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Revision of the Western Australian pebble-mimic dragon species-group (*Tympanocryptis cephalus*: Reptilia: Agamidae)

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Abstract

Recent work on species complexes of the pebble-mimic dragons of the Australian genus *Tympanocryptis* has greatly clarified evolutionary relationships among taxa and also indicated that species diversity has been severely underestimated. Here we provide a morphological and molecular appraisal of variation in the *T. cephalus* species-group and find evidence for recognizing five species-level lineages from Western Australia. Four species-level lineages are strongly supported with a combined mitochondrial and nuclear DNA Bayesian analysis (a fifth population from the Gascoyne region lacked tissue samples). Morphologically, we found subtle, yet consistent, differences among the populations in scalation, color and pattern. True *T. cephalus* Günther is restricted to the coastal Pilbara region and characterized by five dark blotches on the dorsum, keeled ventrals, and other characters. Two other lineages within the Pilbara, from the Hamersley range and Fortescue/northern Pilbara region, differed from *T. cephalus senso stricto* by possessing a more elongate body and a plain dorsum. Furthermore, the Hamersley lineage differed from the Fortescue lineage by possessing slightly more reddish coloration and feeble keeling on the snout. Although there are few specimens and no tissue samples available for the Gascoyne population, these individuals are larger, have rugose scales on the snout, and possess scattered enlarged tubercles with three large blotches on the dorsum. The name *T. cephalus gigas* Mitchell is available for this population. The most widespread lineage, and the one best represented in collections and in field guides, occurs throughout central Western Australia. These Goldfield populations are characterized by a protruding snout, narrow rostral, and uniform reddish-brown coloration, often with a dark wash. Based on the genetic and morphological differences, we redescribe *T. cephalus*, resurrect and elevate *T. gigas* to a full species and designate a neotype for this taxon, and describe three lineages as new species (*T. diabolicus* **sp. nov.**, *T. fortescuensis* **sp. nov.**, *T. pseudopsephos* **sp. nov.**).

Key words: agamid lizard, cryptic species, Gascoyne, morphology, mtDNA, nDNA, neotype, Pilbara, taxonomy, *Tympanocryptis diabolicus* **sp. nov.**, *Tympanocryptis fortescuensis* **sp. nov.**, *Tympanocryptis gigas*, *Tympanocryptis pseudopsephos* **sp. nov.**

Introduction

Lizards of the Australian genus *Tympanocryptis* Peters, 1864 are highly cryptic, with complex patterns on the body similar to the backgrounds on which they occur, and a tendency to remain motionless when predators approach. There are 11 species currently recognized (Melville *et al.* 2014). Most are small (~50 mm snout-vent length [SVL]), with a stout body, short round head, and short thin tail. Some have adopted extreme 'pebble-mimicking' camouflage, with the head and body resembling a small and large stone, with a gray tail that resembles a twig (Pianka & Vitt 2003, p. 68; Wilson 2012, p. 96).

Recently, Shoo *et al.* (2008) conducted a phylogenetic study of the genus, focusing on arid zone pebble-mimic forms. They found that *T. cephalus* Günther, 1867 was restricted to Western Australia, as the type location is near Karratha in the Pilbara region. They also found that populations previously assigned to *T. cephalus* from the Northern Territory, South Australia and Queensland (Houston & Hutchinson 1998; Wilson & Swan 2003) were not

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closely related to *T. cephalus*, and fell into different, unrelated lineages. Within *T. cephalus* from Western Australia, they found evidence for several evolutionary independent lineages, with highest diversity in the Pilbara region (shown in Fig. 1, along with the new taxonomic names). These findings necessitate a taxonomic reappraisal of the *T. cephalus* species-group from Western Australia.

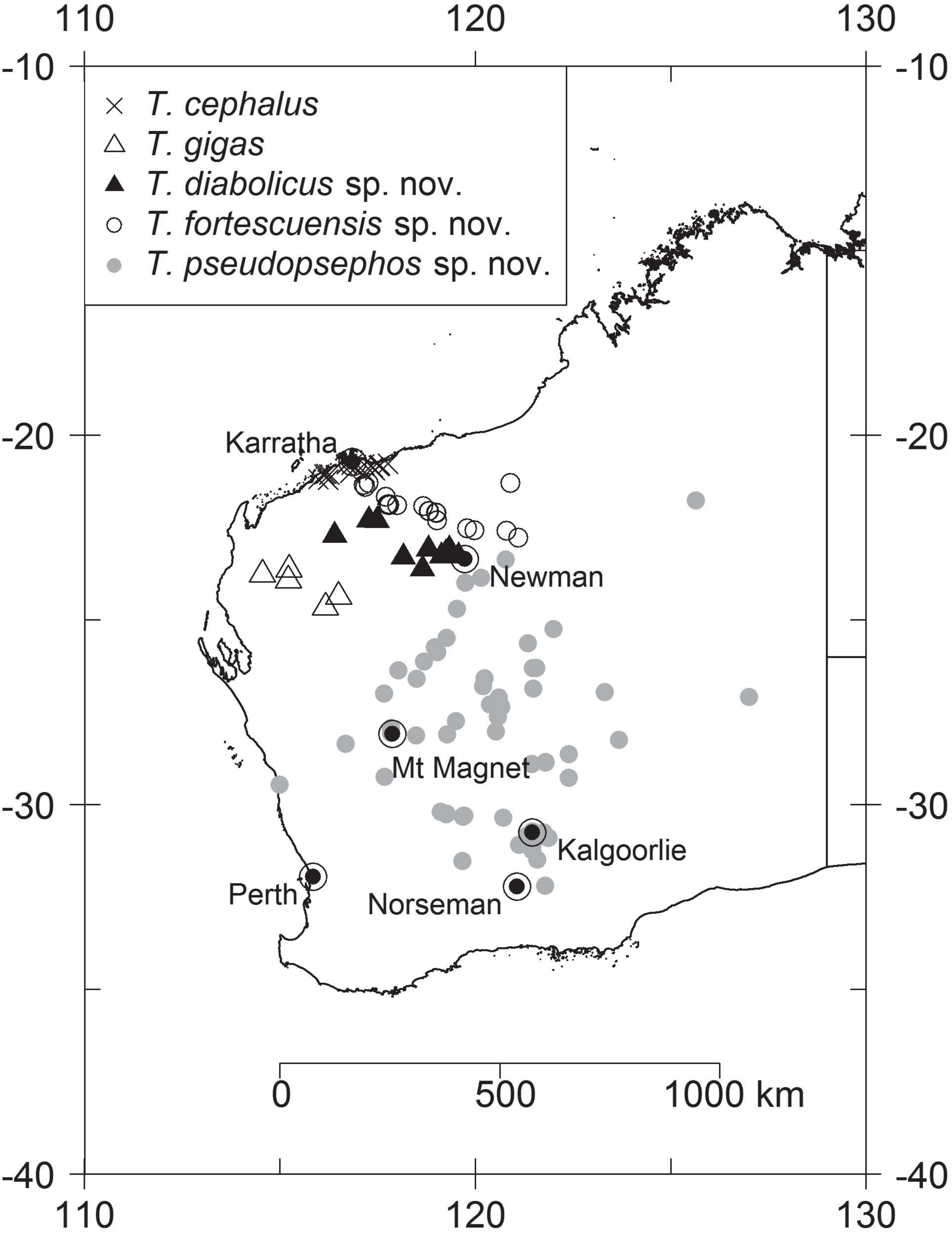


FIGURE 1. Distribution map of the *Tympanocryptis cephalus* species-group in Western Australia.

Here we provide further molecular genetic analyses of the western lineages, expanding on those presented in Shoo *et al.* (2008), along with a detailed morphological assessment of the lineages recovered. Taken together, there was evidence for recognizing five species-level lineages within the western *T. cephalus* species-group. We redescribe *T. cephalus senso stricto* from near Karratha, resurrect and elevate *T. gigas* from Gascoyne to full species, and describe three new species, two from the Pilbara and one widely-distributed species from the Goldfields region of Western Australia.

Methods

Specimens examined. Almost all specimens of *T. cephalus* from the Western Australian Museum, Perth (WAM) and the South Australian Museum, Adelaide (SAMA) were examined. All type material cited herein is lodged in these two museums plus the Natural History Museum (BMNH) (see type lists below, and Appendix 1). Our preference was to measure individuals for which genetic information was available in Shoo *et al.* (2008) and the new molecular genetic analyses here. In the cases where a genotyped individual was of poor quality or a juvenile, we chose a high quality specimen from the same series to measure.

Phylogenetic relationships. In order to further investigate phylogenetic relationships within the *T. cephalus* species-group, additional nuclear genes were sequenced which could be added to the previously published dataset of Shoo *et al.* (2008). The previous study included the genes *ND2* (mtDNA) and the nuclear gene *RAG1*. Here, we sequenced 43 *Tympanocryptis* and two outgroup samples included in Shoo *et al.* (2008) for the nuclear genes *GAPD* and *BDNF* (see Melville *et al.* [2008] for primer sequences). DNA was isolated using Protenase K digestion and chloroform–isoamyl alcohol extraction. PCR amplifications were performed in 41 µl volumes of reaction mixture comprising 4 µl of 10° buffer, 2.4 µl of 25 mM $MgCl_2$, 2 µl of 10 mM dNTP, 0.5 µl each of forward and reverse primer (10 µM), 29.4 µl of autoclaved Milli-Q H_2O, 0.2 µl of HotStar Taq (QIAGEN), and 2 µl of genomic DNA diluted 10 or 100 times. A touchdown protocol was used for PCR amplifications: an initial step of 95°C for 15 min followed by eight cycles of denaturation at 95°C for 30 s, annealing at 70°C for 20 s and extension at 72°C for 90 s with annealing temperature stepping down 5°C every second cycle; this was then followed by 40 cycles of denaturation at 95°C for 30 s, annealing at 52°C for 30 s and extension at 72°C for 45 s with a final extension step 72°C for 4 min. Negative controls were run for all amplifications. PCR products were purified using SureClean Plus (BIOLINE). Purified product was sent to Macrogen (South Korea) for sequencing.

Phylogenetic analysis of the 45 samples were undertaken for each of the gene regions (*ND2*, *RAG1*, *BDNF*, *GAPD*) individually using a Bayesian approach. Subsequently, a Bayesian framework for species tree estimation was applied to incorporate all of the gene regions together. MrModeltest 2.3 with the Akaike Information Criterion was used to estimate the best model of evolution for each gene region, and these models were then used for all subsequent analyses. Bayesian analyses were performed in Mr. Bayes 3.2 using the evolutionary model selected by MrModelTest 2.3 with parameters estimated from data during the analysis. Four Markov chains were used in each of two simultaneous runs starting from different random trees. Analyses were run for 10 million generations for each dataset. Standard deviation of split frequencies was used as a convergence diagnostic to confirm suitability of run length. For all analyses, it was confirmed that potential scale reduction factor values were close to 1.0, indicating that an adequate sample of the posterior probability distribution had been achieved (Ronquist *et al.* 2012). In addition, the output was examined using Tracer v1.5 (Rambaut & Drummond 2007) to check that stationarity had been reached.

We used a Bayesian framework for species tree estimation, incorporating all gene regions (*ND2*, *RAG1*, *BDNF*, *GAPD*), to determine phylogenetic relationships between putative species. We used *BEAST, enabled in BEAST v1.7.5, to co-estimate the four gene trees embedded in a shared species tree (see Heled & Drummond 2010). Unlinked substitutions models were employed across the loci, and models of sequence evolution were implemented based on preliminary analyses using MrModelTest 2.3. A Yule process species tree prior was specified and the gene tree priors were automatically specified by the multispecies coalescent. The analysis was run for 20 million generations. The output was examined using Tracer v1.5 (Rambaut & Drummond 2007) to check that stationarity had been reached.

Morphological assessment. The following linear measurements were taken with digital vernier calipers to the nearest 0.1 mm: snout–vent length (SVL), inter limb length from the base of the axilla to the base of the joint of the thigh (TrunkL), tail length (TailL), head length from tip of snout to angle of jaw (HeadL), head width at widest point (HeadW), head depth immediately behind eye, at the deepest point (HeadD), snout length from tip of snout to anterior margin of eye (SnoutL), snout width at nostrils (SnoutW), eye length (EyeL), forelimb length from axilla to wrist (ArmL), hand length (from wrist to tip of 4th finger, excluding claw and sheath (HandL), hindlimb length from outside joint of the knee to outside joint of the ankle (LegL), foot length (from base of foot to tip of 4th toe, excluding claw and sheath; FootL), inter orbital length (from anterior tip of the eye to posterior edge of the nostril; InterOrb). The following meristic counts were made: number of internasal scales across top of snout between nostrils (IntNas), number of scale rows across the head between supraciliary ridges (IntSup), number of supralabial (SupLab) and infralabial (InfLab) scales, number of subdigital lamellae on 4th finger (4FLam) and 4th toe (4TLam) from point of divergence of the digit up to (but not including) the claw sheath.

A multivariate discriminant function analysis (DFA) was implemented in SYSTAT 13 to assess how accurately individuals could be assigned to their genetic lineage based on morphology. To account for body size, measurements were regressed against SVL and the residuals were used for further analyses. Univariate analyses revealed significant differences between the sexes in all putative species for all measurements ($\alpha = 0.05$); therefore, we analysed the sexes separately.

In addition to the linear measurements and counts, we examined the appearance of scales on the body and compared color and pattern. Where available, color photographs of individuals (vouchered or not) were used to describe color patterns in life.

Results

Phylogenetic relationships. Details of sequencing length, number of parsimony informative characters and models of evolution are provided in Table 1. A Bayesian analysis of the mtDNA (*ND2*) provides strong evidence of four independent evolutionary lineages within *T. cephalus sensu lato* (Fig. 2). Henceforth, these lineages are referred to as Karratha, Hamersley, Fortescue, and Goldfields according to their geographic location. We note that tissue samples for the Gascoyne lineage were not available for DNA sequencing in either Shoo *et al.* (2008) or the current study, despite further collecting efforts. Additional phylogenetic support for a number of these lineages is provided with the nuclear genes (see Appendix 2). In these analyses, Karratha is a well-supported independent lineage across all gene regions, with Hamersley and Fortescue together forming a well-supported lineage in *RAG1* and *BDNF* (except for WAM R158146 in *RAG1*). However, Hamersley and Fortescue were not supported as independent lineages to each other in any of the nuclear gene regions. For the slowly-evolving *GAPD* gene, Karratha was recovered as independent, but the other three lineages were not differentiated from each other.

TABLE 1. Details of sequence length, number of parsimony informative characters, models of evolution, Mr Bayes settings and mean log likelihood of Bayesian tree for each of the genes used in phylogenetic analyses.

Gene region	Length (BP)	Number of parsimony informative characters	Model of evolution	Mr Bayes settings	Log likelihood (-ln)
ND2	1840	618	GTR+I+Γ	Lset nst = 6; rates = invgamma; Prset statefreqpr = dirichlet (1,1,1,1)	-12800.0
RAG1	1376	108	GTR+ Γ	Lset nst = 6; rates = gamma; Prset statefreqpr = dirichlet (1,1,1,1)	-3640.0
BDNF	682	25	HKY + I	Lset nst = 2; rates = propinv; Prset statefreqpr = dirichlet (1,1,1,1)	-1480.0
GAPD	278	35	HKY + Γ	Lset nst = 2; rates = gamma; Prset statefreqpr = dirichlet (1,1,1,1)	-995.0

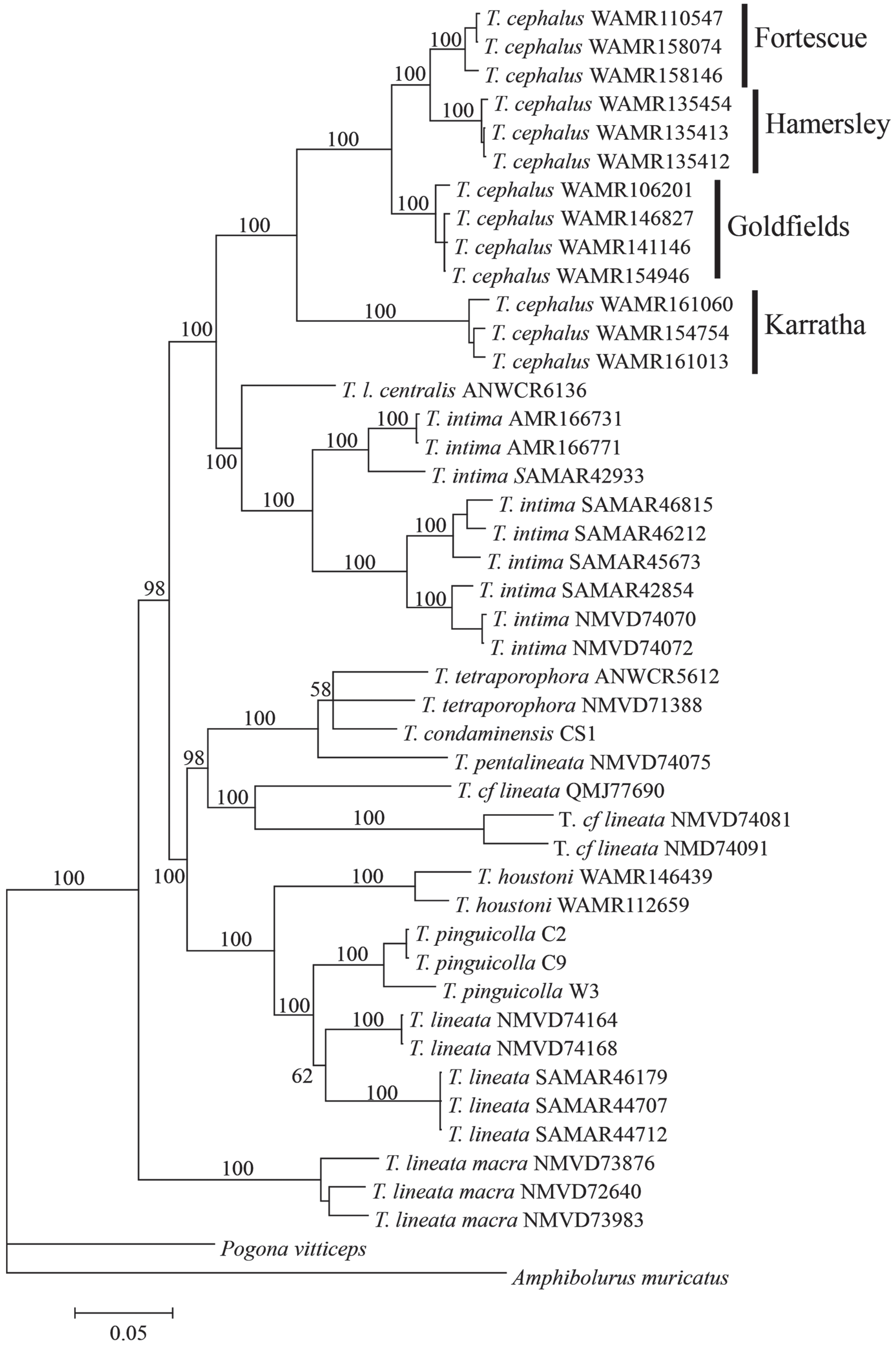


FIGURE 2. Bayesian phylogenetic tree based on 1840 bp mitochondrial DNA (*ND2*) from previously published samples (Shoo *et al.* 2008). Bayesian posterior probabilities are provided on branches.

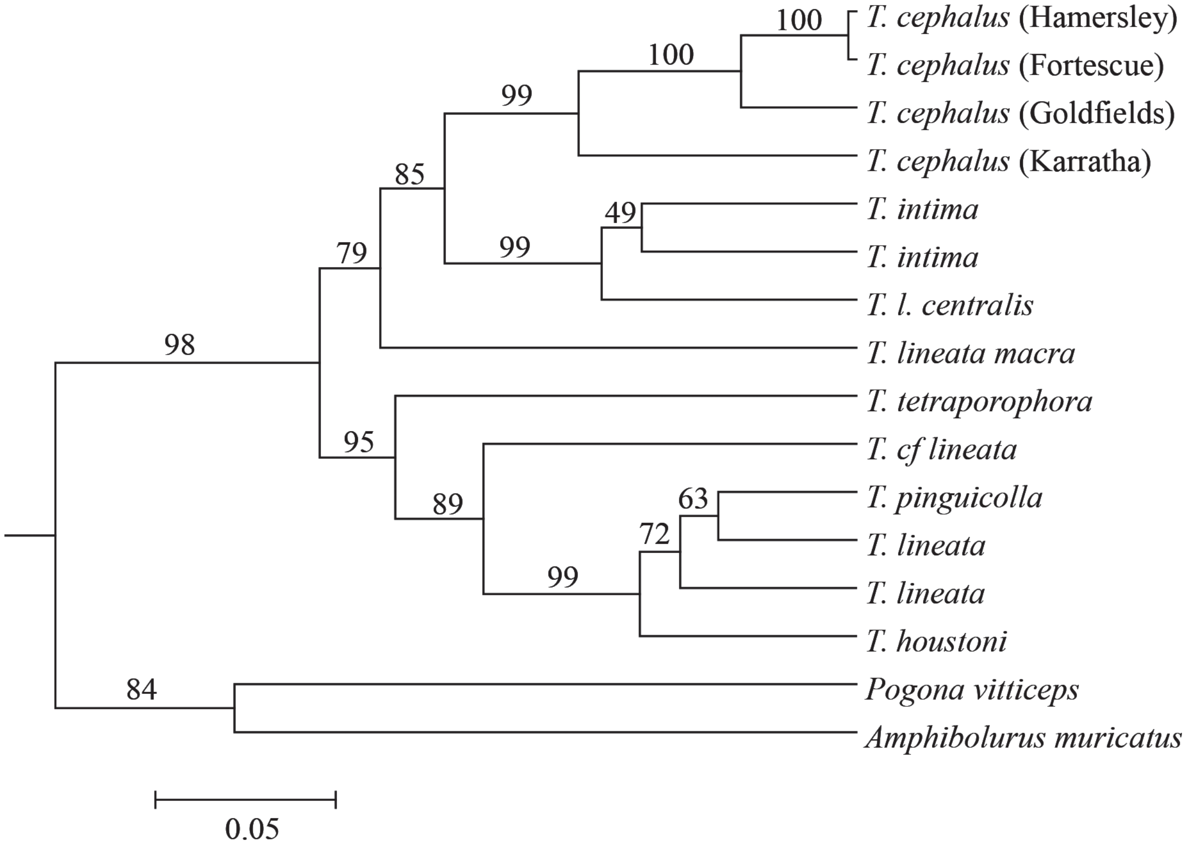


FIGURE 3. Species tree phylogeny based on datasets inferred using *Beast across four gene regions (*ND2*, *RAG1*, *BDNF*, *GAPD*). Clade posterior probabilities are indicated on branches. Individual gene trees from the analyses are provided in Appendix 2.

Bayesian analyses incorporating all four gene regions for the *BEAST species tree estimations were characterized by high (> 200) effective sample sizes, and convergence of the individual runs was confirmed from assessments using Tracer. The maximum clade credibility trees from the posterior sets of species trees differed between each gene (Appendix 3). The topology of the full *Beast dataset was similar to that of the mtDNA tree (Fig. 3). In the species tree phylogengy, Karratha was well supported as the basal lineage within *T. cephalus sensu lato*, with the Goldfields lineage recovered as a well supported sister group to Hamersley and Fortescue, with the latter two groups also being well supported. The taxonomic implications of these analyses is that there is strong support across multiple genes for species-level recognition of the Karratha, Goldfields and Hamersley + Fortescue lineages, with the Hamersley and Fortescue lineages only strongly supported by the mtDNA data.

Morphological analysis. A morphological summary is presented in Appendix 4. The most notable differences in individual characters are the relatively large average SVL, HeadW, HeadD, and TailL of Gascoyne individuals compared to the other forms. In addition, females tended to have longer TrunkL than males across all groups.

DFA revealed significant discrimination between species for both males (Wilks' $\lambda = 0.03$, $F_{80,\,101} = 1.92$, $P = 0.001$) and females (Wilks' $\lambda = 0.003$, $F_{80,\,57} = 2.41$, $P < 0.001$). Canonical variables (CV) 1, 2, and 3 together explained 93% of the variation in males and 97% in females (Table 2). For males, HeadD and HeadW contributed most strongly to CV1, while SnoutW, InterOrb, and EyeL contributed most strongly to CV2, and HeadD to CV3. Thus, in males, Fortescue had shallower, wider heads than Goldfields, while Gascoyne and Goldfields had smaller SnoutW, InterOrb, and EyeL than Karratha (Fig. 4a). There was morphological overlap with correct assignment of males to their genetic species: 100% for Fortescue and Gascoyne, 89% for Karratha, 88% for Hamersley, and 86% for Goldfields. Females, however, were correctly assigned to genetic species in 100% of cases. In females (Fig. 4b), HeadD, HandL, and SnoutL contributed most strongly to CV1, while HeadD most strongly to CV2 and IntNas and HandL to CV3. As a result, female Karratha had shallower heads with longer snouts than Gascoyne or

Hamersley, while Fortescue had shallower heads than Karratha, Gascoyne or Hamersley. In addition, female Goldfields had fewer internasal scales and shorter hand length than Gascoyne or Fortescue.

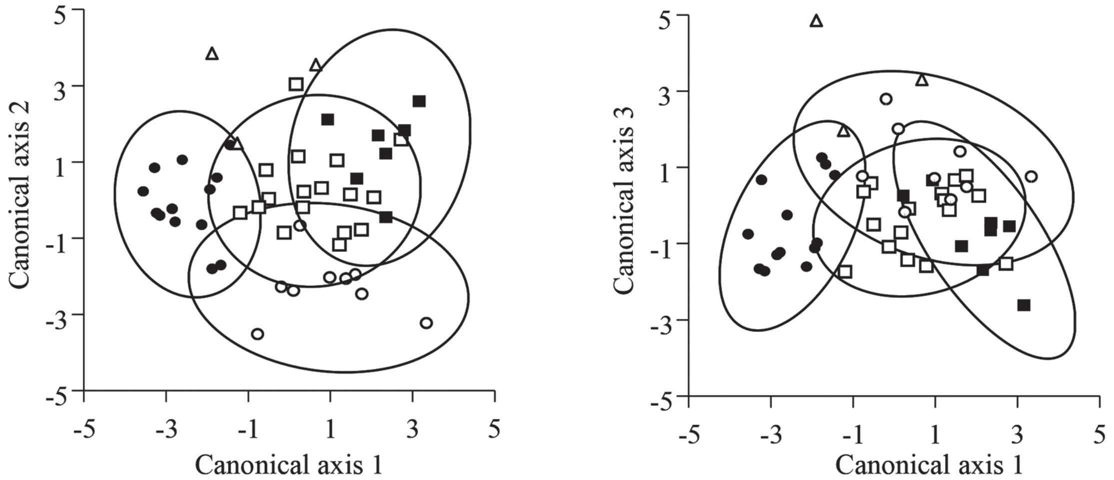
TABLE 2. Pooled within class canonical functions for the first three canonical variables of males and females for (a) morphological variables and (b) lineages. Morphometric variables most strongly correlated with canonical variables are in bold. Refer to text for explanations of morphological variables.

(a)	Males			Females		
Variable	Can 1	Can 2	Can 3	Can 1	Can 2	Can 3
SVL	0.01	0.06	0.05	0.06	0.01	0.03
TrunkL	-0.14	-0.01	-0.06	0.47	0.32	-0.25
TailL	-0.12	0.02	0.05	-0.00	0.13	0.02
HeadL	0.55	0.84	0.79	1.58	-1.11	-0.87
HeadW	**2.01**	1.82	-1.18	1.73	1.71	2.02
HeadD	**-2.02**	-1.14	**3.20**	**3.20**	**-5.88**	-1.64
SnoutL	-1.33	0.79	**-2.45**	**-2.52**	-1.99	**3.03**
SnoutW	-0.21	**-2.45**	0.17	-0.60	0.92	0.37
EyeL	1.39	-1.91	-1.46	0.07	1.21	-0.73
ArmL	0.05	-0.16	-0.58	-0.74	-0.94	0.66
HandL	-0.33	0.16	0.23	**2.70**	-1.01	**-2.47**
LegL	0.03	-1.11	0.17	-2.13	0.14	0.58
FootL	-0.68	0.45	-0.87	1.00	1.65	-0.33
InterOrb	0.04	**-2.06**	0.50	-2.17	-0.40	1.86
IntNas	0.02	-0.48	0.31	0.78	-1.79	-1.95
IntSup	-0.16	-0.18	0.34	0.22	-0.50	-0.25
SupLab	0.43	-0.12	-0.15	-0.69	0.46	0.23
InfLab	-0.13	0.13	-0.05	0.43	-0.06	-0.40
4FLam	-0.38	0.18	0.17	0.59	0.63	0.12
4TLam	0.04	-0.05	-0.03	0.01	0.11	-0.18
Eigenvalue	2.950	1.987	1.223	11.99	3.67	2.47
Proportion of Variance	0.44	0.30	0.18	0.64	0.20	0.13

(b)	Males			Females		
Variable	Can 1	Can 2	Can 3	Can 1	Can 2	Can 3
Karratha	0.959	-2.307	0.973	-4.603	-1.890	0.305
Gascoyne	-0.824	2.910	3.364	5.105	-2.258	-2.194
Hamersley	0.619	0.232	-0.321	3.686	-1.925	-0.266
Fortescue	-2.467	-0.113	-0.540	-1.290	2.238	-1.483
Goldfields	2.199	1.366	-0.910	1.904	0.786	1.805

In contrast to the quantitative characters, differences in color, pattern, and scalation were more apparent, revealing clearly diagnosable groups that corresponded with the genetic lineages recovered above. Karratha individuals were distinguished by a series of five dark blotches along the vertebral zone of the dorsum, whereas the other lineages were either plain or did not exhibit such a reliable pattern of blotching. In addition, there were other scalation differences such as wide rostral scale, keeled ventrals, and no prominent row of enlarged scales on the front of the thigh that distinguish the Karratha form. The two other Pilbara lineages (Hamersley and Fortescue) differed from Karratha individuals by having a more elongate appearance with a relatively plain dorsum. Of these two closely-related sister lineages, Hamersley individuals had a rich red coloration and feeble keels on the snout, whereas Fortescue individuals tended to be browner with more pronounced keels on the snout.

(a) Males



(b) Females

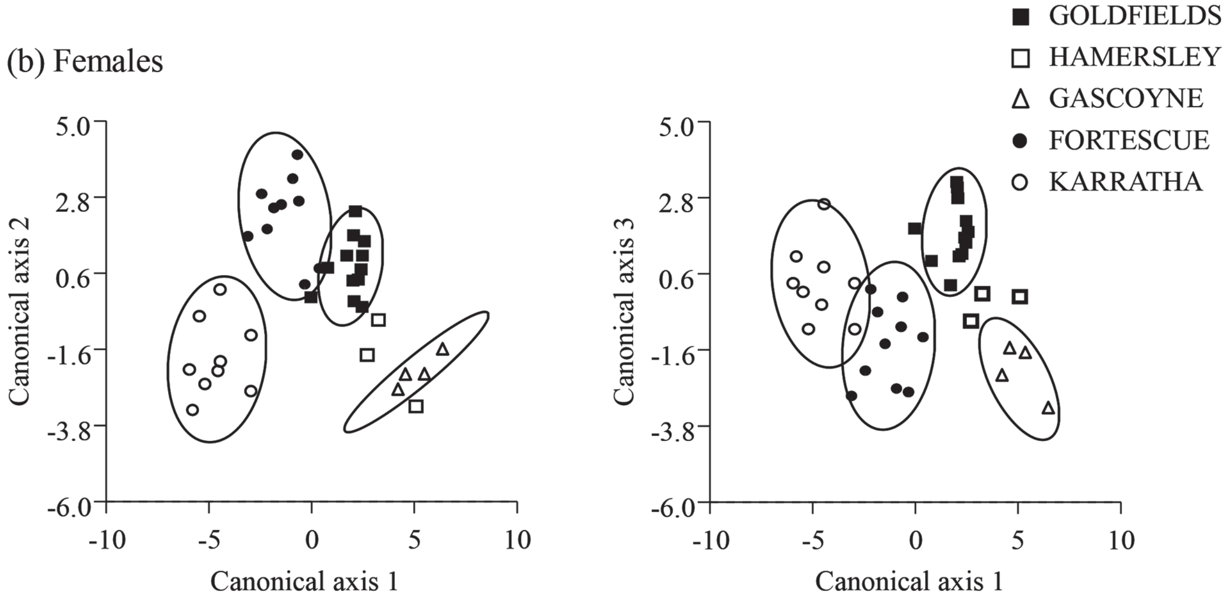


FIGURE 4. Discriminant function analyses based on the morphological dataset for (a) males and (b) females. Ellipses represent 95% confidence levels.

Outside of the Pilbara, two forms occur: the Gascoyne population for which the name *T. cephalus gigas* Mitchell, 1965 would apply, and a widespread southern form that occurs from just outside the Pilbara (~24ºS latitude) south to near Norseman (~32.2ºS latitude). The Gascoyne form is characterized by much larger maximum body size, rugose scales lacking keels on snout, no prominent ridge of enlarged scales on leading edge of thigh, and enlarged scales on dorsum not in transverse rows. The latter character is presumably diagnostic of the *T. cephalus* species-group, indicating that this taxon may fall outside of *T. cephalus senso lato* and may actually be more closely related to other *Tympanocrytpis* species.

The widespread Goldfields form is the one that typically appears in field guides and photographs (e.g. Storr *et al.* 1983; Wilson & Knowles 1988; Bush *et al.* 2007). This taxon is characterized by having a snout with a slight 'duck-like' appearance, i.e. with the line of the mouth protruding outwards, giving the snout a concave appearance when viewed laterally. This form also possesses a relatively narrow rostral scale, a well-defined row of scales on the leading edge of the thigh, and uniform reddish-brown ground color, often with a dark charcoal wash over the body and head.

All five lineages are allopatric and appear to replace one another geographically (Fig. 1). The three Pilbara forms are not each other's closest relatives as the Goldfields form is sister to the Hamersley + Fortescue forms (see above). Thus the type population for the *T. cephalus* near Karratha is sister to all other genotyped populations within the species-group.

Taxonomic conclusions. We found morphological and molecular genetic evidence to support the recognition of five species within *T. cephalus* as currently conceived. Figure 5 shows images in life of all five of the forms we recognize as full species here. For four of these lineages, we used the genetic evidence presented above and from Shoo *et al.* (2008) to guide our morphological analyses. There are no tissue samples for the fifth species, *T. gigas*, but it is one of the most distinctive taxa within the *T. cephalus* species-group, bearing in mind our earlier caveat that it may more closely related to other *Tympanocryptis* species. Although the Hamersley and Fortescue populations were not supported as independent by the nuclear DNA indicating a relatively recent split within the *T. cephalus* species-group, subtle morphological differences and evidence of independent evolutionary trajectories from the mitochondrial DNA led us to recognize both lineages as full species, rather than recognizing two subspecies (e.g. Zink 2004; Torstrom *et al.* 2014).

Taxonomy

Tympanocryptis Peters, 1863

Type species. *T. lineata* Peters, 1863, by monotypy.

Tympanocryptis cephalus Günther, 1867

Coastal pebble-mimic dragons
Figs. 5A, 6, 7

Lectotype. BMNH 1946.8.12.78, from Nicol (Nickol) Bay (= Karratha), Western Australia (Fig. 6). Lectotype designation by Cogger *et al.* (1983).

Diagnosis. Distinguished from other *Tympanocryptis* by the following combination of character states: presence of two pre-cloacal pores, lack of longitudinal stripes on the dorsum, presence of enlarged scales with raised spines arranged in transverse rows, snout straight or convex, scales on snout with low keels, rostral width ~3–4 times height, weakly defined row of enlarged scales at anterior and dorsal edge of thigh, scales on dorsal surface of thigh not aligned, ventrals with low keels, and irregular dark blotches along midline of dorsum.

Description. A small to medium-sized (to 64 mm SVL), moderately rotund dragon; head small with angular snout; moderately short neck; moderate gracile limbs, ArmL%SVL—0.193 (0.014), LegL%SVL—0.256 (0.020); gracile digits; short tail. Head small, HeadL%SVL—0.311 (0.017), HeadW%SVL—0.241 (0.014), HeadD%SVL—0.159 (0.01); neck ~3/4 of widest part of head; snout moderate, SnoutL%HeadL—0.253 (0.018), convex when viewed in profile, narrowing to blunt tip; canthus well-defined and angular, forming continuous line with projecting brow ridge; nostril located below canthus in enlarged scale, opening projecting dorsally and posteriorly; eye moderate, EyeL%HeadL—0.257 (0.023); eyes with laterally-projecting scaly eyelids forming a weak fringe, not projecting past brow when viewed dorsally; tympana covered with fine scales, partly encircled by scattered enlarged scales with low spines; rostral scale ~3–4 times wider than tall; scales on snout with low keels, not tending to align; scales on crown slightly larger with lower keels; scales on back of head small with variably-sized low scattered spines; 11–15 supralabial scales, above which are 3–4 rows of scales with low horizontally-orientated keels continuing to temporal region, uppermost row slightly more prominent and forming edge of eye socket; loosely defined cluster of enlarged spines at posterior and lateral corners of head; mental twice as long as wide; 12–15 infralabials with low keels; 4–5 rows below infralabials of scales with low keels parallel to angle of jaw, gulars kite-shaped with low keels; prominent gular fold.

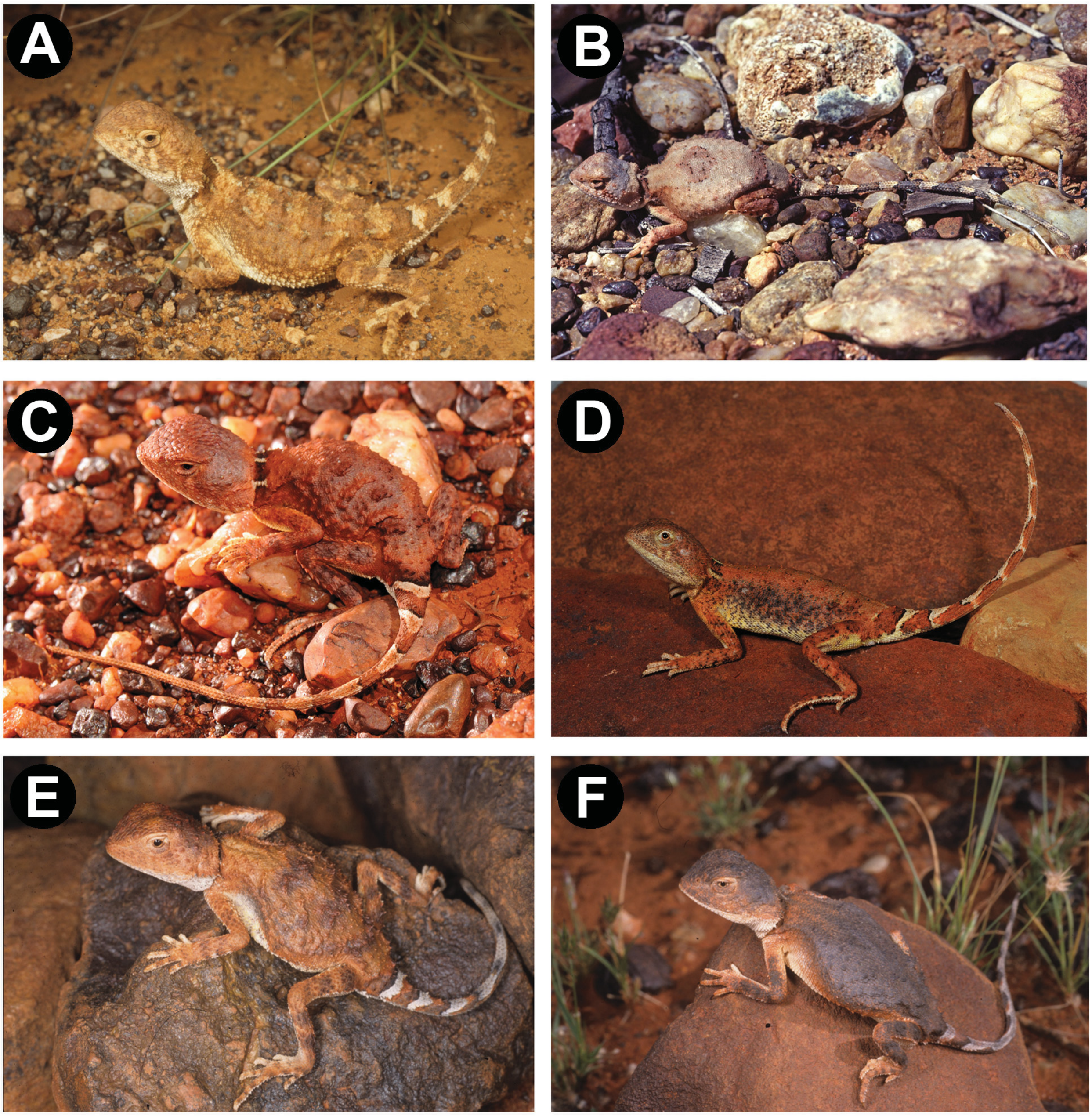


FIGURE 5. Photographs in life of *Tympanocryptis cephalus* species-group members (left to right, top to bottom): a) *T. cephalus* (photo—G. Harold), b) *T. gigas* (M. Peterson), c) *T. diabolicus* **sp. nov.** (M. Peterson), d) *T. fortescuensis* **sp. nov.** (G. Harold), e) *T. pseudopsephos* **sp. nov.**—plain form (G. Harold), f) *T. pseudopsephos* **sp. nov.**—with charcoal wash on dorsum (G. Harold).

Body dorsoventrally compressed, ovoid in dorsal view with widest part 2–3 times wider than neck and pelvis; TrunkL%SVL—0.453 (0.037); dorsum with heterogeneous scales in size and shape; largest scales with sharp spines angled 10–30° posteriorly and ~5–7 times larger than smallest scales; large dorsal scales with spines tending to occur in transversely-aligned clusters of ~4–6; smaller dorsal scales rugose or with weak, low keels, arranged in loose whorls around clusters of large, spiny scales; enlarged dorsolateral edge of pelvis always with a cluster of enlarged spines at posterior edge where skin is fused to bone; ventral scales homogeneous, approximately half the size of large dorsal scales, kite-shaped and arranged in diagonal rows, median keel low with posterior spine at most only slightly protruding past posterior edge of scale.

Limbs covered in elongate kite or teardrop-shaped scales with prominent low keels, spine usually protruding beyond distal edge of scale; arms and legs moderately long, ArmL%SVL—0.193 (0.014), LegL%SVL—0.256 (0.020); scales on dorsal surface of upper arm large with keels tending to align; keels of dorsal scales on lower arm aligned to form lines that extend to hand and fingers; keels of ventral scales mostly aligned forming lines along the length of the arm to palmar surfaces; scales on underside of digit with two rows of spiny lamellae; claw long and recurved, lower portion terminating with circular opening, upper portion continuing past ultimate lamellae to form sharp claw; finger length: 4 > 3 > 2 = 5 > 1. Scales on legs kite or teardrop-shaped; tops of upper and lower leg with large heterogeneous non-aligned scales, otherwise with low keels that align and extend to feet and toes; scales at insertion of limb to body small and lacking keels, abrupt transition from dorsal to posterior edge of leg (large to small scales); scales on underside of toes as for fingers; toe length: 4 >> 3 > 2 = 5 > 1.

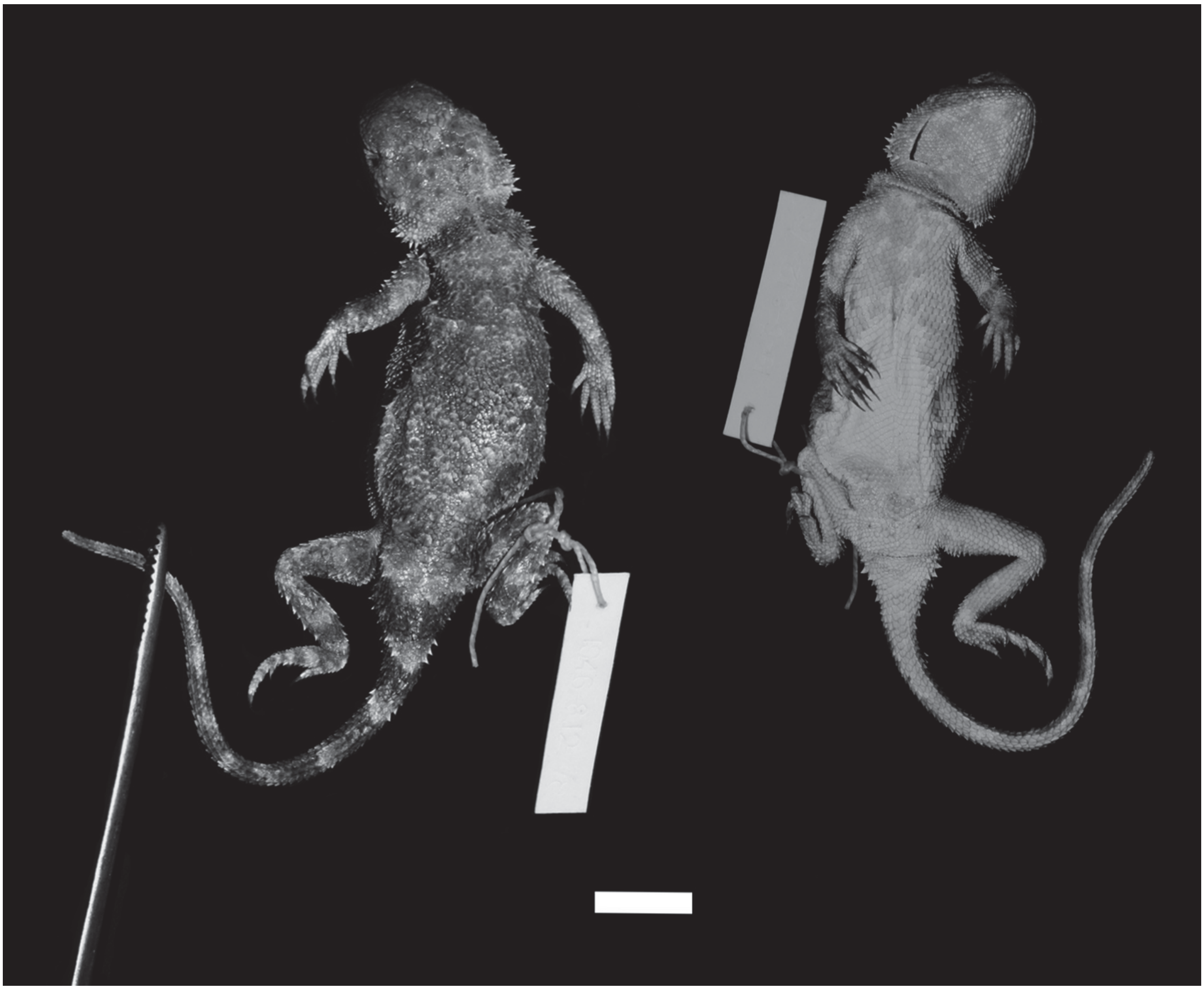


FIGURE 6. Lectotype of *Tympanocryptis cephalus* (BMNH 1946.8.12.78) (scale bar = 1 cm).

Pre-cloacal pores 2, set among 3–5 scales, positioned anterior to distal edges of cloaca, midway between anterior and posterior edge of leg; tail relatively short and thin with blunt tip, TailL%SVL—1.231 (0.134); scattered enlarged scales aligning along most of the length of the tail to terminus; lateral surfaces of tail base with short protruding spines.

Coloration and pattern. In life (based on WAM R165248; Fig. 5A), ground color light to medium brown, vertebral zone of dorsum with 5 tan irregularly-shaped blotches, series continuing to tail as 10–12 pale irregular bands that alternate with ground color, anterior edge of pale bands edged with black; limbs and digits weakly banded; sides of head below eye and naris paler than top of head, with 3–4 darker lines originating from eye to supralabial scales; nuchal region dark brown with three discrete pale bands. In preservative, the warmer hues tend to be lost, leaving a light brown ground color with pale tubercles in higher contrast (Fig. 7); by-catch individuals from glycol invertebrate pits tend to be a dark reddish-brown; WAM R165248 (Fig. 5A) and WAM R161047 appear to have vestiges of longitudinal lines; ventral surfaces pale, occasionally with reddish hue, ventral surface of tail lacking dark bands.

FIGURE 7. Variation in *Tympanocryptis cephalus* (scale bar = 1 cm).

Habitat. Very little data exists on this species, but WAM specimen records indicate its occurrence on red rocky loams or clayey substrates, with *Triodia*, Snakewood (*Acacia xiphophylla*), or annual grasses as the vegetation type. The Pilbara Biodiversity Survey data also indicated a preference for clayey substrates (Doughty *et al.* 2011).

Distribution. Confined to a coastal strip near Karratha and Roebourne in the Pilbara region, Western Australia (Fig. 1). The westernmost record is from Mardie Pool, with the easternmost record 200 km distant at Balla Balla Creek (~ 50 km east of Roebourne). Records occur from the coast and inland to about 40 km. Thus the total range of this species at current estimate is approximately 5,000 km^2.

Etymology. The word *cephalus* is a Latinized version of the Greek *cephalos*, meaning 'head'. Presumably this refers to the distinctive short head of this this species relative to other Australian agamid lizards at the time of description, as no explicit etymology was given. We maintain usage of *cephalus* as a noun in apposition, in contrast to occasional use of *cephala* (e.g. Storr 1964, 1982).

Comparisons with other species. *Tympanocryptis cephalus* is most likely to be confused with *T. gigas*, *T. fortescuensis* **sp. nov.**, and *T. diabolicus* **sp. nov.**, as these species all occur in the Pilbara or Gascoyne regions. *Tympanocryptis cephalus* is distinguished from *T. gigas* by possessing enlarged dorsal scales in short transverse rows on the dorsum (*versus* scattered spines not arranged in rows), scales on snout with low keels (*versus* rugose or with feeble keels), ventrals keeled (*versus* smooth), and smaller average body size.

From *T. diabolicus* **sp. nov.** and *T. fortescuensis* **sp. nov.**, *T. cephalus* is distinguished by generally longer transverse rows of enlarged scales on dorsum (5–7 *versus* 2–5), slightly wider rostral (3.5 *versus* 3.0 times wider than high), enlarged row of scales at front of thigh not forming a conspicuous ridge, and usually possessing a series of dark blotches along the midline; further distinguished from *T. diabolicus* **sp. nov.** by scales on snout possessing low keels (*versus* rugose scales or feebly keeled) and scales on upper thigh not aligned.

From the more geographically distant *T. pseudopsephos* **sp. nov.**, *T. cephalus* is distinguished by straight or convex snout (*versus* concave), low keels on snout (*versus* rugose or feebly keeled scales), rostral scale 3.5 times wider than high (*versus* 2 times), enlarged row of scales at front of thigh not forming a conspicuous ridge, keels on dorsal surface of upper arm not aligned, ventrals with low keels and spine protruding past posterior edge of scale (*versus* smooth with no spines), and more brownish coloration with vertebral series of irregular dark blotches.

Remarks. A theme during the history of this taxon is that most treatments and field guides focused on the more widely distributed Goldfields form, and indeed similar forms from South Australia and Queensland as well. The two syntypes of *T. cephalus* were collected from Nicol (= Nickol) Bay, where the town of Karratha is today, by F. Duboulay. For many years, the two syntypes were the only specimens from this region, and they were located at the Natural History Museum in London. Mitchell (1948) had no access to specimens from the Pilbara, but had photographs of the syntypes supplied by the Natural History Museum and provided some comments on these. Storr (1964) had access to only a single specimen (WAM R12495 from Mardie), and nearly 20 years later, only eight further specimens (but representing all three Pilbara species) were available to Storr (1982) for his taxonomic comments.

The lectotype (Fig. 6) is in agreement with specimens from the Pilbara coast by possessing dorsal blotching along the midline and low keels on the scales of the snout and ventrum, and ridge of scales on leading edge of thigh not well defined. The genetic analyses clearly indicate the coastal Pilbara population is the basal split within Western Australian *T. cephalus senso lato*.

As mentioned above, very few specimens of this species were available for study to Mitchell and Storr. Based on records in the WAM collections, only five specimens of true *T. cephalus* were available up to 1985. Since then, only one further specimen had been collected until the WA Department of Environment & Conservation's (now Parks & Wildlife) Pilbara Biodiversity Survey (PBS) from 2002–2007 (McKenzie *et al.* 2009; Doughty *et al.* 2011). This survey employed many pitfall trap arrays, and for the first time sufficient material was captured to provide the tissue samples necessary for the analysis of Shoo *et al.* (2008) and this study, as well as the specimens examined for morphology in this study (the same applies to the other two Pilbara species described below). This is perhaps due to the habits and predator evasion tactics employed by these species. Owing to the need to remain motionless to avoid predators individuals are not likely to move when a human approaches and so they remain undetected. In contrast, short movements are likely to occur regularly for thermoregulation and foraging, and when pitfall traps with low mesh fencing are employed, capture rates can be relatively high.

***Tympanocryptis gigas* Mitchell, 1948**

Gascoyne pebble-mimic dragons
Figs. 5B, 8, 9

Tympanocryptis cephalus gigas Mitchell, 1948

Holotype. SAMA R2434, from between Ashburton and Gascoyne Rivers, Western Australia (presumed lost).

Paratypes. SAMA R2434, two specimens, as for holotype.

Taxonomic history and neotype designation. Mitchell (1948) erected *T. cephalus gigas* for a population of large-bodied animals in the Gascoyne region of Western Australia, with the type locality of 'between the Ashburton and Gascoyne Rivers, W.A.' (an area approximately 100,000 km^2). Although he only examined three specimens, he believed the consistent differences in several characters, the large body size, and its occurrence in an ecologically different area merited at least subspecific designation. In a paper on the *T. lineata* species-group, Storr (1982) synonomized *T. cephalus gigas* with *T. cephalus* based on a larger sample of specimens, including some near the type location of *T. cephalus*. He concluded, 'These specimens do not differ substantially from those elsewhere; the attempt to divide *cephala* (sic) into subspecies is therefore abandoned' (p. 65).

The holotype and two paratypes of *T. cephalus gigas* all bear the same South Australian Museum registration number—SAMA R2434. The holotype has been missing since 1976 (Houston 1976; M. Hutchinson, pers. comm.), and is presumed lost or destroyed. The two paratypes from the same series, however, are extant and are clearly labeled as such with '2434' and 'PARATYPE' on Dymo tags (Fig. 8). Of these two specimens, the male is 66.5 mm SVL and is in relatively good condition, whereas the female is 57.0 mm SVL and is in poorer condition with damage to the dorsum resulting in large discolored patches (Fig. 9).

To stabilize use of the name *Tympanocryptis gigas* (elevated from a currently synonomized subspecies of *T. cephalus*), we designate as neotype the male and larger of the two paratype specimens. We also provide new South Australian Museum numbers (provided below) for the neotype and the remaining paratype to avoid any confusion with the missing holotype, which remains as SAMA R2434.

Neotype. SAMA R68044 (male), collected from 'between the Ashburton and Gascoyne Rivers, W.A.'; originally one of two paratypes with the number SAMA R2434.

Paratype. SAMA R68045 (female), details as for neotype; originally one of two paratypes with the number SAMA R2434.

Diagnosis. Distinguished from other *Tympanocryptis* by the following combination of character states:

presence of two pre-cloacal pores, lack of longitudinal stripes on the dorsum, presence of scattered enlarged scales with raised spines, snout convex, scales on snout rugose with at most feeble keels, rostral width ~2 times height, row of enlarged scales at anterior and dorsal edge of thigh, scales on dorsal surface of thigh heterogeneous and not aligned, ventrals smooth, and brown ground color with large dark blotches in center of dorsum and anterior to legs, tail with alternating dark and pale bands, posterior edge of dark bands with narrow black and white bands.

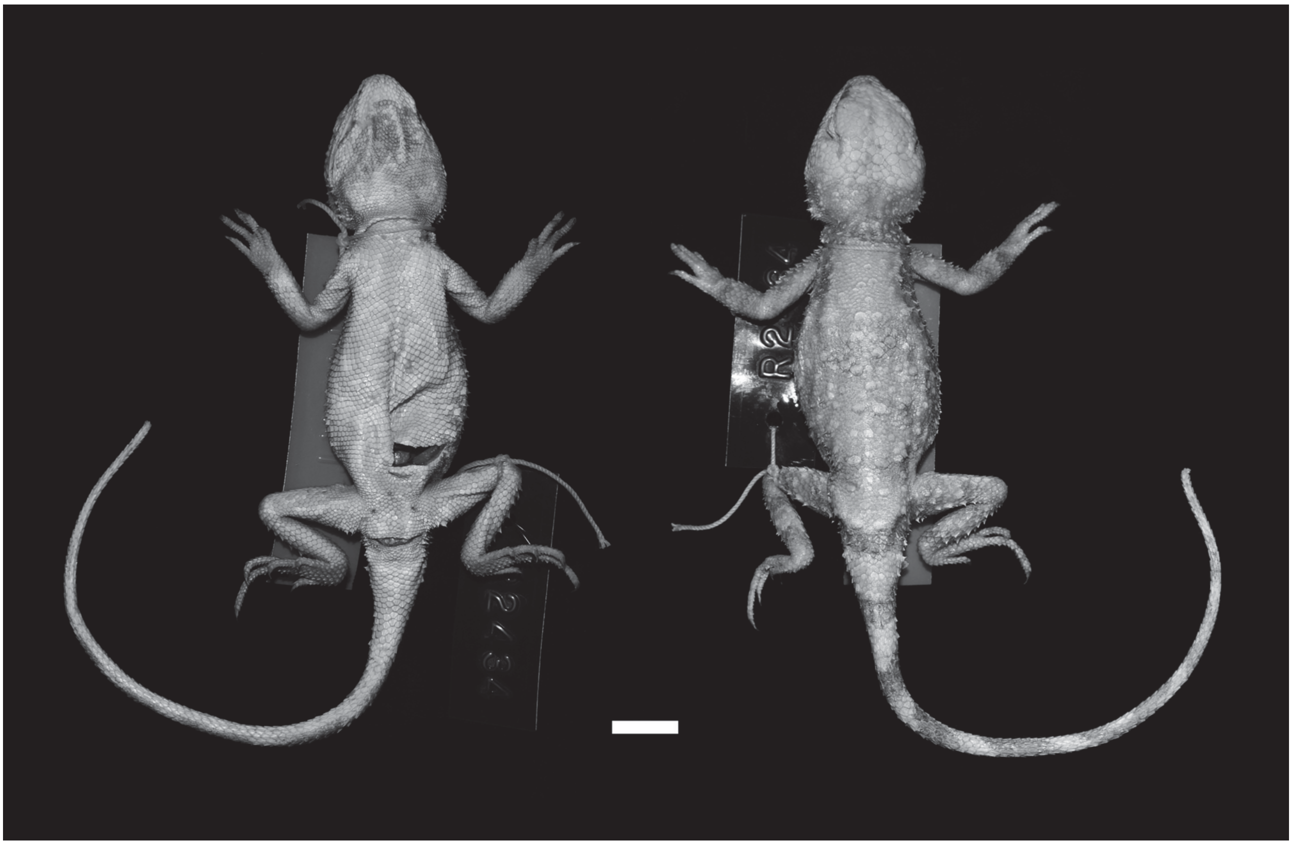


FIGURE 8. Neotype of *Tympanocryptis gigas* (SAMA R68044; formerly SAMA R2434) (scale bar = 1 cm).

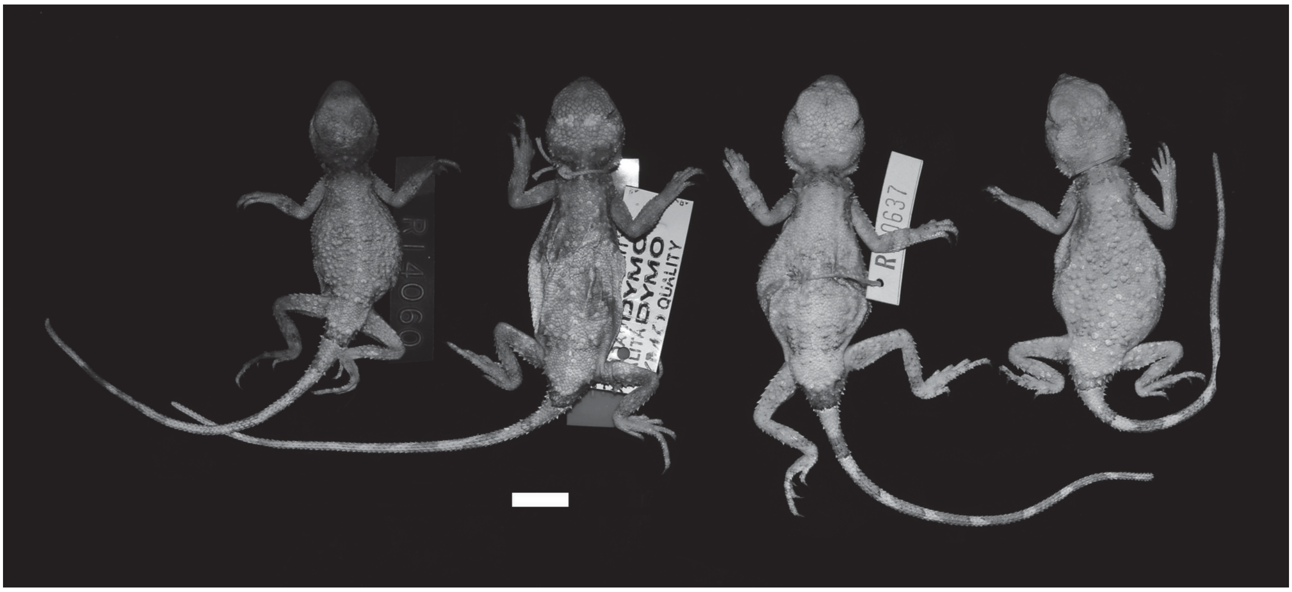


FIGURE 9. Variation in *Tympanocryptis gigas* (paratype SAMA R68045; formerly SAMA R2434 is the second from the left) (scale bar = 1 cm).

Description. A medium-sized (to 66.5 mm SVL), robust dragon; moderate head with blunt snout; short neck; moderately gracile limbs, ArmL%SVL—0.179 (0.010), LegL%SVL—0.228 (0.016); gracile digits; short tail. Head small, HeadL%SVL—0.310 (0.010), HeadW%SVL—0.251 (0.009), HeadD%SVL—0.160 (0.010); neck ~3/4 of widest part of head; snout short, SnoutL%HeadL—0.252 (0.010); snout straight or convex when viewed laterally, narrowing to blunt tip; canthus defined but rounded, forming continuous line with projecting brow ridge; nostril located below canthus in enlarged scale, opening projecting dorsally and posteriorly; eye moderate, EyeL%HeadL—0.236 (0.011); eyes with laterally-projecting scaly eyelids forming a fringe, projecting past brow when viewed dorsally; tympana covered with fine scales, bordered by scattered enlarged scales with spines; scales on snout rugose, occasionally with feeble unaligned keels; scales on crown slightly larger with feeble unaligned keels; scales on back of head small with few variably-sized low scattered spines; rostral scale ~2 times wider than tall; 11–13 supralabial scales, 4–5 rows of scales above supralabial row, keeled, uppermost row slightly larger with larger keels and continuing to temporal region, forming edge of eye socket; loosely defined cluster of enlarged spines at posterior and lateral corners of head; mental 1.5 times long as wide; 13–14 infralabials with low keels; 4–5 rows of scales below infralabials with low keels with parallel to angle of jaw, creating a slightly terraced appearance; gulars kite shaped and smooth; prominent gular fold.

Body slightly dorsoventrally compressed, rectangular or slightly ovoid in dorsal view with widest part ~1–2 times wider than neck and pelvis; TrunkL%SVL—0.487 (0.049); dorsum with heterogeneous scales in size and shape; largest scales with sharp spines angled 10–30° posteriorly and ~2–4 times larger than smallest scales; large dorsal scales with spines scattered, not occurring in transversely-aligned clusters; smaller dorsal scales smooth or rugose, not occurring in regular rows; dorsolateral edge of pelvis occasionally with a cluster of enlarged spines at posterior edge where skin is fused to bone; ventral scales homogeneous, approximately half the size of large dorsal scales, kite-shaped and arranged in diagonal rows; ventral scales smooth, or at most with raised midline (no keels or spines protruding beyond posterior edge of scale).

Limbs largely covered in elongate kite or teardrop-shaped scales with prominent low keels, spine usually protruding beyond distal edge of scale, interspersed with occasional small unkeeled scales; arms and legs moderately long, ArmL%SVL—0.179 (0.010), LegL%SVL—0.228 (0.016); scales on dorsal surface of upper arm large with keels usually not aligning; keels of dorsal scales on lower arm tending to align, often forming lines that extend to hand and fingers; keels of ventral scales mostly aligned forming lines along the length of the arm to palmar surfaces; scales on underside of digit with two rows of spiny lamellae; claw long and recurved, lower portion terminating with circular opening, upper portion continuing past ultimate lamellae to form sharp claw; finger length: 4 > 3 > 2 = 5 > 1; scales on legs kite or teardrop-shaped; tops of upper and lower leg with heterogeneous non-aligned scales, elsewhere with low keels that align and extend to feet and toes; scales at insertion of limb to body small, rectangular and lacking keels; anterior edge of thigh with row of enlarged scales; abrupt transition from dorsal to posterior edge of leg (large to small scales); scales on underside of toes as for fingers; toe length: 4 >> 3 > 2 = 5 > 1.

Pre-cloacal pores 2, set among 5 scales, positioned anterior to distal edges of cloaca, midway between anterior and posterior edge of leg; tail relatively long and thin with blunt tip, TailL%SVL—1.453 (0.128); scattered enlarged scales aligning along most of the length of the tail to terminus; lateral surfaces of tail base with short protruding spines.

Coloration and pattern. In life (from only known photo, Fig. 5B), ground color light brown; limbs slightly darker brown with faint banding; snout and top of head above eyes light brown, followed by grayish band at back of head, above covered tympanum light brown; nuchal region dark brown with three pale longitudinal markings (one at midline, other two behind covered tympanum); dorsum with central oblong darker blotch, edged with medium brown and with black-tipped spines; dark brown band anterior to legs; pelvic region gray; tail with 10 alternating dark brown and pale bands.

In preservative (Fig. 9), most specimens have lost almost all coloration and have faded to a pale yellow or white, except for the tail (except for WAM R19111 which is a brownish-black likely owing to preservation); tails with 8–10 dark bands; on the posterior edge of the dark bands in three individuals (WAM R40655, R40637, R80823), there is an indication of a very thin dark band followed by a thin white band, and in the latter two individuals the dark mid-dorsal and hindlimb bands are discernible; in WAM R40655 the three pale, dark-edged neck streaks are visible, otherwise the nuchal region is a dark brown; ventral surfaces pale, with no dark bands encircling tail (except for WAM R19111).

Ecology and habitats. Unknown.

Distribution. Gascoyne region, Western Australia (Fig. 1). The three original type specimens were listed as being from 'between the Ashburton and Gascoyne Rivers, W.A.' Other records from the WAM collection are from Yinnietharra and Williambury Stations, and Wandagee. A record from Bernier Island (WAM R19111) is somewhat dubious as this is a sandy habitat that is quite different from mainland habitats where other *T. gigas* and other *Tympanocrptis* species frequent. An old specimen from Lyndon (WAM R8832) could not be found.

Etymology. Mitchell (1948) did not explicitly provide an etymology in his description of this taxon as a subspecies of *T. cephalus*. However, the word *gigas* is a Latinized version of the Greek *gantos* for 'giant', presumably in reference to this taxon's relatively large body size to *T. cephalus*. We treat *gigas* as a noun in apposition.

Comparisons with other species. *Tympanocryptis gigas* is most likely to be confused with *T. diabolicus* **sp. nov.** and *T. pseudopsephos* **sp. nov.**, as the latter species occur to the north in the Pilbara or east to the northern Goldfields regions of Western Australia. *Tympanocryptis gigas* is distinguished from *T. diabolicus* **sp. nov.** by possessing scattered enlarged scales on dorsum not arranged in rows (*versus* enlarged scales in short transverse rows), keels on dorsal surface of upper arm not aligned, ventrals smooth (*versus* with low keels), enlarged row of scales at front of thigh not forming a conspicuous ridge, scales on top of thigh heterogeneous and keels not aligned, and larger average body size.

Tympanocryptis gigas can be distinguished from *T. pseudopsephos* **sp. nov.** by larger body size, oblong (*versus* rotund) body shape, convex snout (*versus* concave), possessing scattered enlarged scales on dorsum not arranged in rows (*versus* enlarged scales in short transverse rows), enlarged row of scales at front of thigh not forming a conspicuous ridge, and heterogeneous scales on upper surface of thigh.

Remarks. Based on its distinctive morphology compared to other *T. cephalus* species-group members, we have herein raised *T. cephalus gigas* to a full species—*T. gigas*. We have, however, lingering doubts as to its inclusion in this species-group. Notably, average body size is much larger than the other species considered here (Appendix 3), although sample sizes for *T. gigas* remain small. Significantly, the dorsal scalation appears to diverge from typical *T. cephalus* group members, as the enlarged scales with spines tend not to occur in conspicuous transverse rows. These differences highlight the need for tissue for genetic analyses to confidently place this taxon within the *Tympanocryptis* species-group. At present, however, we suggest leaving *T. gigas* in the *T. cephalus* species-group (an unofficial, convenient taxonomic unit) until further evidence is available.

***Tympanocryptis diabolicus* sp. nov.**

Hamersley pebble-mimic dragons
Figs. 5C, 10, 11

Holotype. WAM R135413, an adult male collected at Mount Brockman (22°17'31"S, 117°16'23"E), Western Australia, on 20 November 1998 by S. Anstee (Fig. 10).

Paratypes. WAM R135411 (male), Mount Brockman (22°17'31"S, 117°16'23"E); WAM R135412 (male), Mount Brockman (22°17'31"S, 117°16'23"E), WAM R135454 (male), Mount Brockman (22°17'31"S, 117°16'23"E), WAM R170204 (male), 53 km north-north-west of Tom Price (22°18'21"S, 117°28'47"E); WAM R170281 (male), 51 km east-south-east of Paraburdoo (23°17'33"S, 118°09'23"E)

Diagnosis. Distinguished from other *Tympanocryptis* by the following combination of character states: presence of two pre-cloacal pores, lack of longitudinal stripes on the dorsum, presence of enlarged scales with raised spines arranged in transverse rows of 2–5 scales or scattered on dorsum, snout straight or concave, scales on snout smooth to rugose with feeble keels, rostral width ~2–3 times height, keels on scales of upper arm aligned, well-defined row of enlarged scales at anterior and dorsal edge of thigh forming conspicuous ridge, scales on dorsal surface of thigh aligned, ventrals with low keels, and rich reddish-brown ground coloration with some irregular dark blotching along midline of dorsum.

Description. A small (to 60.5 mm SVL), rotund dragon; small head with blunt snout; short neck; moderately short gracile limbs, ArmL%SVL—0.189 (0.018), LegL%SVL—0.250 (0.017); gracile digits; short tail. Head small, HeadL%SVL—0.310 (0.018), HeadW%SVL—0.249 (0.016), HeadD%SVL—0.158 (0.010); neck ~3/4 of widest part of head; snout short, SnoutL%HeadL—0.256 (0.021); snout straight or concave when viewed laterally, if concave then snout tip projects forward, narrowing to blunt tip; canthus defined but rounded, forming a continuous line with projecting brow ridge; nostril located below canthus in enlarged scale, opening projecting dorsally and posteriorly; eye moderate, EyeL%HeadL—0.253 (0.019); eyes with laterally-projecting scaly eyelids forming a fringe, rarely projecting past brow when viewed dorsally; tympana covered with fine scales, encircled by scattered enlarged scales with raised apex; scales on snout rugose, occasionally with feeble unaligned keels; scales on crown slightly larger with feeble unaligned keels; scales on back of head small with few variably-sized low scattered spines; rostral scale ~2–3 times wider than tall; 10–14 supralabial scales, 5 rows of scales above supralabial row, keeled, uppermost row slightly larger with larger keels and continuing to temporal region, forming edge of eye socket; loosely defined cluster of enlarged spines at posterior and lateral corners of head; mental 1.5–2 times long as wide; 12–15 infralabials with low keels; 4–5 rows of scales below infralabials with low keels parallel to angle of jaw, creating a slightly terraced appearance; gulars kite or teardrop-shaped and smooth; prominent gular fold.

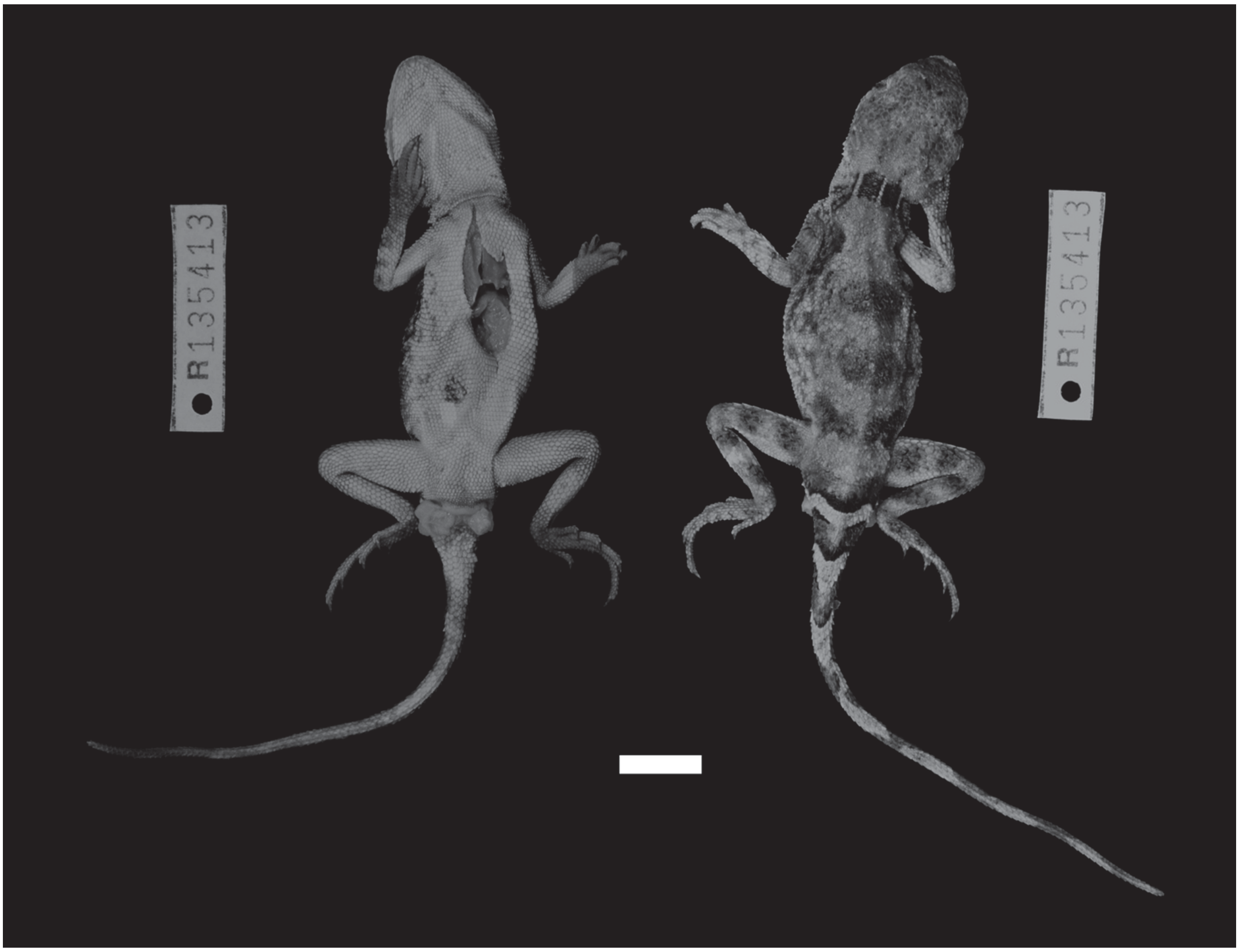


FIGURE 10. Holotype of *Tympanocrtyptis diabolicus* **sp. nov.** (scale bar = 1 cm).

Body dorsoventrally compressed, ovoid in dorsal view with widest part ~1.5–2 times wider than neck and pelvis; TrunkL%SVL—0.463 (0.034); dorsum with heterogeneous scales in size and shape; largest scales with low spines angled 10–30° posteriorly and ~2–5 times larger than smallest scales; large dorsal scales with spines tending to occur in oblique or transversely-aligned clusters of ~2–6; smaller dorsal scales smooth to rugose, arranged in loose whorls around clusters of large, spiny scales; dorsolateral edge of pelvis always with a cluster of enlarged spines at posterior edge where skin is fused to bone; ventral scales homogeneous, approximately half the size of large dorsal scales, kite or teardrop-shaped and arranged in diagonal rows, median keels low.

Limbs covered in elongate kite or teardrop-shaped scales with prominent low keels, spine usually protruding beyond distal edge of scale; arms and legs moderately long, ArmL%SVL—0.189 (0.018), LegL%SVL—0.250

(0.017); scales on dorsal surface of upper arm large with keels aligned; keels of dorsal scales on lower arm aligned, forming lines that extend to hand and fingers; keels of ventral scales mostly aligned forming lines along the length of the arm to palmar surfaces; scales on underside of digit with two rows of spiny lamellae; claw long and recurved, lower portion terminating with circular opening, upper portion continuing past ultimate lamellae to form sharp claw; finger length: 4 > 3 > 2 = 5 > 1; scales on legs kite or teardrop-shaped; tops of upper and lower leg with large non-aligned relatively homogeneous scales, elsewhere with low keels that align and extend to feet and toes; scales at insertion of limb to body small, rectangular and lacking keels; anterior edge of thigh with enlarged scales forming conspicuous ridge; abrupt transition from dorsal to posterior edge of leg (large to small scales); scales on underside of toes as for fingers; toe length: 4 >> 3 > 2 = 5 > 1.

Pre-cloacal pores 2, set among 3–6 scales, positioned anterior to distal edges of cloaca, midway between anterior and posterior edge of leg; tail moderately short and thin with blunt tip, TailL%SVL—1.317 (0.172); scattered enlarged scales aligning along most of the length of the tail to terminus; lateral surfaces of tail base with few, short protruding spines.

Measurements for the type series are presented in Table 3.

TABLE 3. Summary of meristic (mm) and mensural data for the type series of *Tympanocryptis diabolicus* **sp. nov.**

R#	135413	135454	170204	135412	135411	170281
Sex	Male	Male	Male	Male	Male	Male
SVL	54.5	60.5	47.5	60.0	58.5	59.0
TrunkL	24.7	28.8	22.8	27.9	27.8	26.7
TailL	71.5	84.5	63.0	57.0	58.0	78.5
HeadL	16.2	17.2	13.9	16.9	17.4	18.0
HeadW	13.0	13.4	11.7	13.4	12.8	13.5
HeadD	8.6	8.9	7.0	8.3	8.6	9.0
SnoutL	4.0	4.4	3.8	3.9	3.8	4.7
SnoutW	6.1	6.2	5.4	6.2	6.1	6.7
EyeL	4.2	4.7	3.7	4.2	4.3	4.2
InterOrb	1.7	1.9	2.0	2.1	2.2	2.3
ArmL	11.1	12.0	6.1	10.3	11.2	11.5
HandL	8.9	8.5	6.9	7.4	7.5	8.6
LegL	14.5	15.5	12.3	13.1	15.2	14.2
FootL	16.1	17.3	14.3	16.9	16.9	16.5
HeadW/SVL	0.2	0.2	0.3	0.2	0.2	0.2
FootL/SVL	0.3	0.3	0.3	0.3	0.3	0.3
TailL/SVL	1.3	1.4	1.3	1.0	1.0	1.3

Coloration and pattern. In life (Fig. 5C), ground color a rich reddish-brown with variable shading, often with grayish black wash over head, body, and limbs; limbs with subtle bands; nuchal region dark brown, interrupted by three short white lines edged with black; tail with ~8 alternating pale and ground color bands, anterior edge of pale bands edged with black, pale bands tending to coalesce on posterior half of tail forming pale stripe. In preservative, ground color fading to light grayish-brown, in some individuals dark blotches more well-defined and usually number 3–4, some individuals with no blotches but darkened dorsolateral zones (WAM R164063, R170281; Fig. 11); axillary region often with darkened scales in mosaic pattern; ventral surfaces pale white or with reddish hue in some individuals (WAM R135413; Fig. 10).

Habitat. Little is known of this species' habitat preferences from collector's notes. This species was combined with *T. fortescuensis* **sp. nov.** in the analysis of the PBS data (Doughty *et al.* 2011), which indicated a strong preference for clayey substrates, with many of the sites having small rocks and pebbles strewn across the surface (McKenzie *et al.* 2009).

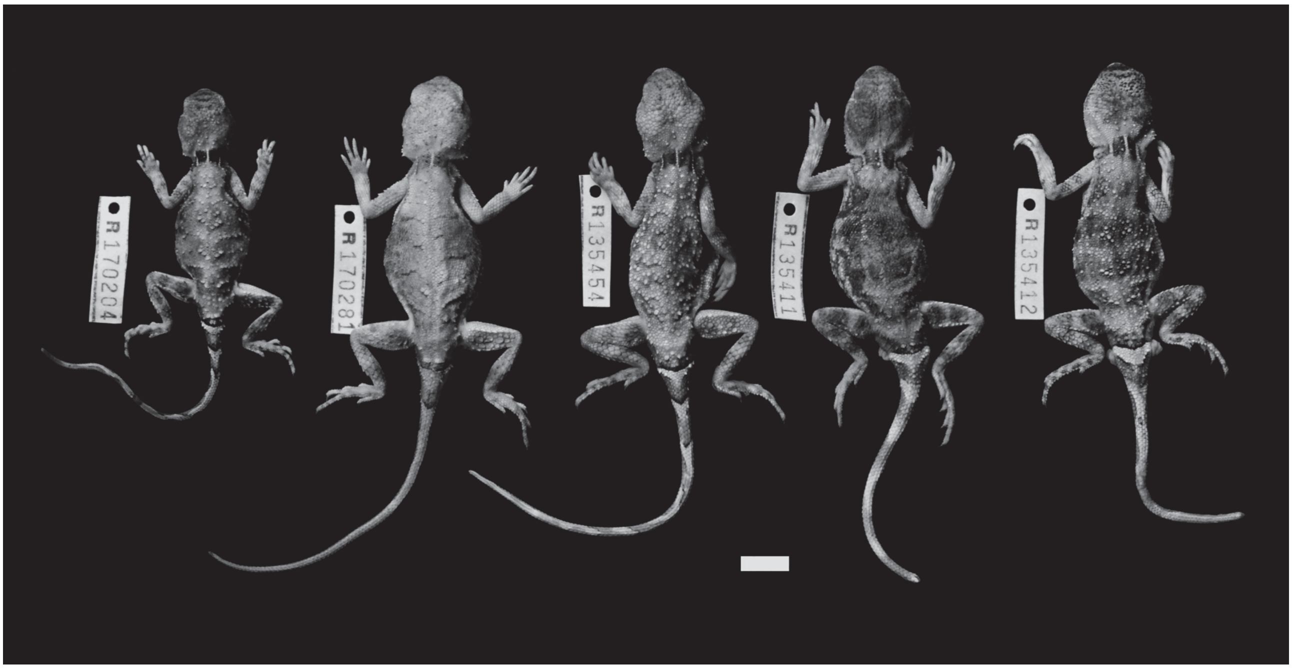


FIGURE 11. Paratypes of *Tympanocryptis diabolicus* **sp. nov.** (scale bar = 1 cm).

Distribution. Restricted to the Hamersley Range in the Pilbara region of Western Australia (Fig. 1). Western records include a specimen from Mt De Courcey in the south-west Hamersley Range, Mt Brockman, and Tom Price. Other locations include Paraburdoo, Rhodes Ridge, Giles Point, and Turee Ck. The easternmost records are from Mt Newman. The distribution of *T. diabolicus* **sp. nov.** runs along the northern edge of the Hamersley range, in parallel to *T. fortescuensis* **sp. nov.** which occurs along the Fortescue Marsh.

Etymology. '*diabolicus*' means 'devil' in Latin, in reference to the rich red coloration possessed by most individuals of this species. Used as a noun in apposition.

Comparisons with other species. Based on its central location relative to the distribution of the other taxa treated here, we provide comparisons of *T. diabolicus* **sp. nov.** to all of these species. *Tympanocryptis diabolicus* **sp. nov.** is distinguished from *T. cephalus* by possessing enlarged dorsal scales in short transverse rows in rows of 2–5 scales (*versus* 5–7), scales on snout rugose with feeble keels (*versus* with low keels), enlarged row of scales forming ridge on leading edge of thigh (*versus* poorly defined), and rich reddish-brown coloration with only weak blotching along midline (*versus* brown with dark blotches).

Tympanocryptis diabolicus **sp. nov.** is distinguished from *T. gigas* by smaller body size, more rotund body shape, enlarged scales on dorsum arranged in short transverse rows (*versus* slightly enlarged scales scattered on dorsum), keels on dorsal surface of upper arm aligned, conspicuous ridge on front of thigh formed by enlarged row of scales, scales on top of thigh homogeneous with keels forming lines, ventrals with low keels (*versus* smooth), and rich reddish-brown coloration with only weak blotching along midline (*versus* light brown with dark blotches in center of dorsum and anterior to legs).

Tympanocryptis diabolicus **sp. nov.** is distinguished *T. pseudopsephos* **sp. nov.** by rostral scale 3 times wider than high (*versus* 2 times), keels on dorsal surface of upper arm aligned, keels of scales on top of thigh aligned, and ventrals with low keels (*versus* smooth or slightly raised).

Tympanocryptis diabolicus **sp. nov.** is distinguished from the closely-related *T. fortescuensis* **sp. nov.** by scales on snout rugose with feeble keels (*versus* with low keels) and ground color a rich reddish-brown with some evidence of blotching along midline of dorsum (*versus* light brown rarely with blotching along midline).

Remarks. The genetic differences between *T. diabolicus* **sp. nov.** and *T. fortescuensis* **sp. nov.** are on the order of 5%, with an estimated time of divergence of 2.8 million years (Shoo *et al.* 2008). Although not as great differences among other *Tympanocryptis* species, we believe species recognition for this taxon is warranted owing to the strong overall genetic support presented here (Fig. 3) and in Shoo *et al.* (2008), the non-overlapping distribution of the species, and the two key morphological differences between the species: coloration and pattern, and the keeling on the snout.

Tympanocryptis fortescuensis sp. nov.

Fortescue pebble-mimic dragons
Figs. 5D, 12, 13

Holotype. WAM R158076, an adult male collected 4 km south-south-east of Wanna Wanna Pool (21°23'41"S, 117°10'14"E), Western Australia, on 9 October 2004 by J. K. Rolfe and B. Durrant (Fig. 12).

Paratypes. WAM R108817 (male), 37 km north-north-east of Auski Roadhouse (22°03'S, 118°48'E); WAM R110129 (male), 12 km east-south-east of Mount Billroth (21°39'45"S, 117°42'17"E); WAM R113625 (female), 37 km north-north-east of Auski Roadhouse (22°03'S, 118°49'E); WAM R121974 (male), Roy Hill Station (22°34'18"S, 119°58'39"E); WAM R158074 (female), 4 km south-south-east of Wanna Wanna Pool (21°23'41"S, 117°10'14"E).

Diagnosis. Distinguished from other *Tympanocryptis* by the following combination of character states: presence of two pre-cloacal pores, lack of longitudinal stripes on the dorsum, presence of enlarged scales with raised spines arranged in transverse rows of 2–5 scales on dorsum, snout straight or convex, scales on snout smooth with low keels, rostral width ~2–3 times height, keels on scales of upper arm aligned, well-defined row of enlarged scales at anterior and dorsal edge of thigh forming conspicuous ridge, scales on dorsal surface of thigh usually aligned, ventrals with low keels, and light reddish-brown coloration, often with blackish sides.

Description. A small to medium-sized (to 65.0 mm SVL), slightly rotund dragon; small head; blunt snout with slightly protruding mouth; short neck; moderately short gracile limbs, ArmL%SVL—0.196 (0.017), LegL%SVL—0.259 (0.020); moderately short gracile digits; short tail. Head small, HeadL%SVL—0.307 (0.017), HeadW%SVL—0.235 (0.018), HeadD%SVL—0.155 (0.009); neck ~3/4 of widest part of head; snout short, SnoutL%HeadL—0.266 (0.016); snout convex, straight or slightly concave when viewed laterally, if concave then snout tip projects forward, narrowing to blunt tip; canthus defined but rounded, forming continuous line with projecting brow ridge; nostril located below canthus in enlarged scale, opening projecting dorsally and posteriorly; eye moderate, EyeL%HeadL—0.248 (0.018); eyes with laterally-projecting scaly eyelids forming a fringe, rarely projecting past brow when viewed dorsally; tympana covered with fine scales, surrounded by several scattered enlarged scales with moderately raised apex; scales on snout rugose and usually with low unaligned keels; scales on crown slightly larger with moderately strong unaligned keels; scales on back of head small with several variably-sized low scattered spines; rostral scale ~2–3 times wider than tall; 11–15 supralabial scales, 4–5 rows of scales above supralabial row, keeled, uppermost row slightly larger with larger keels and continuing to temporal region, forming edge of eye socket; loosely defined cluster of enlarged spines at posterior and lateral corners of head; mental 1.5–2 times long as wide; 12–15 infralabials with low keels; 4–5 rows of scales below infralabials with medium to low keels parallel to angle of jaw, creating a terraced appearance; gulars kite or teardrop-shaped and smooth; prominent gular fold.

Body dorsoventrally compressed, slightly ovoid in dorsal view with widest part ~1.5–2 times wider than neck and pelvis; TrunkL%SVL—0.464 (0.029); dorsum with heterogeneous scales in size and shape; largest scales with low spines angled 10–30° posteriorly and ~2–5 times larger than smallest scales; large dorsal scales with spines tending to occur in oblique or transversely-aligned clusters of ~2–6; smaller dorsal scales smooth to rugose, arranged in loose whorls around clusters of large, spiny scales; dorsolateral edge of pelvis always with a cluster of enlarged spines at posterior edge where skin is fused to bone; ventral scales homogeneous, approximately half the size of large dorsal scales, kite or teardrop-shaped and arranged in diagonal rows, median keel low.

Limbs covered in elongate kite or teardrop-shaped scales with prominent medium high keels, spine usually protruding beyond distal edge of scale; arms and legs moderately long, ArmL%SVL—0.196 (0.017), LegL%SVL—0.259 (0.020); scales on dorsal surface of upper arm large with keels usually forming lines; keels of dorsal scales on lower arm aligned, forming lines that extend to hand and fingers; keels of ventral scales mostly aligned forming lines along the length of the arm to palmar surfaces; scales on underside of digit with two rows of spiny lamellae; claw long and recurved, lower portion terminating with circular opening, upper portion continuing past ultimate lamellae to form sharp claw; finger length: 4 > 3 > 2 = 5 > 1. Scales on legs kite or teardrop-shaped; tops of upper and lower leg with large non-aligned relatively homogeneous scales, elsewhere with low keels that align and extend to feet and toes; scales at insertion of limb to body small, rectangular and lacking keels; anterior edge of thigh with enlarged scales forming conspicuous ridge; abrupt transition from dorsal to posterior edge of leg (large to small scales); scales on underside of toes as for fingers; toe length: 4 >> 3 > 2 = 5 > 1.

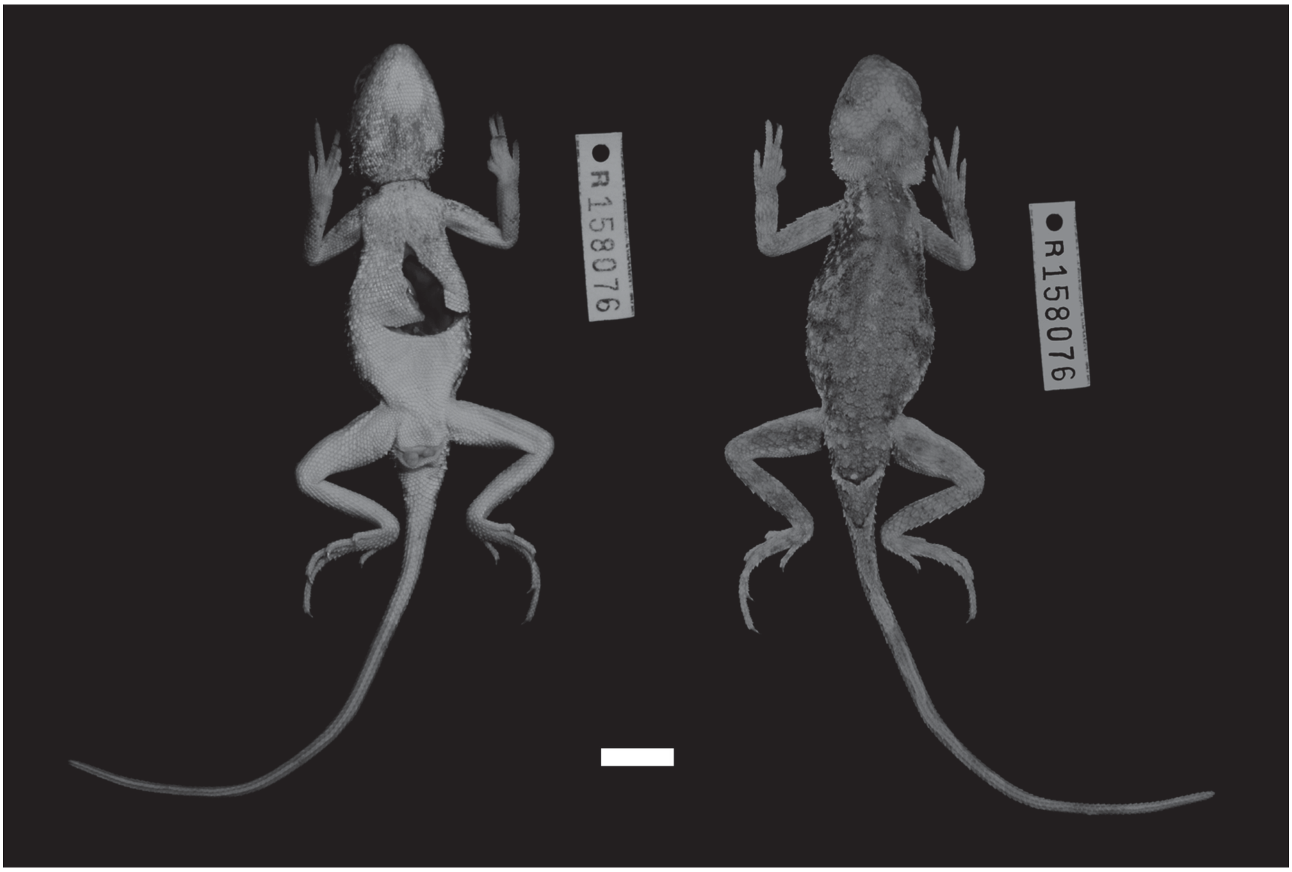


FIGURE 12. Holotype of *Tympanocryptis fortescuensis* **sp. nov.** (scale bar = 1 cm).

FIGURE 13. Paratypes of *Tympanocryptis fortescuensis* **sp. nov.** (scale bar = 1 cm).

Pre-cloacal pores 2, set among 4–6 scales, positioned anterior to distal edges of cloaca, midway between anterior and posterior edge of leg; tail moderately short and thin with blunt tip, TailL%SVL—1.388 (0.127); scattered enlarged scales aligning along most of the length of the tail to terminus; lateral surfaces of tail base with few, short protruding spines.

Measurements for the type series are presented in Table 4.

TABLE 4. Summary of meristic (mm) and mensural data for the type series of *Tympanocryptis fortescuensis* **sp. nov.**

R#	158076	110129	121974	113625	158074	108817
Sex	Male	Male	Male	Female	Female	Male
SVL	56.0	50.5	58.0	59.0	49.0	65.0
TrunkL	24.4	22.2	24.6	26.0	23.3	30.7
TailL	78.5	70.0	90.5	92.0	65.5	98.0
HeadL	16.3	15.5	16.8	19.1	15.1	19.4
HeadW	12.1	11.6	13.5	12.3	11.4	14.2
HeadD	8.4	7.6	8.6	8.5	7.4	9.8
SnoutL	4.0	4.0	4.1	4.6	3.9	5.1
SnoutW	5.5	5.6	6.0	6.3	5.5	6.9
EyeL	4.1	3.6	4.4	4.3	3.6	4.7
InterOrb	1.8	1.7	1.9	2.1	2.1	2.3
ArmL	11.8	10.2	10.9	12.3	10.2	11.8
HeadL	7.8	7.9	9.2	9.4	7.8	8.1
LegL	15.5	14.1	14.6	14.3	12.9	16.8
FootL	18.1	16.6	16.3	17.4	14.7	17.8
HeadW/SVL	0.2	0.2	0.2	0.2	0.2	0.2
FootL/SVL	0.3	0.3	0.3	0.3	0.3	0.3
TailL/SVL	1.4	1.4	1.6	1.6	1.3	1.5

Color and pattern. In life (Fig. 5D), ground color light to medium reddish-brown, usually uniform but occasionally with subtle variations in shade forming just discernible blotches; limbs weakly banded; nuchal region dark brown with three pale lines edged with black; lateral surfaces stippled with black; tail with ~10 alternating bands of ground color and pale white, anterior edge of pale bands edged with black, pale bands sometimes joining posteriorly to form an irregular stripe on top of tail; chest and chin sometimes suffused with a light yellow. In preservative, most individuals gray with some reddish hues (Fig. 13); dark upper axillary and dorsolateral zones more apparent; flanks with irregular pale dark flecking forming irregular wavy lines; tail with ~8–10 alternating dark and pale bands, but most individuals with pale bands coalescing to form a pale stripe along posterior half of tail; ventral surfaces pale, some with a reddish hue (Fig. 12).

Habitat. Most collectors' notes of specimens indicate a preference for cracking clays in the Pilbara region, with one record from a mulga woodland on a clayey loam with small scattered rocks. As mentioned above, this species was combined with *T. diabolicus* **sp. nov.** in the PBS analysis (Doughty *et al.* 2011), which indicated a preference for clay (alluvial) surfaces with strewn rock and tussock grass.

Distribution. Restricted to the Pilbara region of Western Australia. Generally recorded from the Fortescue Marsh area, from near Balfour Downs in the south-east Pilbara, then angling to Millstream-Chichester National Park. There is an outlying record (WAM R160032) from Meentheena Nature Reserve towards the north-east Pilbara, indicating it could be more widely distributed north of the Fortescue River.

Etymology. The specific name is in reference to the Fortescue basin or marsh, formed by the Fortescue River, where this species occurs.

Comparison with other species. *Tympanocryptis fortescuensis* **sp. nov.** is mostly likely to be confused with *T. cephalus* and *T. diabolicus* **sp. nov.** It is distinguished from *T. cephalus* by possessing enlarged dorsal scales in short transverse rows in rows of 2–5 scales (*versus* 5–7), enlarged row of scales at front of thigh forming a conspicuous ridge (*versus* weakly-defined row), scales on upper thigh usually aligned, and uniform light reddish-brown dorsum with at most only subtly discernible blotches along midline (*versus* brown with dark blotches).

Tympanocryptis fortescuensis **sp. nov.** is distinguished from *T. diabolicus* **sp. nov.** by having scales on snout with low keels (*versus* rugose with feeble keels) and light brown coloration rarely possessing dorsal blotches (*versus* rich reddish-brown occasionally with blotches).

Remarks. This species is very similar to *T. diabolicus* **sp. nov.**, differing in coloration and pattern, and having more well-defined keels on the snout. Genetic differences are ~5% between the two taxa (Shoo *et al.* 2008), and they are geographically separated with *T. diabolicus* **sp. nov.** occurring on the uplands of the Hamersley Range, whereas *T. fortescuensis* **sp. nov.** occurs on the Fortescue Marsh itself and in cracking clay habitats in the Chichester Range.

Tympanocryptis pseudopsephos **sp. nov.**

Goldfields pebble-mimic dragons
Figs. 5E, 5F, 14, 15

Holotype. WAM R154790, an adult male collected 31 km south-west of Doolgunna Homestead (25°52'33"S, 119°01'41"E), Western Australia, on 5 April 2004 by B. Maryan and B. Budrey (Fig. 14).

Paratypes. WAM R114550 (female), 67 km south of Capricorn Roadhouse, 18 km east of Bulloo Down homestead (24°00'S, 119°45'E); WAM R136459 (female), Norseman Area (32°12'S, 121°47'E); WAM R164347 (male), 46.1 km east of Leonora (28°51'36"S, 121°48'12"E); WAM R164350 (female), 11.8 km east of Leonora (28°54'23"S, 121°26'44"E); WAM R167478 (male), 49.5 km north of Leinster (27°22'36"S, 120°35'10"E).

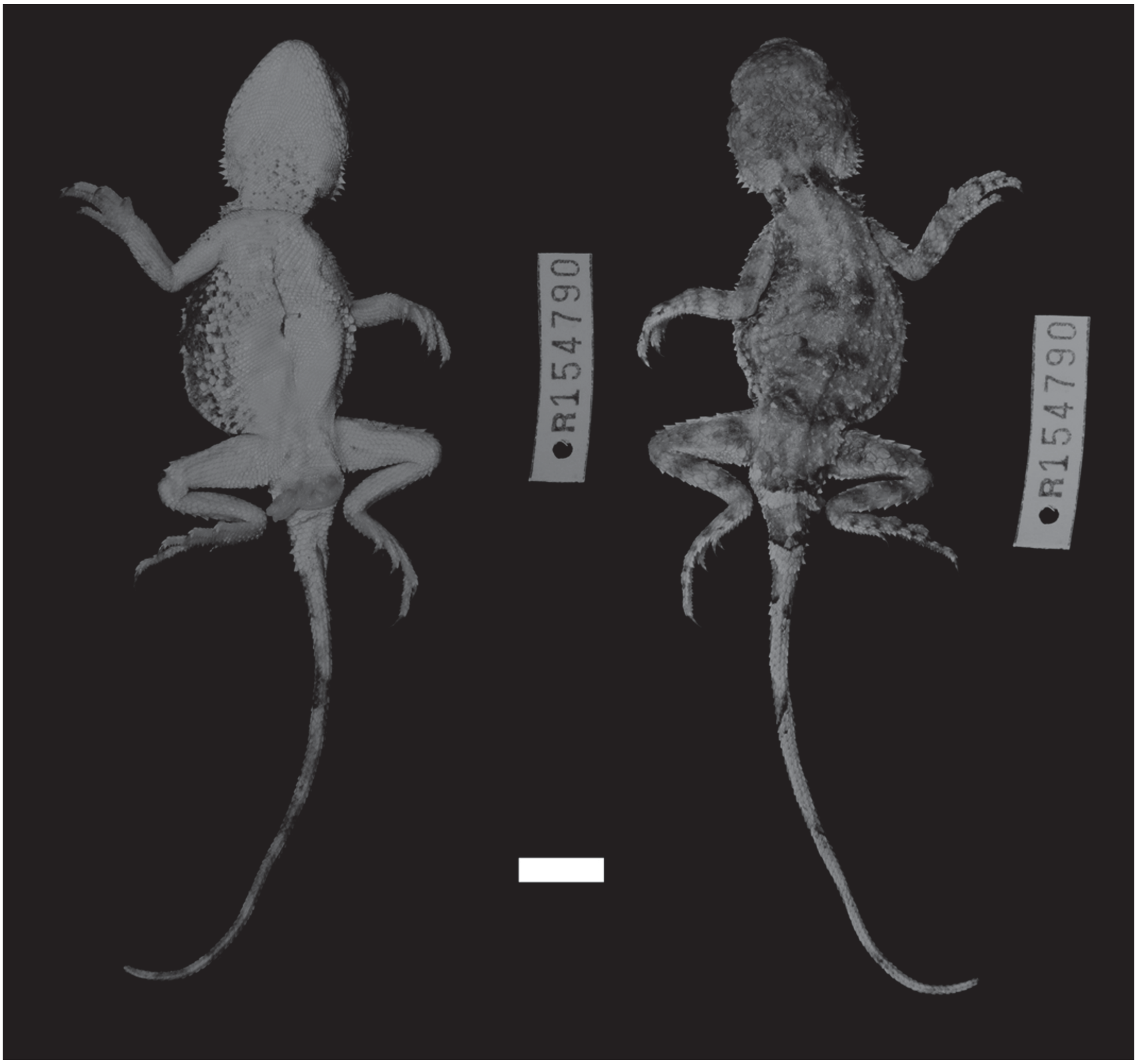


FIGURE 14. Holotype of *Tympanocryptis pseudopsephos* **sp. nov.** (scale bar = 1 cm).

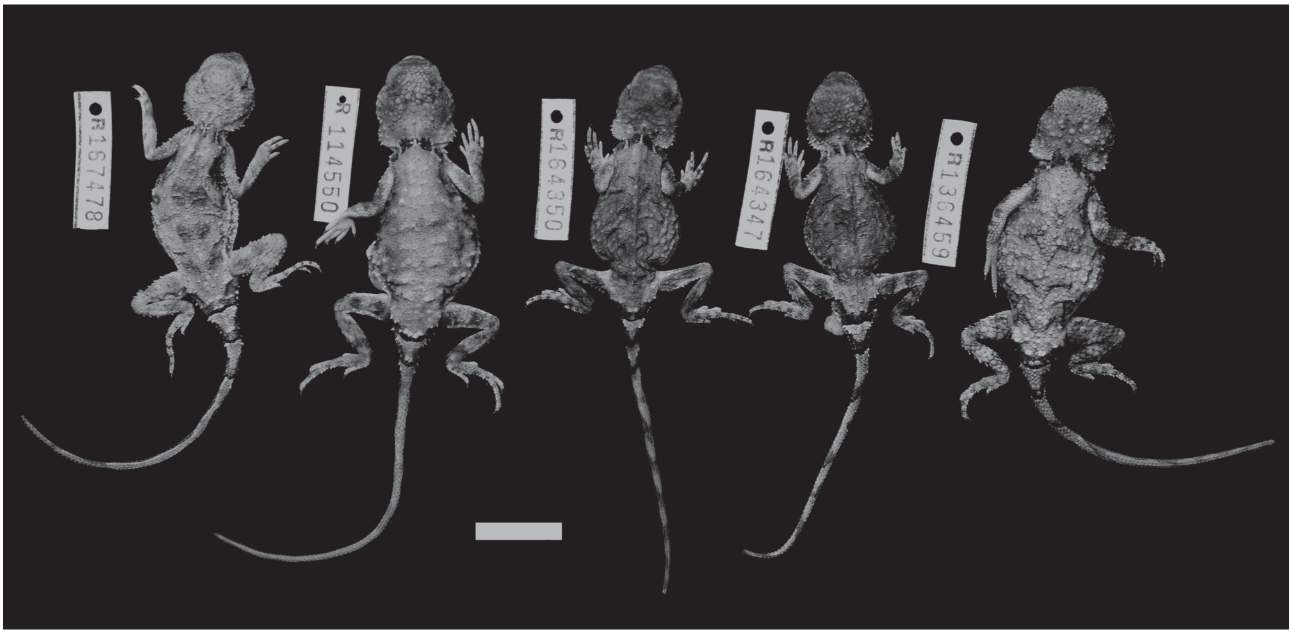


FIGURE 15. Paratypes of *Tympanocryptis pseudopsephos* **sp. nov.** (scale bar = 1 cm).

Diagnosis. Distinguished from other *Tympanocryptis* by the following combination of character states: rotund body shape, presence of two pre-cloacal pores, lack of longitudinal stripes on the dorsum, presence of enlarged scales with raised spines arranged in short transverse rows of 4–7 scales, concave snout formed by protruding mouth, scales on snout rugose with feeble keels, rostral width ~1–2 times height, keels on scales of upper arm not aligned, well-defined row of enlarged scales at anterior and dorsal edge of thigh forming conspicuous ridge, scales on dorsal surface of thigh not aligned, ventrals smooth, and reddish-brown ground color, lacking lines but often possessing a dark charcoal-like wash over the head and dorsum.

Description. A small-bodied (to 56.5 mm SVL), rotund dragon; small head with blunt snout with protruding mouth; short neck; moderately short gracile limbs, ArmL%SVL—0.185 (0.016), LegL%SVL—0.235 (0.017); moderately short gracile digits; short tail. Head small, HeadL%SVL—0.307 (0.017), HeadW%SVL—0.258 (0.013), HeadD%SVL—0.158 (0.008); neck ~3/4 of widest part of head; snout short, SnoutL%HeadL—0.259 (0.025); snout straight or concave when viewed laterally, if concave then snout tip projects forward; line of mouth slightly projecting forming a shelf-like appearance, narrowing to blunt tip; canthus defined but rounded, forming continuous line with projecting brow ridge; nostril located below canthus in enlarged scale, opening projecting dorsally; eye moderate, EyeL%HeadL—0.258 (0.022); eyes with laterally-projecting scaly eyelids forming a fringe, often projecting past brow when viewed dorsally; tympana covered with fine scales, encircled by scattered enlarged scales with raised apex; scales on snout rugose, occasionally with feeble unaligned keels; scales on crown slightly larger with feeble unaligned keels; scales on back of head small with few variably-sized low scattered spines; rostral scale ~ 1–2 times wider than tall; 10–15 supralabial scales, 4–5 rows of scales above supralabial row, keeled, uppermost row slightly larger with larger keels and continuing to temporal region, forming edge of eye socket; loosely defined cluster of enlarged spines at posterior and lateral corners of head; mental 1.5 times long as wide; 11–16 infralabials with low keels; 4–5 rows of scales below infralabials with low keels parallel to angle of jaw, creating a slightly terraced appearance; gulars kite-shaped and smooth; prominent gular fold.

Body dorsoventrally compressed, ovoid in dorsal view with widest part ~2 times wider than neck and pelvis; TrunkL%SVL—0.473 (0.048); dorsum with heterogeneous scales in size and shape; largest scales with sharp spines angled 10–30° posteriorly and ~4–7 times larger than smallest scales; large dorsal scales with spines tending to occur in transversely-aligned clusters of ~4–6; smaller dorsal scales rugose or with weak, low keels, arranged in loose whorls around clusters of large, spiny scales; dorsolateral edge of pelvis always with a cluster of enlarged spines at posterior edge where skin is fused to bone; ventral scales homogeneous, approximately half the size of large dorsal scales, kite-shaped and arranged in diagonal rows; ventral scales smooth, or at most with raised midline (no keel or protruding spine).

Limbs largely covered in elongate kite or teardrop-shaped scales with prominent low keels, spine usually protruding beyond distal edge of scale, interspersed with occasional small unkeeled scales; arms and legs moderately long, ArmL%SVL—0.185 (0.016), LegL%SVL—0.235 (0.017); scales on dorsal surface of upper arm large with keels tending not to align; keels of dorsal scales on lower arm tending to align, often forming lines that extend to hand and fingers; keels of ventral scales mostly aligned forming lines along the length of the arm to palmar surfaces; scales on underside of digit with two rows of spiny lamellae; claw long and recurved, lower portion terminating with circular opening, upper portion continuing past ultimate lamellae to form sharp claw; finger length: 4 > 3 > 2 = 5 > 1; scales on legs kite or teardrop-shaped; tops of upper and lower leg with large heterogeneous non-aligned scales, elsewhere with low keels that align and extend to feet and toes; scales at insertion of limb to body small, rectangular and lacking keels; anterior edge of thigh with enlarged scales forming conspicuous ridge; abrupt transition from dorsal to posterior edge of leg (large to small scales); scales on underside of toes as for fingers; toe length: 4 >> 3 > 2 = 5 > 1.

Pre-cloacal pores 2, set among 3–5 scales, positioned anterior to distal edges of cloaca, midway between anterior and posterior edge of leg; tail short and thin with blunt tip, TailL%SVL—1.268 (0.102); scattered enlarged scales aligning along most of the length of the tail to terminus; lateral surfaces of tail base with short protruding spines.

Measurements for the type series are presented in Table 5.

TABLE 5. Summary of meristic (mm) and mensural data for the type series of *Tympanocryptis psuedopsephos* **sp. nov.**

R#	154790	164347	114550	167478	136459	164350
Sex	Male	Male	Female	Male	Female	Female
SVL	49.5	44.5	52.5	46.5	49.5	44.5
TrunkL	18.6	19.3	21.7	25.1	21.3	20.3
TailL	69.5	55.5	73.0	68.0	58.5	55.0
HeadL	16.4	13.7	16.8	14.3	14.4	14.3
HeadW	13.1	11.7	13.7	12.7	12.6	11.2
HeadD	8.3	6.9	7.9	7.5	8.1	6.9
SnoutL	3.9	3.4	4.3	3.6	3.7	3.6
SnoutW	5.9	5.0	6.1	5.9	6.1	5.1
EyeL	4.1	3.7	3.8	3.8	3.8	3.5
InterOrb	1.8	1.7	1.7	1.8	2.1	2.3
ArmL	9.2	8.1	9.6	8.3	9.3	9.4
HeadL	7.3	6.4	8.5	7.3	7.8	8.9
LegL	12.4	10.8	12.7	11.2	11.5	11.2
FootL	15.5	12.0	14.6	13.8	14.0	13.5
HeadW/SVL	0.3	0.3	0.3	0.3	0.3	0.3
FootL/SVL	0.3	0.3	0.3	0.3	0.3	0.3
TailL/SVL	1.4	1.3	1.4	1.5	1.2	1.2

Coloration and pattern. In life (Figs. 5E, 5F), ground color medium to dark reddish-brown, often with dark grayish black wash over head, dorsum, and limbs; in some individuals this is quite extensive (e.g. Fig. 5F); limbs weakly banded; nuchal region dark brown with 3 pale stripes; tail with ~8 alternating bands of pale white and ground color, anterior edge of pale bands dark, pale bands sometimes coalescing to form continuous stripe along top of tail towards tip. In preservative, ground color usually a grayish-brown, dark blotching on dorsum and banding on limbs dark gray to brown (Fig. 15); some individuals with dark stippling near gular fold; pale bands on tail yellowy-white; ventrum pale with yellow or light orange hue (Fig. 14).

Habitat. Recorded from Mallee and Mulga woodlands, often with stones strewn on the ground.

Distribution. Widely distributed throughout the Goldfields region of Western Australia (Fig. 1). From just outside the south-eastern edge of the Pilbara, then south to near Norseman. Two older western records are from

Yalgoo (WAM R13639) and Dongara (WAM R13476), although the latter record is likely in error given the habitat preferences of this species. A recent eastern record (WAM R163342) is from Neale Junction towards the South Australian border.

Etymology. *pseudopsephos* means 'false pebble', with *pseudo* Latin for 'false' and *psephos* is Greek for 'pebble'. The name is an allusion to the pebble-mimicking abilities of this species.

Comparisons with other species. Based on its widespread distribution, we provide comparisons of *T. diabolicus* **sp. nov.** to all species treated here except *T. cephalus*.

Tympanocryptis pseudopsephos **sp. nov.** is distinguished from *T. gigas* by smaller body size, more rotund body shape, concave (*versus* convex) snout, possessing enlarged scales on dorsum arranged in short transverse rows (*versus* slightly enlarged scales scattered on dorsum), conspicuous ridge on front of thigh formed by enlarged row of scales, and scales on top of thigh homogeneous.

Tympanocryptis pseudopsephos **sp. nov.** is distinguished from *T. diabolicus* **sp. nov.** by possessing enlarged dorsal scales in short transverse rows in rows of 4–7 scales (*versus* 2–5), snout concave (versus straight or convex), rostral scale width 2 times height (*versus* 3 times), keels of scales on upper arm not aligned, scales on upper thigh not aligned, and ventrals smooth or slightly raised (*versus* with low keels).

Tympanocryptis pseudopsephos **sp. nov.** is distinguished from *T. fortescuensis* **sp. nov.** by possessing enlarged dorsal scales in short transverse rows in rows of 4–7 scales (*versus* 2–5), concave snout (*versus* straight to convex), scales on snout rugose with feeble keels (*versus* with low keels), rostral scale 3 times wider than high (*versus* 2 times), keels on dorsal surface of upper arm not aligned, keels of scales on top of thigh not aligned (*versus* usually aligned), ventrals smooth or slightly raised (*versus* with low keels), and reddish-brown color overlain with black (*versus* light brown).

Remarks. *Tympanocryptis pseudopsephos* **sp. nov.** is usually the taxon depicted in field guides (e.g. Storr *et al.* 1983; Wilson & Knowles 1988; Wilson & Swan 2003; Cogger 2014), as this species is the most widely-distributed of the *T. cephalus* species-group members and therefore most likely to be encountered and photographed. This also extends to diagnoses and descriptions in such guides and keys, and also often in taxonomic treatments as well. For example, in Mitchell's 1948 revision of the group, the specimen WAM R7067 figured under the *T. cephalus cephalus* section is a *T. pseudopsephos* **sp. nov.** from 48 km east of Kalgoorlie. Moreover, Mitchell commented that his description of the 'inland form' (i.e. *pseudopsephos*) differed slightly from that in Günther's (1867) original description, Boulenger's (1885) figure, and photographs of the types sent to him by the Natural History Museum: '…the [two syntype] specimens...differ in scalation detail from inland specimens. It has been suggested to me by a fellow worker that this inland form should be described as a new race. However, after considering that no similar specimens have been taken, it is assumed that the type specimens are merely local variants, and not typical representatives of the species which Gunther in fact described.' (p. 64). We now know that the syntypes were of true *T. cephalus* and that the 'inland form' is the distinct *T. pseudopsephos* **sp. nov.** Historically, a lack of specimens has hindered taxonomic understanding in *Tympanocryptis*, and indeed continues to hinder revision of other arid zone forms.

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APPENDIX 1. Non-type material examined.

Tympanocryptis cephalus

Males: SAMA R22854, 21 km north of Roebourne (20°39'S, 117°09'E); WAM R53331, 40 km east of Roebourne (20°57'S, 117°26'E); WAM R129130, 15 km north-east of Fortescue Roadhouse (21°12'S, 116°14'E); WAM R152053, 4 km south of Karratha (20°46'17"S, 116°50'59"E); WAM R159045, 2 km south-west of Marda Pool (21°03'14"S, 116°08'01"E); WAM R160945, 4 km south of Karratha (20°46'17"S, 116°50'59"E); WAM R161047, 13 km east-south-east of Marda Pool (21°03'42"S, 116°15'54"E); WAM R161060, 13 km east-south-east of Marda Pool (21°03'42"S, 116°15'54"E); WAM R165248, 12.2 km east-north-east of Karratha (20°46'15"S, 116°42'55"E); WAM R166115, Dampier Area (20°46'36"S, 116°42'05"E).

Females: WAM R52153, Well 52 Old north-west Coastal Highway (20°48'S, 116°50'E); WAM R110514, 13 km east-south-east of Marda Pool (21°03'42"S, 116°15'54"E); WAM R152052, 4 km south of Karratha (20°46'17"S, 116°50'59"E); WAM R154753, 26 km east-south-east of Roebourne (20°52'S, 117°23'E); WAM R154754, 25 km east-south-east of Roebourne (20°47'S, 117°09'E); WAM R154925, 50 km east of Roebourne (20°49'39"S, 117°31'50"E); WAM R160960, 4 km south of Karratha (20°46'17"S, 116°50'59"E); WAM R160971, 13 km east-south-east of Marda Pool (21°03'42"S, 116°15'54"E); WAM R161013, 2 km south-west of Marda Pool (21°03'14"S, 116°08'01"E); WAM R161076, 13 km east-south-east of Marda Pool (21°03'42"S, 116°15'54"E); WAM R165247, 12.2 km east-north-east of Karratha (20°46'15"S, 116°42'55"E).

Tympanocryptis gigas

Male: WAM R14060, Wandagee (23°46'S, 114°33'E).

Females: WAM R19111, Bernier Island (23°46'S, 114°33'E); WAM R40637, Yinnietharra (20°39'S, 116°10'E).

Tympanocryptis diabolicus **sp. nov.**

Males: WAM R13640, Turee Creek (23°37'S, 118°39'E); WAM R17689, Turee Creek (23°37'S, 118°39'E); WAM R30928, Mount Newman (23°16'S, 119°34'E); WAM R138231, Hamersley Range National Park (23°05'S, 118°48'E); WAM R152126, 3.2 km south-west of Giles Point (23°15'58"S, 119°08'02"E); WAM R152127, 3.2 km south-west of Giles Point (23°15'58"S, 119°08'02"E); WAM R152167, 16 km south-west of Rhodes Ridge (23°11'06"S, 119°14'16"E); WAM R160687, 16 km south-west of Rhodes Ridge (23°11'06"S, 119°14'16"E); WAM R162235, 16 km south-west of Rhodes Ridge (23°11'06"S, 119°14'16"E); WAM R164063, 51 km east-south-east of Paraburdoo (23°17'33"S, 118°09'23"E); WAM R164064, 51 km east-south-east of Paraburdoo (23°17'33"S, 118°09'23"E).

Females: WAM R152165, 16 km south-west of Rhodes Ridge (23°11'06"S, 119°14'16"E); WAM R160591, 10.5 km west of Mount De Courcey (22°42'40"S, 116°24'01"E); WAM R160686, 16 km south-west of Rhodes Ridge (23°11'06"S, 119°14'16"E).

Tympanocryptis fortescuensis **sp. nov.**

Males: WAM R40199, Oakover River Crossing, 6 km north of Talawana (22°46'S, 121°06'E); WAM R40200, Oakover River Crossing, 6 km north of Talawana (22°46'S, 121°06'E); WAM R110150, 12 km east-south-east of Mount Billroth (21°39'45"S, 117°42'17"E); WAM R110238, 19 km north-west of Roy Hill (22°30'29"S, 119°47'03"E); WAM R150773, 18.5 km south-east of Mount Florance Homestead (21°53'29"S, 118°00'00"E); WAM R150864, 12 km east-south-east of Mount Billroth (21°39'45"S, 117°42'17"E); WAM R161119, 6 km north of Cowraline Camp (22°18'06"S, 119°00'48"E); WAM R161830, 12 km east-south-east of Mount Billroth (21°39'45"S, 117°42'17"E); WAM R164129, 19 km north-west of Roy Hill (22°30'29"S, 119°47'03"E).

Females: WAM R40201, Oakover River Crossing, 6 km north of Talawana (22°46'S, 121°06'E); WAM R110103, 11 km south-west of Coolawanyah (21°52'35"S, 117°44'28"E); WAM R110140, 8 km south of Coolawanyah (21°52'55"S, 117°47'40"E); WAM R151896, 6 km north of Cowraline Camp (22°18'06"S, 119°00'48"E); WAM R154963, Fortescue Marsh (22°06'16"S, 119°00'26"E); WAM R159687, 19 km north-west of Roy Hill (22°30'29"S, 119°47'03"E); WAM R160032, 46 km east of Meentheena Outcamp (21°17'16"S, 120°53'29"E); WAM R161146, 19 km north-west of Roy Hill (22°30'29"S, 119°47'03"E).

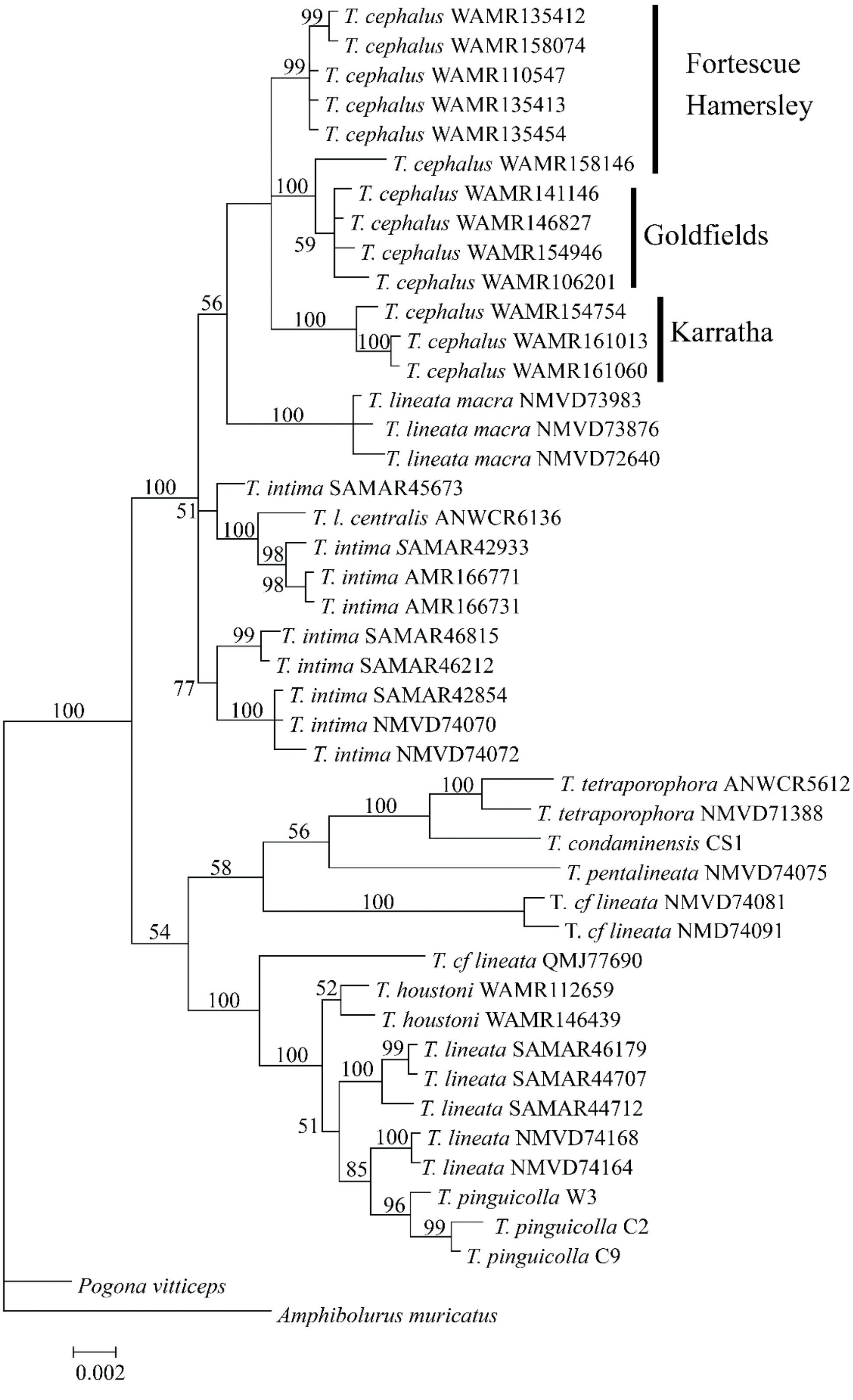
Tympanocryptis pseudopsephos **sp. nov.**

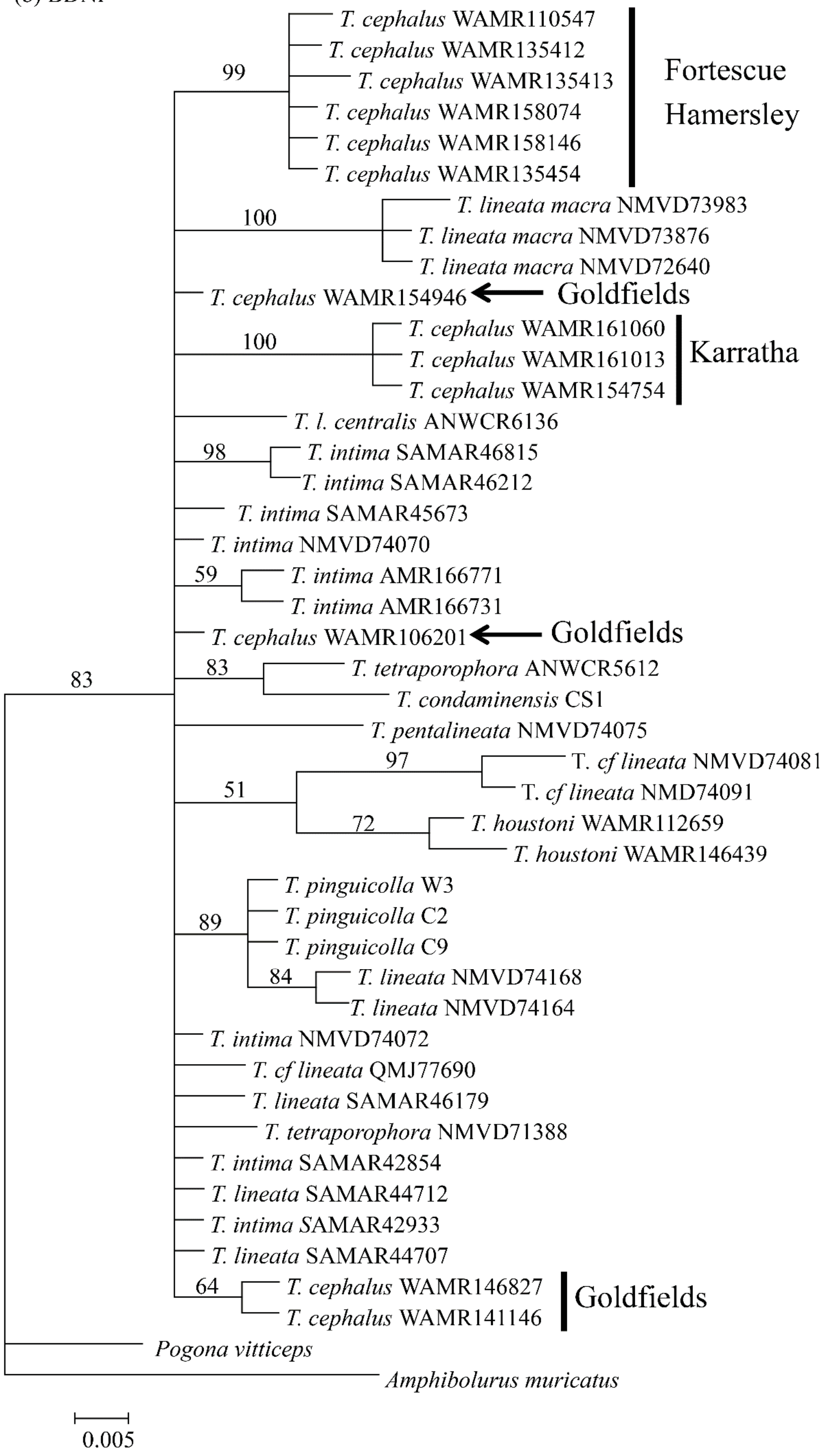
Males: WAM R94719, Glenayle Station (25°15'S, 122°00'E); WAM R100967, Wanjarri Nature Reserve, 3.4 km east of Kathleen Valley Woolshed (27°21'S, 120°40'E); WAM R106201, 10 km north of Mount Magnet (27°58'S, 117°51'E); WAM R146827, Leonora Laverton Road, 47 km east of Leonora (28°51'08"S, 121°48'26"E); WAM R167468, 31.1 km west-north-west of Lake Way (27°12'29"S, 120°34'24"E).

Females: SAMA R1664, Broad Arrow (30°27'S, 121°20'E); SAMA R2439B, Murchison District; WAM R25121, Jiggalong Mission (23°22'S, 120°47'E); WAM R85436, Mount Jackson (30°12'S, 119°07'E); WAM R114911, 12 km north-north-east of Noonyerina Hill (25°29'S, 119°16'E); WAM R141146, 5 km south-west of Vivien Mine (28°00'53"S, 120°31'51"E); WAM R144701, Bungalbin Hill Area (30°20'S, 119°41'E); WAM R154946, Cosmos Mine (27°36'54"S, 120°34'33"E); WAM R164353, 45.2 km east of Leonora (28°51'51"S, 121°47'41"E); WAM R167460, 22.4 km north-west of Lake Way (27°06'14"S, 120°36'21"E); WAM R167482, 47.5 km north of Lake Way (27°21'00"S, 120°37'03"E).

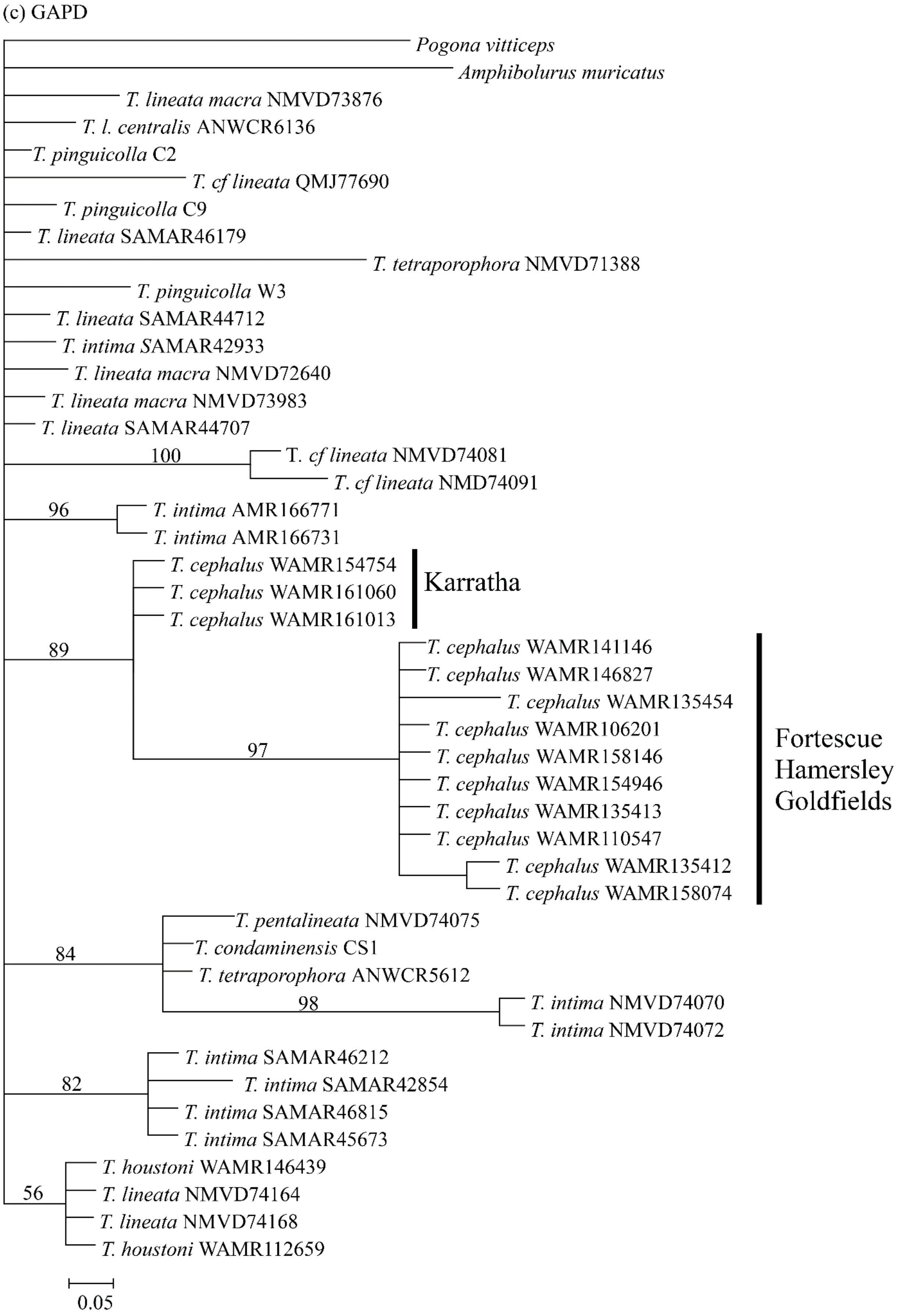
APPENDIX 2. Bayesian analyses of nuclear genes: (a) RAG1, (b) BDNF, and (c) GAPD. See methods for details of analyses.

(a) RAG1




(b) BDNF

99
T. cephalus WAMR110547
T. cephalus WAMR135412
T. cephalus WAMR135413
T. cephalus WAMR158074
T. cephalus WAMR158146
T. cephalus WAMR135454
Fortescue
Hamersley
100
T. lineata macra NMVD73983
T. lineata macra NMVD73876
T. lineata macra NMVD72640
T. cephalus WAMR154946
Goldfields
100
T. cephalus WAMR161060
T. cephalus WAMR161013
T. cephalus WAMR154754
Karratha
T. l. centralis ANWCR6136
98
T. intima SAMAR46815
T. intima SAMAR46212
T. intima SAMAR45673
T. intima NMVD74070
59
T. intima AMR166771
T. intima AMR166731
T. cephalus WAMR106201
Goldfields
83
83
T. tetraporophora ANWCR5612
T. condaminensis CS1
T. pentalineata NMVD74075
97
T. cf lineata NMVD74081
T. cf lineata NMD74091
51
72
T. houstoni WAMR112659
T. houstoni WAMR146439
89
T. pinguicolla W3
T. pinguicolla C2
T. pinguicolla C9
84
T. lineata NMVD74168
T. lineata NMVD74164
T. intima NMVD74072
T. cf lineata QMJ77690
T. lineata SAMAR46179
T. tetraporophora NMVD71388
T. intima SAMAR42854
T. lineata SAMAR44712
T. intima SAMAR42933
T. lineata SAMAR44707
64
T. cephalus WAMR146827
T. cephalus WAMR141146
Goldfields
Pogona vitticeps
Amphibolurus muricatus
0.005


(c) GAPD
Pogona vitticeps
Amphibolurus muricatus
T. lineata macra NMVD73876
T. l. centralis ANWCR6136
T. pinguicolla C2
T. cf lineata QMJ77690
T. pinguicolla C9
T. lineata SAMAR46179
T. tetraporophora NMVD71388
T. pinguicolla W3
T. lineata SAMAR44712
T. intima SAMAR42933
T. lineata macra NMVD72640
T. lineata macra NMVD73983
T. lineata SAMAR44707
100
T. *cf lineata* NMVD74081
T. cf lineata NMD74091
96
T. intima AMR166771
T. intima AMR166731
T. cephalus WAMR154754
T. cephalus WAMR161060
T. cephalus WAMR161013
Karratha
89
T. cephalus WAMR141146
T. cephalus WAMR146827
T. cephalus WAMR135454
T. cephalus WAMR106201
97
T. cephalus WAMR158146
T. cephalus WAMR154946
T. cephalus WAMR135413
T. cephalus WAMR110547
T. cephalus WAMR135412
T. cephalus WAMR158074
Fortescue
Hamersley
Goldfields
T. pentalineata NMVD74075
T. condaminensis CS1
84
T. tetraporophora ANWCR5612
98
T. intima NMVD74070
T. intima NMVD74072
T. intima SAMAR46212
82
T. intima SAMAR42854
T. intima SAMAR46815
T. intima SAMAR45673
T. houstoni WAMR146439
56
T. lineata NMVD74164
T. lineata NMVD74168
T. houstoni WAMR112659
0.05

APPENDIX 4. Summaries of characters and ratios measured for *Tympanocryptis* species. Mean±S.D. (range). See Methods for abbreviations. Sample sizes are listed in column headings, unless noted for individual characters below. Juveniles with SVL < 42 mm were excluded from statistics, but were included in scale counts.

Character	*T. cephalus* N = 22 (11♀, 11♂)	*T. gigas* N = 6 (4♀, 2♂)	*T. diabolicus* **sp. nov.** N = 20 (3♀, 17♂)	*T. fortescuensis* **sp. nov.** N = 23 (10♀, 13♂)	*T. pseudopsephos* **sp. nov.** N = 21 (14♀, 7♂)
SVL	♀♀: 48.9±10.8	♀♀: 54.0±4.8	♀♀: 46.3±7.3	♀♀: 49.9±8.2	♀♀: 49.3±6.1
	(35.0–64.0)	(47.0–57.0)	(39.5–54.0)	(38.0–62.0)	(36.5–56.5)
	♂♂: 47.5±5.5	♂♂: 46.0, 66.5	♂♂: 51.4±7.7	♂♂: 49.5±7.6	♂♂: 46.7±7.9
	(42.0–58.5)		(39.0–60.5)	(41.5–65.0)	(34.0–56.5)
TrunkL	♀♀: 22.0±5.7	♀♀: 27.8±1.7	♀♀: 23.3±3.8	♀♀: 23.7±4.7	♀♀: 23.7±4.3
	(16.1–30.6)	(25.8–29.5)	(19.6–27.2)	(19.0–30.7)	(15.9–30.0)
	♂♂: 21.7±2.6	♂♂: 19.5, 29.5	♂♂: 23.4±3.7	♂♂: 22.5±3.3	♂♂: 21.7±4.7
	(18.6–25.6)		(18.3–28.8)	(17.7–30.7)	(16.2–29.0)
TailL	59.5±12.7	79.9±14.8	66.7±13.8	69.3±14.9	61.5±10.1
	(33.5–82.0)	(58.5–105.0)	(44.0–92.0)	(51.0–81.0)	(40.5–78.0)
HeadL	14.9±1.9	17.0±2.0	15.6±1.9	15.2±2.2	14.8±1.6
	(11.8–19.1)	(14.9–20.8)	(12.2–19.2)	(11.9–19.9)	(11.2–17.2)
HeadW	11.5±1.5	13.8±1.6	12.5±1.4	11.6±1.4	12.4±1.3
	(9.2–15.0)	(11.9–16.6	(10.1–15.0)	(9.6–14.3)	(9.7–14.2)
HeadD	7.6±1.0	8.8±1.3	7.9±0.9	7.7±1.0	7.6±0.9
	(6.1–9.8)	(7.4–11.4)	(6.4–9.2)	(6.2–9.8)	(5.9–9.4)
SnoutL	3.8±0.5	4.3±0.5	4.0±0.4	4.0±0.5	3.8±0.5
	(2.5–4.7)	(3.6–5.1)	(3.5–4.7)	(3.0–5.1)	(3.0–5.0)
SnoutW	5.5±0.6	6.3±0.6	5.8±0.7	5.5±0.8	5.6±0.6
	(4.4–6.6)	(5.6–7.5)	(4.2–7.0)	(4.2–6.9)	(4.1–6.9)
EyeL	3.8±0.5	4.0±0.5	3.9±0.5	3.8±0.5	3.8±0.5
	(2.7–4.7)	(3.4–4.8)	(2.7–4.7)	(3.0–4.7)	(3.0–4.8)
InterOrb	1.8±0.3	1.9±0.3	1.9±0.3	1.8±0.3	1.8±0.3
	(1.4–2.2)	(1.5–2.3)	(1.2–2.5)	(1.3–2.3)	(1.3–2.4)

……continued on the next page

APPENDIX 4. (Continued)

Character	*T. cephalus*	*T. gigas*	*T. diabolicus* **sp. nov.**	*T. fortescuensis* **sp. nov.**	*T. pseudopsephos* **sp. nov.**
	N = 22 (11♀, 11♂)	N = 6 (4♀, 2♂)	N = 20 (3♀, 17♂)	N = 23 (10♀, 13♂)	N = 21 (14♀, 7♂)
ArmL	9.3±1.3	9.8±1.1	9.6±1.8	9.7±1.4	8.9±1.0
	(6.6–12.2)	(8.2–11.3)	(6.1–12.0)	(7.6–12.3)	(6.4–10.9)
HandL	7.1±1.3	8.0±1.1	7.4±1.0	7.6±0.9	7.2±0.9
	(4.9–10.0)	(6.6–9.8)	(5.4–8.9)	(5.9–9.4)	(4.8–8.9)
LegL	12.3±1.8	12.5±1.5	12.7±2.1	12.8±1.9	11.3±1.3
	(8.5–16.6)	(11.0–15.4)	(9.0–15.5)	(9.5–16.8)	(8.6–13.4)
FootL	13.1±1.9	14.4±2.2	14.6±2.2	14.8±1.9	13.0±1.4
	(8.2–17.3)	(12.0–18.6)	(10.9–18.7)	(12.1–18.1)	(10.0–15.5)
SupLab	12.9±1.1	12.3±0.8	12.8±1.0	12.5±1.1	12.3±1.2
	(11–15)	(11–13)	(10–14)	(11–15)	(10–15)
InfLab	13.0±1.0	13.6±0.5	13.4±0.9	13.0±0.9	12.6±1.4
	(12–15)	(13–14)	(12–15)	(12–15)	(11–16)
4FLam	12.9±0.9	14.0±1.5	14.3±1.6	14.4±1.4	13.8±1.4
	(12–15)	(12–16)	(12–17)	(12–18)	(12–16)
4TLam	18.4±1.0	19.4±1.9	19.6±1.8	19.9±1.9	18.5±1.5
	(16–20)	(17–22)	(17–23)	(16–24)	(16–21)
IntSup	13.7±0.9	15.6±0.8	14.0±1.1	14.1±1.2	14.4±1.4
	(12–15)	(14–16)	(12–16)	(12–17)	(12–18)
IntNas	7.3±0.8	7.6±1.4	6.9±0.6	7.0±0.6	6.6±0.8
	(6–9)	(5–9)	(6–8)	(6–8)	(5–7)
HeadW/SVL	0.24±0.01	0.25±0.01	0.25±0.02	0.24±0.02	0.26±0.01
	(0.21–0.26)	(0.24–0.26)	(0.22–0.27)	(0.20–0.27)	(0.24–0.29)
FootL/SVL	0.27±0.02	0.26±0.02	0.29±0.02	0.30±0.02	0.27±0.03
	(0.23–0.31)	(0.23–0.29)	(0.25–0.32)	(0.23–0.33)	(0.23–0.31)
TailL/SVL	1.23±0.13	1.45±0.13	1.32±0.17	1.39±0.13	1.27±0.10
	(0.78–1.49)	(1.24–1.58)	(0.95–1.66)	(1.15–1.71)	(0.99–1.46)