Ancient drainages divide cryptic species in Australia's arid zone: Morphological and multi-gene evidence for four new species of Beaked Geckos (*Rhynchoedura*)

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ABSTRACT

Deserts and other arid zones remain among the least studied biomes on Earth. Emerging genetic patterns of arid-distributed biota suggest a strong link between diversification history and both the onset of aridification and more recent cycles of severe aridification. A previous study based on 1 kb of mtDNA of the monotypic gecko genus *Rhynchoedura* identified five allopatric clades across the vast Australian arid zone. We supplemented this data with 2.2 kb from three nuclear loci and additional mtDNA sequences. Phylogenetic relationships estimated from the mtDNA data with ML and Bayesian methods were largely concordant with relationships estimated with the nDNA data only, and mtDNA and nDNA data combined. These analyses, and coalescent-based species-tree inference methods implemented with *BEAST, largely resolve the relationships among them. We also carried out an examination of 19 morphological characters for 268 museum specimens from across Australia, including all 197 animals for which we sequenced mtDNA. The mtDNA clades differ subtly in a number of morphological features, and we describe three of them as new species, raise a fourth from synonymy, and redescribe it and the type species, *Rhynchoedura ornata*. We also describe a morphologically distinctive new species from Queensland based on very few specimens. The distribution of arid zone clades across what is now relatively homogeneous sand deserts seems to be related to a topographic divide between the western uplands and eastern lowlands, with species' distributions correlated with dryland rivers and major drainage divides. The existence of five cryptic species within the formerly monotypic *Rhynchoedura* points to ancient divergences within the arid zone that likely were driven by wet phases as well as dry ones.

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1. Introduction

Arid zones represent some of the most understudied biomes on Earth, largely due to harsh climatic conditions and inaccessibility. They are widely distributed across mid-latitude continental regions and generally have a geologically recent (<20 million years ago [Mya]) history of aridification (Hartley and Chong, 2002; Clark et al., 2006; Fujioka et al., 2009). These features make them exceptional landscape systems to study the consequences of widespread and severe climate change on evolutionary history. Dated molecular studies of arid zone taxa across the globe show deep divergences in line with the onset and development of aridification (*Asia*: Melville et al., 2009; *Australia*: reviewed in Byrne et al., 2008; *Africa*: Scott et al., 2004; Carranza, 2008; *North America*: Devitt, 2006; *Afro-Arabia*: Fujita and Papenfus, 2010), with intensifying aridity and the movement of mobile sand deserts thought to drive phylogenetic divergences and phylogeographic structuring.

The Australian arid zone comprises the vast central portion of the landmass. The topography of the region is generally subdued, with few major physical barriers. However, the western arid zone is situated upon higher elevation regions associated with the Western Plateau (Mabbutt, 1988), and comprises a number of topographically complex inland ranges, including in the Pilbara, Kimberley, and the Central Ranges (Wasson, 1982). In contrast, the eastern arid zone occupies the desert floodplains of the Interior or Central Lowlands (Wasson, 1982; Mabbutt, 1988). This landscape is dominated by the extensive Lake Eyre and Murray Darling Basins, which are separated by the narrow north–south trending Bulloo-Bancannia Basin (Fig. 1). These desert floodplains are traversed by immense sand-bed channels, largely associated with rivers rising on the uplands of the east and northern margins of the arid zone. Under the current climatic regime, with the
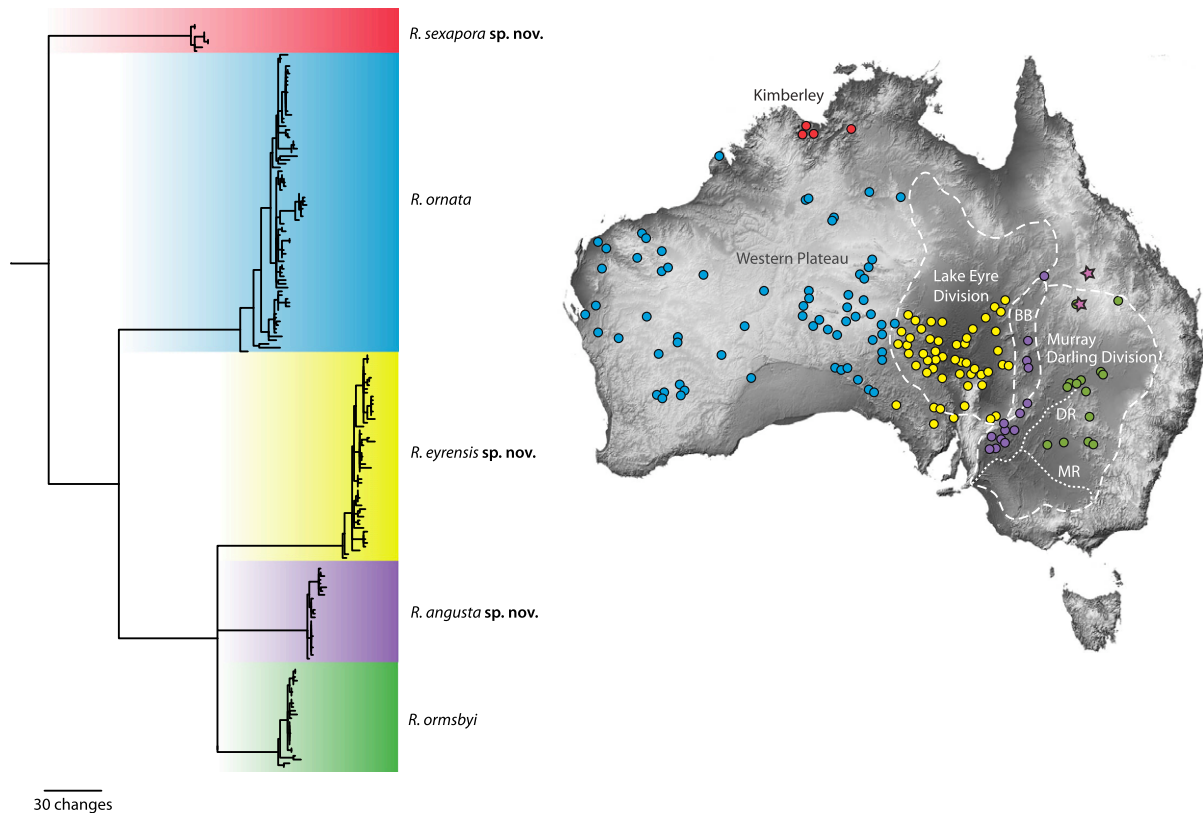
Fig. 1. Phylogeny of *Rhynchoedura* based on 197 mtDNA sequences and their distribution across Australia. These same 197 individuals formed the core material for the morphological data set. The topology of the mtDNA-only data set and additional analyses based on multiple nDNA data sets and nDNA-only data sets are concordant except for the relationships between the three south-eastern species. Here we show the relationships among the three south-eastern species as a polytomy to reflect this uncertainty (see Fig. 2). A parsimony-based phylogeny is shown for ease of interpretation of branch lengths. Dashed lines on the map represent approximate basin boundaries and fine dotted lines represent present-day river courses. BB = Bulloo-Bancannia Division, DR = Darling River, MR = Murray River. Colored dots indicate our sampling for each *Rhynchoedura* taxon, which match clade names from Pepper et al. (2011b) as follows: *R. sexapora* sp. nov. = "Kimberley/Top End", *R. ornata* = "western/central desert", *R. eyrensis* sp. nov. = "southern desert", *R. angusta* sp. nov. = "NSW desert narrow", *R. ormsbyi* = "NSW desert". The distribution of *R. mentalis* sp. nov., for which no genetic samples exist, is represented by the pink stars.

exception of the perennial Murray–Darling system, the northern rivers are characterized by unpredictable and highly variable hydrological regimes, with episodic extensive floods and dry no-flow periods (Carini and Hughes, 2004).

Historical fragmentation and isolation in response to climatic and geomorphologic change throughout the Tertiary has undoubtedly had important consequences for the evolution of biota living in the arid zone (Byrne et al., 2008). Following generally humid conditions with high precipitation in the Eocene (Quilty, 1994; Martin, 2006), the onset of aridification in Australia is thought to have begun in the mid-Miocene ~15 Mya (Martin, 2006). Intensifying aridification in the Pleistocene culminated in the development of extensive inland sand dune systems ~1 Mya (Fujioka et al., 2009). Despite this overarching trend of decreasing precipitation, there was a resurgence of a warm, wet climate in the early Pliocene (Quilty, 1994; Martin, 2006), as well as short duration wet periods associated with interglacial cycles of the Pleistocene (Quilty, 1994).

Molecular studies of arid zone biota are key to understanding the unique biotic diversity that has evolved in concert with progressive and intensifying aridification, particularly as sedimentary palaeorecords and fossil data are frustratingly incomplete (Quilty, 1994). For aquatic taxa distributed throughout the ephemeral dry-land river systems, recent climatic events relating to severe arid cycling of the Pleistocene appear to have been important for diversification, when connectivity of freshwater environments was substantially more restricted (Murphy and Austin, 2004; Carini and Hughes, 2004; Hughes and Hillyer, 2006; Masci et al., 2008; Faulks

et al., 2010). In contrast, genetic studies of terrestrial biota more often show evidence of older diversification of lineages relating to aridification events of the Miocene and Pliocene (reviewed in Byrne et al., 2008), with a number of small, terrestrial vertebrates displaying complex phylogeographic patterns indicative of habitat specialization (Chapple and Keogh, 2004; Pepper et al., 2006, 2008; Couper and Hoskin, 2008; Shoo et al., 2008), persistence and diversification within mesic refugia (Blacket et al., 2001; Fujita et al., 2010; Pepper et al., 2011a,b), and recent range expansion into the deserts (Jennings et al., 2003; Fujita et al., 2010; Oliver and Bauer, 2011; Pepper et al., 2011a,b). Of particular importance for understanding and interpreting the geographic distribution of genetic diversity in the context of aridification history, widespread arid zone species often are found to comprise substantial cryptic diversity (Rabosky et al., 2004; Pepper et al., 2006, 2008, 2011a,b; Doughty and Hutchinson, 2008; Maryan et al., 2007; Oliver et al., 2009, 2011; Sistrom et al., 2009; Melville et al., 2011).

The Beaked Geckos (*Rhynchoedura*) comprise a monotypic gecko genus widely distributed throughout the Australian arid zone (see Supplementary Fig. 1 for all museum records), with a highly specialized morphology that presumably has evolved to enable efficient feeding on termites (Pianka, 1986). The head is narrow and pointed, and at the tip of the snout the rostral (upper) and mental (lower) scales are enlarged and form a beak-like structure. Due to the highly derived 'beaked' morphology, all *Rhynchoedura* specimens have been assigned to the species *Rhynchoedura ornata* with no mention of morphological variation in scientific publications or field guides based on examination of specimens (e.g. Storr et al.,

1990; Cogger, 2000). Recently, however, Pepper et al. (2006) included several representatives of *R. ornata* from Western Australia as an outgroup for a phylogeographic analysis of *Lucasium* (*Diplodactylus*) *stenodactylum*. A single specimen from the eastern Kimberley region in northern Western Australia was highly divergent from other more southerly-distributed arid zone samples. Examination of this specimen revealed a distinctive morphotype that had not been commented on by previous workers and provided the motivation for the current study. A thorough mtDNA screen of almost all available tissue samples of *Rhynchoedura* throughout the Australian arid zone revealed five divergent clades (Pepper et al., 2011b). Here we sequence three additional nuclear genes to further assess genetic diversity within the group and to test the genetic boundaries of the mtDNA clades using both traditional and coalescent-based species tree inference methods. In addition, we carried out morphological examination of 268 specimens from Australian museum collections to revise the taxonomy of the genus in light of all the available evidence. Our dense sampling permits a detailed examination of the relationship between genetic diversity in a terrestrial vertebrate and regional landscapes across the entire Australian arid zone.

2. Materials and methods

2.1. Taxonomic sampling

We chose specimen tissues from existing collections of the Western Australian Museum (WAM), the South Australian Museum (SAMA), the Australian Museum (AMS), and the Queensland Museum (QM) to provide the widest geographic sampling possible. The majority of our mtDNA phylogeny was reproduced using previously published material (Pepper et al., 2011b); however, we included 10 additional samples to provide a clearer picture of the distribution of genetic diversity across the historically under-represented regions of Queensland and the core of the central sand deserts in Western Australia. In addition to the mtDNA dataset, we present new material from three additional nuclear genes that were sequenced for a subset of individuals in the mtDNA phylogeny. Museum accession numbers and collection localities are given in Supplementary Table 1. We used *Lucasium stenodactylum*, a member of the most likely sister genus to *R. ornata* (Oliver et al., 2007a) as the outgroup.

2.2. DNA sequencing and alignment

For all new samples, we followed the protocol of Pepper et al. (2006), targeting a ~1200 base pair (bp) fragment of the mitochondrial genome, extending from tRNA[Met] through the entire protein-coding gene *nd2* (NADH dehydrogenase subunit II) and the genes encoding tRNA[Trp], tRNA[Ala], and tRNA[Asn]. For a subset of 43 individuals representing the five mtDNA lineages of Pepper et al. (2011b), we sequenced an additional 838 bp fragment of the recombination activating gene-1 exon (*rag1*). For details of PCR amplification and sequencing, including reactions and primer combinations, see Pepper et al. (2006). The utility of nDNA markers for recovering relationships among closely related groups can be limited due to slower rates of molecular evolution relative to mtDNA (Hare, 2001). Given non-coding nDNA typically evolves faster than adjacent coding sequence, we also sequenced two recently developed intron markers (developed for another group of Australian geckos), *bzw1* (738 bp) and *snrpd3* (638 bp) for the same 43 individuals, using the PCR, sequencing and primer combinations of Fujita et al. (2010). Alignment of sequences was first performed automatically using the software MUSCLE (Edgar, 2004), then refined by eye in Se-Al (Rambaut, 1996). The few heterozygotes found in

the nDNA genes were coded as such in the alignments prior to analyses. Protein-coding regions were translated into amino acid sequences using the vertebrate mitochondrial genetic code and were checked for internal stop codons and frame-shift mutations.

2.3. Phylogenetic analyses

Phylogenetic analyses were conducted using maximum likelihood (ML) and Bayesian methods. A partitioned ML analysis of our complete *nd2* dataset, totaling 197 taxa, was conducted using RAxML-VI-HPC v7.0.4 (Stamatakis, 2006). The analysis implemented the general time-reversible substitution model with gamma-distributed rates among sites (GTR + G), with the data partitioned into 1st + 2nd + 3rd codon sites. Ten runs with different starting trees were performed, and the most likely tree chosen from this set. Support values were estimated from 100 bootstrap replicates using the –f i search function.

For each marker we also constructed an un-rooted gene tree under a Bayesian framework in MrBayes version 3.2.1 (Huelsenbeck and Ronquist, 2001), partitioning each gene by codon position where applicable. We also conducted a partitioned analysis on our combined mtDNA and nDNA (concatenated) dataset (see below for details on choosing the partition strategy). Because we had no appropriate outgroup sample for *bzw1* and *snrpd3*, the outgroup for these sequences was coded as missing data. Each analysis consisted of four independent runs of four chains each. Analyses were run for 20 million generations with samples taken every 2000 generations. Acceptable convergence to the stationary distribution was checked by inspecting the posterior samples using the diagnostic software Tracer v1.5 (Rambaut and Drummond, 2007). All runs produced the same topology with very similar posterior probabilities, so we combined runs to generate a single consensus tree.

We used Bayes factors (Kass and Raferty, 1995) to determine the best partitioning strategy for our concatenated dataset (Brandley et al., 2005). We compared among (1) unpartitioned, (2) partitioned by nDNA and mtDNA, and (3) partitioned by gene and codon partition where applicable, using the best-fit models of molecular evolution determined under the Akaike Information Criterion (AIC) in MrModeltest v2.3 (Nylander, 2004) (Supplementary Table 2). The ratio of the harmonic mean likelihoods for competing partition models were computed using Tracer v1.4 (Rambaut and Drummond, 2007).

2.4. Bayesian species tree estimation

The distinction between gene trees and species trees is now widely recognized (Maddison, 1997; Degnan and Rosenberg, 2006), and a number of multilocus phylogenetic methods are emerging that incorporate information available from incomplete lineage sorting under a coalescent framework in order to infer the species phylogeny (reviewed by Edwards, 2009). We used the hierarchical model implemented in *BEAST v. 1.6.0 (Heled and Drumond, 2010), that co-estimates the species tree and all gene trees in one Bayesian MCMC analysis, to estimate a species tree phylogeny for *Rhynchoedura*. The *BEAST analysis requires a priori designation of species. To be conservative in our approach, we used only those 43 individuals for which we had complete data for each gene, and used the results of our partitioned Bayesian analysis of the concatenated nDNA and mtDNA analysis, which suggested five species. We also ran additional *BEAST analyses based on the nDNA. We partitioned our data by codon position for *nd2* and *rag1*, and by gene for the two introns. Initially we ran the analysis using the same models as the MrBayes analyses, selected under the AIC in MrModeltest. However, many of the parameters failed to converge which we attribute to prob-

lems with over-parameterisation. Instead, we used simpler models selected under the BIC in Modelgenerator (Keane et al., 2006) (*bzw1*: HKY + I; *nad2*: TrN + I; *rag1*: HKY; *snrpd3*: HKY + G), but removed the invariant sites parameter from *bzw1* and *nad2*. We used a strict molecular clock, as trial analyses suggested the MCMC had difficulty fitting a relaxed clock to our data. Using the diagnostic software Tracer v.1.5 (Rambaut and Drummond, 2007) we were able to determine that the coefficient of variation frequency histograms for all loci abutted against zero, meaning our data could not reject the use of a strict clock (Drummond et al., 2007). Using a Speciation: Yule Process tree prior, we conducted four separate runs, with samples drawn every 10,000 steps over a total of 100 million steps, with the first 10% discarded as burn-in. Acceptable convergence to the stationary distribution was checked by inspecting the posterior samples using Tracer. Effective sample sizes were >600 for all parameters, indicating sufficient sampling from the posterior. All runs produced the same topology with very similar posterior probabilities, so we combined runs to generate a single consensus tree.

2.5. Morphology

We examined specimens of *Rhynchoedura* housed in Australian museum collections, with detailed measurements recorded for a total of 268 specimens, 197 of which also were included in our mtDNA data set. Supplementary Table 1 gives locality information for all samples used, and Supplementary Table 3 presents the morphological characters measured and their descriptions. Measurements were made with electronic callipers to the nearest 1 mm, 0.5 mm or 0.1 mm as appropriate, while fine-scale measurements (i.e. orbit length) were made using a microscope eyepiece. Individuals were sexed by presence (males) of conspicuous bulges posterior to cloaca. We assigned the 197 individuals that we had mtDNA data to the relevant clade, and for the remaining specimens we used morphology and geographic distribution to assign them to clades. Preliminary analyses for *R. ornata*, the lineage for which had the largest sample size (113), did not reveal any evidence for sexual size dimorphism in the morphological characters we examined, so we pooled the sexes in our analyses.

We analyzed the morphological data in two ways. First we tested for significant differences in mean SVL among lineages with a one-way ANOVA. Because SVL was significantly different, we used ANCOVAs to analyze all body size variables with either SVL or HeadL as the covariate, as appropriate. We first tested for homogeneity of slopes and then deleted the interaction term if non-significant to test for differences in the interceps. If the intercepts were significantly different, we then used Tukey's post hoc test (alpha = 0.05) to further examine the differences among clades. We used ANOVAs to test for differences in the remaining continuous variables (AdjMen, IntNar, NarScales). Second, we analyzed the data with Principal Components Analysis (PCA; JMP 8.0), which does not identify groups *a priori*, to examine the patterns of relationship among all the morphological characters. We calculated standard principal components (PC) with variance–covariance and did two separate PCAs. The first included only continuous body size variables (the first 12 characters in Supplementary Table 3) and the second included all variables except for the number of mental scales. In each analysis the first PC was interpreted as largely representing variation in body size and the second PC summarized shape differences among clades. We present these data in terms of the mtDNA clades recovered from the molecular analysis, except for a distinctive morphotype from Queensland for which no tissues were available for analysis.

3. Results

3.1. Phylogenetic analyses

The final *nd2* mtDNA alignment consisted of 1035 nucleotide positions. The *rag1* nuclear exon consisted of 838 positions, the bzw1 intron consisted of 738 positions, and the snrpd3 intron consisted of 638 positions. The best-fit nucleotide substitution models selected for the mtDNA and nuclear data partitions for each analysis are provided in Supplementary Table 2.

The ML analysis of the large mtDNA nd2 dataset recoverd the same topology as Pepper et al. (2011b), comprising five well-supported divergent clades (Fig. 1): Kimberley/Top End, western/central desert, southern desert, NSW desert, and NSW desert narrow. The new mtDNA sequences added to our existing data set all grouped with the known mtDNA clades. The Bayesian analyses of the individual nDNA data sets showed varying levels of incomplete lineage sorting and so were unable to differentiate all of the major mtDNA clades. However, the Kimberley/Top End clade was recovered as monophyletic in both intron loci. When the nDNA genes were analyzed together, however, the topology generated from the concatenated nDNA data were in broad agreement with the mtDNA data results (Supplementary Fig. 2). When the mtDNA and nDNA data were combined the concatenated data resolved all taxa into monophyletic groups (Fig. 2A). For the concatenated analysis, Bayes Factors favored the gene and codon partition strategies (Supplementary Table 4). There was some conflict with the phylogenetic relationships inferred from the combined data compared to that of the mtDNA alone, where southern desert and NSW desert narrow are sister taxa, albeit with relatively low support (Fig. 2B). Fig. 1 shows a phylogeny of the full mtDNA data set constrained to summarize the results based on analyses of all the molecular data, including nDNA.

3.2. Bayesian species tree estimation

Our *BEAST analyses utilizing the combined mtDNA and nDNA data, as well as the nDNA data alone, produced the same topology as the partitioned Bayesian analysis of the concatenated data. The *Kimberley/Top End* clade is strongly supported as the most divergent lineage (pp 1.00), with w*estern/central* inferred to be the sister lineage to the three eastern lineages (pp 1.00). While there is good support for *NSW desert* being the sister lineage to s*outhern desert* and *NSW desert narrow* (combined data: pp 0.99, nDNA only: pp 0.89), there is less support for a sister relationship of s*outhern desert* and *NSW desert narrow* in the combined data analysis (pp 0.78) (Fig. 2).

3.3. Morphology

Supplementary Table 5 summarizes the morphological measurements and the results of the statistical tests. The ANCOVAs on body size variables and one-way ANOVAs on mean values of scale characters all show statistically significant differences across the clades in all variables except TrunkL (although this approached significance). We summarize the results of our PCA analyses in Fig. 3, where we show mean PC scores and standard deviations for the two analyses. For the PCA based on 12 body size variables, PC1 explains 62.0% of the variation, PC2 explains 8.3% of the variation and the mean PC scores varied significantly (PC1: $F_{5,262} = 3.48$, $P = 0.0046$; PC2: $F_{5,262} = 10.51$, $P = 0.0001$). For the PCA based on all variables, except for the number of mental scales, PC1 explains 39.8% of the variation, PC2 explains 11.8% of the variation and the mean PC scores varied significantly (PC1: $F_{5,262} = 4.75$, $P = 0.0004$; PC2: $F_{5,262} = 43.75$, $P = 0.0001$).
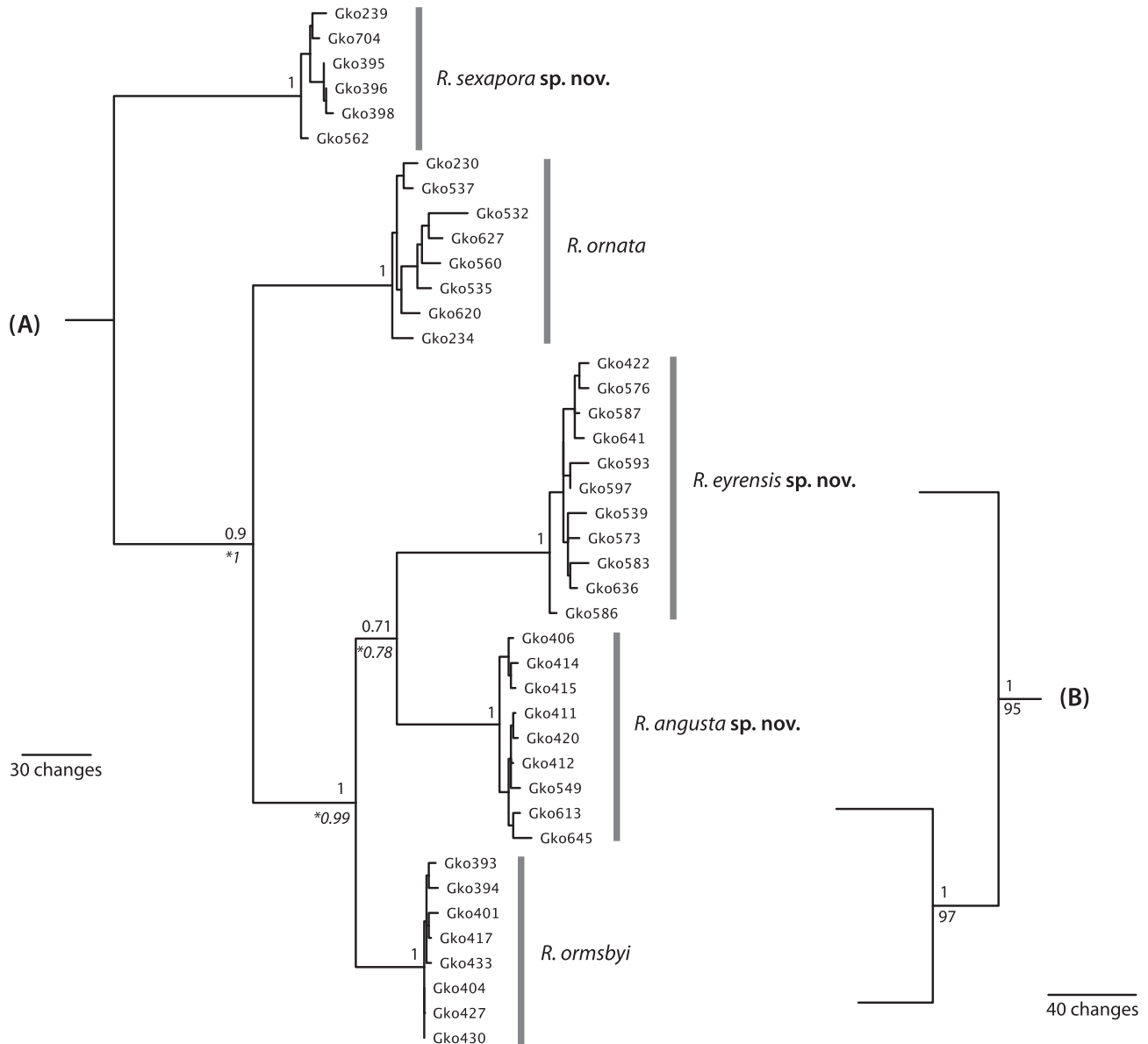
Fig. 2. (A) Phylogenetic tree showing the relationships among _Rhynchoedura_ taxa. Numbers above nodes represent posterior probabilities from the concatenated Bayesian analysis while numbers below the nodes with a '*' represent posterior probabilities from the *BEAST species-tree analysis of the mtDNA and nDNA data. (B) Phylogenetic relationships of the three south-eastern taxa inferred using mtDNA only. Numbers above the nodes represent posterior probabilities from the Bayesian analysis and numbers below the nodes represent bootstrap support from the RAxML analysis. Parsimony-based phylogenies are shown for ease of interpretation of branch lengths.

While there is considerable overlap among clades in most of the variables measured, our analyses show that most variables show significant differences among species (Supplementary Table 5) and our PCA analyses show consistent differences in body size (PC1) and shape (PC2). This result persisted even if we analyzed only the three south eastern clades which did not differ in body size (PC1: $F_{2,99} = 0.9642$, $P = 0.3849$) but did differ significantly in shape (PC2 on continuous characters only: PC2: $F_{2,99} = 36.7086$, $P = 0.0001$) and shape and scale differences (PC2 on all characters except number of mental scales: $F_{2,99} = 67.000$, $P = 0.0001$). Nonetheless, while these significant differences are based on a multivariate perspective of morphological differences, it remains that the three south eastern clades are difficult to distinguish based on individual characters.

Additional qualitative differences in scalation and coloration also were apparent among clades, which we describe below as a series of new species. Due to their relatively conservative morphology, we provide a generic diagnosis and description for

Rhynchoedura, before focusing on characters that vary among species for the redescription and descriptions of species.

3.4. Criteria for species recognition

Species concepts have been discussed among systematic biologists for many years. Over the last decade or so, the debate has become less strident and more focused on points of agreement. As discussed by De Queiroz (2007), different species concepts agree that the primary definition of a species is a goup of metapopulations that are evolving independently. The diagnosis of such separately-evolving entities is an issue for some 'cryptic' taxa that have not differentiated morphologically from close relatives. In this study, we found that Beaked Gecko populations from south-eastern Australia are recently diverged (<1.5 Mya, see Discussion) Pleistocene lineages (compared to the older _western/central desert_ divergence and much older _Kimberley/Top End_ divergence) and have undergone very little evolutionary change in morphology.
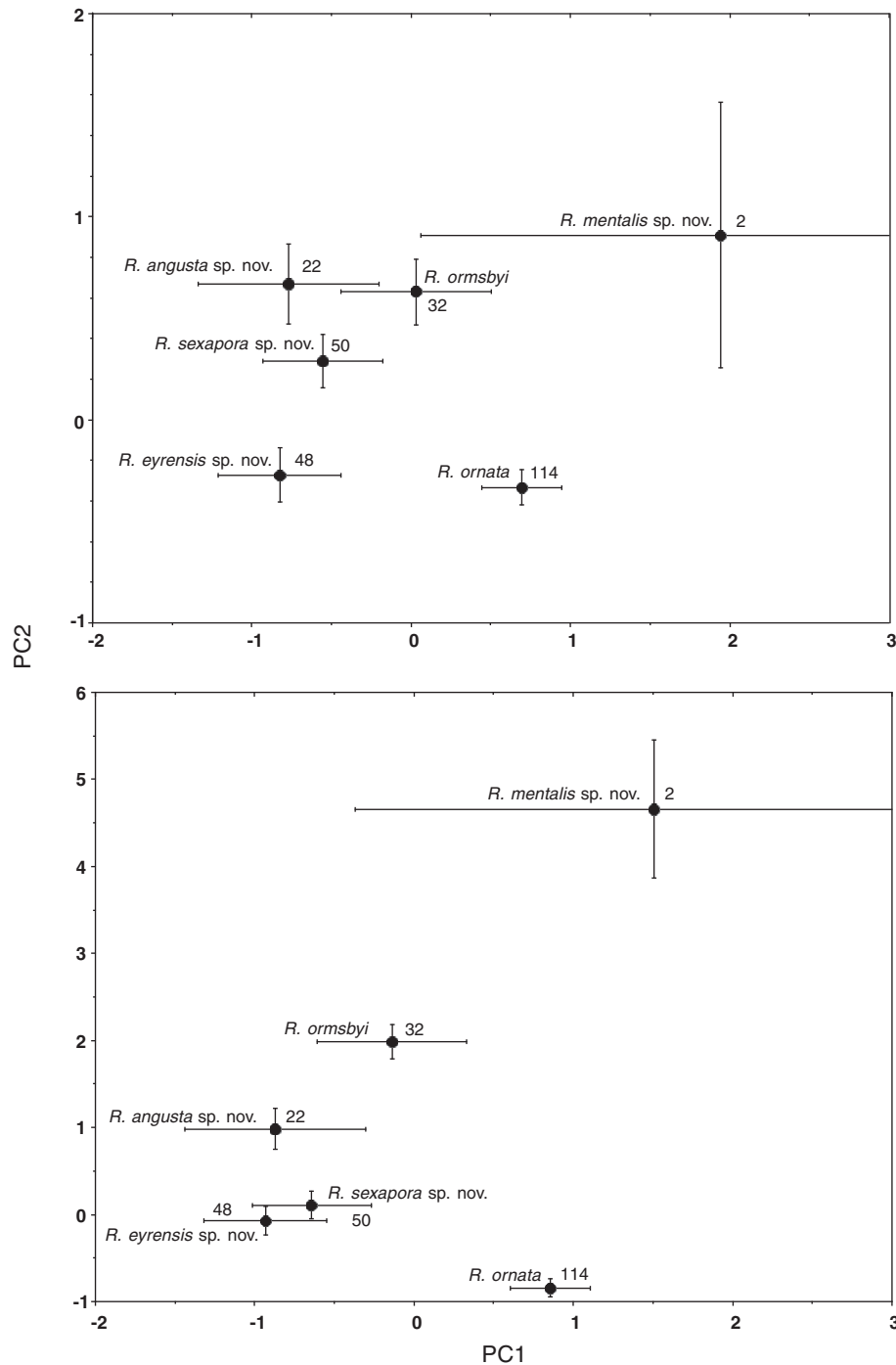
Fig. 3. Summary of results for the PCAs of the morphological data for 268 *Rhynchoedura* specimens. Mean PC scores and standard deviations are shown with sample sizes noted.

However, the molecular evidence for both divergent evolution and lack of mixing of gene pools establishes in our view that we have several groups of metapopulations that no longer engage in reticulate evolution with neighboring populations, even though these populations are closely abutting or possibly overlapping. Thus, for recognizing the three south-eastern taxa as full species we have largely relied on the molecular evidence, as our morphological data indicate widely overlapping characters with no clear way to reliably diagnose an ungenotyped individual. Nevertheless, the three south-eastern species are largely allopatric and have some subtle morphological differences which we report below. True *R. ornata*

from WA are diagnoseable by some morphological characters, although there is still overlap with the three south-eastern taxa. The more distantly-related northern species and the distinct QLD species have conspicuous morphological differences that reliably distinguish them from the other species and so are unproblematic.

3.5. Taxonomy

3.5.1. Rhynchoedura Günther, 1867

Rhynchoedura Günther, 1867, Ann. Mag. Nat. Hist., Ser. 2, 20: 50. *Type species*: *R. ornata*, by monotypy.

The diagnosis and description below apply to all *Rhynchoedura* species. For the species described and redescribed below, only characters that depart from the generic diagnoses and descriptions are provided for brevity.

Diagnosis. A genus of diplodactylid geckos defined by small body size (to 57 mm SVL), slender cylindrical body shape, head small and narrow with protruding eyes with overhanging brow, short sharp snout terminating in beak-like projections formed by enlarged rostral and mental scales, labial scales not enlarged relative to neighboring scales, neck and tail long and slender; limbs short and gracile, digits covered in fine scales terminating in a sharp claw surrounded by a sheath of modified scales (no expanded apical plates), 2–6 pre-anal pores, cloacal spurs comprising 1–3 enlarged pointed scales, and body covered with fine homogeneous scales. Internal morphology: lacrimal contacting dorsally expanded lateral process of prefrontal, four phalanges on fourth finger, vertebral count 27, and lateral and medial pairs of cloacal bones absent (Oliver et al., 2007a).

Dorsal pattern is complex, consisting of a dark background color often with a light vertebral zone with transverse barring; usually small to large white to yellow spots covering entire dorsum and head or confined to flanks; labials and scales bordering eye whitish to yellow; usually a pale spot dorso-posterior to eye; transition to ventrum abrupt; ventrum immaculate to pale off-white; original tail pattern mirrors pattern on body.

3.5.2. Rhynchoedura ornata Günther, 1867

Rhynchoedura ornata Günther, 1867, Ann. Mag. Nat. Hist., Ser. 2, 20: 51.

Western Beaked Gecko (Fig. 4A, Supplementary Figs. 3 and 4).

Holotype. BMNH 1946.8.20.50, from Nickol Bay, WA (Supplementary Fig. 3).

Diagnosis. Morphologically distinguished from *Rhynchoedura sexapora* sp. nov. by two oblong, enlarged preanal pores, relatively flat dorsal and ventral scales approximately equal in size, and small scales on digits, and from *Rhynchoedura mentalis* sp. nov. by having a single enlarged mental scale and cloacal spurs formed by a single enlarged scale; morphologically similar to remaining species of *Rhynchoedura*, but reaches a larger maximum size (to 57 mm SVL) and usually has an ungrooved rostral scale.

Description. Body size relatively large (to 57.0 mm SVL); rostral without medial groove; two oblong enlarged (4–6 typical scales long) pre-anal pores in contact and medial edge angled slightly anteriorly (Fig. 5a); cloacal spurs in males comprising a single enlarged scale, often ringed at the base by slightly larger scales than surrounding scales.

Dorsal pattern complex and highly variable (Supplementary Fig. 4), consisting of a dark ground color with a discernible pale amoeboid vertebral zone with irregular edges and often forming wide transverse bars; the entire dorsal surface including the top of the head is overlain with medium to large pale white to sulfur
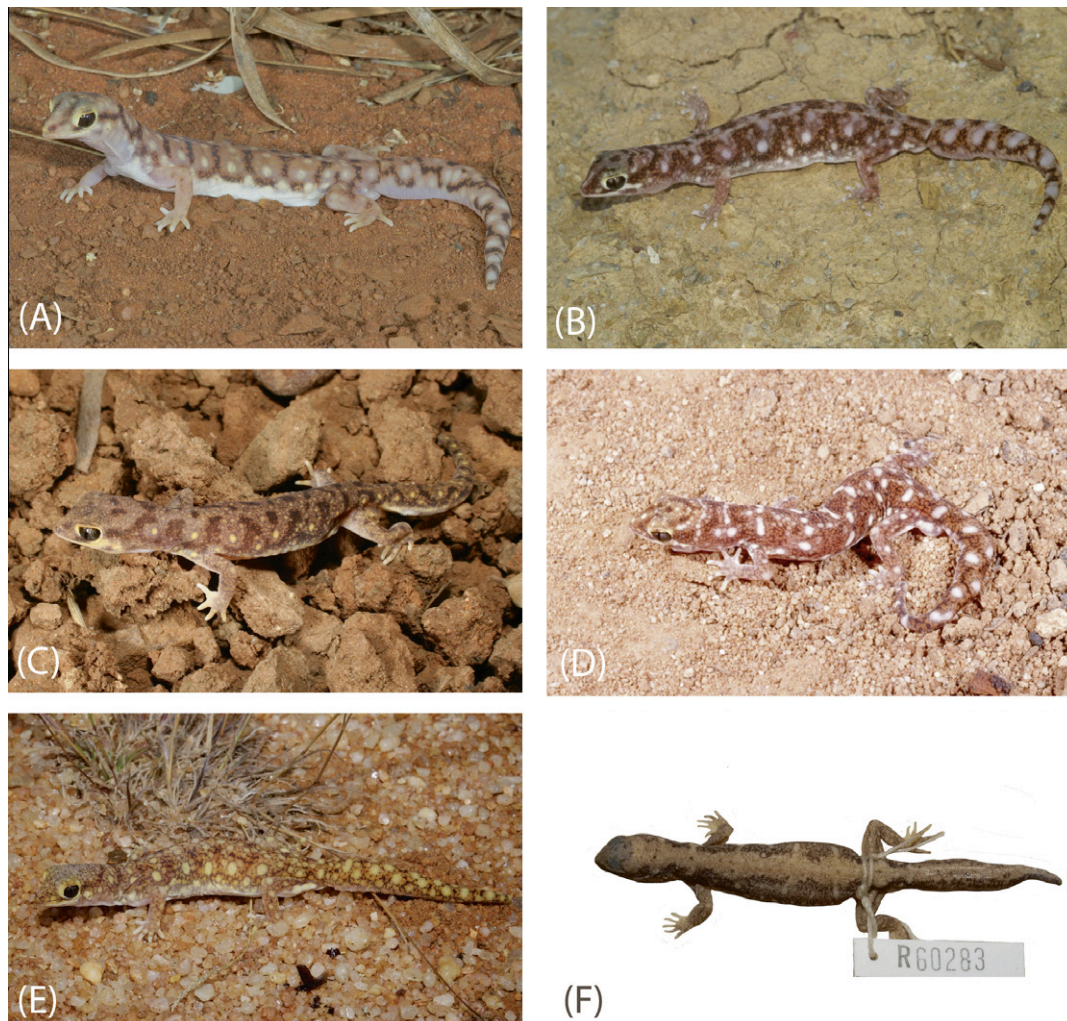
Fig. 4. (A) *Rhynchoedura ornata* in life: Tanami Desert, NT (image: Stewart Macdonald); (B) *R. eyrensis* sp. nov. in life: Stuart Creek, SA (image: Mark Hutchinson); (C) *R. sexapora* sp. nov. in life: Kimberley, WA (image: Paul Doughty); (D) *R. ormsbyi* in life: Nocoleche Nature Reserve, NSW (image: Ross Sadlier); (E) *R. angusta* sp. nov. in life: Noonbah Station, QLD (image: Angus Emmott); (F) *R. mentalis* sp. nov.: Mariala National Park, QLD (holotype).
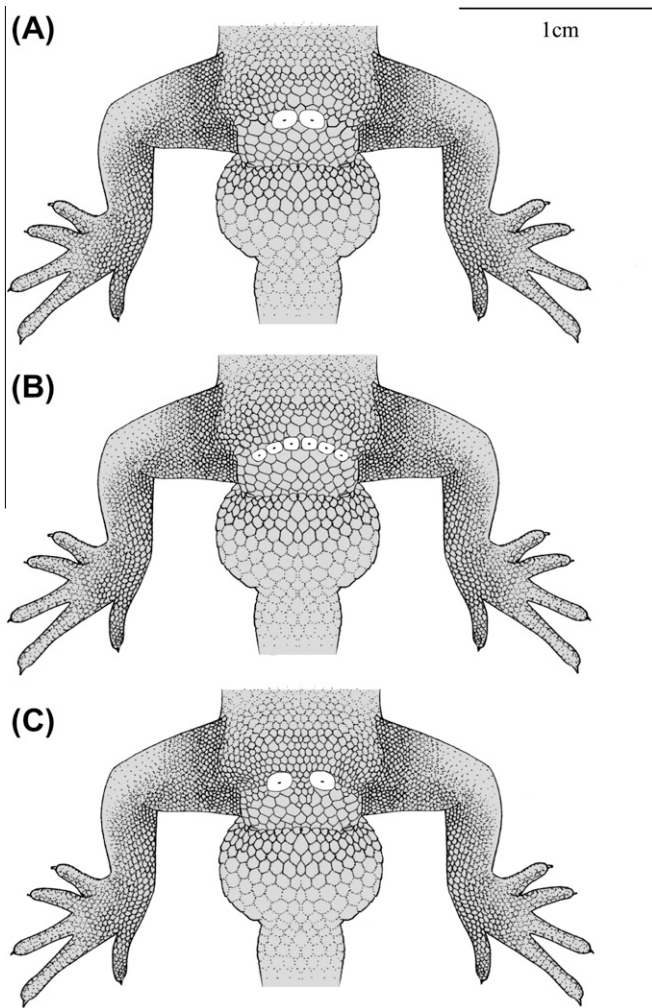
Fig. 5. Arrangement of the pre-anal pores in *Rhynchoedura* species: (A) typical *Rhynchoedura* arrangement (*ornata*, *angusta* sp. nov., *eyrensis* sp. nov., *ormsbyi*), (B) *R. sexapora* sp. nov., (C) *R. mentalis* sp. nov.

spots with brown borders, often giving the appearance of a dark reticulum; labial and scales bordering eye pale to yellow; usually a pale spot dorso-posterior to eye; ventral surface immaculate to a pale off-white; canthal stripes present and often extend to above eye; often a diffuse streak behind eye, sometimes connecting with dark nuchal band; transition from dorsal to ventral pattern abrupt; limb pattern as for dorsum except more subdued; tail as for body.

Habitat. Widely distributed in the western arid zone, including sandy deserts, spinifex grasslands, and mulga woodlands.

Distribution. This species occurs in the western arid zone of Australia, including north to the Great Sandy Desert, south to the edge of the arid zone (excluding the wheatbelt), and east to the western portions of the NT and SA (Fig. 1).

3.5.3. Rhynchoedura sexapora sp. nov

Northern Beaked Gecko (Figs. 4c and 5b, Supplementary Figs. 5 and 6).

Holotype. WAM R170241 (formerly AMS R139904) (male), collected from El Questro Station, WA (−16.01861°S, 128.00389°E), on 1 September 1992 by H. Cogger et al. (Supplementary Fig. 5).

Paratypes. WAM R164785 (female), 35 km W Kununurra, WA (−15.8486°S, 128.4244°E); WAM R132755 (female), Carlton Hill Station, WA (−15.0400°S, 128.8914°E); AMS R117265 (male), track to Hann Yards, Barnett River, WA (−16.7833°S, 125.8500°E); AMS

R139902 (male), AMS R139905 (female), AMS R139903 (female), El Questro Station, WA (−16.0186°S, 128.0039°E).

Diagnosis. Morphologically distinguished from congeners by six (occasionally four) slightly enlarged round pre-anal pores in a shallow 'V' pointing anteriorly (Fig. 5b) and dorsal scales moderately gabled, ventrals slightly larger than dorsal scales (rather than all scales flat and subequal). Further distinguished from *R. mentalis* sp. nov. by having a single mental scale and cloacal spurs formed by a single enlarged scale. Dorsal pattern differs from other species (except *R. mentalis* sp. nov.) by having a brown background color darker and with smaller pale spots (Fig. 4c, Supplementary Fig. 6).

Description. Body size relatively small (to 48.5 mm SVL) with small limbs; projecting rostral and a single enlarged mental scale surrounded by only slightly enlarged scales; rostral with median groove; limbs relatively short; dorsal scales moderately gabled with apex directed posteriorly; ventral scales flatter than dorsals and slightly larger; six (occasionally four) pre-anal pores that are only slightly enlarged and round (Fig. 5b); pores in close contact forming a weak chevron directed anteriorly, cloacal spurs in males comprising a single enlarged scale, often ringed at the base by slightly larger scales.

Dorsal pattern complex and variable (Supplementary Fig. 6); dark brown ground color with lighter tan vertebral zone with short transverse processes or connected blotches that extend to flanks; covered with small pale spots, especially towards flanks and less dense and smaller in vertebral zone; head pale without conspicuous spotting; eye rimmed with white to yellow; canthal stripe poorly defined or absent; diffuse streak behind and above eye diffuse, rarely connecting to a nuchal band; labials pale; a pale spot or blotch behind and below eye; pattern on limbs similar but subdued and tips of digits pale; tail as for body.

Habitat. Occurs on many different soil types within subtropical forests of northern Australia. Collector's notes indicate occurring on many surfaces, such as laterite, sandplains, stony soils, basalt flats, 'hard red brown clay', reddish sand or soil and sandy loams. Known to shelter in spider burrows during the day.

Distribution. This species occurs in the Kimberley region in WA and extends east to below the NT's Top End region (Supplementary Fig. 7).

Etymology. sexapora is derived from the Latin *sex* (six) and *porus* (pore), referring to the condition of the pre-anal pores. Used as an adjective: 'six-pored'.

3.5.4. Rhynchoedura mentalis sp. nov

Brigalow Beaked Gecko (Figs. 4f, 5c, and 6b, Supplementary Fig. 8).

Holotype. AMS R60283 (female), collected 54 km north of Blackall, QLD (−17.6167°S, 123.6000°E), on 30 December 1977 by P. Rankin and G. Husband (Fig. 4f, Supplementary Fig. 8).

Paratype. QM J88376 (male), collected from Mariala National Park, QLD (−26.09°S, 145.07°E).

Diagnosis. Distinguished from all other *Rhynchoedura* by possession of three enlarged mental scales and cloacal spurs comprising two to three enlarged scales; further distinguished from *R. sexapora* sp. nov. by two round, enlarged preanal pores, and dorsal and ventral scales flat and similar in size.

Description. SVL to 50.0 mm; snout terminating in a beak-like structure formed by a projecting rostral and three enlarged mental scales; rostral without medial groove; two round slightly enlarged pre-anal pores separated by 2–3 scales; cloacal spurs in males comprising 2–3 enlarged scales, often ringed at the base by scales slightly larger than surrounding scales.

Dark brown to black ground color; tan vertebral stripe with straight edges (AMS R60283) to pale vertebral stripe formed by irregularly-shaped interconnected blotches (QM J74892 and J88376); top of head pale, not covered in spots; flanks with small
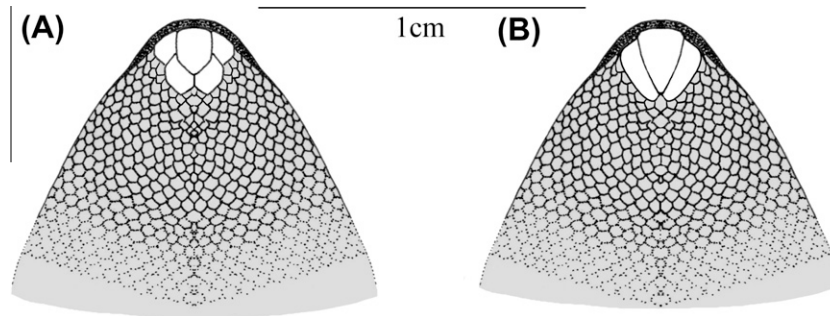
Fig. 6. Ventral view of chin showing arrangement of the mental scales in *Rhynchoedura* species: (A) typical *Rhynchoedura* configuration; (B) configuration in *R. mentalis* sp. nov.

fine spots, not occurring in vertebral zone; AMS R60283 (holotype) has short transverse blotches connected to the vertebral stripe (Supplementary Fig. 8).

Habitat. All specimens have been collected from near mulga (*Acacia aneura*) sites with clay soils.

Distribution. *R. mentalis* sp. nov. is only known from three specimens in QLD. Two specimens were collected from Mariala National Park and the other specimen from between Blackall and Longreach. It is thus the most restricted species of *Rhynchoedura*, although further surveys from the region may expand its distribution in the mulga woodlands of inland QLD and possibly to NSW.

Etymology. *mentalis* refers to this species' unique mental scale configuration within *Rhynchoedura*. Used as a noun in apposition.

Remarks. We recommend the conservation status of *R. mentalis* sp. nov. is listed as 'data deficient'. Its known geographic range is very small (Fig. 1) and it is only known from three individuals in museum collections (all Australian museum specimens have been examined, thus it is unlikely there are further unidentified specimens). Two specimens come from Mariala National Park, where the species is likely secure.

No tissue samples currently exist to test the genetic affinities of *R. mentalis* sp. nov. with other *Rhynchoedura*. The pre-anal pore configuration appears to be intermediate between the presumably ancestral multiple-pore arrangement in *R. sexapora* sp. nov. and the unique highly derived arrangement in the other species.

3.5.5. Rhynchoedura ormsbyi Wells & Wellington, 1985

Rhynchoedura ormsbyi Wells & Wellington, 1985, Aust. J. Herpetol., Supplementary Ser. 1: 15.

Eastern Beaked Gecko (Fig. 4d, Supplementary Fig. 9).

Holotype. AMS R116979, formerly AM Field series no 16781, from Round Hill Nature Reserve, NSW.

Diagnosis. Morphologically distinguished from *R. sexapora*, and *R. mentalis* by a combination of a single enlarged mental scale, two oblong enlarged pre-anal pores in contact, cloacal spurs formed by a single enlarged scale, and dorsal and ventral scales flat and similar in size; smaller species than *R. ornata* (max SVL 50 mm), and can be further distinguished by usual presence of a rostral with a strong medial groove. Scalation and proportions similar to *Rhynchoedura eyrensis* sp. nov. and *Rhynchoedura angusta* sp. nov. but dorsum covered with small to medium pale white to sulfur spots. *R. ormsbyi* also has a longer internarial distance (Inar) relative to head length, round rather than elongate mental scale (lower mental length/width [MenL/W] ratio), fewer adjacent mental scales (AdjMen), more internarial scales (IntNar), and longer mental groove than both *R. angusta* sp. nov. and *R. eryensis* sp. nov.

Description. SVL to 50.0 mm; snout terminating in a beak-like structure formed by a projecting rostral and a single enlarged mental scale (Fig. 6a); rostral usually with a strong medial groove that typically extends down more than 50% (and up to 100%) of the

scale; digits surrounded by fine scales; two enlarged oblong pre-anal pores in contact and angled slightly anteriorly (Fig. 5a); cloacal spurs in males comprising a single enlarged scale, often ringed at the base by scales slightly larger than surrounding scales.

Dorsal pattern complex and variable (Supplementary Fig. 9), consisting of a dark ground color with a discernible pale vertebral zone with wavy edges, but not tending to form transverse bars; the entire dorsal surface including the top of the head is overlain with numerous small pale white to sulfur spots with brown borders, with spots tending to be larger on the flanks and occur on top of darker lateral markings; labial and scales bordering eye pale to yellow; canthal stripe and streak posterior to eye poorly defined, if connecting to a nuchal band there is usually a medial gap; white spot behind lower corner of eye conspicuous; upper labials pale white to yellow, especially posteriorly; ventral surface immaculate to a pale off-white; transition from dorsal to ventral pattern abrupt, although outlines of spots sometimes discernible on venter below transition; limb pattern as for dorsum except more subdued; tail as for body.

Habitat. Distributed in the low-lying eastern arid zone, comprising alluvial floodplains and mulga and eucalypt woodlands.

Distribution. Distributed in the eastern lowlands (Fig. 1), in the northern part of the Murray–Darling basin and throughout the Cobar Peneplain and Mulga Lands bioregions in NSW and QLD.

Remarks. In their self-published catalog, Wells and Wellington (1985) proposed the name *R. ormsbyi* for populations from 'New South Wales'. The holotype is from Round Hill Nature Reserve near Euabalong, NSW, which is in the distributional range of our lineage *NSW desert*.

3.5.6. Rhynchoedura eyrensis sp. nov

Eyre Basin Beaked Gecko (Fig. 4b, Supplementary Figs. 10 and 11).

Holotype. SAMA R54267 (male), collected 2.8 km northwest of Kannakaninna waterhole, Kalamurina Station, SA (−27.8506°S, 137.8692°E) on 12 November 2000 by Jeff Foulkes (Supplementary Fig. 10).

Paratypes. SAMA R46205 (male) collected from Halifax Hill, SA (−29.6839°S, 135.8153°E); SAMA R52745 (female) collected from Plumbago Station, SA (−32.0500°S, 139.8333°E); SAMA R52795 (female) collected from Hamilton Homestead, SA (−26.7553°S, 135.1194°E); SAMA R52824 (male) collected from Macumba Station, SA (−26.8233°S, 136.0719°E); SAMA R52870 (female) collected from Todmorden Station, SA (−27.2044°S, 134.9944°E).

Diagnosis. Morphological diagnosis as for *R. ormsbyi*, except that *R. eyrensis* sp. nov. tend to have larger pale spots that often merge to form elongated blotches. *Rhynchoedura eyrensis* sp. nov. also tends to have shorter arms and legs (relative to SVL) and more narial scales (NarScales) than both *R. angusta* sp. nov. and *R. ormsbyi*.

Description. Body size relatively small (to 51.0 mm SVL); snout terminating in a beak-like structure formed by a projecting rostral and a single enlarged mental scale (Fig. 6a); rostral usually with a medial groove that typically extends down 30% (but up to 70%) of the scale; digits surrounded by fine scales; two enlarged oblong pre-anal pores in contact and angled slightly anteriorly (Fig. 5a); cloacal spurs in males comprising a single enlarged scale, often ringed at the base by scales slightly larger than surrounding scales.

Dorsal pattern complex and variable (Supplementary Fig. 11), consisting of a dark ground color with a discernible pale vertebral zone with wavy edges sometimes forming transverse bars comprising merged spots; the entire dorsal surface including the top of the head is overlain with small to medium pale white to sulfur spots with brown borders, with spots tending to be larger on the flanks and occur on top of darker lateral markings; labial and scales bordering eye pale to yellow; canthal stripe and streak posterior to eye poorly defined, if connecting to a nuchal band there is usually a medial gap; white spot behind lower corner of eye conspicuous; upper labials pale white to yellow, especially posteriorly; ventral surface immaculate to a pale off-white; transition from dorsal to ventral pattern abrupt, although outlines of spots sometimes discernible on venter below transition; limb pattern as for dorsum except more subdued; tail as for body.

Habitat. Occurs on many different soil types within the eastern arid zone, including floodplains, and sandy and stony desert terrains.

Distribution. This species is widely distributed throughout the eastern half of SA, probably extending into the south-eastern NT and south-western QLD, including in the Simpson, Strzelecki, and Sturt Stony Deserts and the Channel Country.

Etymology. eyrensis refers to the distributional area of this species across the Lake Eyre Basin in central/southern Australia.

3.5.7. Rhynchoedura angusta sp. nov

Border Beaked Gecko (Fig. 4e, Supplementary Figs. 12 and 13).

Holotype. AMS R152940, an adult male collected 5 km south of Millers Tank on Miller Road, Sturt National Park, NSW ($-29.0333°$S, $141.7333°$E) on 30 September 1998 by G. Swan et al. (Supplementary Fig. 12).

Paratypes. AMS R150161 (female), collected from Mootwingee National Park, NSW ($-31.28333°$S, $142.25°$E); AMS R152927 (male) ($-29.0558°$S, $141.8983°$E); AMS R155270 (female) ($-29.0311°$S, $141.4508°$E); AMS R152966 (male) ($-29.0494°$S, $141.8608°$E); AMS R152941 (male) ($-29.0333°$S, $141.7333°$E) all collected from Sturt National Park, NSW.

Diagnosis. Morphological diagnosis as for R. ormsbyi except that R. angusta sp. nov. tend to have fewer small, well-defined spots. R. angusta sp. nov. tends to have longer arms (relative to SVL), smaller distance from nostril to eye (NarEye) relative to HeadL, and fewer NarScales than R. eyrensis.

Description. Body size relatively small; snout terminating in a beak-like structure formed by a projecting rostral and a single enlarged mental scale (Fig. 6a); rostral usually with a medial groove that typically extends down 30% (but up to 55%) of the scale; digits surrounded by fine scales; two enlarged oblong pre-anal pores in contact and angled slightly anteriorly (Fig. 5a); cloacal spurs in males comprising a single enlarged scale, often ringed at the base by scales slightly larger than surrounding scales.

Dorsal pattern complex and variable (Supplementary Fig. 13), consisting of a dark ground color with a discernible pale vertebral zone with wavy edges tending to form transverse bars comprising merged spots; the entire dorsal surface including the top of the head is overlain with small to medium pale white to sulfur spots with brown borders, with spots tending to be of similar size across the dorsum and occur on top of darker lateral markings; labial and scales bordering eye pale to yellow; canthal stripe and streak pos-

terior to eye poorly defined, if connecting to a nuchal band there is usually a medial gap; white spot behind lower corner of eye conspicuous; upper labials pale white to yellow, especially posteriorly; ventral surface immaculate to a pale off-white; transition from dorsal to ventral pattern abrupt, although outlines of spots sometimes discernible on venter below transition; limb pattern as for dorsum except more subdued; tail as for body.

Habitat. Distributed in the alluvial floodplains of the Channel Country, on Mitchell grass and Spinifex grasslands.

Distribution. This species has a narrow north–south trending distribution conforming to the Bulloo-Bancannia drainage division, that extends north of Renmark, SA to Longreach in central Queensland (Fig. 1).

Etymology. angusta is Latin for narrow/constricted, in reference to the narrow north–south distribution of this species. Used as a noun in apposition. Also in reference to Angus Emmott for his contribution to herpetology, and the collection locality of the northernmost extent of this species on his Noonbah Station property in Queensland.

3.5.8. Distinguishing among species

We recognize six species within Rhynchoedura. R. sexapora and R. mentalis are the most easy to diagnose based on the configuration of pre-anal pores and mental scales. R. sexapora is the only species to possess more than two pre-anal pores – usually six (occasionally four). R. mentalis is the only species with three enlarged mental scales (all other species have one mental scale which is smaller) and the two pre-anal pores are separated by several scales (versus in contact in R. ornata, R. ormsbyi, R. eyrensis, and R. angusta).

Aside from the two morphologially distinct species mentioned above, the other four taxa have few discrete morphological characters to differentiate them. R. ornata, however, can be differentiated from the south-eastern species, R. eyrensis, R. angusta, and R. ormsbyi, by larger maximum body size and the rostral is usually ungrooved. In addition, R. ornata occupies the western and central deserts and so far as we know is allopatric to the three south-eastern taxa.

The three south-eastern species R. eyrensis, R. angusta, and R. ormsbyi are morphologically very similar. The small morphological differences present among the three south-eastern taxa (see diagnosis for R. ormsbyi), apply to pooled population samples, and identifying an individual without locality data will be difficult without genotyping. Importantly, the three south-eastern species appear to be allopatric based on our extensive sampling and so geographic location will be essential in identification if a tissue sample (e.g. tail tip) is not available. R. mentalis appears to be sympatric with R. ormsbyi but can be distinguished by the mental scales and pre-anal pores (see above).

4. Discussion

Our study based on mitochondrial DNA, three nuclear DNA genes, and a comprehensive assessment of morphological variation, with dense sampling from across the vast arid zone range of Rhynchoedura, provides multiple lines of evidence for six species within the traditionally recognized monotypic genus. The mtDNA data alone provides strong support for five genetic groups (no genetic information is available for R. mentalis). Uncorrected pairwise genetic distances between these lineages range from 9% (angusta and ormsbyi) to 20% (angusta and sexapora) for the mtDNA data. When comparing nDNA versus mtDNA-based topologies for the Rhynchoedura lineages, there is conflict regarding the relationships of the three south-eastern taxa. This explains the lower support of these relationships in the *BEAST analysis of all the

molecular data compared to the *BEAST analysis of the nDNA loci alone, but each individual data set and the combined data provide clear evidence for species-level differences among these clades, as well as a robust, though not fully resolved, hypothesis of the relationships among them (Figs. 1 and 2, Supplementary Fig. 2). Our molecular data also provide one of the most comprehensive assessments of genetic variation across the Australian arid zone, with important implications for our understanding of arid zone diversity and biogeography.

4.1. Systematics

We interpret and revise the taxonomy of *Rhynchoedura* using the information from our collective analyses of the multi-gene data, including species tree reconstruction with *BEAST, in conjunction with morphological and distributional data. Our morphologicial analysis based on measurements of 268 individuals showed strong morphological conservatism across *Rhynchoedura*. When examined in light of the genetic clades, there were varying levels of corroborating evidence from morphology. The endemic Queensland species, *R. mentalis*, for which only three specimens exist and none with tissue samples taken, has a unique configuration of mental scales, pre-anal pores, and an unusual dorsal pattern featuring a wide vertebral stripe. The northern species, *R. sexapora*, is easily distinguished from all other *Rhynchoedura* by six (occasionally four) pre-anal pores instead of two. Discrimination of the arid zone lineages based on morphology alone is problematic because there are no simple binary characters that consistently differ among them. *R. ornata* is consistently larger in adult body size, often possesses larger and more striking dorsal spots, and rarely has a groove in the rostral scale, unlike the south-eastern species. Although we were able to distinguish the three south-eastern species, *R. eyrensis*, *R. angusta*, and *R. ormsbyi*, from each other in our PCA, assignment of individuals to species will rely in practice on location data (their distributions are allopatric) or genotyping.

The Australian arid zone has long been recognized for its spectacularly rich and diverse lizard communities (Pianka, 1969, 1981, 1986,1989; Cogger, 1984; James and Shine, 2000). However, a number of recent molecular studies have highlighted the extraordinary underestimation of species diversity within the arid zone, with many 'species' actually comprising species complexes of multiple, morphologically similar, yet genetically distinctive taxa (see Section 1). Our study of *Rhynchoedura* adds to this growing body of literature, and demonstrates how genetic data can be essential for species delimitation in morphologically conservative groups, especially geckos (Aplin and Adams, 1998; Pepper et al., 2006, 2011a,b; Oliver et al., 2007b, 2011; Doughty et al., 2010; Fujita et al., 2010).

4.2. Biogeography

Our dense sampling of *Rhynchoedura* across the arid zone allows a detailed assessment of the geographic structure of mtDNA clades in relation to landscape features. All taxa for which we have genetic material are well sampled throughout their range. *R. sexapora* is the most divergent species genetically and it also is the most geographically disjunct. This species has a distribution in the Kimberley region that extends east to below the Top End (Fig. 1, Supplementary Fig. 7), adding to the growing body of evidence that this isolated region harbors a unique and diverse biota (Bowman et al., 2010). The contacts between each of the arid zone taxa are extremely sharp (Fig. 1, Supplementary Fig. 1). At the broadest geographic scale, the strong influence of topography is immediately apparent. The distribution of *R. ornata* appears to be limited to the western uplands. This region is associated with the geographic extent of the Australian Craton, a vast and ancient geological struc-

ture representing the foundations of the Australian continent (Wasson, 1982) (Fig. 1, where high elevation is expressed in pale shades). In contrast, the three south-eastern *Rhynchoedura* lineages are distributed throughout the basins of the central lowlands (Fig. 1, where low elevation is expressed in dark gray). To our knowledge, the broad topographic distinction between the western uplands and central lowlands has not been commented on in previous molecular studies. Examination of the published literature, however, reveals coincident geographic patterns of divergence across other arid zone taxa. In particular, the detailed study of Shoo et al. (2008) of the pebble-mimic dragons shows a similar east/west division and the distribution of major clades is likely related to this topographic divide. Given the substantial environmental and climatic differences between these upland and lowland regions, further molecular studies across this landscape juncture are needed to test the generality of this biogeographic pattern. *R. mentalis* appears to be found in sympatry with *R. ormsbyi*, at least in part of their range in Mariala National Park in southern QLD (Fig. 1). However, a lack of genetic material and only three specimens from geographically close collection localities precludes us from commenting on the phylogeographic patterns of *R. mentalis*.

In a recent study of Australian arid zone biogeography using a number of gecko taxa, Pepper et al. (2011b) dated the age of lineage diversification in *Rhynchoedura* as well as the time to most recent common ancestor (TMRCA) of each of the mtDNA clades. While deep lineage divergences were inferred to be of mid-Miocene age (10–15 Mya), the lack of genetic variation within clades was attributed to substantial population bottlenecks following the onset of Pleistocene aridification in the Australian arid zone, with the south-eastern lineages (*southern desert*, *NSW desert narrow* and *NSW desert*) inferred to have TMRCA's of <1.5 Mya. This arid history offers a plausible explanation for the genetic architecture of *Rhynchoedura* lineages (reviewed in Pepper et al., 2011b). However, the present day geographic distributions of the south-eastern *Rhynchoedura* lineages show an intriguing correlation to the three main drainage divides and river channels of the Interior Lowlands (Fig. 1). For example, the distribution of *R. eyrensis* conforms to the extent of the Lake Eyre topographic basin, one of the largest internally draining systems in the world (Alexandrre et al., 2004). The easternmost lineage *R. ormsbyi* is distributed throughout the Murray-Darling drainage division. This immense catchment system incorporates a number of Australia's longest rivers, and the distribution of *R. ormsbyi* appears to be limited in its southern extent by the Murray River. *R. angusta* has a peculiar narrow north–south distribution between the Lake Eyre and Murray Darling drainage divisions, a pattern remarkably similar to that of the Bulloo-Bancannia Basin. While the southernmost samples of *R. angusta* extend south of the Bulloo-Bancannia Basin, in this region they appear to be bound by the Darling River to the east, and the Flinders, Lofty, and Olary Ranges to the west.

The precursors of these major drainage divides are ancient, and are thought to already have been established in the Cretaceous (Quilty, 1994). While tectonic movements such as uplift of the eastern highlands and concomitant subsidence of the basins would undoubtedly have influenced the direction of channels within them since this time (Alley, 1998), the strong visual correlation between evolutionary lineages and drainage boundaries suggests broad-scale hydrology has played a role in driving the diversification of south-eastern *Rhynchoedura*. Despite the overarching trend towards permanent aridification of the arid zone from the mid-Miocene, where particularly dry phases would likely have lead to population contractions such as during the Pleistocene (Pepper et al., 2011a), discharge from eastern river systems is thought to have been substantially greater during intermittent wet intervals of the Miocene and Pliocene (Kershaw et al., 2003; Martin, 2006),

and would have been both temporally and spatially great enough to create barriers to dispersal for expanding *Rhynchoedura* populations, allowing them to diverge in allopatry. The ongoing cyclical nature of wet and dry phases, particularly during the Pleistocene where regular cycling between glacial and interglacial climates corresponded to periods of severe aridity and intervening wet interglacial periods in Australia, presumably could have reinforced this biogeographic pattern until the present time.

The structuring of genetic lineages by rivers and drainage divides in eastern Australia is well documented in arid and semi-arid freshwater biota (Unmack, 2001; Nguyen et al., 2004; Murphy and Austin, 2004; Carini and Hughes, 2004; Hughes and Hillyer, 2006; Thacker et al., 2007; Masci et al., 2008). Because freshwater fauna are biogeographically constrained by spatially and temporally disconnected drainages, they are considered more likely to reflect historical hydrological connections than terrestrial species (Avise, 2000). However, the biogeographic patterns observed in *Rhynchoedura* offer a unique perspective on terrestrial arid zone biogeography, one where deep genetic patterns may have been shaped not only by aridification, but also by drainage divisions and rivers during extreme wet periods. This result contrasts to studies of mesic-adapted arid zone reptiles that, as would be expected, show diversification between major lineages that is likely linked to extreme dry phases and divergence in refugia (Fujita et al., 2010; Pepper et al., 2011a,b). In addition, differences in habitat across the vast arid zone are likely to be important in unravelling the evolutionary history of *Rhynchoedura*, and a better understanding of the spatial distribution of sand dune systems, soils, and vegetation would be beneficial in a more complete understanding of genetic differentiation within the Beaked Geckos and other widely distributed arid zone taxa.

4.3. Conclusions

Genetic studies of widespread taxa in the Australian arid zone are scarce. Our biogeographic inference of *Rhynchoedura* is largely pattern-based, but given our sampling there are broad patterns that can be tested with unrelated taxa (Crisp et al., 2011). Despite vastly different ecologies, we have uncovered biogeographic patterns remarkably concordant with freshwater taxa, indicating the profound influence of palaeo and modern drainages on the evolutionary histories of both terrestrial and aquatic biota. These broad patterns will likely be reflected in other arid-adapted terrestrial vertebrates as molecular studies across this region accumulate. Indeed, examination of the published literature reveals the Lake Eyre and Murray Darling Basin regions are likely reflected in a number of other small arid zone vertebrates, including two Dasyurid marsupials (Blacket et al., 2000, 2001), a scincid lizard (Chapple and Keogh, 2004), and a dragon lizard (Shoo et al., 2008). As the current work demonstrates, using genetic information in conjunction with landscape history can offer insights into the historical biogeography of desert regions, in spite of the inherently poor records of palaeolandscapes and palaeoclimate in the arid zone. With the addition of finer-scale phylogeographic and phylogenetic studies, along with the development of sophisticated biogeographic models, a much better understanding of the complex history of the Australia arid zone may be possible.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.ympev.2011.08.012.

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Supplementary Figure 1
Distribution of Australian museum records (WAM, SAMA, AMS, QM, ANWC, NTM) (black dots) overlain with genotyped specimens for each Rhynchoedura taxon (colored dots). Colors are based on their mtDNA clade: Kimberely/Top End = red, western/central desert = blue, southern desert = yellow, NSW desert narrow = purple, NSW desert = green.

Supplementary Figure 2
Phylogenetic tree showing the relationships among Rhynchoedura taxa, based on a concatenated MrBayes analysis of nDNA data only. Numbers above nodes represent posterior probabilities. Individuals are colored based on their mtDNA clade: Kimberely/Top End = red, western/central desert = blue, southern desert = yellow, NSW desert narrow = purple, NSW desert = green.

Supplementary Figure 3
Holotype of Rhynchoedura ornata (BMNH 1946.8.20.50).

Supplementary Figure 4
Variation of dorsal pattern within Rhynchoedura ornata.

Supplementary Figure 5
Rhynchoedura sexapora sp. nov. (holotype, WAM R170241, formerly AMS R139904).

Supplementary Figure 6
Variation of dorsal pattern within Rhynchoedura sexapora sp. nov.

Supplementary Figure 7
Distribution of Rhynchoedura sexapora sp. nov. in northern Australia.

Supplementary Figure 8
Rhynchoedura mentalis sp. nov. (holotype, AMS R60283, paratype QM J88376).

Supplementary Figure 9
Variation of dorsal pattern within Rhynchoedura ormsbyi.

Supplementary Figure 10
Rhynchoedura eyrensis sp. nov. (holotype, SAMA R54267).

Supplementary Figure 11
Variation of dorsal pattern within Rhynchoedura eyrensis sp. nov.

Supplementary Figure 12
Rhynchoedura angusta sp. nov. (holotype, AMS R152940).

Supplementary Figure 13
Variation of dorsal pattern within Rhynchoedura angusta sp. nov.

Supplementary Figure 1
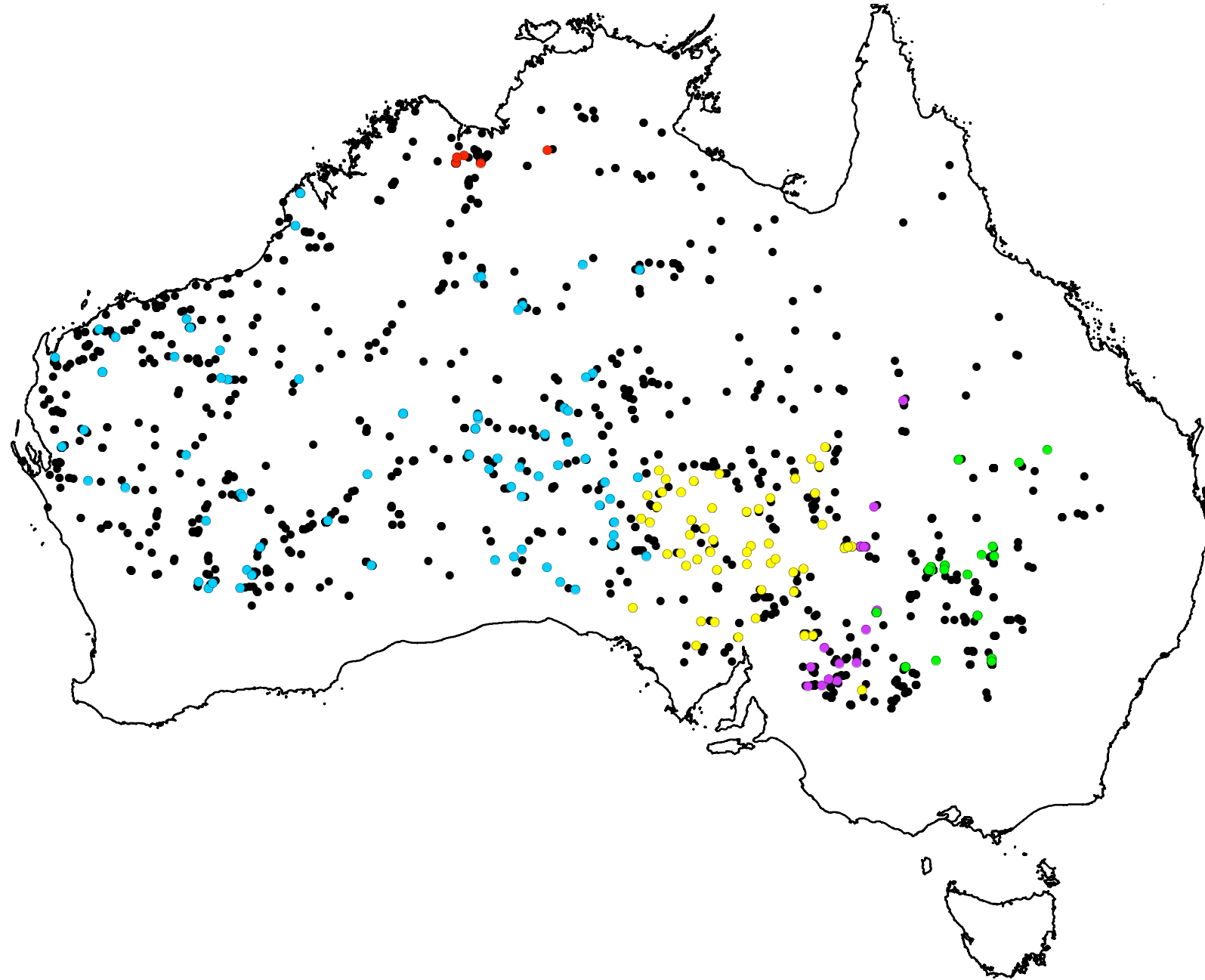
Supplementary Figure 2
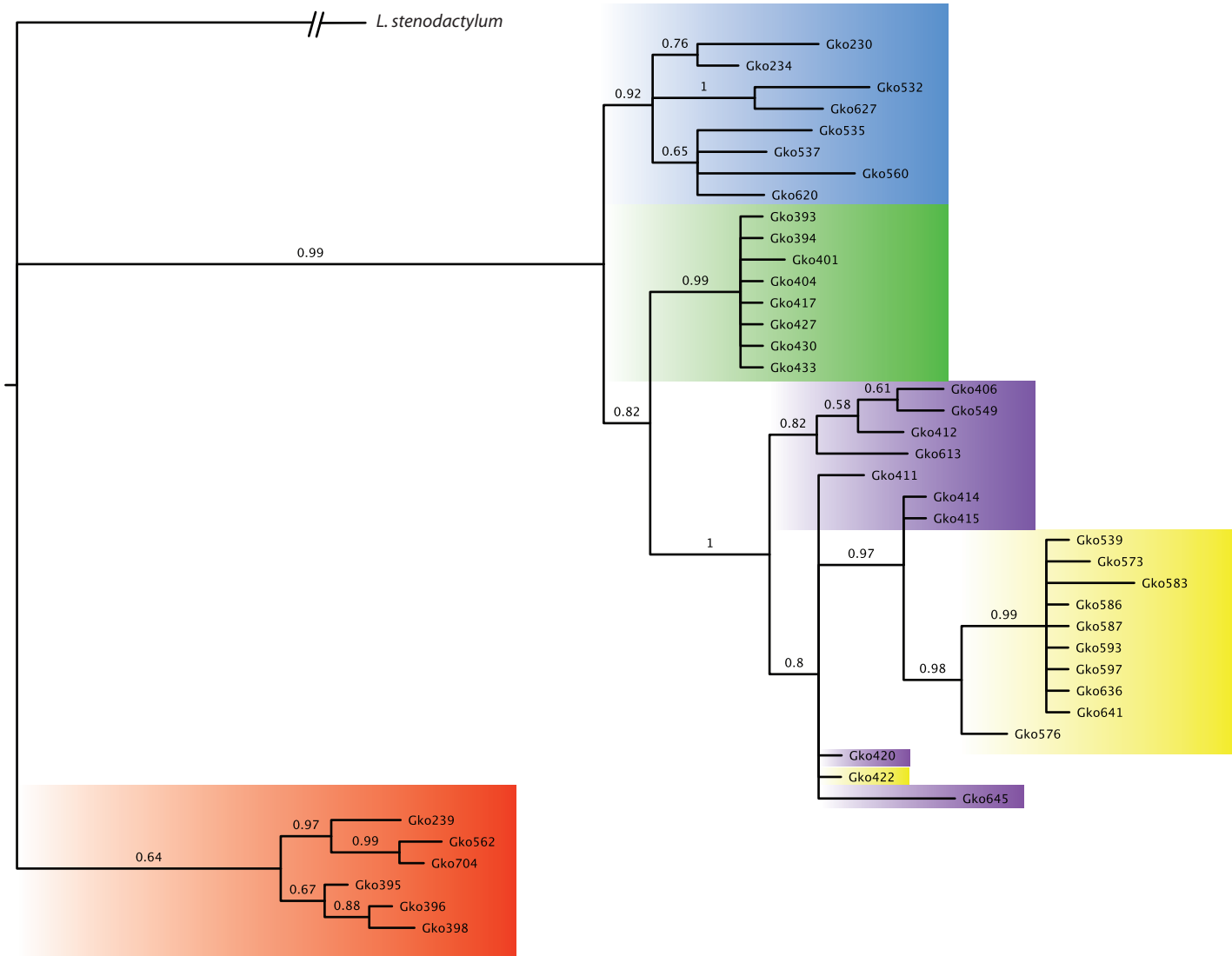
Supplementary Figure 3

Supplementary Figure 4

Supplementary Figure 5

1cm

Supplementary Figure 6

Supplementary Figure 7

Supplementary Figure 8

J 88376

R60283

1cm

Supplementary Figure 9

Supplementary Figure 10

1cm

Supplementary Figure 11

Supplementary Figure 12

Supplementary Figure 13

Supplementary Table #1. Museum accession numbers and collection locality information for all samples used in this study. Bold indicates the individual was sequenced for three nDNA loci.

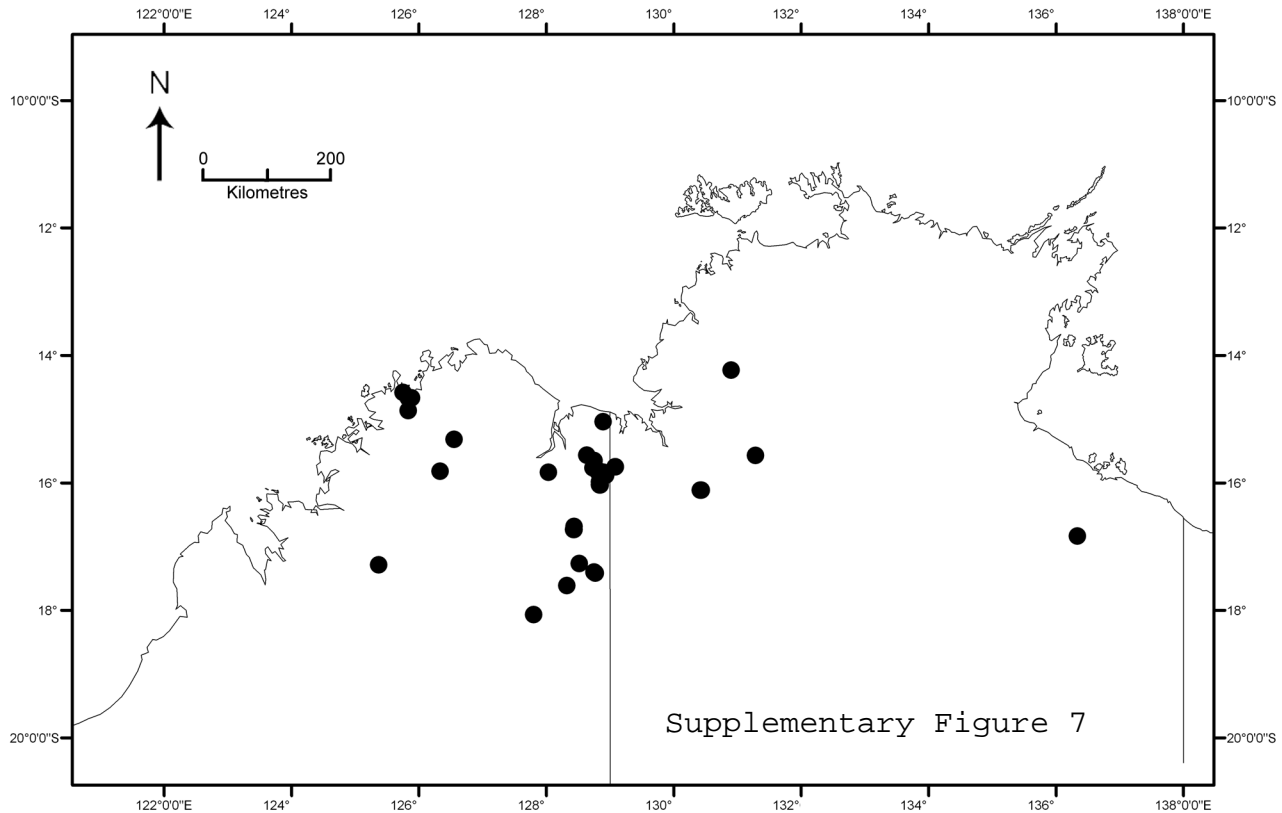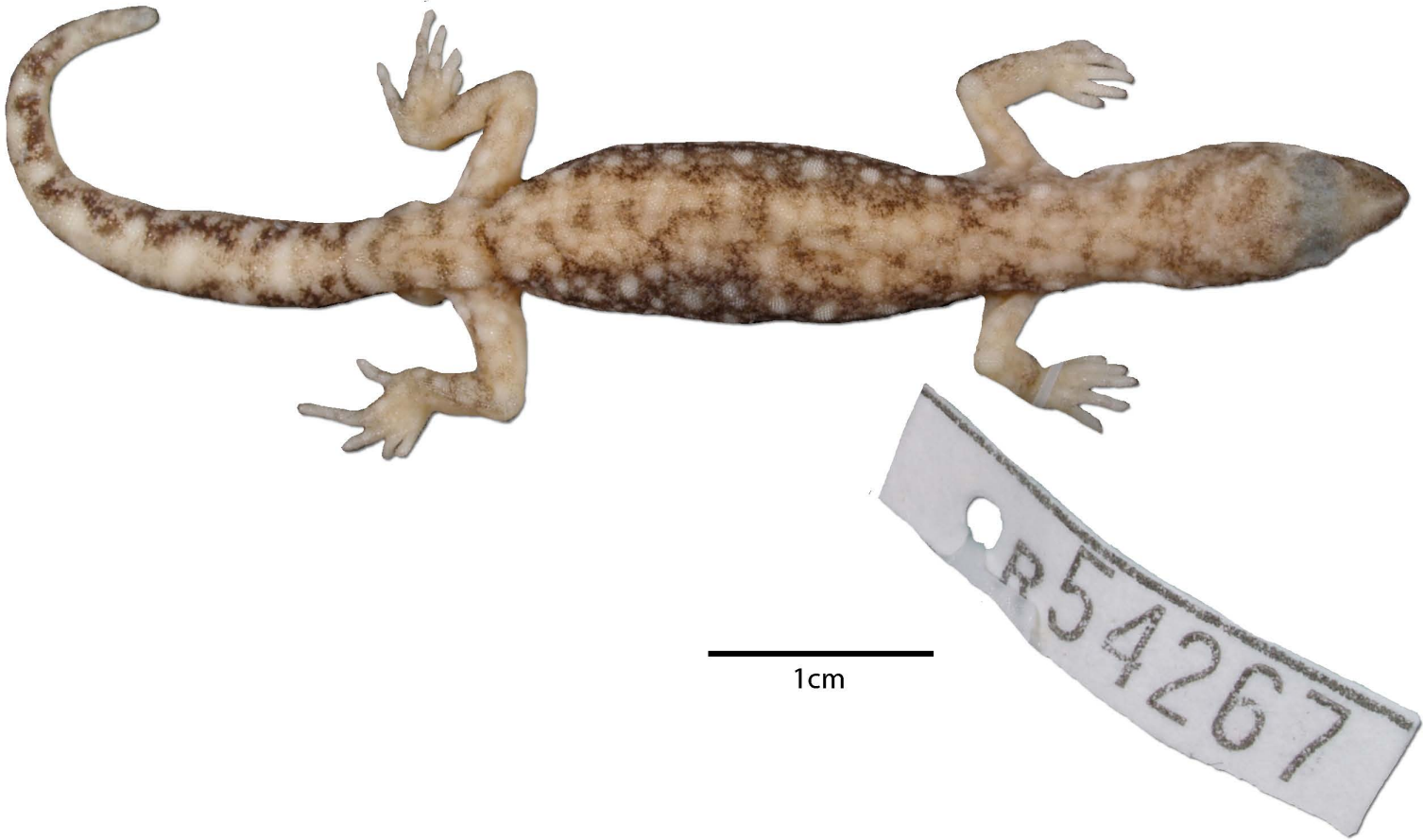| ID#	Museum #	Genus	species	Latitude	Longitude	State	Locality (nearest)
Gko230	WAMR84540	*Rhynchoedura*	*ornata*	-25.05000	128.66667	WA	Giles Creek
Gko231	WAMR84541	*Rhynchoedura*	*ornata*	-25.05000	128.66667	WA	Giles Creek
Gko232	WAMR84592	*Rhynchoedura*	*ornata*	-29.06667	121.35000	WA	Leonora
Gko233	WAMR100521	*Rhynchoedura*	*ornata*	-29.83333	120.91667	WA	Menzies
Gko234	WAMR102502	*Rhynchoedura*	*ornata*	-23.11306	116.01167	WA	Barlee Range
Gko235	WAMR110582	*Rhynchoedura*	*ornata*	-19.90278	128.76333	WA	Tanami Desert
Gko236	WAMR110583	*Rhynchoedura*	*ornata*	-19.90278	128.76333	WA	Tanami Desert
Gko237	WAMR112972	*Rhynchoedura*	*ornata*	-17.05972	122.71667	WA	Broome
Gko238	WAMR112983	*Rhynchoedura*	*ornata*	-17.05972	122.71667	WA	Broome
Gko239	WAMR132719	*Rhynchoedura*	*sexapora* sp. nov.	-15.77167	128.28806	WA	Wyndham
Gko240	WAMR144746	*Rhynchoedura*	*ornata*	-30.46667	119.60000	WA	Bungalbin Hill
Gko241	WAMR157554	*Rhynchoedura*	*ornata*	-21.67389	115.88917	WA	Pannawonica
Gko242	WAMR158315	*Rhynchoedura*	*ornata*	-22.63056	114.39250	WA	Giralia
Gko388	AMSR135427	*Rhynchoedura*	*ormsbyi*	-29.33333	146.21667	NSW	Morton Plains Station
Gko389	AMSR137630	*Rhynchoedura*	*ormsbyi*	-29.66667	144.60000	NSW	Wanaaring
Gko390	AMSR137631 (holotype)	*Rhynchoedura*	*ormsbyi*	-29.66667	144.60000	NSW	Wanaaring
Gko391	AMSR138130	*Rhynchoedura*	*ormsbyi*	-29.32028	145.84639	NSW	Enngonia
Gko392	AMSR138441	*Rhynchoedura*	*ormsbyi*	-29.71667	144.11667	NSW	Wanaaring
Gko393	AMSR138442	*Rhynchoedura*	*ormsbyi*	-29.81667	144.58333	NSW	Wanaaring
Gko394	AMSR138443	*Rhynchoedura*	*ormsbyi*	-29.98333	145.36667	NSW	Wanaaring
Gko395	AMSR139902	*Rhynchoedura*	*sexapora* sp. nov.	-16.01861	128.00389	WA	El Questro Station
Gko396	AMSR139903	*Rhynchoedura*	*sexapora* sp. nov.	-16.01861	128.00389	WA	El Questro Station
Gko397	AMSR139904 (holotype)	*Rhynchoedura*	*sexapora* sp. nov.	-16.01861	128.00389	WA	El Questro Station
Gko399	AMSR141041	*Rhynchoedura*	*ormsbyi*	-29.35694	146.27111	NSW	Beulah Station
Gko398	AMSR139905	*Rhynchoedura*	*sexapora* sp. nov.	-16.01861	128.00389	WA	El Questro Station
Gko400	AMSR145587	*Rhynchoedura*	*angusta* sp. nov.	-31.28333	142.28333	NSW	Mootwingee National Park
Gko401	AMSR145587	*Rhynchoedura*	*ormsbyi*	-31.28333	142.28333	NSW	Mootwingee National Park
Gko402	AMSR145588	*Rhynchoedura*	*angusta* sp. nov.	-31.28333	142.28333	NSW	Mootwingee National Park
Gko403	AMSR150159	*Rhynchoedura*	*angusta* sp. nov.	-31.20000	142.30000	NSW	Mootwingee National Park
Gko404	AMSR151586	*Rhynchoedura*	*ormsbyi*	-31.38167	145.70500	NSW	Cobar
Gko405	AMSR151587	*Rhynchoedura*	*ormsbyi*	-31.38167	145.70500	NSW	Cobar
Gko406	AMSR152924	*Rhynchoedura*	*angusta* sp. nov.	-29.03333	141.73333	NSW	Sturt National Park
Gko407	AMSR152925	*Rhynchoedura*	*angusta* sp. nov.	-29.03333	141.73333	NSW	Sturt National Park
Gko408	AMSR152927	*Rhynchoedura*	*angusta* sp. nov.	-29.05583	141.89833	NSW	Sturt National Park
Gko409	AMSR152930	*Rhynchoedura*	*angusta* sp. nov.	-29.05417	141.89083	NSW	Sturt National Park
Gko410	AMSR152935	*Rhynchoedura*	*angusta* sp. nov.	-29.05583	141.89833	NSW	Sturt National Park
Gko411	AMSR152940 (holotype)	*Rhynchoedura*	*angusta* sp. nov.	-29.03333	141.73333	NSW	Sturt National Park
Gko412	AMSR152941	*Rhynchoedura*	*angusta* sp. nov.	-29.03333	141.73333	NSW	Sturt National Park
Gko413	AMSR152946	*Rhynchoedura*	*angusta* sp. nov.	-29.05583	141.89833	NSW	Sturt National Park
Gko414	AMSR152961	*Rhynchoedura*	*angusta* sp. nov.	-29.05417	141.89833	NSW	Sturt National Park
Gko415	AMSR152966	*Rhynchoedura*	*angusta* sp. nov.	-29.04944	141.86083	NSW	Sturt National Park
Gko416	AMSR152982	*Rhynchoedura*	*eyrensis* sp. nov.	-29.08333	141.21667	NSW	Sturt National Park
Gko417	AMSR153315	*Rhynchoedura*	*ormsbyi*	-33.12444	143.27444	NSW	Spring Hill
Gko418	AMSR153316	*Rhynchoedura*	*ormsbyi*	-33.12444	143.27444	NSW	Spring Hill
Gko419	AMSR153317	*Rhynchoedura*	*ormsbyi*	-33.12444	143.27444	NSW	Spring Hill
Gko420	AMSR155270	*Rhynchoedura*	*angusta* sp. nov.	-29.03111	141.45083	NSW	Sturt National Park
Gko421	AMSR155276	*Rhynchoedura*	*eyrensis* sp. nov.	-29.04444	141.30722	NSW	Sturt National Park
Gko422	AMSR155340	*Rhynchoedura*	*eyrensis* sp. nov.	-29.04417	141.30417	NSW	Sturt National Park
Gko423	AMSR155351	*Rhynchoedura*	*eyrensis* sp. nov.	-29.03111	141.45083	NSW	Sturt National Park
Gko424	AMSR155352	*Rhynchoedura*	*angusta* sp. nov.	-29.04444	141.30722	NSW	Sturt National Park
Gko425	AMSR155354	*Rhynchoedura*	*eyrensis* sp. nov.	-29.08333	141.20000	NSW	Sturt National Park
Gko426	AMSR155371	*Rhynchoedura*	*eyrensis* sp. nov.	-29.04444	141.30722	NSW	Sturt National Park
Gko427	AMSR156652	*Rhynchoedura*	*ormsbyi*	-32.86500	146.18917	NSW	Yarra Property, Mt Hope
Gko428	AMSR156653	*Rhynchoedura*	*ormsbyi*	-32.86500	146.18917	NSW	Yarra Property, Mt Hope
Gko429	AMSR156700	*Rhynchoedura*	*ormsbyi*	-32.84889	146.18278	NSW	Yarra Property, Mt Hope
Gko430	AMSR156701	*Rhynchoedura*	*ormsbyi*	-32.84889	146.18278	NSW	Yarra Property, Mt Hope
Gko431	AMSR156720	*Rhynchoedura*	*ormsbyi*	-32.94417	146.19222	NSW	Yarra Property, Mt Hope
Gko432	AMSR156764/NR9657	*Rhynchoedura*	*ormsbyi*	-29.85389	144.13444	NSW	Nocoleche Nature Reserve
Gko433	AMSR166770/NR9656	*Rhynchoedura*	*ormsbyi*	-29.84417	144.05417	NSW	Nocoleche Nature Reserve
Gko434	AMSR166799/NR9727	*Rhynchoedura*	*ormsbyi*	-29.84417	144.05417	NSW	Nocoleche Nature Reserve
Gko529	SAMAR42576	*Rhynchoedura*	*ornata*	-28.21667	133.36667	SA	Tallaringa
Gko530	SAMAR46239	*Rhynchoedura*	*eyrensis* sp. nov.	-27.68750	134.63944	SA	Arcreekaringa Station
Gko531	SAMAR42833	*Rhynchoedura*	*angusta* sp. nov.	-24.10000	143.18333	QLD	Noonbah Station
Gko532	NMVD67857	*Rhynchoedura*	*ornata*	-24.34590	131.68420	NT	Kathleen Creek, Watarrka
Gko533	SAMAR53747	*Rhynchoedura*	*ornata*	-30.13310	139.61070	SA	Mulga Homestead
Gko534	SAMAR38783	*Rhynchoedura*	*ornata*	-19.66667	134.23333	NT	Tennant Creek
Gko535	SAMAR40564	*Rhynchoedura*	*ornata*	-24.43333	131.81667	NT	Kings Creek Station
Gko536	SAMAR59491	*Rhynchoedura*	*ornata*	-29.73250	131.08583	SA	Maralinga
Gko537	SAMAR60328	*Rhynchoedura*	*ornata*	-29.50000	129.32917	SA	Oak Valley
Gko538	SAMAR60424	*Rhynchoedura*	*ornata*	-29.38361	129.97611	SA	Oak Valley
Gko539	SAMAR60460	*Rhynchoedura*	*eyrensis* sp. nov.	-27.19444	135.65028	SA	Macumba Homestead
Gko540	SAMAR60946	*Rhynchoedura*	*eyrensis* sp. nov.	-32.04639	140.11389	SA	Bimbowrie Station
Gko541	SAMAR49777	*Rhynchoedura*	*eyrensis* sp. nov.	-30.57500	139.47444	SA	Balcanoona Station
Gko543	WAMR166334	*Rhynchoedura*	*ornata*	-25.93250	128.44110	WA	Morgan Range
Gko545	SAMAR58950	*Rhynchoedura*	*ornata*	-29.13111	130.23500	SA	Oak Valley
Gko546	SAMAR33345	*Rhynchoedura*	*angusta* sp. nov.	-32.46667	140.51667	SA	Maldorky Hill
Gko547	SAMAR32967	*Rhynchoedura*	*ornata*	-20.86667	130.26667	NT	Sangster's Bore
Gko548	QMJ48069	*Rhynchoedura*	*eyrensis* sp. nov.	-25.67560	140.54080	QLD	Betoota
Gko549	QMJ48534	*Rhynchoedura*	*angusta* sp. nov.	-27.69540	142.20760	QLD	Cooroo
Gko551	WAMR91452	*Rhynchoedura*	*ornata*	-29.67270	125.13450	WA	Blue Robin Hill
Gko552	SAMAR43887	*Rhynchoedura*	*eyrensis* sp. nov.	-26.73722	139.52056	SA	Koonchera Waterhole
Gko555	SAMAR30989	*Rhynchoedura*	*eyrensis* sp. nov.	-27.22778	140.19028	SA	Coongie Lakes Area
Gko559	SAMAR26672	*Rhynchoedura*	*ornata*	-29.35833	134.46667	SA	Mabel Creek Homestead
Gko560	SAMAR32616	*Rhynchoedura*	*ornata*	-28.64889	133.35361	SA	Tallaringa Well

Gko561	SAMAR32621	*Rhynchoedura*	*ornata*	-28.94889	133.30417	SA	Tallaringa Well
Gko562	No voucher	*Rhynchoedura*	*sexapora* sp. nov.	-15.59700	131.10410	NT	Victoria R. Gregory National Park
Gko563	NTMR16429	*Rhynchoedura*	*ornata*	-19.49000	132.30000	NT	Green Swamp Well,Tanami
Gko566	SAMAR36106	*Rhynchoedura*	*ornata*	-25.23333	131.01667	NT	Yulara
Gko567	SAMAR36175	*Rhynchoedura*	*ornata*	-25.48333	131.81667	NT	Curtin Springs
Gko570	SAMAR40942	*Rhynchoedura*	*eyrensis* sp. nov.	-28.08472	134.29556	SA	Mt Furner
Gko571	SAMAR42084	*Rhynchoedura*	*ornata*	-26.34972	130.17167	SA	Illintjitja
Gko572	SAMAR44896	*Rhynchoedura*	*eyrensis* sp. nov.	-28.93500	138.61778	SA	Dulkaninna
Gko573	SAMAR44938	*Rhynchoedura*	*eyrensis* sp. nov.	-29.61417	138.68361	SA	Mookawarinna Hill
Gko575	SAMAR45030	*Rhynchoedura*	*eyrensis* sp. nov.	-26.31806	140.33611	SA	Elbow Well
Gko576	SAMAR45060	*Rhynchoedura*	*eyrensis* sp. nov.	-29.46306	138.84444	SA	Toopawarinna Bore
Gko577	SAMAR45099	*Rhynchoedura*	*eyrensis* sp. nov.	-29.79167	139.80194	SA	Moolawatana
Gko578	SAMAR45687	*Rhynchoedura*	*eyrensis* sp. nov.	-27.38778	138.66611	SA	Mt Gason
Gko579	SAMAR45765	*Rhynchoedura*	*eyrensis* sp. nov.	-26.05639	140.06917	SA	Frew Well
Gko580	SAMAR46046	*Rhynchoedura*	*eyrensis* sp. nov.	-28.30000	140.45000	SA	Moomba Gas Field
Gko581	SAMAR46205	*Rhynchoedura*	*eyrensis* sp. nov.	-29.68389	135.81528	SA	Halifax Hill
Gko582	SAMAR46457	*Rhynchoedura*	*eyrensis* sp. nov.	-29.21639	136.63083	SA	Beresford Rail Station
Gko583	SAMAR46488	*Rhynchoedura*	*eyrensis* sp. nov.	-29.27139	135.63278	SA	Mungutana Dam
Gko584	SAMAR46398	*Rhynchoedura*	*eyrensis* sp. nov.	-29.64111	137.88944	SA	Callanna Bore
Gko585	SAMAR46299	*Rhynchoedura*	*eyrensis* sp. nov.	-29.84472	136.87167	SA	White Cliff
Gko586	SAMAR46351	*Rhynchoedura*	*eyrensis* sp. nov.	-29.47111	136.18778	SA	Binda Boudna Hill
Gko587	SAMAR46430	*Rhynchoedura*	*eyrensis* sp. nov.	-29.28889	135.18333	SA	Bacadinna Hill
Gko588	SAMAR46560	*Rhynchoedura*	*eyrensis* sp. nov.	-28.63972	135.94111	SA	Patsy Dam
Gko589	SAMAR46932	*Rhynchoedura*	*eyrensis* sp. nov.	-26.45806	134.89861	SA	Top Camp Well
Gko592	SAMAR47241	*Rhynchoedura*	*eyrensis* sp. nov.	-28.81778	136.73611	SA	Armistice Bore Anna Creek Station
Gko593	SAMAR47256	*Rhynchoedura*	*eyrensis* sp. nov.	-28.43250	136.45333	SA	Four Hills Trig Peake Station
Gko594	SAMAR47324	*Rhynchoedura*	*eyrensis* sp. nov.	-28.13583	136.00167	SA	Peake Station
Gko596	SAMAR48378	*Rhynchoedura*	*eyrensis* sp. nov.	-28.21583	134.58306	SA	Mount Barry Station
Gko597	SAMAR48486	*Rhynchoedura*	*eyrensis* sp. nov.	-27.31944	134.50167	SA	Todmorden Station
Gko598	SAMAR48540	*Rhynchoedura*	*eyrensis* sp. nov.	-27.74583	136.69944	SA	Macumba Station
Gko599	SAMAR50016	*Rhynchoedura*	*eyrensis* sp. nov.	-26.57639	136.94639	SA	Approdinna Attora Knolls
Gko601	SAMAR50374	*Rhynchoedura*	*eyrensis* sp. nov.	-30.50667	138.36889	SA	Mt Aroona
Gko605	SAMAR52795	*Rhynchoedura*	*eyrensis* sp. nov.	-26.75528	135.11944	SA	Hamilton Homestead
Gko606	SAMAR52824	*Rhynchoedura*	*eyrensis* sp. nov.	-26.82333	136.07194	SA	Akoalyerilla Hill Macumba Station
Gko607	SAMAR52847	*Rhynchoedura*	*ornata*	-26.69222	134.17222	SA	Lambina Homestead
Gko608	SAMAR52870	*Rhynchoedura*	*eyrensis* sp. nov.	-27.20444	134.99444	SA	Todmorden Homestead
Gko609	SAMAR54162	*Rhynchoedura*	*eyrensis* sp. nov.	-27.77833	138.27583	SA	Kalamurina Homestead
Gko610	SAMAR54230	*Rhynchoedura*	*eyrensis* sp. nov.	-29.02111	138.02278	SA	Clayton Homestead
Gko611	SAMAR54267 (holotype)	*Rhynchoedura*	*eyrensis* sp. nov.	-27.85056	137.86917	SA	Kannakaninna W/Hole, Kalamurina Station
Gko612	SAMAR55253	*Rhynchoedura*	*angusta* sp. nov.	-33.77667	139.95944	SA	Gluepot Homestead
Gko613	SAMAR41226	*Rhynchoedura*	*angusta* sp. nov.	-33.76389	140.43056	SA	Hideaway Hut
Gko614	SAMAR41265	*Rhynchoedura*	*angusta* sp. nov.	-33.59722	140.95833	SA	Twenty Three Mile Dam
Gko616	SAMAR41409	*Rhynchoedura*	*angusta* sp. nov.	-33.52778	140.65000	SA	Round Dam
Gko617	SAMAR41518	*Rhynchoedura*	*angusta* sp. nov.	-33.11944	140.05000	SA	Elmore Dam
Gko618	SAMAR29556	*Rhynchoedura*	*ornata*	-26.65000	130.81667	SA	Musgrave Ranges
Gko620	E. Pianka	*Rhynchoedura*	*ornata*	-28.16680	123.66300	WA	Laverton
Gko622	SAMAR46123	*Rhynchoedura*	*ornata*	-26.05333	129.40806	SA	Pipalyatjara
Gko623	SAMAR47393	*Rhynchoedura*	*ornata*	-27.43028	133.23750	SA	Wallatinna Homestead
Gko624	SAMAR47456	*Rhynchoedura*	*ornata*	-27.64528	132.88583	SA	Oolarinna East Bore
Gko625	SAMAR48705	*Rhynchoedura*	*ornata*	-27.01417	129.87000	SA	Mt Lindsay
Gko626	SAMAR50122	*Rhynchoedura*	*ornata*	-26.06083	132.39917	SA	Sentinel Hill
Gko627	SAMAR51533	*Rhynchoedura*	*ornata*	-26.26944	131.47139	SA	Amata
Gko628	SAMAR51617	*Rhynchoedura*	*ornata*	-26.85528	133.05250	SA	Indulkana
Gko631	SAMAR22593	*Rhynchoedura*	*eyrensis* sp. nov.	-32.11667	137.58333	SA	Uro Bluff
Gko633	SAMAR25442	*Rhynchoedura*	*eyrensis* sp. nov.	-32.39583	136.16667	SA	Mt Ive Station
Gko635	SAMAR36873	*Rhynchoedura*	*eyrensis* sp. nov.	-31.48333	138.17500	SA	Mern Merna Station
Gko636	SAMAR44780	*Rhynchoedura*	*eyrensis* sp. nov.	-31.58333	136.33333	SA	Mahenewo Station
Gko638	SAMAR45969	*Rhynchoedura*	*ornata*	-26.40500	129.12972	SA	Pipalyatjara
Gko639	SAMAR46646	*Rhynchoedura*	*eyrensis* sp. nov.	-29.23333	137.88333	SA	Muloorinna Homestead
Gko640	SAMAR48577	*Rhynchoedura*	*ornata*	-27.33694	130.23750	SA	Mt Cheesman
Gko641	SAMAR50245	*Rhynchoedura*	*eyrensis* sp. nov.	-31.58972	136.78611	SA	Oakden Hills Station
Gko642	SAMAR52745	*Rhynchoedura*	*eyrensis* sp. nov.	-32.05000	139.83333	SA	Camel Humps Rg, Plumbago Station
Gko643	SAMAR54101	*Rhynchoedura*	*eyrensis* sp. nov.	-31.11861	134.00722	SA	Yellabinna Reserve
Gko645	AMSR118614	*Rhynchoedura*	*angusta* sp. nov.	-31.85310	141.91510	NSW	E Broken Hill
Gko646	AMSR118617	*Rhynchoedura*	*eyrensis* sp. nov.	-33.90110	141.78480	NSW	Wentworth
Gko647	AMSR118619	*Rhynchoedura*	*angusta* sp. nov.	-33.00000	141.02170	NSW	Loch Lily
Gko648	AMSR118620	*Rhynchoedura*	*angusta* sp. nov.	-32.98333	141.61667	NSW	Coonbah
Gko649	AMSR118621	*Rhynchoedura*	*ormsbyi*	-32.90260	144.30130	NSW	Ivanhoe
Gko650	Steve Morton	*Rhynchoedura*	*ornata*	-21.00890	130.12640	NT	Sangster's Bore
Gko651	NTMR13652	*Rhynchoedura*	*ornata*	-23.18310	132.65480	NT	Yuendemu Road
Gko652	NTMR13666	*Rhynchoedura*	*ornata*	-23.28990	132.41700	NT	Yuendemu Road
Gko654	SAMAR32094	*Rhynchoedura*	*ornata*	-30.48778	132.05972	SA	Immarna Siding
Gko655	SAMAR32126	*Rhynchoedura*	*ornata*	-30.25556	131.55000	SA	Maralinga
Gko657	SAMAR51850	*Rhynchoedura*	*eyrensis* sp. nov.	-29.90972	139.45889	SA	Mt Fitton
Gko658	WAMR166332	*Rhynchoedura*	*ornata*	-24.69640	128.76280	WA	Pungkulpirri Waterhole
Gko659	WAMR166340	*Rhynchoedura*	*ornata*	-24.59970	128.74470	WA	Pungkulpirri Waterhole
Gko660	SAMAR62132	*Rhynchoedura*	*ornata*	-25.93080	128.44940	WA	BlaCreekstone
Gko675	WAMR102178	*Rhynchoedura*	*ornata*	-22.60270	118.45970	WA	Mt Windell
Gko676	WAMR102502	*Rhynchoedura*	*ornata*	-23.11300	116.01170	WA	Barlee Range
Gko677	WAMR104052	*Rhynchoedura*	*ornata*	-21.60910	118.97420	WA	Woodstocreek Station
Gko678	WAMR110693	*Rhynchoedura*	*ornata*	-28.16160	119.52500	WA	Sandstone
Gko679	WAMR110753	*Rhynchoedura*	*ornata*	-23.37880	120.25640	WA	Newman
Gko680	WAMR110788	*Rhynchoedura*	*ornata*	-21.94130	116.45390	WA	Pannawonica
Gko682	WAMR110903	*Rhynchoedura*	*ornata*	-19.88940	128.86000	WA	Tanami Downs
Gko686	WAMR110981	*Rhynchoedura*	*ornata*	-27.24190	120.69780	WA	Lake Way
Gko687	WAMR112022	*Rhynchoedura*	*ornata*	-27.02550	116.78140	WA	Boolardy Station
Gko688	WAMR112104	*Rhynchoedura*	*ornata*	-25.93470	118.84330	WA	Meekatharra
Gko689	WAMR119999	*Rhynchoedura*	*sexapora* sp. nov.	-15.83330	128.03330	WA	Cockburn Range
Gko695	WAMR122590	*Rhynchoedura*	*ornata*	-25.65380	114.62560	WA	none
Gko696	WAMR123804	*Rhynchoedura*	*ornata*	-25.08800	115.38000	WA	none
Gko697	WAMR125470	*Rhynchoedura*	*ornata*	-23.31660	120.03330	WA	Newman

Gko699	WAMR126403	*Rhynchoedura*	*ornata*	-30.28330	119.75000	WA	Bungalbin Sandplain
Gko700	WAMR126566	*Rhynchoedura*	*ornata*	-30.45000	120.68330	WA	Kalgoorlie
Gko702	WAMR127571	*Rhynchoedura*	*ornata*	-30.02000	121.07750	WA	Goongarrie
Gko704	WAMR132783	*Rhynchoedura*	*sexapora* sp. nov.	-16.03220	128.84500	WA	Lake Argyle
Gko705	WAMR136253	*Rhynchoedura*	*ornata*	-26.79580	115.51690	WA	Muggon
Gko706	WAMR137011	*Rhynchoedura*	*ornata*	-27.35000	120.76670	WA	Wanjarri National Park
Gko707	WAMR144557	*Rhynchoedura*	*ornata*	-30.25000	119.26670	WA	Mount Jacreekson
Gko708	WAMR145610	*Rhynchoedura*	*ornata*	-22.39000	119.99000	WA	Port Hedland
Gko709	WAMR146721	*Rhynchoedura*	*ornata*	-21.32470	118.86330	WA	Port Hedland
Gko724	QMA006665/J88379	*Rhynchoedura*	*ormsbyi*	-26.09000	145.07000	QLD	Mariala National Park
Gko729	QMA001481/J82497	*Rhynchoedura*	*ormsbyi*	-26.20000	147.13000	QLD	Mt Maria
Gko733	QMA006667/J88235	*Rhynchoedura*	*ormsbyi*	-25.74806	148.08361	QLD	Womblebank
Gko734	QMA006666/J88378	*Rhynchoedura*	*ormsbyi*	-26.09000	145.07000	QLD	Mariala National Park
Gko782	WAMR84573	*Rhynchoedura*	*ornata*	-26.58330	125.00000	WA	Gahnda Rockhole
Gko783	WAMR108808	*Rhynchoedura*	*ornata*	-18.15000	122.55000	WA	Thangoo Homestead
Gko784	WAMR142541	*Rhynchoedura*	*ornata*	-23.35130	122.66330	WA	Lake Dissappointment
Gko785	WAMR164239	*Rhynchoedura*	*ornata*	-24.51690	126.21280	WA	Clutterbuck Hills, Gibson Desert
Gko786	WAMR164338	*Rhynchoedura*	*ornata*	-24.51690	126.21280	WA	Clutterbuck Hills, Gibson Desert

Supplementary Table 2. Nucleotide substitution models
selected by MrModelTest2 for the gene data partitions
based on the Akaike Information Criterion.

Gene data partitions	Nucleotide substitution model
nd2	GTR+I
nd2; Codon 1	HKY+I
nd2; Codon 2	HKY+I
nd2; Codon 3	GTR+G
rag1	HKY
rag1; Codon 1	HKY
rag1; Codon 2	F81
rag1; Codon 3	HKY
bzw1	GTR+I
snrpd3	HKY+G
Concatenated (1 partition)	GTR+I+G
Concatenated (2 partition)	GTR+I+G

Supplementary Table 3. Summaries of characters measured.

Character	Abbreviation	Measurement
Body proportions		
Snout to vent length	SVL	From tip of the snout to cloaca
Trunk length	TrunkL	From axilla to groin
Head length	HeadL	From tip of snout to retroarticular process
Head width	HeadW	At widest point
Foreleg length	ArmL	From elbow to tip of fourth finger
Leg length	LegL	From upper surface of knee to tip of fourth toe
Tail length	TailL	From tip of the tail to cloaca, original tails only
Internarial distance	Inar	Measured at medial edges of nares
Orbit length	OrbL	From anterior to posterior corners of eye
Distance from nostril to eye	NarEye	From nostril to anterior corner of eye
Distance from snout to eye	SnEye	From snout to anterior corner of eye
Distance from eye to ear	EyeEar	From posterior edge of eye to anterior margin of ear
Scale and other characters		
Mental length/width	MenL/W	Ratio of Length/Width of mental scale
Adjacent mental scales	AdjMen	Number of scales in contact with the mental scale
Internarial scales	IntNar	Number of internarial scales
Narial scales	NarScales	Number of scales including main nasal scale surrounding the nostril
Rostral groove	GrooveL%	Proportional length of groove on rostral scale
Groove strength	GrooveS	Strength (0=absent, 1=weak, 2=strong) of the groove on rostral scale
Pre-anal pores	AnPor	Number of pre-anal pores
Mental scales	MenScales	Number of mental scales

Supplementary Table 4. Bayes factors comparisons of different data partitions for the combined data. Standard errors (S.E.) were estimated using a bootstrap procedure with 1,000 replicates in Tracer v.1.4 (Rambaut and Drummond, 2007). Negative values indicate support for the alternative model.

Concatenated Data	Ln P(model| data) (harmonic mean)	S.E.	Alternative Models		
			Unpartitioned	2-Partitions (nDNA & mtDNA)	8-Partitions (by genes & codons)
Unpartitioned	-9214.974	+/- 0.288	_	-62.296	-237.167
2-Partitions (nDNA & mtDNA)	-9071.533	+/- 0.263	62.296	_	-174.871
8-Partitions (by genes & codons)	-8668.876	+/- 0.435	237.167	174.871	_

Supplementary Table 5. Summaries of characters and ratios measured for members of *Rhynchoedura.* Mean±SD (range). See Table 1 for abbreviations of characters used. As SVL differed among taxa we used ANCOVAs with either SVL or HeadL as the covariate, as appropriate, for body size characters. ANOVAs were used for other characters. *Rhynchoedura mentalis* sp. nov. was excluded from these analyses due to small sample sizes.

Character	*R. ornata*	*R. sexapora* sp. nov.	*R. eyrensis* sp. nov.	*R. angustus* sp. nov.	*R. sulcata* sp. nov.	*R. mentalis* sp. nov.	Statistics
Sample Size	N = 113	N = 50	N = 48	N =22	N = 32	N = 2	
SVL	45.2±5.0 (32.0–57.0)	41.8±3.7 (32.0–48.5)	43.6±5.0 (33.0–51.0)	44.2±3.5 (39.0–51.0)	44.5±3.8 (33.5–50.0)	46.0±5.7 (42.0–50.0)	ANOVA: $F_{4,266}=4.732$, $P=0.0011$
TrunkL	21.8±3.3 (14.5–29.6)	20.5±2.4 (16.1–27.2)	20.7±3.4 (14.2–26.6)	21.3±2.8 (14.5–26.2)	21.8±2.7 (14.9–26.3)	23.0±1.8 (21.8–24.2)	ANCOVA slopes: $F_{4,256}=1.227$, $P=0.2997$; ANCOVA intercepts: $F_{4,260}=2.164$, $P=0.0734$; Covariate: SVL
HeadL	8.2±0.7 (6.6–9.8)	8.0±0.6 (6.3–9.0)	7.9±0.7 (6.3–9.5)	7.8± 0.5 (6.8–8.9)	7.8± 0.5 (6.8–8.5)	8.2±0.4 (8.0–8. 5)	ANCOVA slopes: $F_{4,256}=0.511$, $P=0.7279$; ANCOVA intercepts: $F_{4,260}=8.717$, $P<0.0001$; Covariate: SVL
HeadW	6.5±0.6 (4.7–8.0)	6.6±0.5 (5.4–7.6)	6.2±0.7 (4.7–7.3)	6.4±0.5 (5.3–7.6)	6.4± 0.5 (5.2–7.6)	7.3±0.1 (7.2–7.3)	ANCOVA slopes: $F_{4,256}=1.057$, $P=0.3784$; ANCOVA intercepts: $F_{4,260}=11.264$, $P<0.0001$; Covariate: SVL
ArmL	9.3±0.9 (7.0–11.0)	9.0±0.8 (8.0–10.0)	9.0±1.1 (7.0–11.0)	9.5±0.9 (7.0–11.0)	9.5±0.8 (8.0–11.0)	10.3±0.4 (10.0–10.5)	ANCOVA slopes: $F_{4,256}=1.777$, $P=0.1338$; ANCOVA intercepts: $F_{4,260}=2.666$, $P=0.0329$; Covariate: SVL
LegL	12.3±1.1 (9.0–15.0)	11.9±0.8 (10.0–13.5)	11.7±1.2 (9.0–14.0)	12.2±1.2 (10.0–14.0)	12.9±1.0 (10.0–14.0)	13.8±1.1 (13.0–14.5)	ANCOVA slopes: $F_{4,256}=1.024$, $P=0.3956$; ANCOVA intercepts: $F_{4,260}=7.532$, $P<0.0001$; Covariate: SVL

TailL	32.3±3.3 (24.0–38.5) N = 65	28.9±3.1 (23.5–36.0) N = 26	30.1±4.5 (20.5–37.0) N = 25	29.9±2.3 (26.0–34.5) N = 18	31.0±2.5 (23.0–34.0) N = 18	-	ANCOVA slopes: $F_{4,143}$=0.280, P=0.8907; ANCOVA intercepts: $F_{4,147}$=2.870, P=0.0252; Covariate: SVL
Inar	1.19±0.12 (0.88–1.50)	1.16±0.12 (0.94–1.40)	1.07±0.12 (0.76–1.24)	1.07±0.07 (0.88–1.20)	1.15±0.09 (0.99–1.38)	1.21±0.09 (1.15–1.27)	ANCOVA slopes: $F_{4,256}$=0.742, P=0.5641; ANCOVA intercepts: $F_{4,260}$=12.420, P<0.0001; Covariate: HeadL
OrbL	2.69±0.26 (1.92–3.40)	2.51±0.30 (1.93–3.25)	2.48±0.26 (2.00–3.00)	2.39±0.19 (2.09–2.86)	2.45±0.21 (1.98–2.80)	2.68±0.12 (2.60–2.75)	ANCOVA slopes: $F_{4,256}$=0.929, P=0.4478; ANCOVA intercepts: $F_{4,260}$=8.344, P<0.0001; Covariate: HeadL
NarEye	3.09±0.26 (2.50–3.68)	2.93±0.21 (2.48–3.25)	3.04±0.24 (2.48–3.44)	2.91±0.20 (2.48–3.30)	2.95±0.23 (2.26–3.30)	2.96±0.06 (2.92–3.00)	ANCOVA slopes: $F_{4,256}$=0.883, P=0.4746; ANCOVA intercepts: $F_{4,260}$=5.811, P=0.0002; Covariate: HeadL
SnEye	3.69±0.36 (2.74–4.47)	3.61±0.30 (2.95–4.04)	3.63±0.34 (3.01–4.46)	3.55±0.24 (2.96–3.99)	3.68±0.27 (2.90–4.18)	3.90±0.11 (3.82–3.98)	ANCOVA slopes: $F_{4,256}$=1.426, P=0.2258; ANCOVA intercepts: $F_{4,260}$=4.667, P=0.0012; Covariate: HeadL
EyeEar	2.14±0.23 (1.56–2.65)	2.24±0.23 (1.75–2.75)	2.07±0.25 (1.60–2.80)	2.12±0.19 (1.71–2.48)	2.10±0.23 (1.65–2.65)	2.15±0.08 (2.09–2.20)	ANCOVA slopes: $F_{4,256}$=0.813, P=0.5178; ANCOVA intercepts: $F_{4,260}$=6.428, P<0.0001; Covariate: HeadL
MenL/W	1.54±0.26 (1.09–2.50)	1.40±0.26 (1.00–2.20)	1.78±0.36 (0.77–3.00)	1.60±0.34 (1.00–2.17)	1.26±0.23 (0.82–1.78)	-	-
AdjMen	4.9±0.6 (3–8)	4.6±0.7 (4–6)	4.8±0.8 (3–7)	4.7±0.5 (4–5)	4.1±0.4 (4–5)	-	ANOVA: $F_{4,265}$=8.077, P<0.0001
IntNar	2.8±0.5 (1–4)	2.9±0.4 (2–4)	2.1±0.5 (1–3)	2.1±0.5 (1–3)	2.7±0.5 (2–3)	1 N = 1	ANOVA: $F_{4,265}$=30.165, P<0.0001
NarScales	6.2±0.8 (5–9)	6.3±0.8 (5–8)	6.7±0.6 (5–8)	5.6± 1.0 (4–7)	5.7± 0.7 (5–7)	Both with 5	ANOVA: $F_{4,265}$=12.398, P<0.0001

GrooveL%	12.5±22.5 (0–90)	29.1±25.6 (0–90)	29.7±18.2 (0–70)	30.0±15.5 (0–55)	54.5± 18.3 (0–100)	50, 90	ANOVA:$F_{4,265}=26.248$, $P<0.0001$
GrooveS	0 - 71% 1 - 21% 2 - 8%	0 - 30% 1 - 54% 2 - 16%	0 - 15% 1 - 20% 2 - 65%	0 - 9% 1 - 14% 2 - 77%	1 - 23% 2 - 84%	2 - 100%	-
PAPor	2 - 100%	6 - 94% 4 - 6%	2 - 100%	2 - 100%	2 - 100%	2 - 100%	-
MenScales	1 – 100%	1 – 100%	1 – 100%	1 – 100%	1 – 100%	3 – 100%	-