

**A Reassessment of *Saltuarius swaini*
(Lacertilia: Diplodactylidae)
in Southeastern Queensland and New South Wales;
Two New Taxa, Phylogeny, Biogeography and Conservation**

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ABSTRACT. The *Saltuarius swaini* lineage comprises four species: *S. swaini* (Wells & Wellington, 1985), *S. wyberba* (Couper *et al.*, 1997), *S. moritzi* n.sp. and *S. kateae* n.sp. These are diagnosed by scalation and colour pattern differences; high levels of discrimination between these species were obtained in genetic and multivariate morphological analyses. Two species, *Saltuarius swaini* and *S. wyberba*, occur in both southeastern Queensland and northeastern N.S.W. The former is a rainforest obligate, the latter saxicolous. *Saltuarius moritzi* and *S. kateae* n.spp. are restricted to northeastern N.S.W. The former is widespread and the least specific in geological and substrate associations. The latter is restricted to the Mt Marsh area. The genus has a rainforest ancestry. Divergence within the “*S. swaini*” lineage may date to the latest Eocene–Early Miocene. We hypothesize that populations of ancestral leaf-tailed geckos would have been severely fragmented since the Mid Tertiary forcing retreat to rainforest refugia and driving allopatric speciation. Some populations shifted from trees to rocks. All four taxa are well-represented in existing reserves. *Saltuarius swaini*, a species with a continuous rainforest history and low levels of genetic variation, may be disadvantaged by ecological stasis in the face of global warming.

COUPER, PATRICK J., ROSS A. SADLIER, GLENN M. SHEA, & JESSICA WORTHINGTON WILMER, 2008. A reassessment of *Saltuarius swaini* (Lacertilia: Diplodactylidae) in southeastern Queensland and New South Wales; two new taxa, phylogeny, biogeography and conservation. *Records of the Australian Museum* 60(1): 87–118.

Leaf-tailed geckos are a distinctive, easily recognized element of the Australian fauna and one species, *Phyllurus platurus*, has occupied the homes and gardens of Sydney residents since the time of first European settlement (Bauer, 1990; Greer, 1989). Yet, until the early 1990s, the diversity within this group was largely unassessed. Aaron Bauer, in

his landmark work on the phylogenetic systematics and biogeography of the Carphodactylini (1990) recognized only four species: *P. platurus* (Shaw, in White 1790), *P. cornutus* (Ogilby, 1892), *P. caudiannulatus* (Covacevich, 1975) and *P. salebrosus* (Covacevich, 1975). These constitute less than one third of the taxa known today.

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Leaf-tails have attracted considerable interest in both taxonomic and molecular studies during the last 13 years. This, to a large degree, was sparked by the discovery of two highly distinctive, previously uncollected, taxa on the Mackay Coast in 1991 (Queensland Museum [QM], Qld National Parks and Wildlife Service) and the subsequent publication of a major revision (Couper *et al.*, 1993). A generic split was proposed; the small leaf-tails with simply-flared tails (*P. platurus* and *P. caudiannulatus*) remained in *Phyllurus* Goldfuss, 1820 while the larger leaf-tails with elaborately-flared tails (*P. cornutus* and *P. salebrosus*) were assigned to *Saltuarius* Couper, Covacevich & Moritz, 1993. The newly discovered taxa were described (*P. isis* and *P. ossa* Couper *et al.*, 1993) and two further taxa were recognized from existing museum collections: *P. nephtys* Couper *et al.*, 1993 (regarded as a population of *P. caudiannulatus* by Covacevich, 1975), and *S. occultus* Couper *et al.*, 1993 (formerly treated as a northern outlier of *P. cornutus*: Cogger, 1983, 1986, 1992; Wilson & Knowles, 1988). Additionally, *P. swaini* Wells & Wellington, 1985 was redescribed and re-located to *Saltuarius*. This taxon encompassed the southeast Queensland (SEQ) and northern New South Wales (NSW) populations formerly treated as *S. cornutus*. Recognition of *P. swaini* was delayed because the type description was “neither complete nor accurate” (Couper *et al.*, 1993).

Ongoing fieldwork and follow-up studies combining morphological data with mitochondrial cytochrome *b* sequence data have resulted in the recognition and description of four additional taxa (*S. wyberba* Couper *et al.*, 1997; *P. championae* Schneider *et al.*, 2000 (in Couper *et al.*, 2000); *P. amnicola* Hoskin *et al.*, 2000 (in Couper *et al.*, 2000); *P. gulbaru* Hoskin *et al.*, 2003), reassignment of *S. occultus* to a new genus, *Orraya* Couper *et al.*, 2000 and the discovery of genetically divergent lineages. Couper *et al.* (1997) flagged specimens from Chaelundi State Forest, NSW (misspelt as Chelundi in that publication from incorrect donor information) as being of interest in their description of *S. wyberba* from the northern Granite Belt. This material was collected approximately 145 km SW of the *S. wyberba* type locality (Girraween National Park, SEQ) and differed at approximately 11% of sites (cytochrome *b*) from this taxon. These authors commented, “Given the level of sequence differences and the discontinuity of suitable habitat, it seems unlikely that the Chelundi and Girraween populations are conspecific. However, in the absence of comprehensive data, their status remains uncertain.”

Field surveys through the northeastern forests of NSW (North-east Forest Biodiversity Study, 1991–1994; NSW National Parks and Wildlife Service, 1994) and targeted searches (1998–2004, by herpetological staff of the Australian Museum [AM] and QM) have added vastly to knowledge of the distribution of leaf-tailed geckos in SEQ and NSW, particularly through the dry forest/rock habitats and wet sclerophyll forests. This work has significantly increased museum holdings and provided fresh material for genetic analyses, and it is now appropriate to reassess the status of the species of *Saltuarius* in southeastern Australia.

Materials and methods

The morphological components of this project utilized 167 specimens belonging to the “*S. swaini*” lineage (inclusive of *S. wyberba*) from the collections of the AM and QM. The genetic component analysed tissues from 35 specimens held by these institutions, many of which were collected specifically for this project (approved by the Australian Museum Animal Research Authority—Animal Care and Ethics Committee 17 Nov. 2004, ACEC Approval Number 04-12). Dr Chris Schneider (Boston University) kindly provided access to his unpublished sequence data and additional sequences for *S. cornutus* were downloaded from Genbank.

Sampling strategy. Prior to obtaining samples for genetic sampling, we mapped the distribution of the “*S. swaini*” lineage in New South Wales and southeastern Queensland, based on voucher specimens in the Australian Museum and Queensland Museum, the two major repositories of reference collections for this region. Genetic sampling attempted to obtain representation from near the type localities of the two described species, *S. swaini* and *S. wyberba*, as well as from all rainforest and extensive rock outcrop areas in the region that were known to be inhabited by *Saltuarius*, and emphasizing apparently isolated habitat blocks. We were able to genetically sample most of the known regional distribution of *Saltuarius* to within 30 km (air distance) of all confirmed localities (i.e., localities represented by historical voucher specimens in museum collections). Up to four individuals per locality were sampled. Finer-scale sampling was not undertaken for logistic reasons, and because previous studies had not recorded sympatry between leaf-tailed gecko species (30 km represents the distance between the geographically closest populations of *S. wyberba* and *S. swaini*, the two most geographically proximate species), and hence we assumed that the samples obtained adequately represented the genetic diversity and lineage representation of each locality. Only a few areas in the south of the overall distribution were not genetically sampled.

Genetics. Total genomic DNA was extracted from all 35 liver and tail tip tissues using a standard kit (DNeasy Tissue Kit, Qiagen). In order to discern the phylogenetic relationships of these new *S. swaini* samples, we targeted the same region of the mitochondrial cytochrome *b* gene used by Couper *et al.* (1997, 2000) to describe a new genus and additional *Saltuarius* and *Phyllurus* species. In addition to the new samples, unpublished sequence data for the same region from *S. swaini* (2), *S. wyberba* (1), *S. moritzi* n.sp. (1) [provided as *S. cf. wyberba*], *S. cornutus* (1) and *S. salebrosus* (2) individuals were provided by Chris Schneider and a further two *S. cornutus* sequences were downloaded from GenBank (see Appendix 1).

Using the primer pairs Ph-1 and MVZ04 listed in Couper *et al.* (1997), a 392bp region of the mitochondrial *cyt b* gene was amplified and sequenced, although PCR conditions and amplification parameters varied slightly from that paper. Each 25µl reaction contained to a final concentration 1× Taq polymerase buffer with a final concentration of 2.5 mM MgCl₂, 0.2µM each primer; 0.8 mM dNTPs and 0.75U of Taq polymerase. The use of the hot start polymerase HotMaster Taq (Eppendorf) required an initial

denaturation at 94°C for 2 min prior to the commencement of the remaining cycle parameters; then followed 35 cycles of 94°C for 20 sec, 45°C for 20 sec, 65°C for 30 sec and a final extension 65°C for 5 min, 22°C for 30 sec.

PCR products were gel purified and sequencing reactions carried out according to standard ABI PRISM dye-deoxy terminator sequencing protocols using Big Dye Terminator version 1.1. Sequences from the new specimens have been deposited in GenBank nucleotide sequence database (see Appendix 1) under the accession numbers EU625300–EU625342.

Chromatographs were checked and all sequences were aligned using Se-Al v2.0a10 (Rambaut, 1996). For phylogenetic analysis among all *swaini*–*wyberba* group sequences we used a Bayesian approach with posterior probabilities calculated using Markov chain, Monte Carlo (MCMC) sampling as implemented in MrBayes v 3.1 (Ronquist & Huelsenbeck, 2003) These analyses used the HKY (Hasegawa, Kishino and Yano model) + Γ (gamma distribution of rates) model of sequence evolution with the shape of the gamma distribution and Tratio priors set to 0.36 and 5.13 respectively, as determined by Modeltest v.3.7. Starting trees were random and 4 simultaneous Markov chains were run for 2.5 million generations with trees sampled every 100 generations. To generate the majority rule consensus tree, burnin values were set at 10 000 generations after empirical values of stabilizing likelihoods indicated that convergence of the MCMC chains had been reached. The posterior probabilities on the consensus tree are indicated only where branch support was greater than 0.5 (Posada & Crandall, 1998). Based on the previous phylogenetic studies, *S. cornutus* and *S. salebrosus* were used as outgroup sequences (Couper *et al.*, 1997, 2000).

Morphometrics. All measurements were taken with Mitutoyo electronic callipers and all bilateral counts were scored for the left side only. Juveniles are excluded from all measurements given as percentage SVL.

Definitions: snout to vent length (SVL), tip of snout to anterior margin of cloaca with body straightened; tail length (T), from posterior margin of cloaca to tip of tail; attenuated tip of original tail (TT), portion of tail distal to lateral flanges; head length (HL), mid anterior margin of ear to tip of snout; head width (HW), widest point across back of skull, corresponding with anterior upper margin of ear openings; head depth (HD), lower jaw to top of head, between eyes; snout length (S), anterior margin of orbit to tip of snout; eye to ear (EE) posterior margin of orbit to mid anterior margin of ear; neck length (NL) axilla to mid posterior margin of ear; length of forelimb (L1), insertion to tip of longest digit, with limb stretched straight perpendicular to body; length of hind limb (L2), insertion to tip of longest digit, with limb stretched straight perpendicular to body; axilla to groin (AG); subdigital lamellae (fourth finger, fourth toe) tip of digit to basal junction of third and fourth digits; supralabial and infralabial scale rows (from rostral and mental scales, terminating posteriorly at the angle of the mouth when the labials cease to be twice the size of adjacent granules). The hands and feet were examined for the presence or absence of enlarged dorsal tubercles and degree of spinosity on the digits. The scale rows on the snout, immediately above the anterior supralabials, were scored as: 1) grading evenly from small to large (dorsal–ventral transect), or 2) heterogeneous, small and large scales intermixed. Spines across

the attenuated tail tip were counted immediately distal to the flared portion of the original tail. The spines across the flared portion of the tail were counted three rows anteriorly to the former count. Aspects of colour/pattern were assessed (as in the descriptions that follow).

Multivariate analyses. We used discriminant function analysis to test the hypothesis that the four major lineages recovered from our genetic analysis were morphologically distinct. In so doing, we assumed that additional genetic lineages were not present. Discriminant function analysis was chosen rather than principal components analysis because the functions derived were capable of predicting identity of individuals of unknown identity from the few areas that were not able to be genetically sampled, and because DFA takes into account within-group covariance between characters. Thorpe (1980) found that the two techniques otherwise gave similar results in recovering known patterns of geographic variation.

Because sample sizes available for morphological study greatly exceeded those used for genetic analysis, to use only individuals of known genotype would have markedly limited sample size, particularly when sexes were analysed separately and juveniles excluded (see below), and resulted in many more unknown than known individuals. Hence, we increased the samples for morphological analyses by including individuals from within 30 km of genetically typed individuals as part of the known sample of each lineage. To reduce the risk of combining multiple genetic lineages into single morphological samples by this approach, we treated any individuals from within the overlap zone of 30 km radii of genetically distinct lineages or more than 30 km from genotyped individuals, as being of unknown identity (for allocation of specimens see Appendix 2). Because the four genetic lineages were geographically disjunct (northeast, northwest, central and south), this approach effectively tested the hypothesis that these four geographic and genetic subunits were morphologically distinguishable, and predicted the identity of unassigned individuals representing (a) regions of close geographic approach of the four geographic blocks (i.e., potential contact zones) and (b) more peripheral regions distant to genetically sampled blocks.

Preliminary morphological analyses of the three genetic species best represented (*S. swaini*, *S. wyberba* and *S. moritzi* n.sp., described herein) were undertaken to test for the existence of sexual dimorphism and allometric growth in head, body and limb proportions. All measurements were converted to natural logarithms, and the relationship between each measurement and snout-vent length (as an estimate of overall size) was calculated, for each sex of each of the three taxa.

Within at least one species for each comparison, there were significant differences in either the slope or (where slopes were not significantly different) the intercepts of the regression lines for the sexes (analysis of covariance), indicating the presence of sexual dimorphism in the relationship. Sexual dimorphism was also detected in some taxa in meristic data (t-tests).

Consequently, subsequent analyses were performed independently for each sex. Unsexed immature specimens were excluded from analyses.

Within each sex, allometry of the relationship between body, head or limb measurements and snout-vent length was

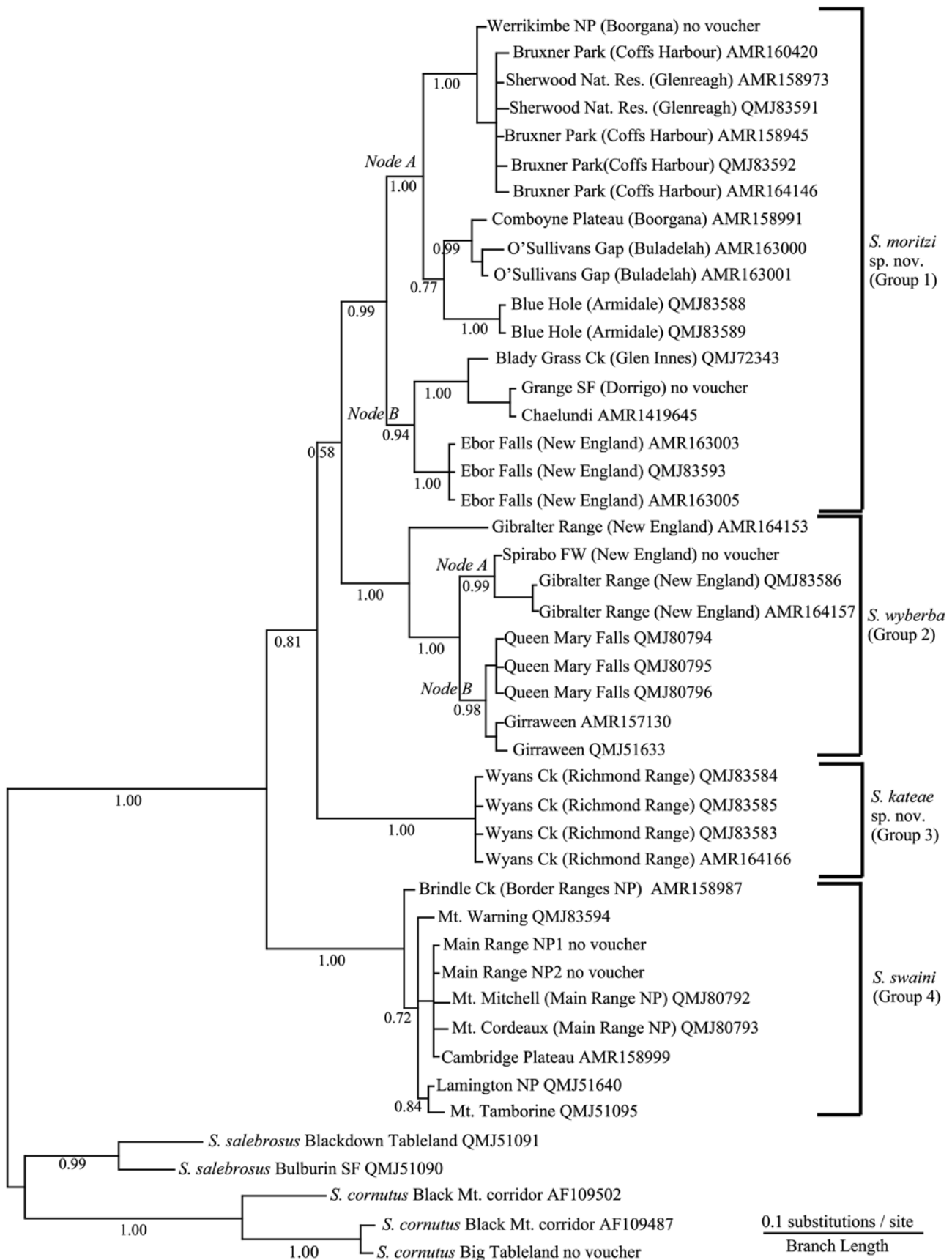


Fig. 1. Phylogeny of *Saltuarius* spp. based on cytochrome b sequence data. Some branches may be represented by multiple individuals with identical sequences. Numbers on the branches represent Bayesian Posterior Probabilities. Branches with <50% support were collapsed.

Table 1. Percent sequence divergence estimates within and between *Saltuarius* species groups. Values on the diagonal are the average within species estimates; values below the diagonal are the average between species estimates. Standard errors and range values (in parentheses) are presented where there are more than 2 non-identical sequences.

	<i>S. moritzi</i> n.sp.	<i>S. wyberba</i>	<i>S. swaini</i>	<i>S. kateae</i> n.sp.	<i>S. cornutus</i>	<i>S. salebrosus</i>
<i>S. moritzi</i> n.sp.	4.69±0.002 (0–8.24)					
<i>S. wyberba</i>	10.59±0.001 (8.45–11.90)	3.17±0.004 (0–7.4)				
<i>S. swaini</i>	13.01±0.001 (11.11–15.28)	14.37±0.001 (13.05–16.24)	0.73±0.001 (0–1.57)			
<i>S. kateae</i> n.sp.	11.47±0.001 (10.06–12.92)	11.34±0.001 (10.88–12.09)	14.23±0.001 (12.89–15.88)	0.00		
<i>S. cornutus</i>	22.19±0.001 (21.01–24.67)	24.52±0.002 (22.23–25.60)	22.65±0.002 (20.44–24.41)	23.10±0.007 (19.21–24.74)	6.06±0.026 (0.83–8.85)	
<i>S. salebrosus</i>	18.45±0.001 (17.15–24.67)	19.57±0.001 (18.70–21.43)	19.38±0.002 (17.96–21.15)	19.03±0.003 (17.86–20.14)	16.73±0.005 (15.77–18.92)	5.78

assessed by two methods. Firstly, allometry was considered to exist if the slope of the regression line of the variable against snout-vent length was more than two standard errors of 1.0 (Zar, 1974). However, sample sizes were small for some of the sexes and taxa, and standard errors often large, and hence for some tests, allometry was not statistically demonstrated, even though the slope of the relationship was further from isometry than for some statistically significant comparisons. Consequently, we considered there was potential for allometric growth if, for all three species studied of that sex, the slope of the regression line was uniformly in the same direction (either less than 1.0 or greater than 1.0). Using both criteria (statistical support and consistency of direction), all measurements showed some potential for allometric growth.

Hence, we used the methods of Thorpe (1975) to remove these potential effects by converting the measurements to the values they would assume for an animal of average size. For these conversions, we separately converted male and female data. For each sex, we used the average slope of the regression lines for the three well-represented species, and the mean snout-vent length of the sexed individuals. To avoid adjusting morphometric data for the effects of allometric growth runs the risk of the subsequent multivariate analyses being affected by changes in sampling distribution of body sizes (young individuals will have different shapes to older, larger adults); similarly, because our analyses combined both morphometric and meristic characters, and because allometric growth was present in the metric characters, we were unable to remove the effect of body size either by use of simple ratios or traditional principal components analyses of untransformed variables.

In our discriminant function analyses, we included those metric and meristic characters that showed significant differences between the putative genetic taxa (analyses of covariance for metric data, with snout-vent length as the independent variable; t-tests for meristic data and snout-vent length itself), and only used characters that were multi-state and variable within species. Hence, we were unable to include some categorical differences in scalation and coloration between putative taxa that were observed during our examination of specimens, even though these often differentiated the four genetic lineages. The characters we included in our multivariate analyses were: snout-vent length; adjusted

axilla-groin length; adjusted hind limb length; adjusted head length; adjusted head width; adjusted head depth; adjusted snout length; adjusted eye-ear length; adjusted neck length; number of supralabials; number of infralabials; number of finger lamellae; number of toe lamellae, and number of scales contacting the postmental.

For females, where each of the four putative taxa was represented by six or more individuals, we treated each of the four taxa as a distinct operational taxonomic unit (OTU). For males, we treated *S. swaini*, *S. wyberba* and *S. moritzi* n.sp. as identified OTUs; however because there was only a single male of *S. kateae* n.sp. (described herein), we treated this as unidentified for the analysis. The female analysis had fewer identified specimens ($n = 40$, representing 6 *S. kateae* n.sp., 18 *S. moritzi* n.sp., 9 *S. swaini* and 7 *S. wyberba*) than the male analysis ($n = 74$, representing 27 *S. moritzi* n.sp., 22 *S. swaini* and 25 *S. wyberba*).

Results

Genetics. The Bayesian consensus tree (Fig. 1) clearly shows *S. swaini* (group 4) and *S. wyberba* (group 2) as very strongly supported clades with posterior probabilities of 1.00 for both groups. Clades (groups) 1 and 3 are equally robust with posterior probabilities of 0.99 and 1.00 respectively and correspond with the two new taxa identified by the morphological assessment. Species groups 1 and 2 exhibit considerable population structuring with strongly supported subgroups represented by nodes A and B in both. Average sequence divergence within each group (1–4) ranges from 0–4.69% (Table 1). The average divergence between these species groups ranges from 10.59–14.37% (Table 1). The extensive structuring within groups 1 and 2 is also represented by a wide range of within species sequence divergence estimates (Table 1). The maximum values of 8.24% and 7.40% within groups 1 and 2 respectively, while close, are still lower than the smallest interspecific divergence estimate of 8.45% (*S. moritzi* n.sp. vs *S. wyberba*).

Morphology. The morphological assessment identified consistent differences in colour/pattern and scalation between the four genetic lineages.

Multivariate analyses. Both analyses provided high levels of discrimination of the identified taxa.

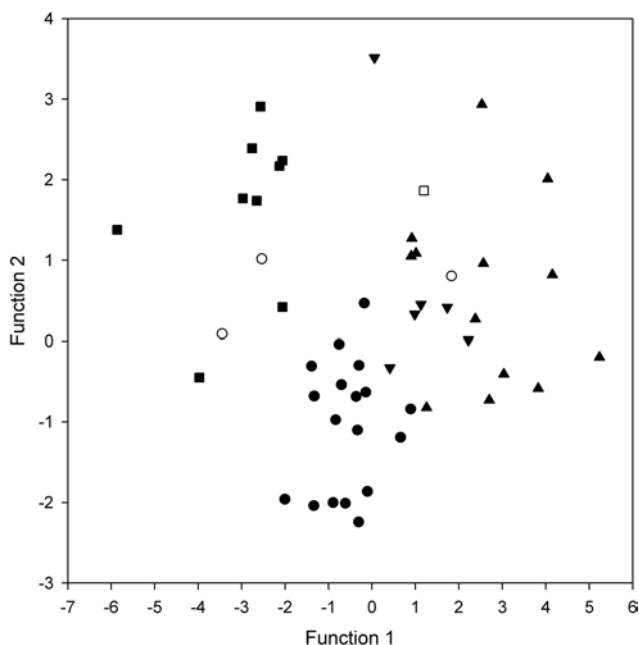


Fig. 2. Scatterplot of scores from discriminant functions 1 and 2 for female *Saltuarius*. ▼ *S. kateae* n.sp., ● *S. moritzi* n.sp., ▲ *S. swaini*, ■ *S. wyberba*. Open symbols are individuals assigned to each species on other criteria (locality, genetic identity, coloration) that were considered by the discriminant functions to belong to other species.

Females:

Saltuarius kateae n.sp. (Group 3 of the genetic analysis). All six individuals were correctly identified.

Saltuarius moritzi n.sp. (Group 1 of the genetic analysis). Eighteen animals were identified *a priori* as this taxon, and three individuals treated as unidentified for the analysis but tentatively expected to belong to this taxon on geographic or coloration grounds. The discriminant function analysis correctly identified 18 of the 21 individuals. The exceptions were one specimen from Giro (AM R150912), from a region not genetically studied, but closest to *S. moritzi* n.sp., which the analysis considered to be *S. swaini*; and two individuals (AM R143592, from Oakwood, treated as *S. moritzi* n.sp. due to its proximity to the Blady Grass Creek genetic sample and AM R43870 from 22 km E of Guyra, treated as unidentified for the analysis because of its distance from genetic samples, but considered to be morphologically most similar to *S. moritzi* n.sp.) which were both identified as *S. wyberba*. Hence, the analysis correctly identified 86% of *S. moritzi* n.sp.

Saltuarius swaini (Group 4 of the genetic analysis). Nine individuals were identified as this species and four individuals treated as unidentified. All 13 *S. swaini* were correctly identified by the analysis.

Saltuarius wyberba. (Group 2 of the genetic analysis). Seven individuals were identified as this species and an additional three individuals, for which precise locality data were unavailable, were expected to be this species. All of the identified *S. wyberba*, and two of the three presumed *S. wyberba*, were correctly identified (90%); the exception, one of the

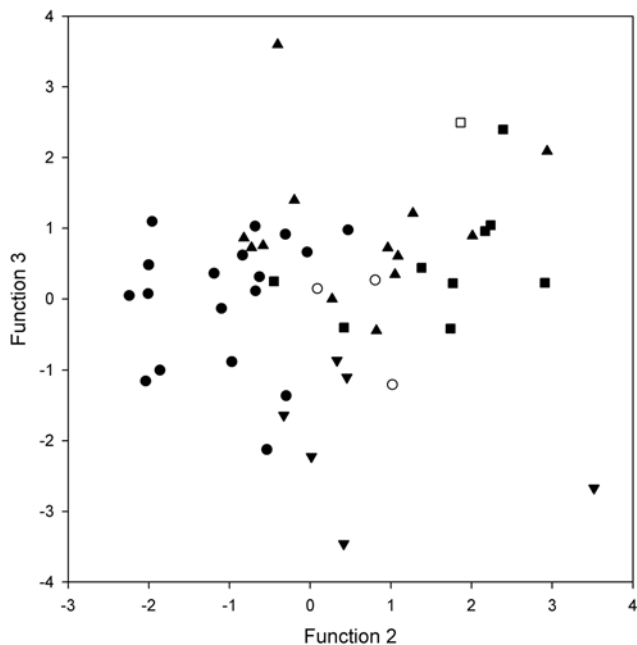


Fig. 3. Scatterplot of scores from discriminant functions 2 and 3 for female *Saltuarius*. ▼ *S. kateae* n.sp., ● *S. moritzi* n.sp., ▲ *S. swaini*, ■ *S. wyberba*. Open symbols are individuals assigned to each species on other criteria (locality, genetic identity, coloration) that were considered by the discriminant functions to belong to other species.

unlocalized specimens (QM J79753), was identified by the analysis as *S. swaini*.

Hence, of 50 females included in the analysis, the discriminant functions misidentified four individuals. If our *a priori* identifications are treated as correct, then the DFA misidentified 8% of individuals. For females, if the four misidentified individuals are excluded, the first discriminant function fully separated *S. wyberba* and *S. swaini*, with *S. kateae* n.sp. and *S. moritzi* n.sp. having intermediate values; the second function in combination with the first function fully separated *S. moritzi* n.sp. from *S. swaini* and *S. wyberba*, the third function fully separated *S. kateae* n.sp. from *S. wyberba* and *S. swaini*, and the combination of second and third functions almost completely separated *S. kateae* n.sp. and *S. moritzi* n.sp. (Figs 2–3).

The first of the three functions extracted contributed 67.3% of the total dispersion, while the first two functions contributed 84.4% of the total dispersion. Head width (negative), number of infralabials and number of supralabials, had the greatest contributions to Function 1, head width (negative), number of supralabials and number of toe lamellae had the highest contributions to Function 2, and head length (negative), head width and toe lamellae had the highest contributions to Function 3.

Males:

Saltuarius moritzi n.sp. In addition to the 27 individuals identified as this species, two additional specimens were treated as unknown. The discriminant analysis correctly identified 25 of the 27 identified individuals and the two unknowns (from the Nambucca River area, with genetic samples of this species to the north, west and south, and from “Brisbane”), an accuracy of 93%. The two incorrectly identified individu-

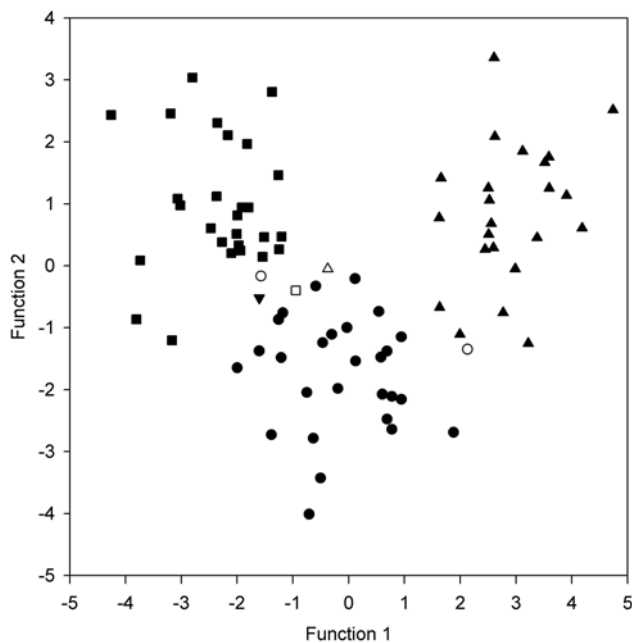


Fig. 4. Scatterplot of scores from discriminant functions 1 and 2 for male *Saltuarius*. ▽ *S. kateae* n.sp., ● *S. moritzi* n.sp., ▲ *S. swaini*, ■ *S. wyberba*. Open symbols are individuals assigned to each species on other criteria (locality, genetic identity, coloration) that were considered by the discriminant functions to belong to other species.

als were from Comboyne Plateau (AM R158990), close to a genetic sample, and geographically distant from *S. swaini*, to which it was identified by the discriminant analysis, and QM J72343, a genetically sampled individual from Blady Grass Creek, which the analysis predicted to be *S. wyberba*.

Saltuarius swaini. In addition to the 22 identified individuals, there were two individuals, from Mt Clunie and Mt Superbus, which although morphologically similar to *S. swaini*, were within 30 km of both *S. swaini* and *S. wyberba* genetic samples, and hence were treated as unidentified. The discriminant analysis correctly identified both of the unidentified individuals, and all but one of the identified individuals (97% accuracy). The exception was an individual from O'Reilly's (QM J51637), which the analysis considered to be *S. moritzi* n.sp.

Saltuarius wyberba. In addition to the 25 identified individuals, there were three specimens treated as unidentified but which we expected to be *S. wyberba* on other morphological grounds. All three, together with 24 of the 25 identified specimens, were correctly identified as *S. wyberba*. The exception was QM J83587, from Gibraltar Range, which the analysis identified as *S. moritzi* n.sp.

Hence, of the 81 males considered, the discriminant analysis misidentified four individuals. If our *a priori* identifications of these four specimens are considered correct, then the DFA misidentified 5% of males. For males, if the four misidentified individuals are excluded, the first function completely separated *S. wyberba* and *S. swaini*, with *S. moritzi* n.sp. intermediate, while the combination of the first and second functions completely separated *S. moritzi* n.sp. from both *S. wyberba* and *S. swaini* (Fig. 4). The single male individual of *S. kateae* n.sp. was intermediate between *S.*

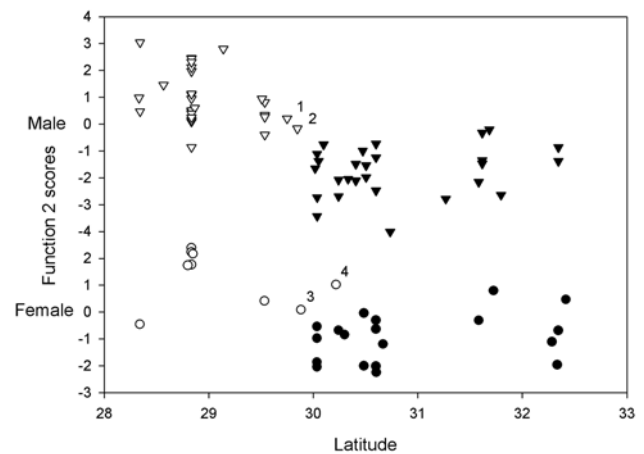


Fig. 5. Latitudinal change in discriminant function 2 scores for males (inverted triangles ▽ and ▼) and females (circles ○ and ●) for *Saltuarius wyberba* (open symbols ▽ and ○) and *S. moritzi* (closed symbols ▼ and ●). Individuals from intermediate localities are indicated by numbers: 1 = Teapot Creek; 2 = Blady Grass Creek; 3 = Oakwood State Forest; 4 = 22 km E of Guyra.

wyberba and *S. moritzi* n.sp., and predicted by the analysis to be *S. wyberba*.

The first of the two functions extracted contributed 72.6% of the total dispersion. Head width (negative), snout-vent length and head depth had the greatest contributions to Function 1, number of infralabials, head depth (negative), head width, snout-vent length and number of scales contacting the mental had the greatest contributions to Function 2.

Systematics of the *Saltuarius swaini* lineage

None of the genetic lineages identified in this study show geographic overlap that would allow for assessment of species boundaries by direct application of interbreeding criteria of the traditional biological species concept. Lack of sympatry between species is typical of the entire Australian leaf-tailed gecko radiation. Instead, we adopt a phylogenetic species concept of the smallest independently evolving diagnosable unit (Cracraft, 1989), that recognizes species by the combination of genetic and morphological criteria, each of which provides evidence of independent evolution between geographically adjoining lineages. We recognize that attempts to use a standard level of sequence divergence as sole criterion for species definition must rest on a dubious assumption that speciation occurs at a relatively continuous rate and, if molecular clock hypotheses are accepted, only occurs beyond a given age. However, we consider that a high level of sequence divergence, commensurate with the level of sequence divergence between known species pairs of closely related taxa, and at a much greater degree than occurs between and within populations within related known species, can be suggestive of species-level distinction. We are encouraged to treat such lineages as full species when they are able to be distinguished morphologically, and when those

differences are maintained on geographic proximity.

Harris (2002) reported percentage differences in the *cytb* gene for congeneric gecko species of three genera (*Hemidactylus*, *Stenodactylus* and *Tarentola*) as low as 10%, and for reptiles in general a mean level of divergence between closely related species-pairs of 13.6%, while Bauer and Lamb (2001) reported interspecific differences as low as 9.7% for Namib day geckos (*Rhoptropus*) using the same gene. There have been recent suggestions that geckos in general may have higher rates of mutational change in mtDNA than other reptiles (Harris *et al.*, 2004, Jesus *et al.*, 2002, 2006), and hence that geckos should show higher levels of sequence divergence between sister-species of the same age as for other reptiles. Certainly there have been some very high levels of sequence divergence in the *cytb* gene detected between congeneric gecko species (Lamb & Bauer, 2000, 2001; Bauer *et al.*, 2002; Carranza *et al.*, 2002). However, most studies using the *cytb* gene in geckos have been based on gekkonine geckos, not diplodactyline geckos, many of the larger genetic distances have not been confirmed to be between sister-species, and the most recent study (Jesus *et al.*, 2006) was unable to exclude the possibility that the comparative nuclear gene they used was not evolving unusually slowly. The only comparable study using *cytb* for diplodactyline geckos is by Couper *et al.* (2000), who reported sequence divergences between other *Saltuarius* and *Phyllurus* species as low as 12.3%.

We begin our assessment of species boundaries in the *Saltuarius swaini* complex by considering the two named species, *S. swaini* (group 4) and *S. wyberba* (group 2). These two taxa approach geographically to within 15 km (Mt Clunie and Mt Superbus *vs* Queen Mary Falls). Samples of the two 30 km apart have been genetically typed (4 *swaini* from Main Range National Park; 3 *wyberba* from Queen Mary Falls) and each sample is genetically homogeneous and nested deeply within its respective species. The two species show 14.37% sequence divergence, comparable to other leaf-tail gecko species pairs. Morphologically, the two species are distinguishable on coloration, size and snout scalation (see direct comparisons below) and are distinguishable in morphological space in multivariate analyses, and these differences are maintained in geographic proximity. Multivariate analyses consistently assigned identity to individuals from localities of closest approach that agreed with the expectations of coloration. Hence, we have no hesitation in continuing to recognize these two species as distinct. *Saltuarius swaini* maintains its genetic and morphological integrity over a latitudinal distance of 102 km while *S. wyberba* similarly maintains its integrity over a latitudinal range of at least 133 km.

The Group 3 lineage, geographically to the south of *S. swaini*, is separated from it by 38 km (Wyans Creek *vs* Cambridge Plateau, type locality for *S. swaini*). At this closest known approach, the genetic and morphological distinction between the two is maintained, and they differ by 14.23% genetic distance, a level very close to that between *S. swaini* and *S. wyberba*. Group 3 is geographically more widely disjunct from *S. wyberba* (60 km from Wyans Creek to Gibraltar Range, the closest genetic sampling, and 47 km from Wyans Creek to Timbarra Plateau, the closest individual morphologically), and apparently isolated from it by the Clarence River valley. The genetic distance between Group 3 and *S. wyberba* is 11.34%, and the two lineages are morphologically distinguishable in scalation, head width (see

comparisons below) and in morphological multivariate space (no individuals of *S. wyberba* and Group 3 were misidentified as each other in either the female or male analyses). Hence, we recognize Group 3 as a species distinct from *S. swaini* and *S. wyberba*, and describe it below as *S. kateae* n.sp.

The remaining lineage, Group 1, represents all southern populations of the *S. swaini* complex, and covers a latitudinal range of at least 271 km. It is genetically divergent from *S. swaini* by 13.01%, geographically widely disjunct from it (137 km between Cambridge Plateau *vs* Chaelundi, and 75 km if the Grange State Forest locality is accepted; see below), with the Clarence River valley forming a geographic barrier to dispersal, and maintains its morphological and genetic distinction at these closest approaches. It is distinguishable from *S. swaini* by coloration, body size and snout scalation (see below). Multivariate analyses misidentified only one of 34 females and two of 53 males as the other species; none of the three misidentified individuals were from near regions of closest geographic approach and all were unambiguously referable to the correct lineage on other morphological grounds. Group 1 is similarly genetically distinct from *S. kateae* n.sp. by 11.47% sequence divergence, geographically widely disjunct from it (101 km between nearest genetic samples from Wyans Creek, and Chaelundi; 45 km if the Grange State Forest locality is accepted), again with the Clarence River valley forming a barrier to contact, and morphologically distinct at this nearest approach, both in multivariate morphological space and in scalation and coloration. No females of either lineage were identified as the other lineage by discriminant function analysis, while the single male *S. kateae* n.sp. was predicted to be Group 1 because it was morphologically closest to that lineage, not because it fell within the morphological space of that group.

Hence, we consider Group 1 to warrant specific distinction from both *S. swaini* and *S. kateae* n.sp. The nature of the interaction between Group 1 and *S. wyberba*, to which it is closest genetically and geographically, warrants further consideration. These two genetic lineages have the lowest level of sequence divergence (10.59%) in the *S. swaini* complex, a divergence near the lower level for sister-species of other geckos (Harris, 2002; Bauer & Lamb, 2001). The extent of sequence divergence within each group is considerably lower (an average of 4.69% for Group 1, over a latitudinal range of 271 km, and 3.17% for *S. wyberba*, over a 133 km latitudinal range), less than half the divergence between the two lineages, and there is a moderate degree of morphological distinction between the two. Multivariate analyses distinguished 47 of 50 (94.0%) Group 3 specimens from 37 of 38 (97.4%) *S. wyberba*. However, the four individuals that proved problematic to the multivariate analyses were from localities either representing the most proximate samples of otherwise unequivocal *S. wyberba* to Group 1 (one of five individuals from Gibraltar Range identified as Group 1), or from a small area (53 km from north to south) to the south and geographically intermediate between *S. wyberba* at Gibraltar Range and Group 1 at Ebor Falls and Chaelundi, raising the possibility of a zone of intermediacy or hybridization between the two putative taxa.

Only four individuals were able to be examined from this intermediate region: J53984 from Teapot Creek; J72343 from Blady Grass Creek; R43870 from 22 miles E of Guyra, and R143592 from Oakwood State Forest. The multivariate analyses identified all four individuals as *S. wyberba*, while

the only one that was able to be genetically examined (J72343) had the *cytb* profile of Group 1. Function 2 of both male and female discriminant function analyses most strongly differentiated these two lineages. A plot of function 2 scores against latitude (Fig. 5) shows little evidence for clinal change; the four specimens from intermediate localities are well within the range of variation of *S. wyberba* and the two lineages show only weak geographic variation across their distribution.

As both genetic and morphological analyses distinguish northern and southern groups, and the morphological distinction between these groups is not clinal, and the genetic differentiation between the two groups is much greater than between populations within the other species of the *S. swaini* complex, we believe that group 1 warrants taxonomic recognition as distinct from *S. wyberba*.

Sampling is as yet insufficient to resolve the discrepancy between genetic and morphological assignment of individuals from a small intermediate zone, and hence we treat this population as *incertae sedis*. As the magnitude of the genetic and morphological differentiation between Group 1 and *S. wyberba* is only a little less than between other pairs of species, we treat Group 1 as a distinct species, which we describe below as *S. moritzi* n.sp. However, we recognize that further work is needed to clarify the exact nature of the interaction between *S. moritzi* n.sp. and *S. wyberba* at closest approach, and it is possible that a subspecific distinction may ultimately best label the interaction.

The two new species are described in the systematics section that follows. *Saltuarius swaini* sensu stricto and *S. wyberba* are redescribed. The former species was composite,

Table 2. Comparison of body proportions (as % SVL) between members of the “*S. swaini*” lineage.

Measurement	<i>S. moritzi</i> n.sp.	<i>S. swaini</i>	<i>S. kateae</i> n.sp.	<i>S. wyberba</i>
Adult body length				
max SVL (mm)	109.3	134.0	105.4	107.7
N	62	46	7	41
Tail length % SVL				
range	63.0–76.0	59.2–72.4	not available	62.3–80.7
mean±sd	68.9±3.53	66.9±4.11		71.2±4.32
N	17	16		14
Attenuated tail % SVL				
range	23.9–31.6	24.4–33.6	not available	20.7–36.8
mean±sd	27.9±2.19	27.4±2.85		29.0±4.07
N	17	16		14
Head length % SVL				
range	25.4–29.8	25.2–28.5	26.5–27.7	24.7–29.3
mean±sd	26.9±0.83	26.2±0.64	27.2±0.48	27.3±0.97
N	49	40	7	36
Head width % SVL				
range	19.9–24.2	18.7–22.0	20.8–22.0	19.8–23.9
mean±sd	21.2±0.78	20.4±0.80	21.3±0.47	22.1±0.95
N	49	40	7	36
Snout length % SVL				
range	11.4–14.1	10.1–13.5	11.8–12.5	11.0–13.7
mean±sd	12.2±0.49	12.2±0.48	12.2±0.22	12.1±0.49
N	49	40	7	36
Eye-ear % SVL				
range	7.4–10.3	7.4–9.4	7.5–9.2	7.5–10.0
mean±sd	8.5±0.61	8.3±0.46	8.3±0.66	8.9±0.63
N	49	40	7	36
Neck length % SVL				
range	15.8–23.0	14.5–22.4	15.0–19.7	15.1–21.3
mean±sd	19.4±1.48	18.6±1.73	17.4±1.52	17.7±1.46
N	49	40	7	35
Axilla-groin % SVL				
range	39.9–50.1	41.3–51.3	44.6–48.0	39.9–48.3
mean±sd	45.1±2.12	46.2±2.30	46.8±1.27	45.0±1.91
N	49	39	7	36
Forelimb % SVL				
range	41.5–51.6	44.0–51.1	44.9–47.4	44.0–50.9
mean±sd	47.4±2.26	48.2±1.60	46.3±0.96	47.2±1.92
N	49	36	7	35
Hind limb % SVL				
range	52.0–62.4	53.2–62.3	55.4–60.4	53.1–63.3
mean±sd	57.7±2.24	58.7±2.24	58.0±2.00	57.4±2.50
N	49	36	7	34

incorporating specimens of *S. moritzi* n.sp. in the latest formal description (Couper *et al.*, 1993); the latter species exhibits colour/pattern and scalation variations that were not encompassed in the type description (Couper *et al.*, 1997).

The two new taxa, along with *S. wyberba*, are sibling species to *S. swaini* (see phylogeny, Fig. 1). They are assignable to *Saltuarius* by the following characters: nostril contacting the rostral (except in *S. kateae* n.sp.); rostral completely divided; moderate to large size (max SVL 105–134 mm); original tail strongly flared with an elaborate outer flange (not yet assessable for *S. kateae* n.sp.); regenerated

tail strongly flared, with only a small attenuated tip. Skeletal features were not assessed, but given the uniformity of these across the genus, they are unlikely vary from the generic description (Couper *et al.*, 1993). The skeletons of *S. swaini* and *S. wyberba* show no significant differences (Couper *et al.*, 1993, 1997). The “*S. swaini*” lineage is morphologically distinguished from its northern congeners by the absence of preanal pores in both sexes (present in males in the northern taxa). Morphometric summaries for the species comprising the “*S. swaini*” lineage are provided in Tables 2 & 3.

Table 3. Comparison of key scalation characters between members of the “*S. swaini*” lineage.

Scale count	<i>S. moritzi</i> n.sp.	<i>S. swaini</i>	<i>S. kateae</i> n.sp.	<i>S. wyberba</i>
Scales contacting posterior margin of mental				
range	1–7	3–8	4–7	4–11
mode	4	6	4	6
mean±sd	4.9±1.15	5.4±1.14	5.0±1.29	6.0±1.42
N	61	45	7	40
Supralabials				
range	10–18	12–18	13–16	11–18
mode	13	14	14	14
mean±sd	13.5±1.35	14.9±1.53	14.4±0.98	14.5±1.43
N	61	46	7	41
Infralabials				
range	9–14	9–16	12–13	10–15
mode	12	12	12	12
mean±sd	11.9±1.20	12.8±1.45	12.1±0.38	12.3±1.10
N	62	46	7	41
Lamellae (4th finger)				
range	17–23	18–26	19–22	16–24
mode	19	22	21	18
mean±sd	19.6±1.43	21.5±1.64	20.4±1.13	19.2±1.61
N	60	46	7	41
Lamellae (4th toe)				
range	19–26	20–28	21–24	19–25
mode	24	23	24	20
mean±sd	22.6±1.75	24.0±1.71	23.3±1.11	21.6±1.66
N	62	46	7	41
Tail tubercles (across flared portion)				
range	4–7	6–13	Not available	4–8
mode	6	10		6
mean±sd	5.4±0.89	9.4±1.74		5.6±1.21
N	27	19		14
Tail tubercles (across attenuated tip)				
range	4–6	5–10	Not available	4–7
mode	4	6		6
mean±sd	4.3±0.60	6.4±1.16		5.4±0.94
N	26	19		14

Saltuarius kateae n.sp.

Fig. 6

Material examined. HOLOTYPE, AM R164163, Wyans Creek Road, 11.4 km W of Old Tenterfield Road (29°08'31"S 152°47'06"E) NSW. R. Sadlier, G. Shea & P. Couper. PARATYPES: QM J83583–85, AM R164161, AM R164166, collection data as for holotype. AM R139790 Mount Marsh SF (29°12'52"S 152°49'17"E) NSW.

Etymology. For Kate Couper for her ongoing support during the field component of this project.

Diagnosis. A medium-sized *Saltuarius* (maximum SVL 105 mm) with smooth throat scales, no preanal pores (in either sex) and an obscure, narrow V-shaped marking running back deeply between the eyes (Fig. 7A). It is distinguished from its congeners by the following combination of character states: rostral shield usually excluded from nostril (Fig. 8A); scales on snout usually grade evenly from small to large (in dorsal–ventral transect, Fig. 9A); dorsal surface of hand free of large conical tubercles; digits without spinose tubercles along dorsal surface (Fig. 10A); body darkly pigmented, reducing extent of dorsal cross-bands between fore and hind limbs (Fig. 6).

Description

SVL (mm): 84.5–105.4 (n = 7, mean = 98.5, SD = 6.61). Proportions as % SVL: T unknown (no original tails in sample); HL = 26.5–27.7 (n = 7, mean = 27.2, SD = 0.48); HW = 20.8–22.0 (n = 7, mean = 21.3, SD = 0.47); S = 11.8–12.5 (n = 7, mean = 12.2, SD = 0.22); EE = 7.5–9.2 (n = 7; mean = 8.3, SD = 0.66); NL = 15.0–19.7 (n = 7, mean = 17.4, SD = 1.52); AG = 44.6–48.0 (n = 7, mean = 46.8, SD = 1.27); L1 = 44.9–47.4 (n = 7, mean = 46.3, SD = 0.96); L2 = 55.4–60.4 (n = 7, mean = 58.0, SD = 2.00).

Head. Large, depressed, triangular, distinct from neck; head depth 39.1–44.3% head width (n = 7, mean = 41.7, SD = 1.71); covered in small granules which are intermixed with larger conical tubercles; skin of head co-ossified with skull; rostral shield fully divided by deep vertical groove (n = 7); rostral shield excluded from nostril (Fig. 8A; except on left side of QM J83585); scales contacting posterior margin of mental shield 4–7 (n = 7, mode = 4, mean = 5.0, SD = 1.29); ear opening elliptical, vertical, much less than half as large as eye; supralabials 13–16 (n = 7, mean = 14.4, mode = 14, SD = 0.98); scales on snout usually grade evenly from small to large (in dorsal–ventral transect, Fig. 9A); infralabials 12–13 (n = 7, mode = 12, mean = 12.1, SD = 0.38). **Neck.** Broad. **Body.** Moderate, depressed, covered in small granules; dorsal granules intermixed with larger conical tubercles; tubercles small to moderate on back, flanks and sides of neck; basal scales surrounding upper flank and back tubercles not, or only slightly, larger than adjacent granules; ventral scales enlarged in pelvic region. Preanal pores absent. Axilla moderately to deeply invaginated. **Limbs.** Long, covered in small pointed tubercles dorsally; lacking enlarged tubercles on ventral surfaces; digits strongly compressed distally; subdigital lamellae (fourth finger) 19–22 (n = 7, mode = 21, mean = 20.4, SD = 1.13); dorsal surface of hand free of large



Fig. 6. *Saltuarius kateae* n.sp. (AM R164163—holotype), Wyans Creek Road, 11.4 km W of Old Tenterfield Road (29°08'31"S 152°47'06"E) NSW (photograph—R. Sadlier, AM).

conical tubercles; dorsal surface of fingers without enlarged, spinose scales; subdigital lamellae (fourth toe) 21–24 (n = 7, mode = 24, mean = 23.3, SD = 1.11); dorsal surface of foot with enlarged conical tubercles centred mainly above 4th and 5th digits; dorsal surface of toes without enlarged spinose tubercles (Fig. 10A). **Original tail,** unknown. **Regenerated tail** approximately 52% SVL when fully regenerated; depressed, broad and strongly leaf-like, contracted at base with short attenuated tip; slight tapering and folding of lateral flange anteriorly; covered with uniform granules and minute, spinose lateral tubercles.

Colour pattern In spirit, head body and limbs finely marbled with grey and mid to dark brown blotches; a narrow brown vertebral stripe (edged with dark brown), broken by 6–7 obscure (brown or greyish) cross-bands between fore and hind limbs. Some individuals are more heavily pigmented, and hence, much darker in overall appearance. Head with an obscure, deep V-shaped marking between eyes (Fig. 7A) and obscure, ragged cross-bands on snout; labials pale, but broken by dark brown blotches. Limbs with obscure, broken bands; digits clearly banded with dark brown and grey.

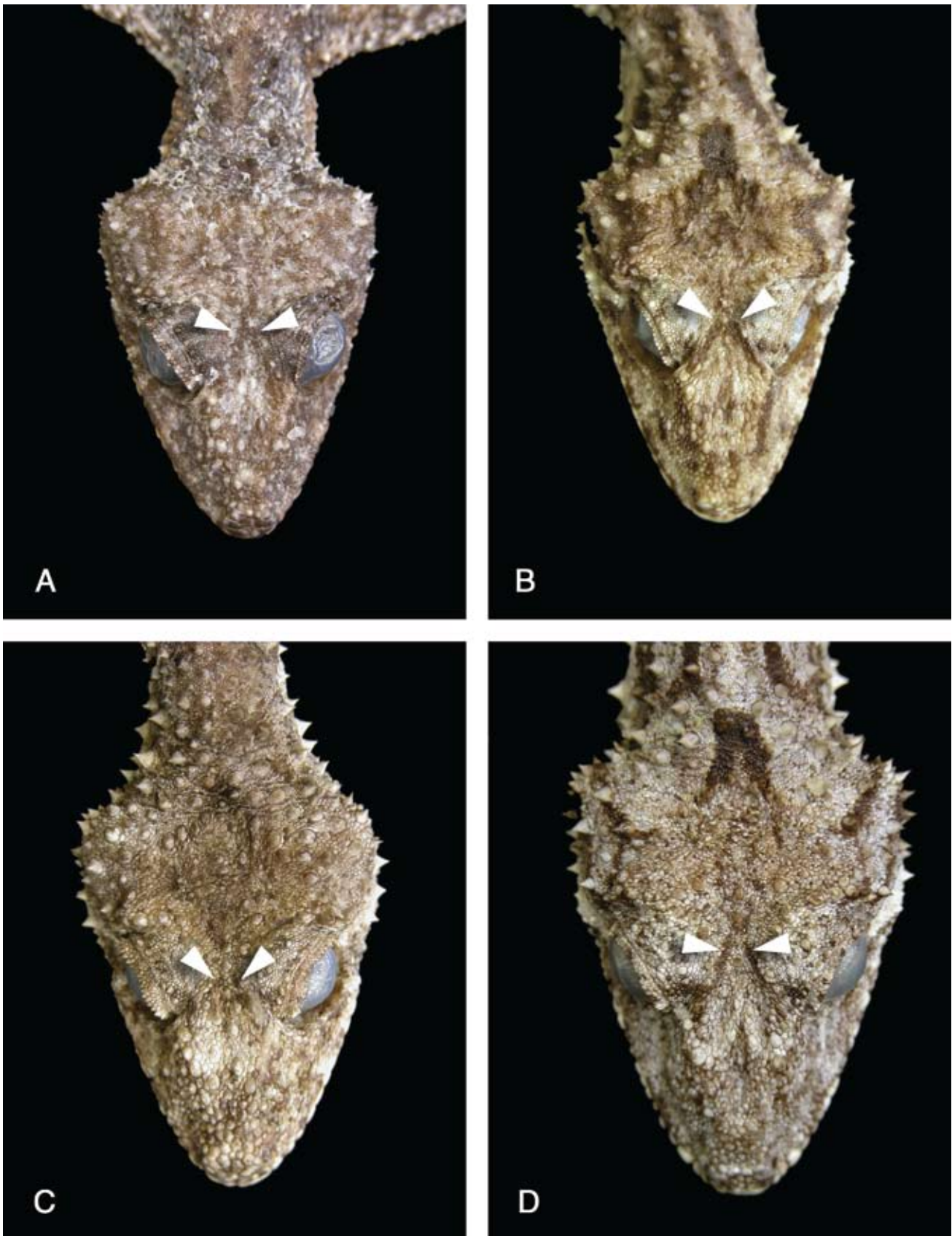


Fig. 7. V-shaped pattern between eyes in (A) *Saltuarius kateae* n.sp. AM R164166; (B) *S. moritzi* n.sp. AM R160420; (C) *S. moritzi* n.sp. AM R158990; (D) *S. swaini* QM J51640; (E, facing page) *S. wyberba* QM J28648.



Fig. 7 (continued). V-shaped pattern between eyes in *S. wyberba* QM J28648.

Venter cream to pale grey, heavily peppered with brown. Regenerated tail greyish with heavy mottling (mid to dark brown) above; ventral surface similar, but with reduced pigmentation.

Measurements and scale counts of holotype. AM R164163 (female) SVL = 100.3 mm, T(regrown) = 52.4 mm, HL = 26.9 mm, HW = 21.1 mm, HD = 8.6 mm, S = 12.3 mm, EE = 8.4 mm, NL = 19.8 mm, L1 = 45.0 mm, L2 = 56.3 mm, AG = 47.0 mm, Lamellae 4th finger 20, Lamellae 4th toe 24, supralabials 15, infralabials 12, scales contacting posterior edge of mental 4.

Genetics. *Saltuarius kateae* n.sp. differs in cytochrome *b* sequences from other members of the “*S. swaini*” lineage at 11.34–14.23% of sites (Table 1). It differs from its northern congeners *S. cornutus* and *S. salebrosus* at 23.10% and 19.03% of sites respectively. No intraspecific sequence divergence was recorded within the Wyans Creek sample.

Distribution. Narrowly restricted between latitudes 29°08'S and 29°13'S in northern NSW. The two known collection sites (Wyans Creek Road and Mt Marsh) lie on the eastern side of the Clarence River at the extreme southern end of the Richmond Range and are approximately 10 km apart (Fig. 11).

Geology. The distribution of *S. kateae* n.sp. is restricted to the southern portion of the Clarence-Moreton Basin on

continental sandstone (Kangaroo Creek Sandstones) of Cretaceous–Jurassic age.

Habitat. Associated with sandstone escarpments in open forest (blackbutt/bloodwood) communities.

Comparison with other species. *Saltuarius kateae* n.sp. is readily distinguished from *S. cornutus* and *S. salebrosus* in lacking preanal pores in both sexes (*vs* present in males). It is further separated from *S. cornutus* by its lower flank tubercles which are not hooked and lack smaller basal spines (*vs* tubercles hooked and surrounded by smaller spines) and from *S. salebrosus* by having a smooth throat (*vs* throat strongly tuberculate). It is most similar to *S. moritzi* n.sp., *S. swaini* and *S. wyberba*. From these it is separated by the rostral / nostril contact (rostral usually excluded from nostril (Fig. 8A) *vs* rostral and nostril usually in contact (Fig. 8B), rarely excluded) and the absence of spinose tubercles from the dorsal surface of all digits (Fig. 10A; *vs* spinose tubercles rarely absent from all digits, Fig. 10B). It is further distinguished from *S. swaini* by max SVL (105.4 mm *vs* 134.0 mm), from *S. moritzi* n.sp. by its darker pigmentation (and associated reduction in the extent of dorsal cross-bands between fore and hind limbs) and from *S. wyberba* by its greater head depth (39–44% head width, *n* = 7, mean = 41.7, SD = 1.71 *vs* 36–42% head width, *n* = 35, mean = 39.3, SD = 1.65).

Remarks. The Clarence River isolates *S. kateae* n.sp. from populations of *S. moritzi* n.sp. to the south and *S. wyberba* to the west. Like *S. kateae* n.sp., *S. swaini* occurs in the Richmond Range, to the east of the Clarence River. However, there is clear habitat separation between the two species.

Saltuarius moritzi n.sp.

Figs 12A–C

Material examined. HOLOTYPE, AM R158990 Comboyne Plateau, Boorgana NR (31°36'56"S 152°24'53"E) NSW. PARATYPES: QM J56894 Evans Rd, Salisbury, Brisbane (found on warehouse wall; said to have arrived in truck-load of ferns from NSW); AM R141964 Chaelundi SF (30°01'07"S 152°30'02"E) NSW; QM J83590–91, AM R158973–74, AM R158977–78, AM R160421 Sherwood NR, near Glenreagh (30°02'10"S 153°00'26"E) NSW; AM R141965 Chaelundi SF, Sundew Lookout (30°03'04"S 152°21'36"E) NSW; AM R153478 Sherwood NR, ridgeline N of Ewens Gap (30°05'52"S 153°01'12"E) NSW; AM R123490 Tallawudjah Ck (30°08'S 152°58'E) NSW; AM R158945–46, QM J83592, AM R160420 Bruxner Park, near Coffs Harbour (30°14'30"S 153°05'36"E) NSW; AM R164146 Coffs Harbour area, 1.9 km towards lookout from intersection of Bruxner Park Rd (30°15'54"S 153°06'41"E) NSW; AM R69866–67, AM R81921, Coffs Harbour (30°18'S 153°08'E) NSW; AM R43875 Dorrigo (30°20'S 152°43'E) NSW; QM J83593, AM R163003, AM R163005 Ebor Falls (30°24'19"S 152°20'20"E) NSW; AM R54071, AM R106749, AM R97670–72 Bellinger River N arm, near Brinerville (30°28'20"S 152°32'37"E) NSW; AM R16905, AM R16989, AM R17008 New England NP, Point Lookout, near Armidale (30°29'S 152°25'E) NSW; AM R43871–73 New England NP, at Point Lookout (30°30'18"S

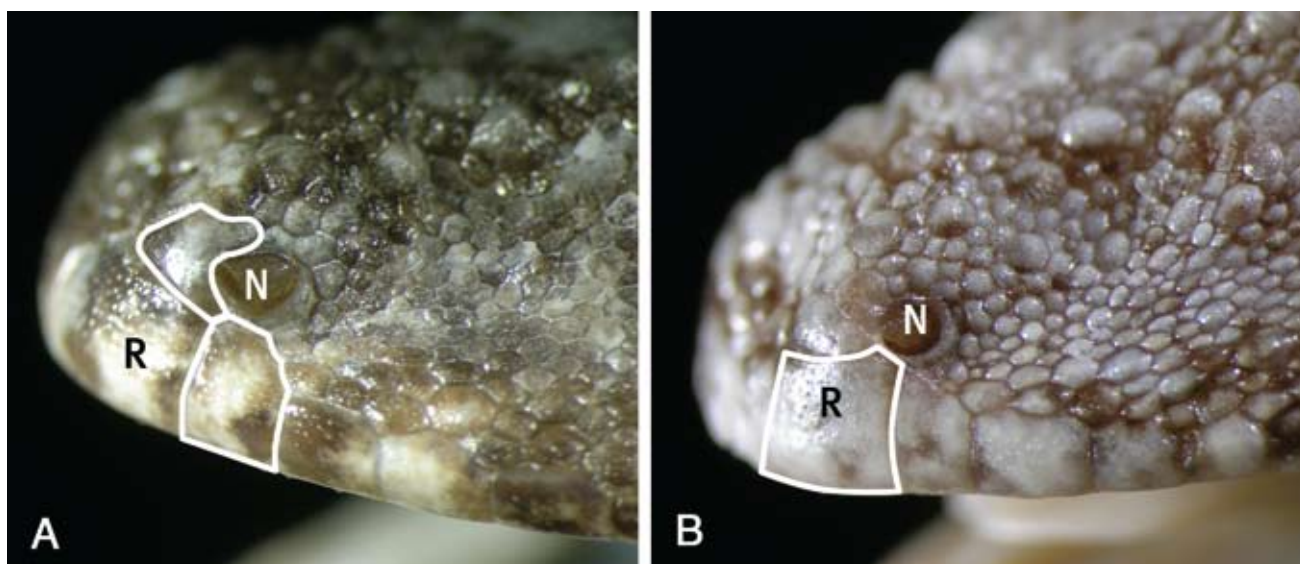


Fig. 8. (A) Rostral scale excluded from nostril, *Saltuarius kateae* n.sp. QM J83583; (B) rostral scale contacts nostril, *S. swaini* QM J51637. Condition (B) also applies for *S. moritzi* n.sp. and *S. wyberba*.

152°23'00"E) NSW; QM J83588–89, AM R163006, AM R163009–10, AM R163012 Blue Hole, SE Armidale on upper reaches of Gara River (30°36'00"S 151°48'09"E) NSW; AM R143590 Gara River—first falls downstream of Blue Hole (30°36'03"S 151°48'13"E) NSW; AM R6792 Purgatory Creek, Taylors Arm, Nambucca River (30°40'S 152°57'E) NSW; AM R6284 Gurravambi, Nambucca River, near Macksville (30°44'S 152°59'E) NSW; AM R103031 Wonders Hill Homestead, 4.5 km N (31°16'S 152°19'E) NSW; AM R71372–73 Lorne SF, Comboyne Peak (31°35'S 152°33'E) NSW; AM R6247 Bulga Tableland, near Bobin, Manning River (31°37'S 152°15'E) NSW; AM R6915 Bulgong, near Wingham (31°37'S 152°18'E) NSW; AM R151753 Kerewong State Forest, 300 m upslope McLeods Ck crossing, McLeods Creek Rd (31°38'10"S 152°32'44"E) NSW; AM R59314 5 km W of Hwy on Middle Brother Mtn (31°41'S 152°42'E) NSW; AM R59313 Middle Brother SF, Bird Tree area (31°41'S 152°42'E) NSW; AM R43874 Lansdowne, Manning River (31°47'39"S 152°32'00"E) NSW; AM R8253 Wallis Lake, Tuncurry (32°17'S 152°29'E) NSW; AM R101338 O'Sullivan's Gap Forestry Reserve, NE of Bulahdelah (32°20'S 152°16'E) NSW; AM R163000–02 O'Sullivan's Gap, c. 10 km N Bulahdelah on Old Pacific Hwy (32°20'38"S 152°15'35"E) NSW; QM J9054 Bulahdelah, 96 km NE Newcastle (32°25'S 152°12'E) NSW; AM R15412 Girvan via Stroud (32°29'S 152°02'E) NSW; AM R143591 Nerong SF, Nerong Rd, 1.2 km N from Boundary Rd (32°31'38"S 152°09'12"E) NSW.

Additional material examined. AM R141966 Grange SF (29°27'03"S 152°23'06"E) NSW; AM R150911–12 Giro SF, Mountain Creek Trail, Qbx Rd (31°43'23"S 151°52'26"E) NSW.

Etymology. For Professor Craig Moritz (University of California at Berkeley) for his contributions to the molecular phylogenetics of Australian rainforest reptiles.

Diagnosis. A medium-sized *Saltuarius* (maximum SVL 109 mm) with smooth throat scales, no preanal pores (in either sex) and often with a prominent, narrow V-shaped marking

running back between the eyes (Fig. 7B). It is distinguished from its congeners by the following suite of characters: rostral shield usually contacts nostril (Fig. 8B); dorsal surface of toes usually with large spinose tubercles (Fig. 10B); scales on snout usually grade evenly from small to large (in dorsal–ventral transect, Fig. 9A), not intermixed with larger granules above the supralabials (Fig. 9B); two narrow pale bands are usually continuous across the flared portion of the original tail (Fig. 13A); enlarged dorsal and lateral tubercles do not extend to tail tip (Fig. 13A); dark markings on head generally not strongly contrasting with base colour.

Description

SVL (mm): 38.3–109.3 ($n = 62$, mean = 85.5, SD = 20.20). Proportions as % SVL: T = 63.0–76.0 ($n = 17$, mean = 68.9, SD = 3.53); TT = 23.9–31.6 ($n = 17$, mean = 27.9, SD = 2.19); HL = 25.4–29.8 ($n = 49$, mean = 26.9, SD = 0.83); HW = 19.9–24.2 ($n = 49$, mean = 21.2, SD = 0.78); S = 11.4–14.1 ($n = 49$, mean = 12.2, SD = 0.49); EE = 7.4–10.3 ($n = 49$, mean = 8.5, SD = 0.61); NL = 15.8–23.0 ($n = 49$, mean = 19.4, SD = 1.48); AG = 39.9–50.1 ($n = 49$, mean = 45.1, SD = 2.12); L1 = 41.5–51.6 ($n = 49$, mean = 47.4, SD = 2.26); L2 = 52.0–62.4 ($n = 49$, mean = 57.7, SD = 2.24). **Head.** Large, depressed, triangular, distinct from neck; head depth 37.3–49.1% head width ($n = 62$, mean = 42.4, SD = 2.66); covered in small granules which are intermixed with larger conical tubercles; skin of head co-ossified with skull; rostral shield fully divided by deep, vertical groove ($n = 57$), not divided ($n = 1$), only half divided ($n = 2$) or divided into three ($n = 1$); rostral shield contacting nostril ($n = 58$), narrowly excluded from nostril ($n = 1$) or narrowly excluded from nostril on one side only ($n = 3$); scales contacting posterior margin of mental shield 1–7 ($n = 61$, mode = 4, mean = 4.9, SD = 1.15); ear opening elliptical, vertical, much less than half as large as eye; supralabials 10–18 ($n = 61$, mode = 13, mean = 13.5, SD = 1.35); scales on snout usually grade evenly from small to large (in dorsal–ventral transect, Fig. 9A), not intermixed with larger granules above the supralabials (Fig. 9B); infralabials 9–14 ($n = 62$, mode = 12, mean =

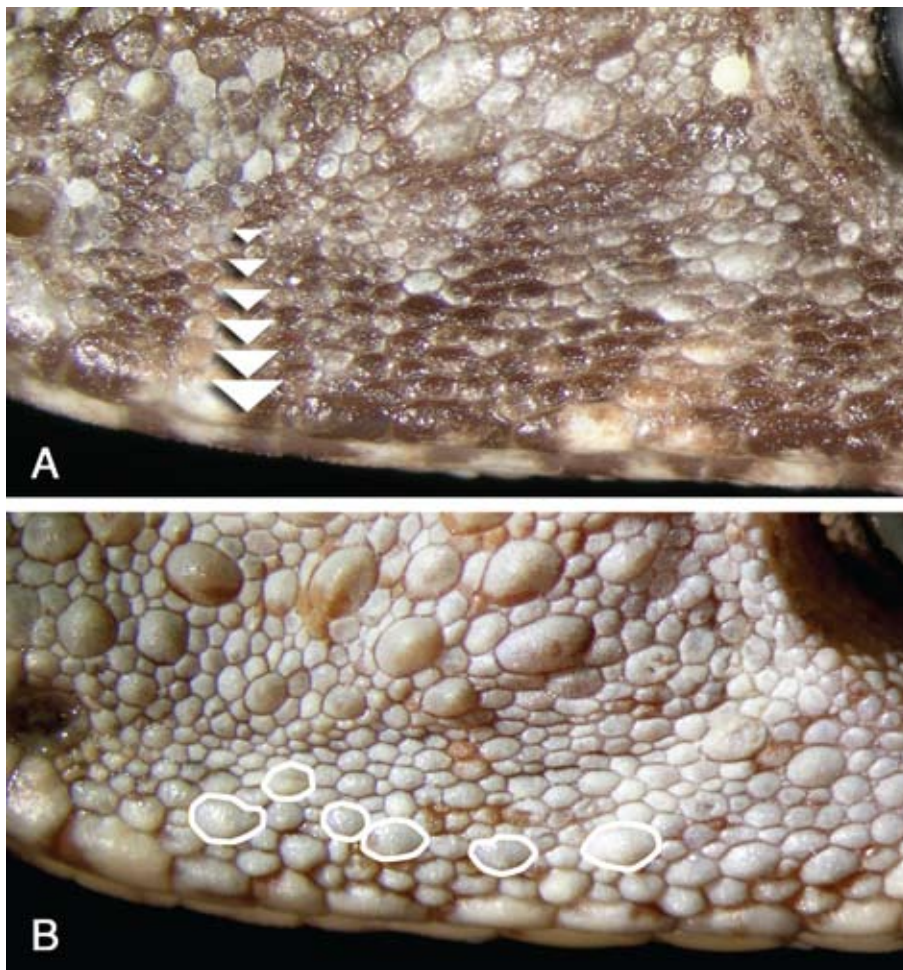


Fig. 9. Scales on snout. (A) grade evenly from large to small (moving up from supralabial row), *Saltuarius kateae* n.sp. AM R164163; (B) heterogeneous, small and large scales intermixed, *S. swaini* QM J8359. Condition (A) also applies for *S. moritzi* n.sp. and *S. wyberba*.

11.9, SD = 1.20). **Neck.** Broad. **Body.** Moderate, depressed, covered in small granules; dorsal granules intermixed with larger conical tubercles; tubercles small to moderate on back and flanks, moderate to pronounced on sides of neck; basal scales surrounding upper flank and back tubercles not, or slightly, larger than adjacent granules; ventral scales enlarged in pelvic region. Preanal pores absent. Axilla slightly to moderately invaginated. **Limbs.** Long, covered in small to moderate pointed tubercles dorsally; lacking enlarged tubercles on ventral surfaces, although some specimens have enlarged granules on the anterior edge of the upper forelimb; digits strongly compressed distally; subdigital lamellae (fourth finger) 17–23 ($n = 60$, mode = 19, mean = 19.6, SD = 1.43); dorsal surface of hand with (83%) or without (17%) enlarged conical tubercles; dorsal surface of fingers, at least some, with (57%) or without (43%) enlarged spinose scales; subdigital lamellae (fourth toe) 19–26 ($n = 62$, mode = 24, mean = 22.6, SD = 1.75); dorsal surface of foot with enlarged conical tubercles; dorsal surface of toes, at least some, with enlarged spinose tubercles (Fig. 10B). **Original tail.** Depressed, broad, contracted at base and attenuated at tip; flared portion with undulating flange bearing sharply pointed tubercles along margin; dorsal surface of tail, except vertebral region of flared portion, covered with large conical tubercles; tail tip slender and free of tubercles (Fig. 13A); number of rows of enlarged spinose tubercles

across flared portion of tail 4–7 ($n = 27$, mode = 6, mean = 5.4, SD = 0.89); number of rows of spinose tubercles across attenuated portion 4–6 ($n = 26$, mode = 4, mean = 4.3, SD = 0.60); attenuated tip accounts for 29.1–47.3% tail length ($n = 28$, mean = 39.3, SD = 3.63); ventral surface smooth with a slight depression along midline. **Regenerated tail.** approximately 61%SVL when fully regenerated; depressed, broad and strongly leaf-like, contracted at base with short attenuated tip; slight tapering and folding of lateral flange anteriorly; covered with uniform granules and minute, spinose lateral tubercles.

Pattern. In spirit, head body and limbs finely marbled with grey and mid to dark brown blotches; a narrow brown or tan vertebral stripe (edged with dark brown), broken by 3–6 obscure to bold (brown or greyish) cross-bands between fore and hind limbs (bands are often edged with dark brown along the anterior edge). Pattern extremely variable (AM R160420 from Bruxner Park greyish with a dark netted pattern on dorsum; AM R101338 from O’Sullivan’s Gap dark brown with a paler vertebral stripe and indistinct vertebral blotches). Head usually with deep V-shaped marking back between eyes (Fig. 7B), but this character is variable and the marking may be indistinct and not penetrate deeply between the eyes (Fig. 7C). Snout with obscure, ragged cross-bands; labials pale, but broken by dark brown blotches. Limbs with obscure, broken

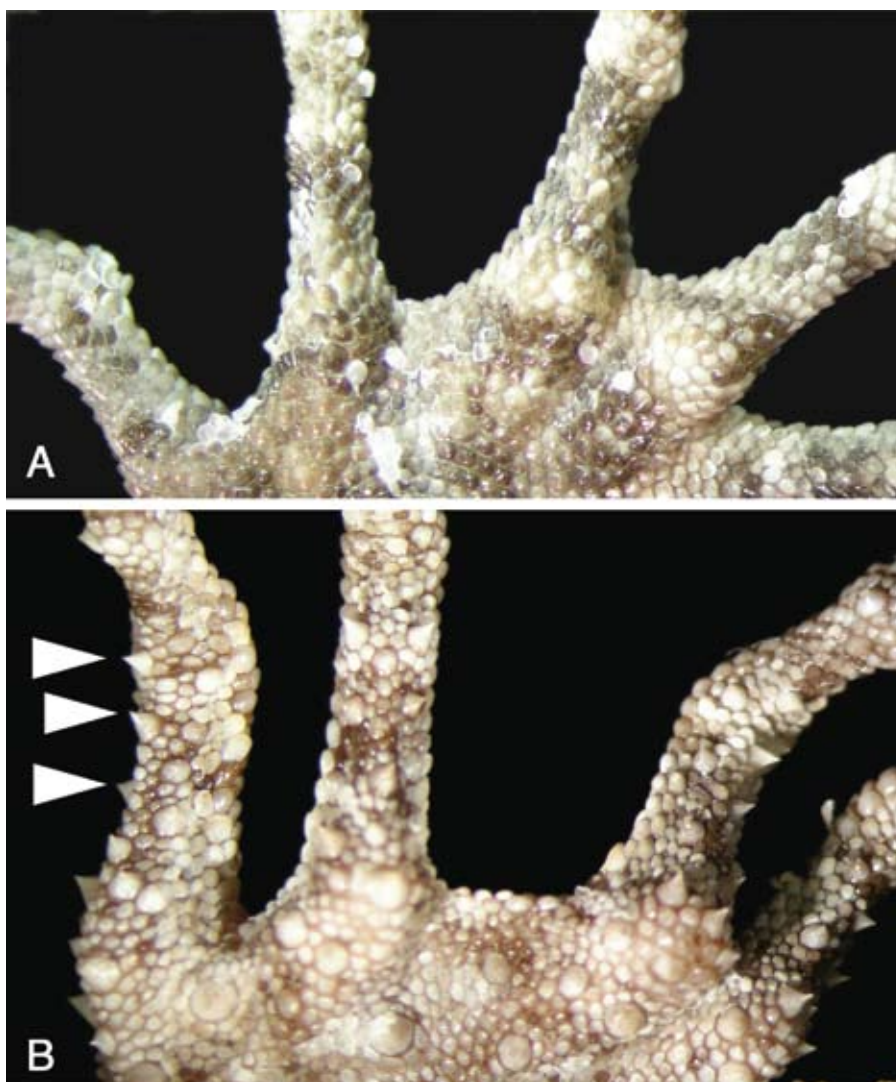


Fig. 10. Dorsal surface of toes. (A) Without enlarged spinose tubercles, *Saltuarius kateae* n.sp. AM R164161; (B) with enlarged spinose tubercles, *S. swaini* QM J54846. Condition (B) also applies for *S. moritzi* n.sp. and *S. wyberba*.

bands; digits banded with dark brown and grey (less visible in darker specimens). Venter cream to pale grey, heavily peppered with fine brown specks. Original tail with irregular pale cross bands (usually 4), these extend to the ventral surface on the attenuated tip. Regenerated tail greyish with dark marbling (mid to dark brown or black) above; ventral surface similar, but may have reduced pigmentation.

Measurements and scale counts of holotype. AM R158990 (male) SVL = 109.3 mm, T = 75.8 mm, TT = 30.0 mm, HL = 28.6 mm, HW = 21.8 mm, HD = 8.7 mm, S = 13.5 mm, EE = 8.1 mm, NL = 21.6 mm, L1 = 52.3 mm, L2 = 62.8 mm, AG = 51.0 mm, Lamellae 4th finger 20, Lamellae 4th toe 22, supralabials 12, infralabials 13, scales contacting posterior edge of mental 4.

Genetics. *Saltuarius moritzi* n.sp. differs in cytochrome *b* sequences from other members of the “*S. swaini*” lineage at 10.59–13.01% of sites (Table 1). It differs from its northern congeners *S. cornutus* and *S. salebrosus* at 22.19% and 18.45% of sites respectively. Average intraspecific sequence divergence is 4.69% (Table 1).

Distribution. Widespread south of the Clarence River between latitudes 29°50'S and 32°32'S. Its distribution extends from coastal areas west through the gorge systems of the New England Tableland (Fig. 11).

Geology. *Saltuarius moritzi* n.sp. occurs in the New England Block, a complex mosaic of Tertiary basalts, intrusive granites and rocks of Silurian, Carboniferous and Permian age. These include sediments of both continental and marine origins.

Habitat. Wet sclerophyll forests, on the trunks of Flooded Gums and the bases of hollow, dead trees, at Coffs Harbour and O'Sullivan's Gap (near Bulahdelah); in closed forests on the bases of emergent *Tristania* sp. at Boorgana Nature Reserve (Comboyne Plateau) and on rock (outcrops, escarpments and gorges) at Sherwood Nature Reserve (Fig. 14A, near Glenreagh), Ebor Falls (Fig. 14B) and Blue Hole (near Armidale).

Comparison with other species. *Saltuarius moritzi* n.sp. is readily distinguished from *S. cornutus* and *S. salebrosus*

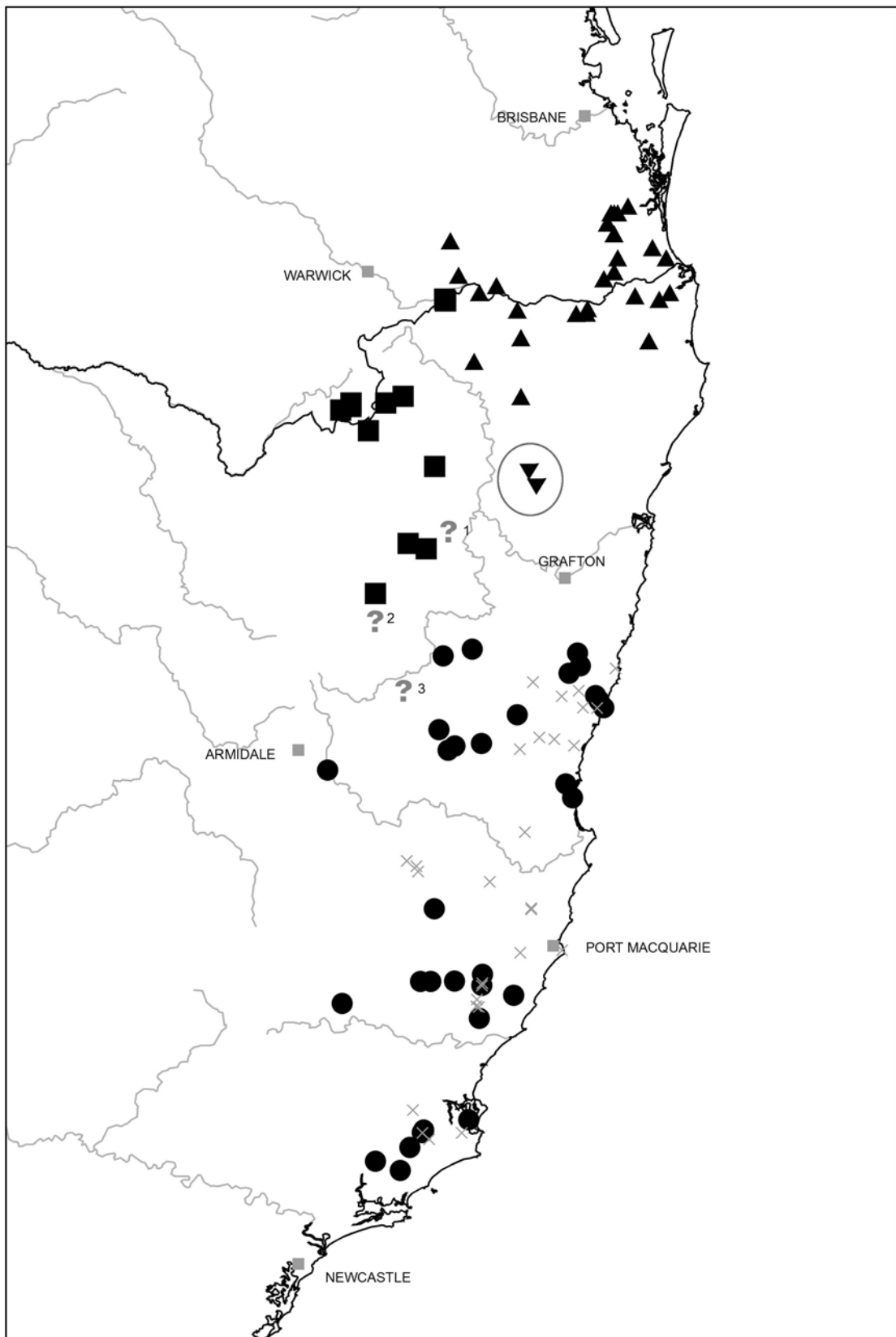


Fig. 11. Distribution for “*Saltuarius swaini*” lineage in southeastern Queensland and northeastern New South Wales. ▲ = *S. swaini*; ▼ = *S. kateae* n.sp.; ■ = *S. wyberba*; ● = *S. moritzi* n.sp.; × = *Saltuarius* records, presumably *S. moritzi* n.sp., from the NSW National Parks and Wildlife Service database; ?1, ?2, ?3 = QM J72343, AM R143592 and AM R43870 respectively—see *Results* and *Future directions* for further discussion. The species’ symbols correspond with those used in Figs 2–4.



Fig. 12. Variation of colour and pattern in *Saltuarius moritzi* n.sp. (A) AM R160420, Bruxner Park, near Coffs Harbour ($30^{\circ}14'30''\text{S}$ $153^{\circ}05'36''\text{E}$) NSW (photograph—Jeff Wright, QM); (B) Ebor Falls ($30^{\circ}24'19''\text{S}$ $152^{\circ}20'20''\text{E}$) NSW (photograph—Glenn Shea); (C) QM J83588, Blue Hole, SE Armidale on upper reaches of Gara River ($30^{\circ}36'00''\text{S}$ $151^{\circ}48'09''\text{E}$) NSW (photograph—Ross Sadlier, AM).

in lacking preanal pores in both sexes (*vs* present in males). It is further distinguished from *S. cornutus* by its lower flank tubercles (tubercles not hooked and not surrounded by smaller spines *vs* tubercles hooked and surrounded by smaller spines) and from *S. salebrosus* by its throat scalation (throat smooth *vs* throat strongly tuberculate). It is most similar to *S. wyberba*. Colour pattern most readily distinguishes these species (Figs 12A,B,C and 15A,B), although both exhibit some variability. *Saltuarius moritzi* n.sp. usually has two clearly defined, narrow, pale bands across the flared portion of the original tail and these are continuous through the vertebral region (Fig. 13A; *vs* anterior band may be obscure, often centred on enlarged tubercles and usually discontinuous through vertebral region, Fig. 13B); the dark bands across the snout and other dark head markings are not usually sharply contrasted with the base colour (*vs* dark head markings often in sharp contrast with base colour) and the V-shaped marking between the eyes is usually narrow and deep (Fig. 7B; *vs* usually wide and shallow, Fig. 7E). *Saltuarius moritzi* n.sp. also tends to be deeper headed than *S. wyberba* (mean HD = 42% HW *vs* 39% HW). It is distinguished from *S. swaini* in having narrow pale bands across the flared portion of the original tail (*vs* broad cream/grey zones, Fig. 13C); by its smaller size (max SVL = 109 mm *vs* 134 mm) and by the arrangement of the snout scales (grade evenly from small to large in dorsal–ventral transect, Fig. 9A *vs* intermixed with larger granules above the supralabials, Fig. 9B). From *S. kateae* n.sp. it is readily distinguished by the rostral/nostri contact (rostral usually in contact with nostril, Fig. 8B *vs* rostral usually excluded from nostril, Fig. 8A) and by the spinosity of the digits (dorsal surface of digits with spinose tubercles, Fig. 10B *vs* spinose tubercles absent, Fig. 10A).

Remarks. Specimen AM R158990 was selected as the holotype of *S. moritzi* n.sp. despite it lying on the morphological boundary of *S. swaini* in the discriminant functions analyses (Fig. 4). This specimen comes from a genetically typed population. It is geographically and genetically remote from *S. swaini*, is well-preserved, adult-sized, possesses an original tail, and displays pattern details characteristic of *S. moritzi* n.sp.

The specimens listed as “additional material examined” are problematic and hence they are excluded from the type series and their morphometrics have been excluded from this species account. Specimen AM R141966 from Grange State Forest (29°27'03"S 152°23'06"E) is excluded (despite its genetic assignment to *S. moritzi* n.sp.—see phylogeny, Fig. 1) for a number of reasons. Firstly, the co-ordinates provided by the collector (see above) do not correspond closely with those of Grange SF (29°28'S 152°34'E, Anon., 1975) and place the specimen geographically between the Mt Spirabo and Gibraltar Range *S. wyberba* populations. Secondly, AM R141966 was processed (tissues sample, specimen fixed and registered) in the same series as AM R141964 from Chaelundi State Forest (30°01'07"S 152°30'02"E). It shows no genetic divergence from this specimen despite a geographic separation of 60 kms or more. Leaf-tail geckos are known to occur at Chaelundi SF (see Couper *et al.*, 1997) and the possibility that both specimens originated from this site cannot be overlooked. Verification of the presence of leaf-tailed geckos in Grange SF and their genetic similarity to Chaelundi populations requires additional survey effort.

Specimens QM J72343 (Blady Grass Ck, approx 1 km upstream of junction with Henry River, SE of Glen Innes (29°50'49"S 152°00'08"E) NSW; Fig. 11: ?1), AM R143592 (Oakwood SF, Oakwood Fire Trail, at Willys Ck (29°52'58"S 152°01'54"E) NSW; Fig. 11: ?2) and AM R43870 (Guyra, 22 miles E (30°13'03"S 152°10'05"E) NSW; Fig. 11: ?3) are excluded (despite the genetic assignment of one, QM J72343 to *S. moritzi* n.sp.) because they were identified as *S. wyberba* in the discriminant analysis (see “future directions” in discussion). Specimens AM R150911–12 come from Giro SF, a region not genetically studied. One of these, AM R150912 was identified as *S. swaini* by the discriminant analysis. Giro SF is well within the known range of *S. moritzi* n.sp. and both specimens are consistent with this species in colour pattern and the arrangement of the snout scales above the anterior supralabials.

Saltuarius swaini (Wells & Wellington, 1985), revised description

Fig. 16

Material examined. QM J12257 Tamborine (27°53'S 153°15'E) SEQ; QM J398, QM J2409, QM J2933–34, QM J3254, QM J4439, QM J8183, QM J8359, QM J8861, QM J10440 Mt Tamborine (27°55'S 153°10'E) SEQ; QM J51095 Mt Tamborine (27°55'S 153°11'E) SEQ; QM J4819 Tamborine Mtn, Eagle Hts (27°55'S 153°12'E) SEQ; QM J148 Canungra Ck (27°58'S 153°09'E) SEQ; QM J3215 Canungra (28°01'S 153°11'E) SEQ; QM J80792, Mt Mitchell, Cunninghams Gap, Main Range NP (28°03'06"S 152°23'38"E) SEQ; QM J80793, QM J81611, Mt Cordeaux, Cunninghams Gap, Main Range NP (28°03'06"S 152°23'38"E) SEQ; QM J4198, QM J5690 Mudgeeraba (28°05'S 153°22'E) SEQ; QM J5649 Flying Fox Valley, Beechmont (28°08'S 153°12'E) SEQ; QM J3313 Tallebudgera (28°08'S 153°26'E) SEQ; QM J8646 Lamington NP, Binna Burra (28°12'S 153°11'E) SEQ; QM J5382 Lamington NP (28°12'S 153°05'E) SEQ; QM J51094 Mt Superbus SF, via Warwick (28°13'S 152°28'E) SEQ; AM R97823 Mt Superbus (28°13'S 152°26'E) SEQ; QM J51637–40 Lamington NP, O'Reillys (28°14'S 153°08'E) SEQ; QM J23937 near Mt Ballow (28°16'S 152°37'E) SEQ; QM J8074, QM J8099 Mt Clunie, Boonah (28°18'S 152°32'E) NSW; QM J1143 Tweed River (28°18'S 153°27'E) NSW; QM J5757 Chillingham, Murwillumbah (28°19'S 153°17'E) NSW; AM R2409 Murwillumbah, Tweed River (28°20'S 153°24'E) NSW; AM R158987 Border Ranges NP, vicinity of Brindle Ck rest area (28°22'37"S 153°03'14"E) NSW; QM J10565 Mt Lindesay (28°23'S 152°43'E) SEQ; QM J54846 Brays Ck, Border Ranges NP (28°24'S 153°03'E) NSW; AM R98333, QM J83594, AM R160423 Mt Warning NP (28°24'05"S 153°16'54"E) NSW; AM R116978 (holotype) Richmond Range SF (28°31'S 152°44'E) NSW; AM R11860 Huonbrook (28°32'S 153°21'E) NSW; AM R92122 6 km NW of Amiens (28°34'S 151°46'E) SEQ; AM R130911 Yabba SF (28°37'57"S 152°30'32"E) NSW; AM R158999 Cambridge Plateau NP, Richmond Range (28°48'S 152°44'E) NSW.

Diagnosis. A large, slender-bodied *Saltuarius* (maximum SVL 134 mm) with smooth throat scales, no preanal pores (in either sex) and a prominent, narrow V-shaped marking



Fig. 13. Spinosity of tail tip and intensity of tail bands in *Saltuarius* spp. (A) Tail tip free of spinose tubercles; pale cross bands continuous on vertebral region, *S. moritzi* n.sp. AM R158990. (B) Tail tip free of spinose tubercles; anterior cross band obscure, centred on enlarged tubercles and usually discontinuous through vertebral region, *S. wyberba* QM J28649. (C) Tail with spinose tubercles extending to tip; broad cream/grey zones on anterior flared portion, *S. swaini* QM J54846.

larger granules above the supralabials (Fig. 9B); spinose tubercles on dorsal surfaces of hands, feet and digits (Fig. 10B); a high tubercule count across flared portion of original tail (mode = 10, mean = 9.42, SD = 1.74); original tail with broad cream/grey zones, as opposed to narrow pale cross bands (Fig. 13C); enlarged dorsal and lateral tubercles extend to tail tip (Fig. 13C).

Re-description

SVL (mm): 45.1–134.0 (n = 46, mean = 105.8, SD = 24.49). Proportions as % SVL: T = 59.2–72.4 (n = 16, mean = 66.9, SD = 4.11); TT = 24.4–33.6 (n = 16, mean = 27.4, SD = 2.85) HL = 25.2–28.5 (n = 40, mean = 26.2, SD = 0.64); HW = 18.7–22.0 (n = 40, mean = 20.4, SD = 0.80); S = 10.1–13.5 (n = 40, mean = 12.2, SD = 0.48); EE = 7.4–9.4 (n = 40, mean = 8.3, SD = 0.46); NL = 14.5–22.4 (n = 40, mean = 18.6, SD = 1.73); AG = 41.3–51.3 (n = 39, mean = 46.2, SD = 2.30); L1 = 44.0–51.1 (n = 36, mean = 48.2, SD = 1.60); L2 = 53.2–62.3 (n = 36, mean = 58.7, SD = 2.24).

Head. Large, depressed, triangular, distinct from neck; head depth 39.6–51.0% head width (n = 46, mean = 43.9, SD = 2.68); covered in small granules which are intermixed with

running back deeply between the eyes (Fig. 7D). It is distinguished from its congeners by the following combined characters: rostral shield usually in contact with nostril (Fig. 8B); scales on snout do not usually grade evenly from small to large (in dorsal–ventral transect), but are intermixed with

Fig. 14. Rock habitats of *Saltuarius moritzi* n.sp. at (A) Sherwood Nature Reserve (30°02'10"S 153°00'26"E): (B) Ebor Falls (30°24'19"S 152°20'20"E). (Photographs—R. Sadlier, AM).



larger conical tubercles; skin of head co-ossified with skull; rostral shield fully divided by deep, vertical groove ($n = 46$), or divided into three ($n = 2$); rostral shield contacting nostril (Fig. 8B); scales contacting posterior margin of mental shield 3–8 ($n = 45$, mode = 6, mean = 5.4, SD = 1.14); ear opening elliptical, vertical, much less than half as large as eye; supralabials 12–18 ($n = 46$, mode = 14, mean = 14.9, SD = 1.53); scale rows on the snout, immediately above the anterior supralabials, do not grade evenly from large to small, but are intermixed with larger scales (Fig. 9B) in 84.8% of specimens, condition ambiguous in 15.2% of specimens; infralabials 9–16 ($n = 46$, mode = 12, mean = 12.8, SD = 1.45). *Neck*. Broad. *Body*. Moderate, depressed, covered in small granules; dorsal granules intermixed with larger conical tubercles; tubercles moderate to large on body and neck; basal scales surrounding upper flank and back tubercles noticeably larger than adjacent granules; ventral scales enlarged in pectoral and pelvic regions. Preanal pores absent. Axilla slightly to moderately invaginated. *Limbs*. Long, covered in moderate pointed tubercles dorsally; lacking enlarged tubercles on ventral surfaces, although some specimens have enlarged granules on the anterior edge of the upper forelimb; digits strongly compressed distally; subdigital lamellae (fourth finger) 18–26 ($n = 46$, mode = 22, mean = 21.5, SD = 1.64); dorsal surface of hand and fingers with enlarged conical tubercles; subdigital lamellae (fourth toe) 20–28 ($n = 46$, mode = 23, mean = 24.0, SD = 1.71); dorsal surface of foot and toes with enlarged conical tubercles (Fig. 10B). *Original tail*. Depressed, broad, contracted at base and attenuated at tip; flared portion with undulating flange bearing sharply pointed tubercles along margin; dorsal surface of tail, except vertebral region of flared portion, covered with large conical tubercles; tail tip slender, with sharp tubercles extending almost to tip (Fig. 13C); number of rows of enlarged spinose tubercles across flared portion of tail 6–13 ($n = 19$, mode = 10, mean = 9.4, SD = 1.74); number of rows of spinose tubercles across attenuated portion of tail 5–10 ($n = 19$, mode = 6, mean = 6.4, SD = 1.16); attenuated tip accounts for 35.3–49.3% tail length ($n = 19$, mean = 40.6, SD = 3.41); ventral surface smooth with a slight depression along midline. *Regenerated*



tail. Approximately 55%SVL when fully regenerated; depressed, broad and strongly leaf-like, contracted at base with short attenuated tip; slight tapering and folding of lateral flange anteriorly; covered with uniform granules and minute, spinose lateral tubercles.

Pattern. The pattern description provided by Couper *et al.* (1993) for this species included specimens of *S. moritzi* n.sp. In spirit, head, body and limbs grey to mid-brown; a



Fig. 15. *Saltuarius wyberba* (A) Girraween NP (28°51'S 151°55'E) SEQ (photograph—Jeff Wright, QM); (B) AM R164152, Gibraltar Range NP, Gwydir Hwy, 4.2 km W rangers station (29°32'06"S 152°16'43"E) NSW (photograph—Ross Sadler, AM).

tan vertebral stripe (edged with dark brown), broken by 3–5 grey cross bands between fore and hind limbs. Head with pronounced, deep V-shaped marking running back between eyes (Fig. 7D) and obscure, ragged cross-bands sometimes present on snout; labials pale, broken by dark brown blotches. Limbs often with obscure broken bands; digits faintly banded. Venter cream to pale grey, marked by small clusters of brown scales (faint to heavy); some specimens with obscure dark barring beneath lower jaw, near angle of mouth. Original tail with grey to brown vertebral zone; dark “lichen-like” blotches on basal, medial and distal portions (broad cream/grey zones on anterior flared portion, Fig. 13C, as opposed to narrow pale cross bands, Fig. 13A,B); pale bands on tail tip obscure, extend to ventral surface. Regenerated tail grey to tan with darker brown marbling above; ventral surface with reduced pigmentation.

Measurements and scale counts of holotype. The measurements provided by Wells and Wellington (1985) vary slightly from those in the current study.

AM R116978 (female) SVL = 124.5 mm, T(regrown) = 57.3 mm, HL = 32.5 mm, HW = 25.6 mm, HD = 11.8 mm, S = 14.79 mm, EE = 10.7 mm, NL = 22.5 mm, L1 = 58.3 mm, L2 = 68.1 mm, AG = 62.8 mm, Lamellae 4th finger 21, Lamellae 4th toe 25, supralabials 15, infralabials 13, scales contacting posterior edge of mental 7.

Genetics. *Saltuarius swaini* differs in cytochrome *b* sequences from other members of the “*S. swaini*” lineage at 13.01–14.37% of sites (Table 1). It differs from its northern congeners *S. cornutus* and *S. salebrosus* at 22.65% and 19.38% of sites respectively. Average intraspecific sequence divergence is .73% (Table 1).



Fig. 16. AM R160423, *Saltuarius swaini*, Mt. Warning NP (28°24'05"S 153°16'54"E) NSW (photograph—Jeff Wright, QM).

Distribution. Occurs in the coastal ranges of southeast Queensland and northern NSW between latitudes 27°53'S–28°48'S. All NSW populations occur east of the Clarence River (Fig. 11).

Geology. The distribution of *S. swaini* lies within the Clarence-Moreton Basin centred on the Main Range, Focal Peak and Mt Warning-Tweed Volcanics and smaller outliers of these blocks. These formations are largely basalt of Miocene age.

Habitat. Subtropical rainforests, often in association with strangler figs and the buttressed roots of large trees.

Comparison with other species. *Saltuarius swaini* is readily distinguished from *S. cornutus* and *S. salebrosus* in lacking preanal pores in both sexes (*vs* present in males). It is further distinguished from *S. cornutus* by its lower flank tubercules (tubercules not hooked and not surrounded by smaller spines *vs* tubercules hooked and surrounded by smaller spines) and from *S. salebrosus* by its throat scalation (throat smooth *vs* throat strongly tuberculate). It is most similar to *S. moritzi* n.sp., *S. kateae* n.sp. and *S. wyberba*, but larger (max SVL = 134 mm *vs* 109 mm, 105 mm and 108 mm respectively). It is further separated by the scales on the snout (dorsal-ventral transect): intermixed with larger granules above the supralabials (Fig. 9B) *vs* even gradation from small to large

(Fig. 9A). *Saltuarius swaini* lacks the narrow pale bands that are present on the flared portion of the original tails of *S. moritzi* n.sp. and *S. wyberba* (original tail pattern could not be assessed for *S. kateae* n.sp.) and these appear as two broad cream/grey zones (Fig. 13C). From *S. kateae* n.sp., it is further separated by the rostral/nostril contact (rostral usually contacts nostril, Fig. 8B vs rostral usually excluded from nostril, Fig. 8A) and the spinosity of the digits (dorsal surface of digits with spinose tubercles, Fig. 10B vs tubercles absent, Fig. 10A).

Remarks. Specimen AM R92122 (listed in material examined) remains problematic. This animal was identified by Couper *et al.* (1994) as belonging to the “rainforest” colour form of *S. swaini* (= *S. swaini* sensu stricto) despite its close geographic proximity to “eucalypt-granite” populations that were later described as *S. wyberba* (Couper *et al.*, 1997). The discriminant analysis herein, further supports the identification of AM R92122 as *S. swaini*, but the locality for this specimen, “6 km NW Amiens” is not compatible with current knowledge of the habitat requirements and geological associations of this taxon. Consequently, this locality should be treated with caution.

Saltuarius wyberba Couper, Schneider & Covacevich, 1997, revised description

Fig. 15A,B

Material examined. QM J70465 Queen Mary Falls, top, near Killarney (28°20'S 152°22'E) SEQ; QM J80794 Queen Mary Falls NP (28°20'30"S 152°22'10"E) SEQ; QM J80795 Queen Mary Falls NP (28°20'29"S 152°22'14"E) SEQ; QM J80796 Queen Mary Falls NP (28°20'31"S 152°22'16"E) SEQ; AM R110510 1.5 km NW Amiens (28°34'S 141°46'E) SEQ; QM J35401 Boonoo Boonoo Falls, via Tenterfield (28°48'S 152°10'E) NSW; QM27349 near Girraween (28°50'S 151°55'E) SEQ; QM J25374 Girraween NP, via Stanthorpe (28°50'S 151°55'E) SEQ; QM J61539–45 Girraween NP, 1.5 km from Bald Rock camp ground (28°50'S 151°56'E) SEQ; QM J28648–49 Girraween area, near Wyberba (28°50'S 151°55'E) SEQ; QM J51633–36 Girraween NP, Natural Arch track (28°50'S 151°55'E) SEQ; QM J50345 Girraween NP (28°51'S 151°55'E) SEQ; QM J29116–17 Stanthorpe area, ?Girraween (28°50'S 151°55'E) SEQ; QM J51093 Girraween NP, edge, outside park (28°50'S 151°56'E) SEQ; QM J30677 Stanthorpe, Aztec Temples, near Underground River (28°50'S 152°05'E) SEQ; QM J54847 Bookookoorara, Boonoo SF (28°50'S 152°02'E) NSW; QM J30420 near Wyberba (28°52'S 151°52'E) SEQ; QM J68108 Basket Ck, S of Bald Mountain NP (28°58'S 152°00'E) NSW; AM R156806 Timbarra Plateau (29°08'17"S 152°19'09"E), NSW; AM R149768 Curramore SF, 6.1 km SE along Black Hole Trail, at Black Hole Ck (29°30'30"S 152°11'24"E) NSW; QM J83586–87, AM R164152–53, AM R164155, AM R164157 Gibraltar Range NP, Gwydir Hwy, 4.2 km W rangers station (29°32'06"S 152°16'43"E) NSW; QM J53984 Teapot Ck, Narrow Pass Fire Trail, Mann River NR (29°45'S 152°02'E) NSW; QM J79754–55, QM J79757–58 no data.

Diagnosis. A medium-sized *Saltuarius* (maximum SVL 108 mm) with smooth throat scales, no preanal pores in either sex

and usually a wide, shallow V-shaped marking between the eyes (Fig. 7E). It is distinguished from its congeners by the following suite of characters: rostral shield usually contacts nostril (Fig. 8B); dorsal surface of toes usually with large spinose tubercles (Fig. 10B); scales on snout usually grade evenly from small to large (in dorsal–ventral transect) (Fig. 9A), not intermixed with larger granules above the supralabials; two narrow pale bands across the flared portion of the original tail, anterior-most usually broken in vertebral region (Fig. 13B); enlarged dorsal and lateral tubercles usually do not extend to tail tip (Fig. 13B); dark markings on head usually strongly contrasting with base colour and mean HD < 40% HW.

Re-description

SVL (mm): 58.3–107.7 (n = 41, mean = 92.8, SD = 10.04). Proportions as % SVL: T = 62.3–80.7 (n = 14, mean = 71.2, SD = 4.32); TT = 20.7–36.8 (n = 14, mean = 29.0, SD = 4.07) HL = 24.7–29.3 (n = 36, mean = 27.3, SD = 0.97); HW = 19.8–23.9 (n = 36, mean = 22.1, SD = 0.95); S = 11.0–13.7 (n = 36, mean = 12.1, SD = 0.49); EE = 7.5–10.0 (n = 36, mean = 8.9, SD = 0.63); NL = 15.1–21.3 (n = 35, mean = 17.7, SD = 1.46); AG = 39.9–48.3 (n = 36, mean = 45.0, SD = 1.91); L1 = 44.0–50.9 (n = 35, mean = 47.2, SD = 1.92); L2 = 53.1–63.3 (n = 34, mean = 57.4, SD = 2.50).

Head. Large, depressed, triangular, distinct from neck; head depth 36.2–42.3% head width (n = 36, mean = 39.2, SD = 1.67); covered in small granules which are intermixed with larger conical tubercles; skin of head co-ossified with skull; rostral shield fully divided by deep, vertical groove (n = 38), only half divided (n = 1), divided into three (n = 1) or not divided (n = 1); rostral shield contacting nostril (Fig. 8B, n = 37), narrowly excluded from nostril on one side (n = 3) or not contacting nostril (n = 1); scales contacting posterior margin of mental shield 4–11 (n = 40, mode = 6, mean = 6.0, SD = 1.42); ear opening elliptical, vertical, much less than half as large as eye; supralabials 11–18 (n = 41, mode = 14, mean = 14.5, SD = 1.43); scales on snout grade evenly from small to large (in dorsal–ventral transect; Fig. 9A); infralabials 10–15 (n = 41, mode = 12, mean = 12.3, SD = 1.10). **Neck.** Broad. **Body.** Moderate, depressed, covered in small granules; dorsal granules intermixed with larger conical tubercles; tubercles moderate on body and large on neck; basal scales surrounding upper flank and back tubercles noticeably larger than adjacent granules; ventral scales enlarged in pelvic region. Preanal pores absent. Axilla slightly to moderately invaginated. **Limbs.** Long, covered in moderate pointed tubercles dorsally; lacking enlarged tubercles on ventral surfaces; digits strongly compressed distally; subdigital lamellae (fourth finger) 16–24 (n = 41, mode = 18, mean = 19.2, SD = 1.61); dorsal surface of hand with (88%) or without (12%) enlarged conical tubercles; dorsal surface of some fingers with (45%) or without (55%) enlarged spinose scales; subdigital lamellae (fourth toe) 19–25 (n = 41, mode = 20, mean = 21.6, SD = 1.66); dorsal surface of foot with enlarged conical tubercles; dorsal surface of some toes usually with (95%) enlarged spinose tubercles (Fig. 10B; sharp in 61% of specimens, blunt in 39% of specimens). **Original tail.** Depressed, broad, contracted at base and attenuated at tip; flared portion with undulating flange bearing sharply pointed tubercles along margin; dorsal surface of tail, except

vertebral region of flared portion, covered with large conical tubercules; tail tip slender and free of tubercules, or with only minute tubercules (Stanthorpe area and further south, Fig. 13B), or tail more bluntly tipped (Queen Mary Falls population) with tubercules almost to tip; number of rows of enlarged spinose tubercules across flared portion of tail 4–8 ($n = 14$, mode = 6, mean = 5.6, SD = 1.21); number of rows of spinose tubercules across attenuated portion of tail 4–7 ($n = 14$, mode = 6, mean = 5.4, SD = 0.94); attenuated tip accounts for 33.17–46.23% tail length ($n = 14$, mean = 40.6, SD = 3.92); ventral surface smooth with a slight depression along midline. *Regenerated tail*. Approximately 58% SVL when fully regenerated; depressed, broad and strongly leaf-like, contracted at base with short attenuated tip; slight tapering and folding of lateral flange anteriorly; covered with uniform granules and minute, spinose lateral tubercules.

Pattern. In spirit, Couper *et al.* (1997) provide the following description of body colour pattern for *S. wyberba*: “Dorsum tan or grey; heavily marked with dark brown/black or grey blotches on head, body and limbs; a narrow vertebral stripe, broken by four irregular tan or grey blotches, extends from neck to base of tail; a wide, open V-shaped marking between the eyes (Fig. 3a); labials light grey, mottled with dark brown; limbs moderately boldly banded; toes prominently banded. Venter cream with clusters of dark brown granules which often form irregular bars below the infralabials and on the anterior margin of the thigh.” This description stands to define the populations in the Stanthorpe area, SEQ. The Queen Mary Falls population is generally consistent with the above description, but the blotches across the vertebral stripe tend to be less pronounced and the “V” between the eyes can be finer and more “*swaini*-like” in some individuals. The Gibraltar Range animals are darker, and hence more uniform in appearance. The vertebral blotches are more restricted and may not extend to the dorsolateral area as in the northern populations. The degree of dark peppering on the ventral surface is also less pronounced. All populations have a series (usually 4) of pale, irregular crossbands on the original tail and these extend to the ventral surface of the attenuated tip. Regenerated tails show considerable variation in base colour and degree of darker marbling.

Measurements and scale counts of holotype. See Couper *et al.*, 1997.

Geology. *Saltuarius wyberba* is largely associated with outcropping of Middle Permian to Early Triassic granitoids in southeastern Queensland and northeastern NSW (for extent of granite occurrence see map in Schaltegger *et al.*, 2005). The Queen Mary Falls population occurs on the southwestern flank of the Main Range Volcano where the geckos are found on a cliff-line of Trachyte with an underlying layer of basalt. These formations are only narrowly separated from the broader granite outcrops of the Stanthorpe region.

Genetics. *Saltuarius wyberba* differs in cytochrome *b* sequences from other members of the “*S. swaini*” lineage at 10.59–14.37% of sites (Table 1). It differs from its northern congeners *S. cornutus* and *S. salebrosus* at 24.52% and 19.57% of sites respectively. Average intraspecific sequence divergence is 3.17% (Table 1).

Distribution. Queensland and northern NSW between latitudes 28°20'S–29°45'S. The most southerly Queensland populations and all NSW populations lie on the western side of the Clarence River. The Queen Mary Falls population (Queensland, northern limit of range) lies in the headwaters of the Condamine River (Fig. 11).

Habitat. Associated with granite outcropping in open forest communities.

Comparison with other species. *Saltuarius wyberba* is readily distinguished from *S. cornutus* and *S. salebrosus* in lacking preanal pores in both sexes (*vs* present in males). It is further distinguished from *S. cornutus* by its lower flank tubercules (tubercules not hooked and not surrounded by smaller spines *vs* tubercules hooked and surrounded by smaller spines) and from *S. salebrosus* by its throat scalation (throat smooth *vs* throat strongly tuberculate). It is most similar to *S. moritzi* n.sp. and colour pattern most readily distinguishes these species, although both are quite variable. *Saltuarius wyberba* usually has two, narrow pale bands across the flared portion of the original tail, the anterior-most may be obscure, often centred on enlarged tubercules and usually discontinuous through vertebral region (Fig. 13B; *vs* anterior band well defined and usually continuous through the vertebral region, Fig. 13A); the dark bands across the snout and other dark head markings are usually sharply contrasted with the base colour (*vs* dark head markings not usually sharply contrasted with base colour) and the V-shaped marking between the eyes is usually wide and shallow (Fig. 7E; *vs* usually narrow and deep, Fig. 7B). *Saltuarius wyberba* also tends to be more dorsoventrally compressed than *S. moritzi* n.sp. (mean HD = 39% HW *vs* 42%). It is distinguished from *S. swaini* in having narrow, pale bands across the flared portion of the original tail (Fig. 13B; *vs* broad cream/grey zones, Fig. 13C); by its smaller size (max SVL = 108 mm *vs* 134 mm) and the arrangement of the snout scales (grade evenly from small to large in dorsal–ventral transect, Fig. 9A *vs* intermixed with larger granules above the supralabials, Fig. 9B). From *S. kateae* n.sp. it is readily distinguished by the rostral/nostril contact (rostral usually in contact with nostril, Fig. 8B *vs* rostral usually excluded from nostril, Fig. 8A) and by the spinosity of the digits (dorsal surface of digits usually with spinose tubercules, Fig. 10B *vs* spinose tubercules absent, Fig. 10A).

Remarks. Specimen QM J53984 (Mann River Nature Reserve; see specimens examined) is not incorporated into the above description. Pattern irregularities and a close geographic proximity to specimens that were genetically typed as *S. moritzi*, but considered to be *S. wyberba* in the discriminant analysis (see “remarks” for *S. moritzi* and “future directions” in discussion) hinder a precise taxonomic assignment. If this specimen proves to be *S. wyberba*, it represents the most southerly record.

Discussion

Biogeography. The three basal lineages in our phylogeny (Fig. 1) are all rainforest inhabitants. *Saltuarius cornutus* and *S. swaini* sensu stricto are both restricted to moist, upland rainforests, the former in northeastern Queensland (NEQ), the latter in SEQ and northern NSW. *Saltuarius*

salebrosus extends from the subtropical rainforests (complex notophyll vine forests) of mid-eastern Queensland, west to the sandstone areas (Blackdown Tableland and Injune) of Central Queensland. Despite its presence in dry, inland areas, this taxon is closely associated with softwood scrubs (dry rainforests), now largely cleared. Where *S. salebrosus* occurs on sandstone and granite rock-faces, there are often pockets of softwood scrub clinging to the gullies and talus slopes of these landforms. In view of these associations, it seems reasonable to suggest that *Saltuarius* spp. are derived from a common rainforest ancestor.

The molecular data provide a time frame for interpreting the phylogeography of the “*S. swaini*” lineage. In an earlier study (Couper *et al.*, 2000), divergence between mtDNA lineages within the leaf-tailed geckos was calibrated by C. Schneider to accrue at the rate of 0.0042 ± 0.0002 per million years. Using this calibration, we infer that divergence between the four clades of the “*S. swaini*” lineage occurred between the latest Eocene and the Late Oligocene. The split between the rainforest-dependent *S. swaini* and the three open forest/saxicolous forms, *S. moritzi*, *S. wyberba* and *S. kateae*, dates to around 34–31 mya. The split amongst the saxicolous forms is more recent, 27–25 mya. The previous calibration has been used to maintain consistency between datasets. However, the dates given should be treated tentatively as cytochrome *b* is likely to be saturated at deeper divergences. Nonetheless, these dates do highlight the antiquity of the speciation events within this group.

By considering the historical geomorphology of the Clarence–Moreton Basin and the New England Block (the geological units which underlie the distributions of the species comprising the “*S. swaini*” lineage) it is possible to gain insights into the current distribution and diversification of the “*S. swaini*” lineage.

The southern portion of the Clarence–Moreton Basin is largely shaped by the erosive processes of the Clarence River (from 80 mya; late Cretaceous) which captured the streams running off the New England Block and cut a series of deep gorges at the base of the Dividing Range. These coalesced to form the Great Escarpment (Haworth & Ollier, 1992). It also features the Tweed, Main Range and Focal Peak Shield Volcanoes (Late Oligocene to Early Miocene, dated at 23.5–20.5 mya, 25–22 mya and 25.5–23.2 mya respectively; Ewart *et al.*, 1987; Willmott, 2004). This landscape, with its diverse topography and abundant rock, provided a canvas for divergence and subsequent speciation in the “*S. swaini*” lineage.

Climate change during the last 65 million years has alternated through three warm, wet intervals (Late Palaeocene to Middle Eocene, Early Miocene and possibly Early Pliocene) and cool, dry periods between; arguments for speciation in this period have largely concluded that there were periods of diversification through range expansion during the warm periods, and phases of extinction or range contraction during the cool periods (Greenwood & Christophel, 2005).

Hypothesized time of divergence in the “*S. swaini*” lineage coincides with the latest Eocene–Early Miocene cool phase; a period with cooler, drier vegetation types and diminished diversity within rainforest communities (Greenwood & Christophel, 2005). Despite a short-lived return to warm-wet conditions in the Early Miocene, climate deterioration continued. The widespread aseasonal wet biome (rainforest and wet heath) contracted, giving way to xerophytic com-

munities dominated by eucalypts, acacias and casuarinas (Galloway & Kemp, 1981) and there were rapid radiations in sclerophyll taxa (25–10 mya) associated with ecological and geographical expansions (Crisp *et al.*, 2004).

Past climate changes have severely affected rainforest communities. The rainforests of southeastern Australia were increasingly “... restricted to edaphically or topographically wetter pockets in the regional vegetational mosaic” (Greenwood & Christophel, 2005). These sheltered areas were well insulated from the effects of fire (Adam, 1992) and were crucial to the survival of rainforest taxa during arid times. Mount Warning, the Dorrigo-Ebor Plateau and the Macleay Gorges have been identified as important in this respect (Floyd, 1990).

We hypothesize that past arid cycles have had severe consequences for ancestral leaf-tails by attenuating populations, eliminating contact zones between populations and preventing gene flow. The gorges associated with the Clarence River (which antedate the initial divergence within the “*S. swaini*” lineage) and the Tweed, Main Range and Focal Peak volcanoes (which developed between the initial isolation of *S. swaini* from the ancestor of the saxicoline lineage, and the speciation of the three saxicoline taxa) were important refugia through dry times and continued to drive the mechanisms for allopatric divergence. The volcanic peaks were significant from the Early/Mid Miocene onwards, by which time large areas of lowland rainforest had contracted out of existence. While some populations remained rainforest-dependent and changed little over time, others become saxicolous and expanded through dry, rocky habitats. Deep rock crevices offered refuge against a generally inimical climate. The Clarence Valley, present since the Cretaceous, and without such crevice-based microhabitats on an alluvial plain, may have acted as a barrier to leaf-tail dispersal throughout, and subsequent to, the period of their speciation.

The leaf-tail populations isolated in the elevated, subtropical rainforests that developed on the Tweed, Main Range and Focal Peak Volcanoes (27°53'–28°48'S) gave rise to *S. swaini*, a taxon with a continuous rainforest ancestry (the basal position of this species in the southern lineage on our phylogeny (see Fig. 1) and its morphological similarities to *S. cornutus*, a rainforest obligate from NEQ, may provide insights into the ancestral form to the “*S. swaini*” lineage). The remaining taxa, *S. moritzi* n.sp., *S. kateae* n.sp. and *S. wyberba*, are likely to have evolved in small isolates of dry rainforest (a depauperate version of the subtropical form; Adam, 1987) that persisted as fragmented remnants on the rocky slopes of gorges and escarpments. The small size of these habitats, coupled with the drier conditions during changed climatic regimes, created selection pressures that favoured occupation of rocky habitats (Fig. 14A,B) which were more insulated from environmental change. This, in turn, initiated the morphological shift to smaller body size and the habitat shift from trees to rocks that characterize these species.

Rock-dwelling populations probably persisted, even where remnant rainforests contracted out of existence. Once rock habitats had been invaded, opportunities were created for range expansions by *S. moritzi* n.sp. and *S. wyberba*. These taxa had access to the extensive gorges and rock outcrops of the New England Block. In some situations, geographically proximate populations of *S. moritzi* n.sp. occur in both rock (in dry forests), and rainforest habitats (e.g., near Coffs

Harbour). This, most likely represents a secondary shift back to the latter. The occurrence of *S. salebrosus* in rainforests and on rock escarpments does indicate the potential for the hypothesized shift between rainforest and rock habitats.

In contrast to the hypothesized range expansions of *S. wyberba* and *S. moritzi* n.sp., *Saltuarius kateae* n.sp. remains narrowly restricted and may be confined to sandstone escarpments north of Grafton. Its distribution is disjunct from the extensive rock habitats of the New England Block, broken by the main channel of the Clarence River and its broad alluvial plains. The significance of the dry Clarence Valley, with its northwest–southeast orientation, as a major barrier restricting the movements of both plants (Floyd, 1990) and animals (land snails, J. Stanic pers. comm.; hexathelid spiders, R. Raven pers. comm.) is clearly recognized. Yet, prior to 27–25 mya (Late Oligocene) the dry forest/saxicolous leaf-tails (*S. moritzi* n.sp., *S. kateae* n.sp. and *S. wyberba*) maintained genetic exchange across this barrier. This may have been facilitated by a series of ranges from south and west of the Clarence River (near where the town of Jackadgery now stands, 29°35'S 152°34'E) running north and east to Mt Marsh (29°20'S 152°51'E). As aridity became more pronounced during the Late Tertiary and Quaternary, moist forest communities in the Clarence Valley gave way to open forests thus enhancing the river's significance as a biogeographic barrier. In the absence of robust phylogenies, it is not possible to speculate when this region became a significant barrier to the aforementioned invertebrate groups.

While there is little sequence divergence within either *S. swaini* (except for the Brindle Ck population, Fig. 1) or *S. kateae* n.sp., there are deep splits within the other taxa that coincide with geography, suggesting relatively ancient fragmentation events. There are two main lineages within *Saltuarius moritzi*: lineage A generally occurs at altitudes below 1000 m, lineage B generally at higher elevations. The divergence between lineages dates between 19.7–11.4 mya and suggests habitat fragmentation tied to the Miocene climate changes together with limited subsequent exchange of individuals between sites.

Within *S. wyberba*, the Gibraltar Range population showed a high level of sequence divergence among individuals, with one specimen differing by 7.32% from the others on the same outcrop. This individual (AM R164153) was consistent in morphology and colour pattern with other specimens (AM R164152, QM J83586–87, AM R164155, AM R164157) from this site. This degree of sequence divergence within a site suggests either a long period of habitation of the immediate region, allowing mitochondrial sequence divergence to occur *in situ*, or secondary contact of two lineages of *S. wyberba*. *Saltuarius wyberba* and *S. moritzi* n.sp. are narrowly separated in the area east of Glen Innes, with no obvious barriers to movement, and a possible zone of contact may exist here. The proximity of the Queen Mary Falls *S. wyberba* population (on rocks/open forest) to the *S. swaini* populations (on trees/primary rainforest) of Main Range is unlikely to result in any genetic exchange as the two taxa are clearly partitioned by niche preference.

In the above overview of the distribution of the “*S. swaini*” lineage, the Clarence River is discussed in detail because of its previously-identified significance as a biogeographic barrier and importance in shaping the landscape in ways that were conducive to leaf-tail speciation. However, the significance of other lesser coastal river systems (Bellinger,

Macleay, Hastings and Manning Rivers) and the erosive processes that shaped them should not be overlooked—these all have a role in forming a landscape that could favour or restrict dispersal of lizards constrained by rainforest or rock crevice habitats. Seemingly small geographic features, like the Henry River Valley (an upper tributary of the Mann River separating *S. wyberba* from *S. moritzi* n.sp.), east of Glen Innes may have presented barriers to dispersal at population and species level. Nix (1991) notes that a “sea” of warm air at lower elevations within a valley can be as effective as an ocean barrier in blocking the movement of mesotherm flora and fauna.

We have identified the Late Eocene (34 mya)–Late Oligocene (25 mya) as an important period for genetic divergence of *Saltuarius* species in temperate southeastern Australia. Similar, though slightly older, dates (38–31 mya) apply to the genetic divergence seen amongst *Phyllurus* spp. on the Mackay Coast in mid-eastern Queensland (Couper *et al.*, 2000). However, phylogeographic studies show that the Quaternary was also important in shaping the current genetic signatures of leaf-tailed geckos from northeastern and mid-eastern Queensland (Schneider *et al.*, 1998 [*S. cornutus*]; Stuart-Fox *et al.*, 2001 [*Phyllurus ossa*]). Processes driven by Quaternary climate changes (during the last 1.8 million years) were “... responsible for the most recent sifting of the rainforest biota” (Adam, 1992).

Conservation. The current study provides high resolution data on species and phylogeographic diversity which is applicable to a process-oriented approach to conservation. Such an approach is discussed by Moritz and McDonald (2005) who state “The overall goal of a conservation strategy should be to protect the processes, both ecological and evolutionary, that sustain diversity at the ecosystem, species, and genetic levels”. In determining conservation priorities for the “*S. swaini*” lineage, it is clear that three of the four species involved (*S. swaini*, *S. moritzi* n.sp., and *S. wyberba*, especially the latter two) also include genetically divergent populations that should be viewed as separate entities for land management issues (see phylogeny, Fig. 1). These reflect genetic isolation stemming from past climate change. All three species, and the divergent populations within, are present in existing reserve systems. *Saltuarius wyberba* and some populations of *S. moritzi* n.sp. are closely associated with exposed rock outcrops, gorges and escarpments, while *S. swaini* is restricted to rainforests that blanket ancient volcanic peaks. These landscapes, largely selected for their scenic values (Fig. 14A,B), feature prominently in national parks and nature reserves. Additionally, these species have populations within state forests where access is restricted. The impacts of selective timber harvesting in forestry reserves are likely to be less severe where the geckos utilize a rock substrate. Tree dwelling populations are likely to have a better chance of recovery where selected harvests leave essential sheltering sites intact (i.e. living and dead trees with hollows). Clear-felling operations that remove these essential components of the habitat are likely to be of concern.

Two species, *S. wyberba* and *S. moritzi* n.sp. may occur widely on private land. As many of these populations are associated with rock outcropping, they are probably largely protected from the direct impacts of grazing. The effects of fire may be of greater concern. Duncan (2005), in assessing the impact of wildfire on terrestrial mollusc populations

stressed the importance of rock for “maintaining long-term species distribution within a range”. Fissures between rocks provide a vertical retreat to cool, moist environments allowing land snails to escape from the heat of fire. Survival following fires was skewed towards juvenile size classes, probably because smaller individuals have the ability to penetrate the substrate more deeply. Many of the rock outcrops supporting leaf-tailed gecko populations are massive, and in these situations fire may only have peripheral effects (leaf-tails living in surface retreats, beneath thin, exfoliating slabs may perish). Yet, fire may alter population structure in smaller rock piles that exist as outliers from larger outcrops. A loss of adult-sized individuals from a population will diminish reproductive success in subsequent seasons.

Saltuarius kateae n.sp. is currently known from two localities, Wyans Creek and Mt Marsh. The former locality is on private land, the latter within Mt Neville Nature Reserve (a large portion of Mount Marsh State Forest (60%) came under the control of the NSW Department of Environment and Conservation on 1 Jan., 1999. The southeast portion is now Banyabba Nature Reserve; the northeastern portion is now Mt Neville Nature Reserve—Guy Hodgson, Dept. of Environment and Conservation, Parks and Wildlife Division, NSW, pers. comm.). This species has the smallest distribution within the “*S. swaini*” lineage, with a range of 0.25° of latitude (*S. swaini* spans 1°, *S. wyberba* < 1.5° and *S. moritzi* n.sp. < 2.5°). The genetic samples used in our analyses came from a single population and showed no divergence. In view of the narrow range of this species, there is probably limited genetic divergence between the Wyans Creek and Mt Marsh populations. The Wyans Creek population is associated with sandstone escarpments and these formations (Kangaroo Creek Sandstones) are well represented in the Banyabba and Mt Neville Nature Reserves (Mick Andren, Dept. Environment and Conservation, NSW, pers. comm.). The predicted presence of *S. kateae* n.sp. in Banyabba Nature Reserve still requires confirmation.

The potential impacts of global warming continue to ring alarm bells in many quarters and there is little doubt that montane communities will be hit hard by human-induced climate change. Rising temperatures promote upward shifts of both flora and fauna (Montaigne, 2004; Kluger, 2006; Grabherr *et al.*, 1994), yet there are tight constraints on these altitudinal movements. A limited dispersal ability equates to a higher extinction risk (Thomas *et al.*, 2004). Williams *et al.* (2003) assessed the impact of climate change on endemic vertebrates living in mountain rainforests of northeastern Queensland. Using bioclimatic models of spatial distribution, they predict high, nonlinear extinction rates due to loss of core environments, with rapid increases in losses beyond an average temperature increase of 2°C. Projections by CSIRO (2001), relative to 1990, predict average temperature increases of 0.4–2.0°C by 2030 and 1.0–6.0°C by 2070 (Hughes, 2003). These predictions present a bleak outlook. Sadler *et al.* (2005) have expressed concern for the montane rainforests of mid-eastern Queensland (Eungella, Clarke Range), where two skinks, *Saproscincus eungellensis* and *Eulamprus luteilateralis* have narrow altitudinal limits; the former restricted to elevations above 700 m, the latter above 900 m. Rising temperatures are likely to elevate the direct risk of extinction for both species and may also benefit the plant pathogen, *Phytophthora cinnamomi*, that is present in these forests, creating indirect effects on habitat suitability.

To assess the impacts of global warming on the members of “*S. swaini*” lineage, it is important to consider the phylogeography (see above) of this group. In discussing how ecological communities adjust to unforeseen change, Leigh and Rubinoff (2005) state, “Populations presumably recover best from disturbances their ancestors have frequently encountered.” This assumption would infer that the rock-dwelling species, *S. moritzi* n.sp. (some populations), *S. kateae* n.sp. and *S. wyberba*, that have experienced greater selection pressures in response to past climatic events are more likely to adjust to rising temperatures than *S. swaini*. Further, large outcrops of deeply cracked rocks provide a stable habitat which provides considerable buffering from thermal extremes. *Saltuarius swaini*, on the other hand, lives in a habitat that will progressively degrade with rising temperatures. Its evolutionary history, involving a continuous rainforest ancestry, may reduce its ability to adapt during rapid climate change. Ecological stasis could leave this species ill equipped to cope with global warming and significantly elevate its extinction risk.

In their assessment of the impact of global warming on endemic vertebrates in the Wet Tropics, Williams *et al.* (2003) concluded that a temperature rise of 5°C would cause total habitat loss for 88% of species and, for the remaining 12% of species, a reduction of core habitat area to an average of 3% of its former area. A temperature increase of 7°C would cause total loss of core habitat for all species. In this study, *S. cornutus*, the northern, ecological equivalent of *S. swaini* (both rainforest endemics with broad altitudinal ranges), was one of the last species to lose its entire core habitat (Williams, pers. comm.). Extrapolating from this study, and allowing that temperature increases predicted by CSIRO run closer to maximum predictions, then *S. swaini* could be drastically reduced to a small remnant population as early as 2070. This, of course, is the worst case scenario and many other rainforest vertebrates from southeastern Queensland and NSW will decline more rapidly than *S. swaini* and some, with narrow altitudinal distributions, could face extinction as early as 2030. An extrapolation of this kind does not take into account the ability of individuals of a species to behaviourally buffer against thermal extremes, nor does it allow that temperature increases may affect rainforests adapted to different climates in different ways. Yet, the rainforests of eastern Australia, both northern and southern, have had similar responses to past climatic events (Greenwood & Christophel, 2005; Martin, 1987, 1997).

A further factor potentially impacting on survival through environmental change is the genetic diversity of populations. With the exception of the sample of *S. wyberba* from Gibraltar Range (AM R164153) and the sample of *S. moritzi* n.sp. from Bruxner Park (AM R164146), we found very low levels of genetic difference among individuals within samples, and in many cases, particularly within *S. swaini*, very limited genetic variation between localities. These apparent low levels of genetic diversity may reflect limited potential to survive severe population decreases, an effect that is likely to be most marked for *S. swaini* and *S. kateae* n.sp.

Future directions. The discriminate functions analyses (DFAs) point to unresolved issues that can only be clarified with further fieldwork, coupled with genetic and morphological studies. Most of the individuals that were incorrectly identified by the DFAs can be considered as true misidenti-

fications, but there are three individuals (from Blady Grass Creek QM J72343, Oakwood AM R143592, and Guyra AM R43870, the first genetically typed as *S. moritzi* n.sp., the second geographically within 30 km of the previous locality, the third more distant, but geographically closest to this locality) which form a geographic cluster. All three were presumed to represent *S. moritzi* n.sp. based on geography and proximity to a single individual genetically typed as this species, but were identified by the morphological analysis as *S. wyberba*. Given the paucity of material from this region and the lack of congruence between the genetic and morphological data for QM J72343, we consider that the identity of *Saltuarius* from this region should be treated as indeterminate pending the collection of larger samples. The Blady Grass Creek, Oakwood and Guyra specimens are all geographically proximate to the presumed break between the distributions of *S. moritzi* n.sp. and *S. wyberba*, raising the possibility of existence of a hybrid zone.

ACKNOWLEDGMENTS. The authors wish to thank the Australian and Queensland Museums for financially supporting this project. We are especially grateful to Chris Schneider (Boston University) for his ongoing support and access to his unpublished sequence data; Harry Hines (QPWS) and Conrad Hoskin (University of Queensland) for field observations, tissue samples and ongoing discussions on leaf-tail distributions; Fred Kraus (Bishop Museum / Hawaii) and Rod Hobson (Qld Parks and Wildlife Service) for their assistance, and excellent company, in the field; Gary Stephenson for pointing us to the Glenreagh collection site; Mick Andren and Guy Hodgson (Dept of Environment and Conservation, NSW) for information on land tenure and topography of the Mt Marsh area; Steve Williams and John Winter for their thoughts on global warming; Tony Ewart for discussions on underlying geology, and Amy and Hannah Couper for allowing their holiday destinations to be within striking range of leaf-tailed gecko habitats. All specimens collected in New South Wales for this project were collected under New South Wales National Parks and Wildlife Service Scientific Authority (A1397) license number S10807 to the Australian Museum, and under Australian Museum Animal Research Authority Project No. 04–12 to Principal Investigator Ross A. Sadler.

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Manuscript submitted 06 July 2007, revised 19 March 2008, and accepted 31 March 2008.

Associate Editor: S. Ingleby

Appendix 1. List of localities, museum registration numbers, Genbank accession numbers and identifications for specimens used in the genetic analyses.

locality	museum registration	Genbank Accession no.	identification
Chaelundi SF, northern NSW	AM R141964–5	EU625300	<i>S. moritzi</i> n.sp.
Bruxner Park, nr Coffs Harbour NSW	AM R160420	EU625301	<i>S. moritzi</i> n.sp.
Blady Grass Ck, nr Glen Innes, NSW	QM J72343	EU625302	<i>S. moritzi</i> n.sp.
O'Sullivan's Gap, Bulahdelah, NSW	AM R163000	EU625303	<i>S. moritzi</i> n.sp.
O'Sullivan's Gap, Bulahdelah, NSW	AM R163001	EU625304	<i>S. moritzi</i> n.sp.
Ebor Falls, New England, NSW	AM R163003	EU625305	<i>S. moritzi</i> n.sp.
Ebor Falls, New England, NSW	QM J83593	EU625306	<i>S. moritzi</i> n.sp.
Ebor Falls, New England, NSW	AM R163005	EU625307	<i>S. moritzi</i> n.sp.
Blue Hole, Armidale, NSW	QM J83588	EU625308	<i>S. moritzi</i> n.sp.
Blue Hole, Armidale, NSW	QM J83589	EU625309	<i>S. moritzi</i> n.sp.
Sherwood NR, Glenreagh, NSW	AM R158973	EU625310	<i>S. moritzi</i> n.sp.
Sherwood NR, Glenreagh, NSW	QM J83591	EU625311	<i>S. moritzi</i> n.sp.
Bruxner Park, nr Coffs Harbour NSW	AM R158945	EU625312	<i>S. moritzi</i> n.sp.
Bruxner Park, nr Coffs Harbour NSW	QM J83592	EU625313	<i>S. moritzi</i> n.sp.
Bruxner Park, nr Coffs Harbour NSW	AM R164146	EU625314	<i>S. moritzi</i> n.sp.
Comboyne Plateau, Boorgana NR, NSW	AM R158991	EU625315	<i>S. moritzi</i> n.sp.
Werrikimbee NP, NSW	no voucher	EU625316	<i>S. moritzi</i> n.sp.
Grange SF, Dorrigo, NSW	AM R141966	EU625317	<i>S. moritzi</i> n.sp.
Main Range NP, SEQ	no voucher	EU625318	<i>S. swaini</i>
Main Range NP, SEQ	no voucher	EU625319	<i>S. swaini</i>
Mt Mitchell, Main Range NP, SEQ	QM J80792	EU625320	<i>S. swaini</i>
Mt Cordeaux, Main Range NP, SEQ	QM J80793	EU625321	<i>S. swaini</i>
Lamington NP, SEQ	QM J51640	EU625322	<i>S. swaini</i>
Mt Tamborine, SEQ	QM J51095	EU625323	<i>S. swaini</i>
Mt Warning, NE NSW	QM J83594	EU625324	<i>S. swaini</i>
Cambridge Plateau, NSW	AM R158999	EU625325	<i>S. swaini</i>
Brindle Ck, Border Ranges NP, NSW	AM R158987	EU625326	<i>S. swaini</i>
Wyans Creek, Richmond Range, NSW	QM J83584	EU625327	<i>S. kateae</i> n.sp.
Wyans Creek, Richmond Range, NSW	QM J83585	EU625328	<i>S. kateae</i> n.sp.
Wyans Creek, Richmond Range, NSW	QM J83583	EU625329	<i>S. kateae</i> n.sp.
Wyans Creek, Richmond Range, NSW	AM R164166	EU625330	<i>S. kateae</i> n.sp.
Spirabo Forest Way, NE NSW	no voucher	EU625331	<i>S. wyberba</i>
Queen Mary Falls, Main Range NP, SEQ	QM J80794	EU625332	<i>S. wyberba</i>
Queen Mary Falls, Main Range NP, SEQ	QM J80795	EU625333	<i>S. wyberba</i>
Queen Mary Falls, Main Range NP, SEQ	QM J80796	EU625334	<i>S. wyberba</i>
Gibraltar Range, New England, NSW	AM R164153	EU625335	<i>S. wyberba</i>
Gibraltar Range, New England, NSW	QM J83586	EU625336	<i>S. wyberba</i>
Gibraltar Range, New England, NSW	AM R164157	EU625337	<i>S. wyberba</i>
Girraween NP, SEQ	AM R157130	EU625338	<i>S. wyberba</i>
Girraween NP, SEQ	QM J51633	EU625339	<i>S. wyberba</i>
south of the Black Mountain corridor, north QLD	no voucher	AF109502	<i>S. cornutus</i> 1
north of Black Mountain corridor, north QLD	no voucher	AF109487	<i>S. cornutus</i> 2
Big Tableland, north QLD	no voucher	EU625340	<i>S. cornutus</i> BT
Blackdown Tableland, QLD	QM J51091	EU625341	<i>S. salebrosus</i>
Bulburin SF, QLD	QM J51090	EU625342	<i>S. salebrosus</i>

 Appendix 2. Allocation of specimens for multivariate analyses (see materials and methods).

1 Specimens identified (from within 30 km of genetic sample)

Females:

Saltuarius kateae n.sp.: AM R164163, AM R164166, AM R139790, QM J83583–85
Saltuarius moritzi n.sp.: AM R8253, AM R16905, AM R16989, AM R69866, AM R71372, AM R101338, AM R143590, AM R143592, AM R158945, AM R158973, AM R158977, AM R163001, AM R163006, AM R163009, QM J9054, QM J83589, QM J83590–83591
Saltuarius swaini: AM R116978, QM J2933–34, QM J4819, QM J5649, QM J8183, QM J8359, QM J8646, QM J51095
Saltuarius wyberba: AM R164152, QM J35401, QM J50345, QM J61543–45, QM J80795

Males:

Saltuarius moritzi n.sp.: AM R6247, AM R6915, AM R43871, AM R43873–75, AM R59313, AM R71373, AM R103031, AM R106749, AM R141964–65, AM R153478, AM R158974, AM R158978, AM R158990, AM R160420–21, AM R163000, AM R163002–03, AM R163010, AM R163012, QM J72343, QM J83588, QM J83592, QM J83593.
Saltuarius swaini: AM R2409, AM R11860, AM R97823, AM R98333, AM R130911, AM R158987, AM R158999, AM R160423, QM J2409, QM J3254, QM J4198, QM J4439, QM J5690, QM J10440, QM J51637–40, QM J54846, QM J80792–93, QM J83594.
Saltuarius wyberba: AM R149768, AM R156806, AM R164153, AM R164157, QM J25374, QM J28648–49, QM J29116–17, QM J30420, QM J51093, QM J51633–36, QM J54847, QM J61539–42, QM J70465, QM J80794, QM J80796, QM J83586–87.

2 Specimens treated as of unknown identity for the purposes of analyses (more than 30 km from a genetic sample or from sites where 30 km radii from different genetic taxa overlapped or no collection data available)

Females:

AM R6792, AM R43870, AM R150912—assumed to be *S. moritzi* n.sp. from locality or overall appearance.
 AM R92122, QM J8099, QM J23937, QM J36116 (no data—excluded from species account): assumed to be *S. swaini* from locality or overall appearance.
 QM J79753 (no data—excluded from species account) QM J79754, QM J79757: assumed to be *S. wyberba* from overall appearance.

Males:

AM R164161: assumed to be *S. kateae* n.sp. from the locality.
 AM R6284, QM J56894: assumed to be *S. moritzi* n.sp. from locality or overall appearance.
 QM J8074, QM J51094: assumed to be *S. swaini* from morphology.
 AM R110510, QM J53984, QM J79758: assumed to be *S. wyberba* from morphology.

3 Specimens that were unable to be used in the analyses because of missing data, but fell within 30 km radii of genetic samples.

Females:

AM R43872: *S. moritzi* n.sp.
 QM J148, QM J8861, QM J81611: *S. swaini*.
 J27349: *S. wyberba*.

Males:

AM R69867, AM R151753: *S. moritzi* n.sp.
 QM J3215, QM J3313: *S. swaini*.
 QM J30677: *S. wyberba*.

4 Specimens that were not used in the analyses because of missing data, and were more than 30 km from genetic samples, or were from regions where different species' 30 km radii overlapped.

Females:

AM R150911: (excluded from species account): assumed to *S. moritzi* n.sp. on morphology.
 QM J47144 (no data—excluded from species account): assumed to be *S. moritzi* n.sp. on morphology.

5 Unsexed specimens that were not used in the analyses (includes juveniles).

AM R15412, AM R17008, AM R54071, AM R59314, AM R81921, AM R97670–72, AM R123490, AM R143591, AM R158946, AM R163005, AM R164146: *S. moritzi* n.sp.
 QM J398, QM J1143, QM J5382, QM J5757, QM J10565, QM J12257: *S. swaini*.
 AM R164155, QM J68108, QM J79755: *S. wyberba*.

6 Specimen not included in analyses with missing data and unknown locality.

Male:

QM J79756: *S. wyberba*.

7 Specimen not included in analyses because of uncertainty of locality data (see remarks *S. moritzi* n.sp.).

AM R141966: assumed to be *S. moritzi* n.sp. on morphology.
