244	0.2081	0.2260	0.2346	0.2585	0.1514	0.1594	0.1727	0.1694	0.1661	0.0050	-		
13	P. nepthys Eungella	0.2980	0.3093	0.2862	0.2862	0.2756	0.2514	0.2610	0.2889	0.2849	0.2810	0.2602	0.2594	-	
14	P. nepthys Finch Hatton	0.2929	0.3041	0.2813	0.2813	0.2806	0.2561	0.2658	0.2840	0.2800	0.2761	0.2555	0.2548	0.0025	-
15	P. isis	0.3051	0.2911	0.2966	0.3065	0.2973	0.2591	0.2688	0.2797	0.2757	0.2718	0.2642	0.2591	0.1544	0.1581
16	P. ossa MtDryander	0.2765	0.2679	0.2909	0.3007	0.2774	0.2453	0.2546	0.2869	0.2876	0.2836	0.2591	0.2585	0.1512	0.1549
17	P. ossa Conway	0.2757	0.2765	0.2966	0.3065	0.2884	0.2457	0.2551	0.2925	0.2933	0.2893	0.2642	0.2636	0.1516	0.1553
18	P. ossa MtOssa	0.3020	0.2831	0.3033	0.3134	0.2748	0.2719	0.2719	0.3042	0.3051	0.3010	0.2992	0.2983	0.1416	0.1452
19	P. championae sp. nov.	0.3001	0.3010	0.3218	0.3271	0.3136	0.2685	0.2786	0.2942	0.2951	0.2911	0.2893	0.2885	0.1563	0.1600
20	P. platurus	0.2510	0.2752	0.2496	0.2586	0.2702	0.2499	0.2596	0.2414	0.2376	0.2339	0.2518	0.2510	0.1936	0.1975
21	P. caudiannulatus	0.2610	0.2853	0.2829	0.2925	0.3130	0.2650	0.2749	0.2789	0.2797	0.2757	0.2983	0.3024	0.2405	0.2450
22	P. cf. caudiannulatus Oakvie	0.2742	0.3010	0.2558	0.2649	0.3094	0.2699	0.2799	0.2781	0.2742	0.2702	0.2642	0.2681	0.2056	0.2097
23	P. amnicola sp. nov.	0.2579	0.2496	0.2688	0.2734	0.2859	0.2563	0.2470	0.2514	0.2476	0.2438	0.2558	0.2508	0.2420	0.2376
24	P. amnicola sp. nov.	0.2534	0.2451	0.2688	0.2734	0.2861	0.2516	0.2424	0.2470	0.2432	0.2395	0.2514	0.2508	0.2376	0.2333
25	Orraya (gen. nov.) occultus	0.2632	0.2640	0.2309	0.2351	0.2575	0.2336	0.2336	0.2565	0.2572	0.2534	0.2489	0.2482	0.2427	0.2383
26	C. laevis BigTableland	0.3033	0.2893	0.2448	0.2491	0.2759	0.2702	0.2801	0.2880	0.2840	0.2880	0.2656	0.2649	0.2521	0.2568
27	C. laevis Atherton	0.3074	0.3033	0.2530	0.2574	0.2803	0.2845	0.2948	0.3020	0.2980	0.3020	0.2558	0.2642	0.2559	0.2606

		15	16	17	18	19	20	21	22	23	24	25	26	27
15	P. isis	-												
16	P. ossa MtDryander	0.1230	-											
17	P. ossa Conway	0.1235	0.0206	-										
18	P. ossa MtOssa	0.1306	0.0595	0.0568	-									
19	P. championae sp. nov.	0.1682	0.1727	0.1694	0.1787	-								
20	P. platurus	0.2000	0.1857	0.1853	0.1941	0.1970	-							
21	P. caudiannulatus	0.2383	0.2145	0.2194	0.2280	0.2223	0.1887	-						
22	P. cf. caudiannulatus Oakvie	0.2333	0.2211	0.2217	0.2145	0.2390	0.1853	0.1452	-					
23	P. amnicola sp. nov.	0.2097	0.2450	0.2468	0.2442	0.2310	0.2123	0.2451	0.2687	-				
24	P. amnicola sp. nov.	0.2139	0.2405	0.2442	0.2398	0.2266	0.2081	0.2407	0.2640	0.0025	-			
25	Orraya (gen. nov.) occultus	0.2290	0.2046	0.1931	0.1970	0.2555	0.2122	0.2563	0.2451	0.2314	0.2272	-		
26	C. laevis BigTableland	0.2555	0.2656	0.2713	0.2829	0.2450	0.2390	0.2831	0.2951	0.2625	0.2579	0.2092	-	
27	C. laevis Atherton	0.2782	0.2791	0.2849	0.2970	0.2580	0.2383	0.2870	0.2749	0.2773	0.2726	0.2127	0.0599	-

Holotype Data. QMJ64847, ♂; SVL 59.28mm; L1 25.57mm; L2 32.80mm; T 48.13mm; TT 24.13mm; HL 17.81mm; HW 14.20mm; S 7.77mm; NL 11.34mm; supralabials 13/14; infralabials 13/13; subdigital lamellae 18/17.

COMPARISON. *P. championae* can be confused with only its congeners. *P. championae* is distinguished from *P. caudiannulatus* by tail shape (leaf-like vs cylindrical); from *P. platurus* by colour pattern of anterior portion of original tail (with white bands vs without white bands); from *P. amnicola* by spinosity of original tail (tail covered with spinose tubercules vs enlarged spinose tubercules restricted to anterior 1/3rd of tail and tail margins); from *P. isis* by spinose flank tubercules (pronounced vs very small); from *P. nepthys* by colour/pattern of ventral surface (plain vs peppered with brown specks) and from *P. ossa* by rostral groove/s (usually one groove dividing rostral, or a straight vertical groove partially dividing rostral vs 1-3 grooves, usually 3, only rarely 1 or 2, partially dividing rostral).

GENETICS. *P. championae* shows 16-24% sequence divergence from all other *Phyllurus* spp. for the cytochrome *b* portion of mtDNA (Table 1). The Cameron Ck and Blue Mtn populations showed no within, or between, population polymorphism. Phylogenetic analyses firmly place *P. championae* within the monophyletic MEQ species group of *Phyllurus* (*P. isis*, *P. nepthys* and *P. ossa*, Fig. 1), though its precise relationship to these taxa is not well resolved.

HABITAT & DISTRIBUTION. *P. championae* is known from only two localities, Cameron Ck (21°34'24"S, 149°11'06"E) and (21km to the west) Blue Mtn (21°36'S, 148°58'E) MEQ, (Fig. 4). The type specimens were collected at altitudes between 200m (Cameron Ck) and 700m (Blue Mtn) in notophyll rainforest/microphyll rainforest.

HABITS. All specimens have been on rocks or on the trunks of trees near rocks. The Cameron Ck (21°34'24"S, 149°11'06"E) specimens were collected on the edges of a permanent creek on the eastern side of Black Mtn (Fig. 7a). Blue Mtn (21°36'S, 148°58'E) specimens were active on a scree slope, in dry rainforest, just below the summit (Fig. 7b). Activity began soon after dark.

REPRODUCTION. Gravid females were present in the Cameron Ck population during Dec., 1996/Jan., 1997. A female measuring 68.7mm SVL and weighing 6.2g (QMJ62757) laid two oval-shaped eggs on 6 Jan., 1997. These measured 18.35 × 9.01mm and 17.72 × 8.90mm and weighed 1.0g and 0.9g, respectively. The relative clutch mass (RCM (1) after Greer, 1989) equalled 30.6%. This corresponds closely with that of *P. platurus* (29%, Greer, 1989).

A male (QMJ64863, SVL 72.3mm) from Blue Mtn, collected on 19 Apr., 1998, was in peak reproductive condition with sperm present in its epididymis (inferred by opacity) and a turgid testis. From this we infer that mating may occur in autumn and that females store sperm through winter. A similar reproductive strategy has been suggested for *P. platurus* (Greer, 1989).

CONSERVATION. *P. championae* appears to be common at both localities from which it is known. Suitable similar habitat in adjacent areas may support this species. Blue Mtn is freehold and thus, potentially, could be cleared. However, given that the known leaf-tail site is on an elevated scree slope, the chance that this area would be further disturbed by stock or humans seems remote. Cameron Ck, the type locality, is in State Forest and may be subject to timber harvesting.

Phyllurus caudiannulatus

The discovery of specimens treated tentatively as *P. caudiannulatus* (QMJ62817, J63849-53, J63857) at Oakview SF (26°07'23"S, 152°19'01"E), SEQ extends the range of this species 195km south of the only other known population (Bulburin SF, 24°31'S, 151°29'E), SEQ. Morphological differences between the Oakview and Bulburin populations cannot be fully assessed presently, due to small sample size. Surveys in the intervening areas should help assess the significance of these differences. For conservation purposes, the Oakview population of '*P. caudiannulatus*' must be recognised as a genetically distinct unit (Fig. 1), given its geographic and genetic isolation and its uncertain taxonomic status.

KEY TO AUSTRALIAN LEAF- TAILED GECKOS

1. Nostril in contact with rostral scale 2
   Nostril not in contact with rostral scale 6
2. Neck extremely elongate and slender . . . . *O. occultus*
   Neck broad 3
3. Throat strongly tuberculate . . . . . *S. salebrosus*
   Throat smooth 4
4. Lower flank tubercules hooked and surrounded by spinose, basal scutes. . . . . *S. cornutus*
   Lower flank tubercules not as above 5
5. Original tail bluntly tipped with large tubercules . . . . . *S. swaini*
   Original tail finely tipped with only minute tubercules . . . . . *S. wyberba*
6. Tail cylindrical . . . . . *P. caudiannulatus*
   Not as above (leaf-shaped). 7
7. Anterior portion of original tail without white crossbands or blotches . . . . . *P. platurus*
   Not as above (with white crossbands) 8
8. Venter distinctly 'peppered' with brown . . . *P. nepthys*
   Not as above (plain) 9
9. Rostral scale completely divided . . . . . *P. championae*
   Not as above (partially divided) 10
10. Rostral scale partially divided by 2 or 3 grooves, occasionally by a single Y-shaped groove . . . *P. ossa*
    Not as above (partially divided by a straight groove). . 11
11. Anterior flared portion of original tail uniformly covered with enlarged spinose tubercules . . . . *P. championae*
    Not as above 12
12. Tail predominantly black, with distinct white blotches present on either side of the vertebral line . . . . *P. isis*
    Not as above (tail predominantly tan/grey, with anterior-most bands broken, but spanning tail width) . . . . . *P. amnicola*

DISCUSSION

Twelve species of leaf-tailed geckos in three genera occur in eastern Australia (13°45'S - 33°53'S). Nine are obligatory rainforest/adjacent wet sclerophyll forest species: McIlwraith Ra., NEQ, *Orraya occultus* (Couper, Covacevich & Moritz, 1993); Wet Tropics (Big Tableland - Paluma), NEQ, *S. cornutus* (Ogilby, 1892); Mt Elliot, NEQ, *Phyllurus amnicola* Hoskin, Couper, Schneider & Covacevich, 2000; Mt

Dryander - Mt Ossa, MEQ, *P. ossa* Couper, Covacevich & Moritz, 1993; Mt Blackwood and Mt Jukes, MEQ, P. isis Couper, Covacevich & Moritz 1993; Clarke Ra. (Mt David - Crediton), MEQ, *P. nepthys* Couper, Covacevich & Moritz, 1993; Black Mountain and Blue Mountain, MEQ, *P. championae* Schneider, Couper, Hoskin & Covacevich, 2000; Many Peaks Ra. and Oakview State Forest, SEQ, *P. caudiannulatus* Covacevich, 1975; Great Dividing Range and foothills and Border Ranges (Mt Tamborine - Buladelah), SEQ-MENSW, *S. swaini* Wells & Wellington, 1985. Two species are confined to heaths associated with either sandstone or granites: Girraween National Park, SEQ, *S. wyberba* Couper, Schneider & Covacevich, 1997; and Hawkesbury R. region, MENSW, *P. platurus* (Shaw, 1790). One species, *S. salebrosus*, occurs amongst sandstone in open forests: Blackdown Tableland - Cracow, MEQ. It is also found in rainforest in the Many Peaks Range (24°31'S, 151°29'E), where it is sympatric with *P. caudiannulatus*. This is the only known area to support more than one species of leaf-tail.

The genetic analyses (Fig. 1, Table 1) show that the depth of divergence amongst leaf-tails is high and that more-than-trivial differences between some taxa/populations remain to be clarified. Relative rates tests show that substitution rates among lineages do not differ significantly suggesting that a molecular clock may apply. By using the break-up of Gondwanaland to estimate substitution rates in this portion of cytochrome *b* among carphodactyline geckos from Australia, New Zealand and New Caledonia (Schneider, unpublished) it is estimated that the Kimura two-parameter distance between two lineages accrues at a rate of ca. 0.0042 ± 0.0002 per million years (0.0021 per lineage per million years). Using this calibration, the split between *Saltuarius* sensu stricto and *Phyllurus* is ca. 58-74mya. The divergence among species in MEQ is ca. 31-38mya, and this is nearly identical to the estimated time of divergence between the Oakview and Bulburin populations of *P. caudiannulatus*. Estimating genetic distances among taxa using only transversions (which are more likely to accrue linearly with time) does not substantially change these time estimates. '*Saltuarius wyberba*' populations from Chaelundi SF, NSW (30°01'07"S, 152°30'02"E) and Girraween, SEQ (28°50'S, 151°56.04E, the type locality) differ to the same degree as *P. isis* (from Mt Blackwood, 21°02'S, 148°56'E) and *P. ossa* (Mt Ossa, 20°56'S, 148°49'E, only 14km to the north). However, more specimens must be examined before the status of the Chaelundi *Saltuarius* specimens can be determined.

Recognition of *Orraya occultus* as distinct from the other large leaf-tails (*Saltuarius* spp.) is significant given the general paucity of endemism in the reptiles of the McIlwraith Ra. rainforest isolate. (Couper et al., 1993 observed this in relation to the Wet Tropics rainforests where 2/3 of the rainforest reptile species are endemic to the area). *Orraya* is the sole terrestrial vertebrate genus not represented in rainforest isolates further south.

The discovery of *P. amnicola* on Mt Elliot, NEQ is noteworthy for two reasons. First, recognition of this species brings to two the number of vertebrate species endemic to Mt Elliot (the other species is the microhylid frog, *Cophixalus mcdonaldi* Zweifel, 1985), highlighting the evolutionary uniqueness of this rainforest isolate. Second, it extends the range of *Phyllurus* some 200km NW of its previously-known, northern limit of occurrence (Mt Dryander, 20°15'S, 148°33'E, MEQ), across what has been termed the 'Burdekin Gap' (Joseph et al., 1993). This expanse of dry woodland between Mt Elliot (19°30'S, 146°58'E), NEQ and Bowen (20°01'S, 148°15'E), MEQ has separated the faunas of two major zoogeographic regions, the Wet Tropics and Central Mackay Coast, for an 'evolutionarily long period' (Joseph et al., 1993). There is a deep divergence between *P. amnicola* and its congeners immediately south of the Burdekin Gap (ca. 50-60 mya). The mtDNA sequence divergence between *P. amnicola* on the one hand, and *P. championae*, *P. isis*, *P. nepthys*, *P. ossa*, on the other, is thus nearly as great as that between these species and those of *Saltuarius* spp. With the recognition of *P. amnicola*, there is now an overlap in the max SVL between the largest member of *Phyllurus* (*P. amnicola*, max SVL = 113mm) and the smallest species of *Saltuarius* (*S. wyberba*, max SVL = 109mm).

Description of *P. championae* brings to four the number of *Phyllurus* species known to be confined to rainforests of the Central Mackay Coast Biogeographic Region, MEQ. Couper et al. (1993) commented on aspects of the zoogeography of the other species confined to this area, all within 100km of each other (*P. isis*, *P. nepthys* and *P. ossa*). It is now clear that the species of leaf-tailed geckos in rainforests of MEQ represent the relictual distribution of an ancient group. It has been thought that

Pleistocene ice age contraction of rainforest resulted in speciation among rainforest endemics, but the deep genetic divergence among leaf-tailed geckos precludes any role for Pleistocene speciation.

Whether *P. caudiannulatus* (sensu stricto) occurs between Bulburin and Oakview State Forests, SEQ or is confined to the northernmost locality, remains to be ascertained. If the latter is the case, the Oakview '*P. caudiannulatus*' may represent another new species, pointing to a replication of patterns of relictual isolation already observed in MEQ.

Most leaf-tails (*Phyllurus* spp., *Saltuarius* spp. and *Orraya occultus*) are very narrowly distributed. Several (*Orraya occultus*, *P. amnicola*, *P. isis* and *P. nepthys*) are known from only single localities. Four other species (*S. cornutus*, *S. swaini*, *S. wyberba* and *P. caudiannulatus*) are narrowly distributed, being confined to small rainforest or rainforest and heath blocks. Under IUCN (1994) criteria, notwithstanding narrow distributions, all species should be categorised 'Data Deficient'. Higher IUCN categories, which reflect concerns based on such single locality/ narrow ranges are all tied to knowledge of declines in populations and/or potential threatening processes. Virtually all known leaf-tail localities are in state conservation or timber reserves where, generally speaking, threats are presently low. Impacts of possible future timber harvest in some areas are not known. However, most of the known, still healthy leaf-tail localities have, in the past, already been selectively logged, some extensively.

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APPENDIX 1

SPECIMENS EXAMINED. The following have been examined in addition to other material cited in Couper et al., 1993.

Morphology:

P. caudiannulatus - QMJ15619 (holotype), J33684-86, J33706, J33709, J62817, J63849-53, J63857

P. isis - QMJ53511 (holotype), J53485-86, J53518, J53480, J53591, J53602-3

P. nepthys - QMJ34058 (holotype), J34057, J35114, J57031, J65511, J65575, J65578, J65580, J65582, J65584, J65674

P. ossa - QMJ53444 (holotype), J53389, J53392, J53426, J53428, J53443, J53445, J53447, J56311, J56773, J56791

P. platurus - QMJ160, J31978, J56880-81, J56895

Orraya occultus - QMJ37040 (holotype), J37037, J37038-9 J60717, J62596
C. laevis - QMJ31004, J65410-11, J65419

Genetics:

Phyllurus amnicola - liver samples from QMJ64406-7 (Mt Elliot - 19°28'S, 146°59'E).
P. caudiannulatus - (Bulburin SF - 24°31'S, 151°29'E) liver sample from QMJ51103.
P. caudiannulatus (Oakview - 26°07'23"S, 152°19'01"E) - liver sample from QMJ62817.
P. championae - liver samples from QMJ62757-58, J62766, J63907 (Cameron Ck - 21°34'24"S, 149°11'06"E) and 4 liver samples from the following series:- J64854, J64857, J64859, J64861-62 (Blue Mtn - 21°36'S, 148°58'E).
P. isis - tail tips from Mt Blackwood (21°02'S, 148°56'E).
P. nepthys - liver samples from QMJ51101 & J51098 (Finch Hatton NP - 21°06'S, 148°38'E).
P. ossa - tail tips from Mt Ossa (20°56'S, 148°49'E), Brandy Ck (20°21'S, 148°41'E) and Mt Dryander (20°15'S, 148°33'E).
P. platurus - liver samples from QMJ56880-1 (via Gosford - 33°24'S, 151°21'E).
Saltuarius cornutus - liver samples from QMJ51632 (Malbon Thompson Ra.- 17°07'S, 145°54'E) and tail tips from Atherton (17°16'S, 145°29'E) and Big Tableland (15°43'S, 145°17'E).
S. salebrosus - liver samples from QMJ51091 (Blackdown Tableland - 23°46'S, 149°06'E) and J51090 (Bulburin SF- 24°31'S, 151°29'E).
S. swaini - liver samples from QMJ51640 (Lamington NP- 28°14'S, 153°08'E) and J51095 (Mt Tamborine - 27°58'S, 153°11'E).
S. wyberba - liver sample from QMJ51633 and tail tips (Girraween NP - 28°50'S, 151°55'E)
S. cf. *wyberba* - (Chaelundi SF population - 30°01'07"S, 15230'02"E & 30°03'04"S, 152°21'36"E) tissues from AMR141964-5.
Orraya occultus - tissues from QMJ60717, J62596 (McIlwraith Ra. - 13°45'S, 143°19'E).
Carphodactylus laevis - tails from Big Tableland (15°43'S, 145°17'E) and Mt Bartle Frere (17°24'S, 145°49'E).