

1447-2554 (On-line)

<https://museumvictoria.com.au/about/books-and-journals/journals/memoirs-of-museum-victoria/>

DOI <https://doi.org/10.24199/j.mmv.2018.77.04>

## Diversity in Australia's tropical savannas: An integrative taxonomic revision of agamid lizards from the genera *Amphibolurus* and *Lophognathus* (Lacertilia: Agamidae)

(<http://zoobank.org/urn:lsid:zoobank.org:pub:22334107-0784-466E-8288-D6E29F87F6E2>)

JANE MELVILLE<sup>1\*</sup>, EUAN G. RITCHIE<sup>1,2</sup>, STEPHANIE N.J. CHAPPLE<sup>1</sup>, RICHARD E. GLOR<sup>3</sup> and JAMES A. SCHULTE II<sup>4</sup>

<sup>1</sup> Department of Sciences, Museum Victoria, GPO Box 666, Melbourne VIC 3001, Australia

<sup>2</sup> School of Life and Environmental Sciences, Deakin University, Burwood VIC 3125, Australia

<sup>3</sup> Herpetology Division, Biodiversity Institute and Department of Ecology and Evolutionary Biology, University of Kansas, Lawrence, KS 66045, USA

<sup>4</sup> Beloit College, 700 College Street, Science Center 338, Beloit, WI 53511, USA

\* Corresponding author. Email: [jmelv@museum.vic.gov.au](mailto:jmelv@museum.vic.gov.au)

### Abstract

Melville, J., Ritchie, E.G., Chapple, S.N.J., Glor, R.E. and Schulte II, J.A. 2018. Diversity in Australia's tropical savannas: An integrative taxonomic revision of agamid lizards from the genera *Amphibolurus* and *Lophognathus* (Lacertilia: Agamidae). *Memoirs of Museum Victoria* 77: 41–61.

The taxonomy of many of Australia's agamid lizard genera remains unresolved because morphological characters have proved to be unreliable across numerous lineages. We undertook a morphological study and integrated this with a recent genetic study to resolve long-standing taxonomic problems in three genera of large-bodied Australian agamid lizards: *Amphibolurus*, *Gowidon* and *Lophognathus*. We had broad geographic sampling across genera, including all currently recognised species and subspecies. Using an integrative taxonomic approach, incorporating mitochondrial (*ND2*) and nuclear (*RAG1*) genetic data, and our morphological review, we found that both generic and species-level taxonomic revisions were required. We revise generic designations, creating one new genus (*Tropicagama* gen. nov.) and confirming the validity of *Gowidon*, giving a total of four genera. In addition, we describe a new species (*Lophognathus horneri* sp. nov.) and reclassify two other species. Our results provide a significant step forward in the taxonomy of some of Australia's most iconic and well-known lizards and provide a clearer understanding of biogeographic patterns across Australia's monsoonal and arid landscapes.

### Keywords

Agamid lizards, *Amphibolurus horneri* sp. nov., *Lophognathus*, *Gowidon*, *Tropicagama* gen. nov., integrative taxonomy, Australia, monsoon tropics

### Introduction

Tropical savannas constitute one of Earth's major biomes, covering 20–30% of the land surface (Myers et al., 2000). Australian tropical savannas are particularly important because they are the largest and least modified tropical savanna woodlands in the world, comprising approximately 25% of the Earth's remaining savannas that are in good ecological condition (Woinarski et al., 2007). The Australian monsoonal tropics, which span the northern third of the continent, are home to a major component of biodiversity, with some areas, particularly the sandstone escarpments, having similar biodiversity levels to Australian rainforests (Bowman et al., 2010). Yet, only recently has research started to uncover unexpected levels of diversity and phylogeographic structure across the monsoonal tropics (Melville et al., 2011; Moritz et

al., 2016; Oliver et al., 2014; Potter et al., 2016; Smith et al., 2011). As a result of these research findings, the current taxonomy in many groups does not reflect actual species diversity.

One lizard group that is in immediate need of a taxonomic revision is the large-bodied agamids of the tropical savannah woodlands. Despite their ubiquity and ecological significance in this biome, major taxonomic problems characterise the group at both the generic and the species levels. Molecular work suggests major taxonomic problems within *Amphibolurus*, *Gowidon* and *Lophognathus* (Hugall et al., 2008; Melville et al., 2011; Schulte et al., 2003). Melville et al. (2011) identified a clade containing five species in three genera: *Amphibolurus muricatus* (White, 1790), *A. norrisi* Witten and Coventry, 1984, *A. burnsi* (Wells and Wellington, 1985), *L. gilberti* Gray, 1842, and *Chlamydosaurus kingi* Gray, 1825. According to

Table 1. Current taxonomic designations of Agamidae genera under revision, including details of synonyms and primary types, from Department of the Environment and Energy (2014). All types have been examined for morphological analysis, except those where they are presumed lost or status unknown.

Species plus junior synonyms	Described	Details of types
1. <i>Amphibolurus muricatus</i> <i>Lacerta muricata</i> <i>Agama jaksoniensis</i>	[White (1790)] White (1790) Cloquet (1816)	BMNH 1946.9.4.44 BMNH 1946.9.4.44 RMNH 3117
3. <i>Amphibolurus norrisi</i>	Witten and Coventry (1984)	NMV D51499
4. <i>Chlamydosaurus kingii</i>	Gray (1825)	Type presumed lost.
5. <i>Amphibolurus burnsi</i>	[Wells and Wellington (1985)]	AM R 116981
6. <i>Lophognathus gilberti</i> <i>Redtenbacheria fasciata</i> <i>Physignathus incognitus</i> <i>Physignathus gilberti centralis</i>	Gray (1842) Steindachner (1867) Ahl (1926) Loveridge (1933)	BMNH 1946.8.28.69 Type not found. ZMB 30086 MCZ 35207
7. <i>Gowidon longirostris</i> <i>Physignathus eraduensis</i> <i>Physignathus longirostris quattuorfasciatus</i>	[Boulenger (1883)] Werner (1909) Sternfeld (1924)	BMNH 1946.8.12.64-65, 1946.8.28.73 Status unknown SMF 10366
8. <i>Gowidon temporalis</i> <i>Lophognathus lateralis</i> <i>Lophognathus labialis</i>	[Günther (1867)] Macleay (1877) Boulenger (1883)	BMNH 1946.8.12.73/63, 1946.8.28.72 AM R31882 BMNH 1946.8.12.72, 1946.8.12.63

Note: BMNH, British Museum of Natural History, London; RMNH, Rijksmuseum van Natuurlijke Historie, Leiden, Holland; AM, Australian Museum, Sydney; NMV, Museum Victoria, Melbourne; ZMB, Zoologisches Museum, Universität Humboldt, Berlin, Germany; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, United States; SMF, Senckenberg Naturmuseum, Frankfurt-am-Main, Germany.

these results, the frill-necked lizard (*Chlamydosaurus kingii*), which has remained monotypic since its description, belongs to this clade, despite its stunning morphological distinctness. Further complicating these results is the possibility that *L. gilberti* is actually a species complex. Molecular work (Melville et al., 2011; Schulte et al., 2003) and field observations (Melville, unpublished data) led to the hypothesis that a number of populations that have been relegated to *L. gilberti*'s synonymy (Table 1, e.g. *Physignathus gilberti centralis* Loveridge 1933) may represent a valid species.

There has been a complex taxonomic history for the genus *Lophognathus*, which was originally erected for a single species (*Lophognathus gilberti*), with the inclusion of multiple species at different times, including *Amphibolurus burnsi* (Wells and Wellington 1985), *Gowidon longirostris* (Boulenger, 1883) and *G. temporalis* (Günther, 1867). The current catalogue (Department of the Environment and Energy, 2014) lists one species in *Lophognathus* (*L. gilberti*) and two in *Gowidon* (*G. temporalis* and *G. longirostris*), although a formal revision of the generic placement of *G. temporalis* into *Gowidon* has not occurred. Molecular work

suggests that *G. temporalis* and *G. longirostris* are not closely related to *L. gilberti*, and that *A. burnsi* is more closely related to *Amphibolurus*, with more recent publications reflecting this placement (e.g. Wilson and Swan, 2017). Based on this confusing taxonomic history and that the morphological characters previously used to define *Gowidon*, *Lophognathus* and *Amphibolurus* do not seem to be diagnostic, a complete review of these species is required.

We undertook a morphological study and an integrative taxonomic review of the genera *Gowidon*, *Amphibolurus* and *Lophognathus* species from northern Australia, incorporating results from the most recent molecular study (Melville et al., 2011). We examined all primary types for the study species, including junior synonyms, and conducted detailed morphological analyses using additional museum specimens that included many of the specimens sequenced in the molecular study (Melville et al., 2011). This comprehensive review of these genera provides a complete taxonomic revision and contributes significantly to our understanding of generic and species-level diversity in the Australian tropical savannas.

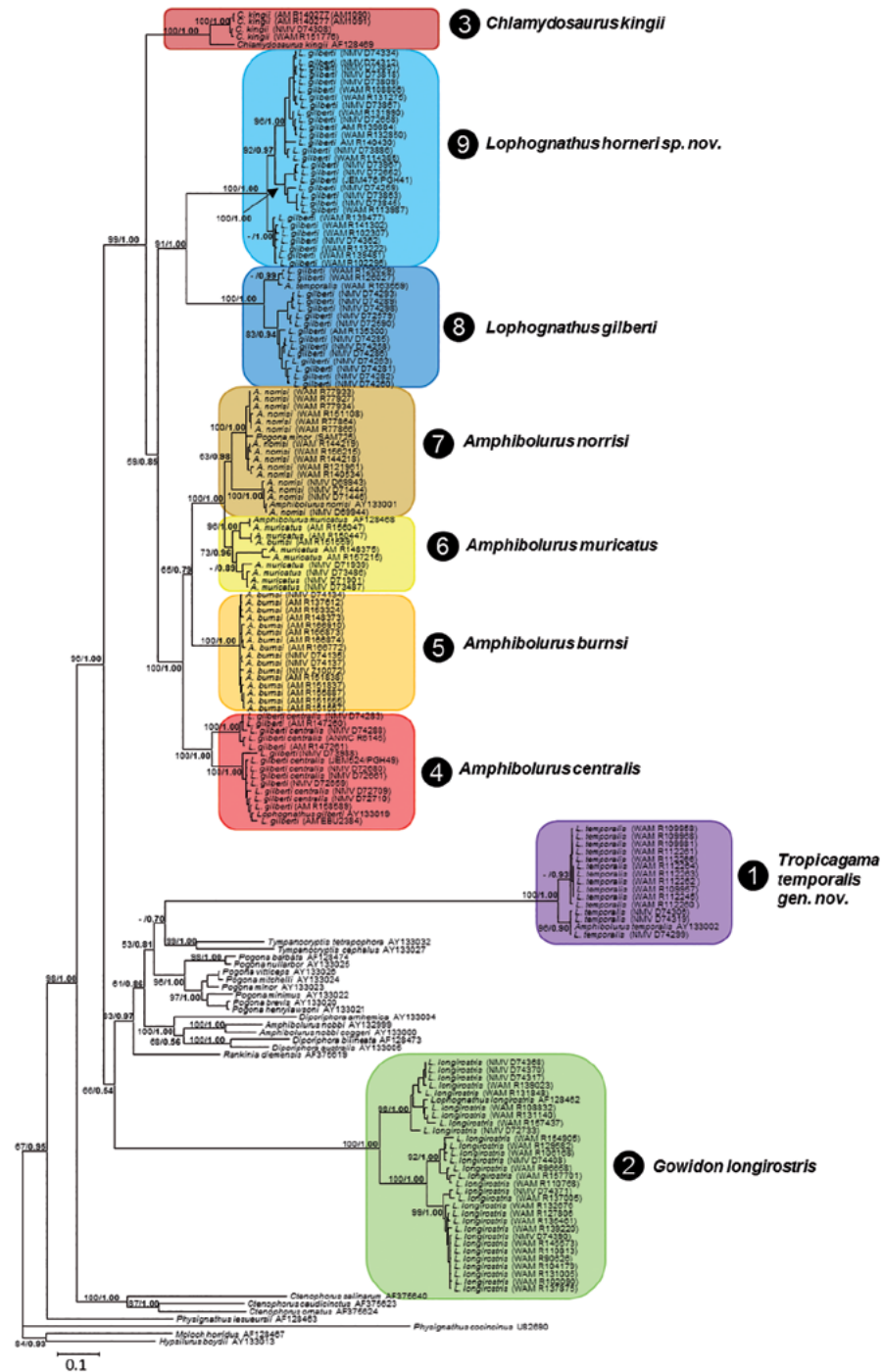


Figure 1. MtDNA phylogenetic tree for the genera *Lophognathus*, *Amphibolurus* and *Chlamydosaurus* reproduced from Melville et al. (2011). Tree presented is a Bayesian 50% majority-rule consensus tree based on ~1200 bp mitochondrial DNA (*ND2*). Bayesian posterior probabilities and ML bootstraps are provided on branches. Sample identification numbers are either Genbank accession numbers for previously published sequences or museum IDs (shown in brackets) for samples sequenced previously. Vertical bars indicate species following the taxonomic revision.

## Materials and methods

### Morphology

Primary types, including all junior synonyms (Table 1), were examined for morphological analysis and taxonomic revision. We also examined additional museum specimens for a morphological analysis of all species currently belonging to *Lophognathus* (see Supplementary Appendix S1 for details). Ten morphometric characters were measured using calipers for all specimens examined: snout–vent length (mm), tail length (mm), upper hindlimb length (proximal hindlimb; mm), lower hindlimb length (distal hindlimb; mm), hindfoot length to end of fourth toe (autopod hindlimb; mm), head length (mm), head width at widest point behind ear (mm), head depth at deepest point between eyes and ears (mm), number of femoral pores and number of preanal pores. In addition to these morphometric measurements, specimens were examined for scalation patterns, colour patterns and other synapomorphies.

Univariate and multivariate analyses were used to examine differences in the morphometric characters between the species. We used SYSTAT Version 10.2 (SYSTAT Software Inc., Richmond, California, USA) for analyses. Before analysis, all morphological variables were regressed against snout–vent length and the residuals were used for subsequent analyses to remove the effect of body size. First, all ten morphometric characters were analysed using analysis of variance with multiple comparisons (Tukey's procedure). Then, principal components analysis was used to reduce the dimensionality of the morphological data (FACTOR procedure of SYSTAT). Principal components were extracted from a correlation matrix of the raw data. Principal components were named by the correlations of the original variables to the principal component; correlations with absolute values greater than 0.5 were considered important. Resultant principal components were explored using analysis of variance with multiple comparisons (Tukey's procedure) to determine whether there were interspecific differences in morphometric characters.

### Species delimitation assessment

We used an integrative taxonomic approach for species delimitation assessment by following the principle that as many lines of evidence as available should be combined to delimit species (Miralles and Vences, 2013), which has been successfully used in Australian dragon lizards (Melville et al., 2014). We first used the mtDNA phylogenetic tree in association with the nuclear tree to determine that no mtDNA introgression exists. Thus, the mtDNA was used to define a starting hypothesis for the clustering of specimens (Miralles and Vences, 2013). Species delimitation was then based on additional support from at least two of the following: (a) sympatric occurrence without admixture, as revealed by consistent differences in morphological or molecular characters at the same geographic location; (b) congruent diagnostic differences between sister lineages in morphological characters; and (c) the absence of haplotype sharing in nuclear loci. Integrative taxonomy therefore minimises the alpha error by only taking into account the most unambiguous species evidence provided by a variety of approaches and attempts to

keep the beta error low by seeking evidence from as many different approaches as possible (Miralles and Vences, 2013).

## Results

### Taxonomic implications of phylogenetic relationships

Results from the comprehensive molecular study (Melville et al., 2011) provide strong evidence that a taxonomic revision of *Lophognathus*, *Gowidon* and *Amphibolurus* is warranted (fig. 1). Within the clade containing *Amphibolurus*, *Chlamydosaurus* and *Lophognathus* (fig. 1), *Chlamydosaurus* forms a monophyletic group that is sister to the other genera. Based on these results, *Chlamydosaurus* is a well-supported genus. However, revision of *Amphibolurus* and *Lophognathus* is required. Molecular results show that *Amphibolurus*, for which *A. muricatus* is the type specimen, consists of *L. gilberti centralis*, *A. burnsi*, *A. muricatus* and *A. norrisi*. The genus *Lophognathus* contains only *L. gilberti*, but there is strong molecular evidence that *L. gilberti* is two species, a northern taxon and a more southern taxon (fig. 1). These two *L. gilberti* lineages are analysed further in the morphological section below, with the southern lineage referred to as *Lophognathus* sp. nov. Additionally, *Gowidon temporalis* and *G. longirostris*, which have previously been placed in *Lophognathus*, form two independent lineages that fall outside the *Amphibolurus*, *Chlamydosaurus* and *Lophognathus* clade. Based on these phylogenetic results, *G. temporalis* and *G. longirostris* should be placed in two separate genera. The name *Gowidon* (Wells and Wellington, 1984) has been used in recent publications (e.g. Wilson and Swan, 2017) based on molecular data (Melville et al., 2011). However, there is no available name for *G. temporalis* and a new genus is required (see taxonomic revision below). These generic designations are analysed further in the morphological section below.

### Morphological analysis

Museum specimens for species in *Lophognathus*, *Gowidon* and *Amphibolurus* were analysed using ten morphometric characters and examined to identify morphological synapomorphies. Initially, the specimens that were sequenced in the molecular study (Melville et al., 2011) were examined to determine diagnostic characters for the six species identified in the phylogenetic analyses: *L. gilberti*, *L. sp. nov.*, *L. gilberti centralis*, *G. longirostris*, *G. temporalis* and *A. burnsi*. Once the diagnostic characters had been established, we then went through museum specimens (Supplementary Appendix S1) and primary types (Table 1) and assigned each of them to one of these species. All specimens were then measured and scored for morphometric and synapomorphic characters. A summary of morphometric characters for each species is presented in Table 2. While there is extensive variation within species in body colour, patterns and scalation, we were able to determine some consistent and diagnostic characters that differed between the taxa. These synapomorphies were particularly related to scalation and colour patterning on the head and upper body. These synapomorphies are covered in detail in the taxonomic revision section below.

*Morphometric analyses* – multivariate methods were used to examine the morphological differences between the six

Table 2. Mean morphological measurements (mm ± standard error) for study species

Species	N	SVL	Tail	Hindlimb proximal	Hindlimb distal	Hindlimb autopod	Head length	Head depth	Head width	Femoral pores	Prealal pores
<i>Amphibolurus burnsi</i>	12	110.3 (± 4.69)	274.0 (± 13.45)	27.7 (± 1.29)	32.8 (± 1.42)	41.8 (± 1.23)	39.7 (± 1.67)	18.4 (± 1.60)	26.9 (± 1.82)	4 (3–5)	4 (4–6)
<i>Lophognathus gilberti centralis</i>	21	100.1 (± 3.62)	273.5 (± 10.36)	23.9 (± 0.92)	30.0 (± 1.15)	37.4 (± 0.91)	34.9 (± 1.38)	15.5 (± 0.81)	22.2 (± 1.47)	4 (2–6)	4 (3–6)
<i>Lophognathus gilberti gilberti</i>	25	86.8 (± 2.76)	246.9 (± 8.00)	21.6 (± 0.61)	27.1 (± 0.83)	36.0 (± 1.09)	30.2 (± 1.09)	13.6 (± 0.56)	18.7 (± 0.93)	4 (2–7)	4 (3–6)
<i>Lophognathus sp. nov.</i>	43	86.2 (± 2.73)	238.1 (± 9.26)	21.6 (± 0.63)	26.6 (± 0.76)	36.2 (± 0.92)	30.0 (± 1.14)	13.1 (± 0.51)	17.8 (± 0.84)	4 (2–8)	4 (3–6)
<i>Gowidon longirostris</i>	31	95.0 (± 1.48)	302.5 (± 5.7)	23.4 (± 0.47)	28.2 (± 0.52)	38.9 (± 0.65)	32.9 (± 0.81)	13.5 (± 0.39)	17.5 (± 0.56)	16 (11–22)	6 (4–7)
<i>Gowidon temporalis</i>	32	93.1 (± 2.33)	277.5 (± 6.56)	23.1 (± 0.56)	27.8 (± 0.78)	39.6 (± 0.76)	31.5 (± 0.98)	14.5 (± 0.52)	18.1 (± 0.93)	2 (1–6)	2 (1–3)

Note: SVL, snout–vent length.

*Lophognathus* species. We conducted a principal components analysis on the measured morphological characters (Table 3). Three morphological measurements were found not to vary significantly between species: proximal hindlimb; distal hindlimb and head length. Consequently, these characters were not included in the multivariate analyses.

Principal components analysis of the morphometric variables revealed that body proportions accounted for almost half of the variance in the data. This first principal component (PC1) explained 46.43% of the variance in morphology. Lizards scoring high on PC1 are large with relatively long hind feet, long tails, and deep or wide heads, while lizards scoring low on PC1 are small with short body proportions (Table 3). The second principal component (PC2) explained 19.69% of the variance in morphology. Lizards with high scores on PC2 had lower numbers of femoral and preanal pores, while lizards scoring low on PC2 had higher numbers of pores (Table 3). The third principal component (PC3) explained 14.40% of the variance in morphology. Lizards with high scores on PC3 had proportionally short hind feet, while lizards scoring low on PC3 had longer hind feet. Analysis of variance indicated a statistically significant difference between species on PC1 ( $F_{5,136} = 12.61$ ,  $P < 0.001$ ), and Tukey's honest significant difference *post hoc* test showed that *L. gilberti* and *L. sp. nov.* scored significantly lower on this principal component than *L. gilberti centralis* ( $P = 0.029$  and  $P = 0.003$ , respectively), *A. burnsi* (both  $P < 0.001$ ) and *G. longirostris* ( $P = 0.039$  and  $P = 0.010$ , respectively) but not *G. temporalis*. In addition, *G. temporalis* had a significantly lower score than *G. longirostris* ( $P < 0.001$ ) on PC1. Thus, relative to body size, *L. gilberti*, *L. sp. nov.* and *G. temporalis* have shorter or smaller body proportions than the other species.

Analysis of variance of PC2 also indicated a statistically significant difference between species ( $F_{5,136} = 56.49$ ,  $P < 0.001$ ). Tukey's honest significant difference *post hoc* test indicated that *G. temporalis* scored significantly higher on PC2 than all of the other taxa (all  $P < 0.001$ ), indicating lower pore numbers, and *G. longirostris* scored significantly lower than all other taxa (all  $P < 0.001$ ), indicating higher pore numbers. Analysis of variance of PC3 indicated a statistically significant difference between species ( $F_{5,136} = 21.08$ ,  $P < 0.001$ ) and Tukey's honest significant difference *post hoc* test indicated that on PC3, *G. temporalis* and *G. longirostris* scored significantly higher than all of the other taxa (all  $P < 0.001$ ), indicating shorter hind feet length, relative to body size.

Although there is a statistically significant separation of these species in morphospace, it is visually difficult to ascertain (fig. 2). There is extensive overlap in morphospace, with *G. temporalis* and *G. longirostris* being the only species with visible separation from the others and that do not overlap each other in morphospace.

#### Species delimitation assessment

All available specimens were separated into groups based on the independent lineages supported in the mtDNA tree and then assessed for fixed and unambiguous morphological character states. We identified five morphologically diagnosable lineages that were also resolved as independent

Table 3. Principal components analysis of lizard morphology. Correlations with absolute values greater than 0.5 are in bold and are considered important.

	PC 1	PC 2	PC 3
<b>% Variance explained</b>	46.43	19.69	14.40
<b>Eigenvalues</b>	3.25	1.38	1.01
<b>Component loadings</b>			
SVL	<b>0.81</b>	0.37	-0.05
Tail	<b>0.78</b>	0.13	0.32
Hind foot	<b>0.55</b>	0.18	<b>-0.77</b>
Head width	<b>0.80</b>	0.10	0.27
Head depth	<b>0.83</b>	0.08	0.02
Femoral pores	0.40	<b>-0.75</b>	-0.42
Preanal pores	0.45	<b>-0.79</b>	0.30
<b>Species</b>			
<i>Amphibolurus burnsi</i>	0.51 ± 0.34	0.65 ± 0.22	-0.71 ± 0.15
<i>Lophognathus gilberti centralis</i>	0.34 ± 0.24	0.44 ± 0.14	-1.09 ± 0.20
<i>Lophognathus gilberti gilberti</i>	-0.51 ± 0.16	0.10 ± 0.13	-0.29 ± 0.20
<i>Lophognathus</i> sp. nov.	-0.54 ± 0.17	-0.12 ± 0.10	-0.24 ± 0.14
<i>Gowidon longirostris</i>	0.85 ± 0.10	-1.32 ± 0.10	0.65 ± 0.12
<i>Gowidon temporalis</i>	-0.28 ± 0.13	1.13 ± 0.13	0.83 ± 0.14

Note: PC, principal component; SVL, snout–vent length.

lineages in the mtDNA and nuclear trees, which were equated to generic level divisions (fig. 3). Within lineages, further morphologically diagnosable lineages, which were also well-supported in the mtDNA and nuclear trees, could be identified. A number of these lineages have wholly or partially overlapping geographic distributions within the Australian tropical savannah (fig. 4): *Lophognathus gilberti gilberti*, *L. gilberti centralis*, *L. gilberti* sp. nov. and *Chlamydosaurus kingi*. Using this species delimitation method, five genera and nine species could be delineated across *Amphibolurus*, *Gowidon* and *Lophognathus* sensu lato.

#### Taxonomic revision

Diagnoses below are given only in terms of synapomorphies. Species diagnoses are only provided for those species for which taxonomic revision is required.

#### Genus *Amphibolurus* Wagler, 1830

*Gemmatophora* Kaup, J.J., 1827. Zoologische Monographien. *Isis Von Oken*, Jena 20: 610–625 [621] [*nom. oblit.*; described as subgenus of *Calotes* Cuvier, 1817]. Type-species *Lacerta muricata* White, 1790 by original designation.

*Amphibolurus* Wagler, J.G., 1830. *Natürliches System der Amphibien, mit vorangehender Classification der Säugethiere und Vögel*. München, Cotta'schen vi 354 pp. [145] [replacement for *Gemmatophora* Kaup, 1827, which Wagler rejected as an invalid

hybrid name (“vox hybrida”)].

*Grammatophora* Duméril, A.M.C. and Bibron, G., 1837. *Erpétologie Générale ou Histoire Naturelle Complète des Reptiles*. Paris, Roret 4: ii 571 pp. [468] [*non Grammatophora* Stephens, 1829 (*nom. nud.*); emendation of *Gemmatophora* Kaup, 1827].

*Petroplanis* Fitzinger, L.J., 1843. *Systema Reptilium*. Vienna, Braumüller u. Seidel vi 106 pp. [83, 84] [*nom. nud.*; introduced in synonymy of *Amphibolurus* Wagler, 1830]. Types species *Petroplanis jacksoniensis* Fitzinger, 1843 (= ? *Agama jacksoniensis* Cloquet, 1816) by monotypy.

*Polylophus* Fitzinger, L.J., 1843. *Systema Reptilium*. Vienna, Braumüller u. Seidel vi 106 pp. [83, 84] [*nom. nud.*; introduced in synonymy of *Amphibolurus* Wagler, 1830]. Types species *Polylophus jacksoniensis* Fitzinger, 1843 (= ? *Agama jacksoniensis* Cloquet, 1816) by monotypy.

Synonymy that of: Cogger, H.G. 1983, in Cogger, H.G., Cameron, E.E., and Cogger, H.M. Amphibia and reptiles. Pp. 108–116 in: Walton, D.W. (ed.) *Zoological catalogue of Australia*. Vol. 1. Netley, South Australia: Griffin Press Ltd. vi 313 pp. [108]

**Diagnosis.** A genus consisting of large agamid lizards in the subfamily Amphibolurinae with exposed tympanum, long robust limbs and a long tail. Gular scales smooth to weakly keeled, ventral scales smooth to strongly keeled. Head wide and deep in comparison with length. Heterogenous body scales, dorsal surface scattered with many spinose scales. Well-developed spinose nuchal and vertebral crest. Two broad pale dorsolateral stripes running from ear or neck to the hip,

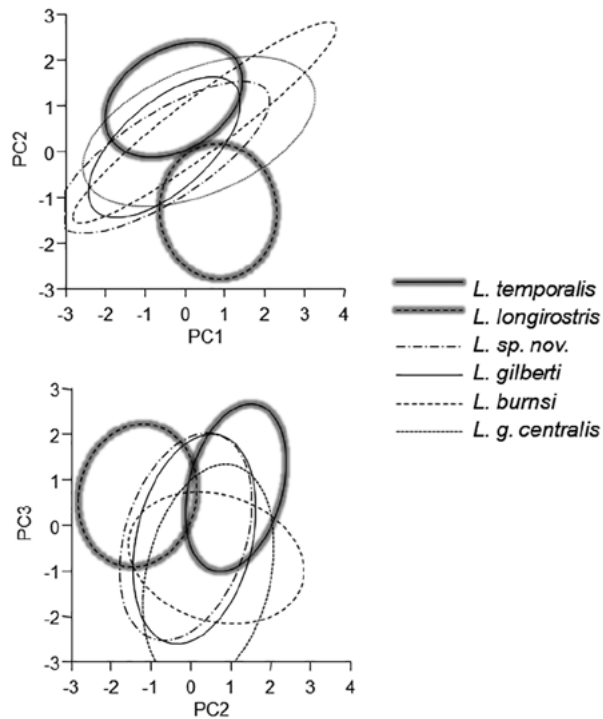


Figure 2. The distribution of *Lophognathus* sensu lato samples included in this study along the first three morphological principal components axes. Distribution of each taxon is delineated by a 95% confidence ellipse. *Lophognathus gilberti* has been separated into *L. sp. nov.*, *L. gilberti centralis*, and *L. gilberti*.

discontinuous with pale lip scales. Dorsolateral stripes intersected by multiple wedges of brown or grey along their length.

**Included species.** *Amphibolurus norrisi* Witten, G.J. and Coventry, A.J., 1984; *Lacerta muricata* White, J., 1790; *Amphibolurus burnsi* Wells, R.W. and Wellington, C.R., 1985; *Physignathus gilberti centralis* Loveridge, A., 1933.

**Distribution.** Continental Australia, including south-eastern Australia extending west across Nullabor Plain, eastern Australia extending north into Queensland, central Australia incorporating Northern Territory, Western Australia and western Queensland. A broad range of habitats occupied, including arid and semi-arid woodlands, dry sclerophyll forests and woodlands, and coastal heathlands.

### *Amphibolurus burnsi*

(fig. 8)

*Amphibolurus burnsi* Wells, R.W. and Wellington, C.R., 1985. A classification of the Amphibia and Reptilia of Australia. *Australian Journal of Herpetology Supplementary Series* 1: 1–61 [18]. Designation that of Melville, J., this work.

**Holotype.** AM R116981 (previously AMF 28917), Collarenebri, New South Wales.

**Diagnosis.** Large robust member of the *Amphibolurus* genus. Large wide head with extensive covering of spinose scales. Posterior ventral portion of head heavily covered with spinose scales. Well-developed spinose nuchal and vertebral crest, which continues down back to hips. At least two more spinose dorsal crests on each side of vertebral crest. Scalation on back strongly heterogeneous, with two dorsolateral rows of spinose scales running from shoulders to hips. Scales on thighs strongly heterogeneous with scattered spinose scales. Prominent row of spinose scales running along the posterior edge of thighs. Shades of brown, grey to almost black. Two broad pale dorsolateral stripes running from ear or neck to the hip, discontinuous with lip scales. Dorsolateral stripes intersected by multiple wedges of brown or grey along their length. Femoral pores 3–5; preanal pores 4–6.

**Description of holotype.** Adult. Large robust lizard with distinct neck, limbs long and robust; canthus well defined; nasal scale below canthal ridge, nare slightly to the posterior–dorsal section of the nasal scale; visible tympanum. Infralabials 12; supralabials 13. Labials elongate somewhat keeled. Scales on dorsal surface of head heterogeneous and strongly keeled. Well-developed spinose nuchal crest. Posterior portion of head heavily covered with spinose scales. Well-developed vertebral crest, which continues down back to hips. Two paravertebral rows of enlarged and prominent spinose scales on each side of vertebral crest, running from shoulders to hips. Scales on thighs strongly heterogeneous with scattered spinose scales. Row of enlarged spinose scales running along posterior edge of thighs. Scales on the dorsal surface of body and tail are strongly keeled and scales on the ventral surface are weakly keeled. Colour dorsally is light to dark brown and grey, with scattered black markings.

**Variation.** Considerable variation in the number and size of spinose scales between males, females and juveniles. In adult males there are numerous long spines (> 2 mm) and the spinose scales are dense across the back of the head, nuchal and ventral crests, and rear of the thighs. In females and juveniles, spinose scales are still present and diagnostic but they are smaller and less dense, providing an overall appearance of the lizards being less spiny. Some individuals, particularly adult males, have a broad pale stripe running along the full extent of the lower lip. However, a white stripe along the upper lip is not present and a well-defined pale stripe between the eyes and ears is not present.

**Distribution and ecology.** Occurs in dry woodlands and associated with eucalypts along inland watercourses. Distributed across southern and central-western Queensland and northern inland New South Wales.

**Remarks.** The distribution of *Amphibolurus burnsi* potentially overlaps with *A. centralis* and *A. muricatus*. *A. burnsi* has been included in the genus *Lophognathus* but DNA sequencing has confirmed that it is unrelated to *Lophognathus* species and demonstrates a clear sister-species relationship with *A. centralis*. Morphologically, *A. centralis* and *A. burnsi* can be distinguished by the latter having heterogeneous scales on the thighs, spinous scales on the thigh and enlarged spinous scales along the rear of the thigh.

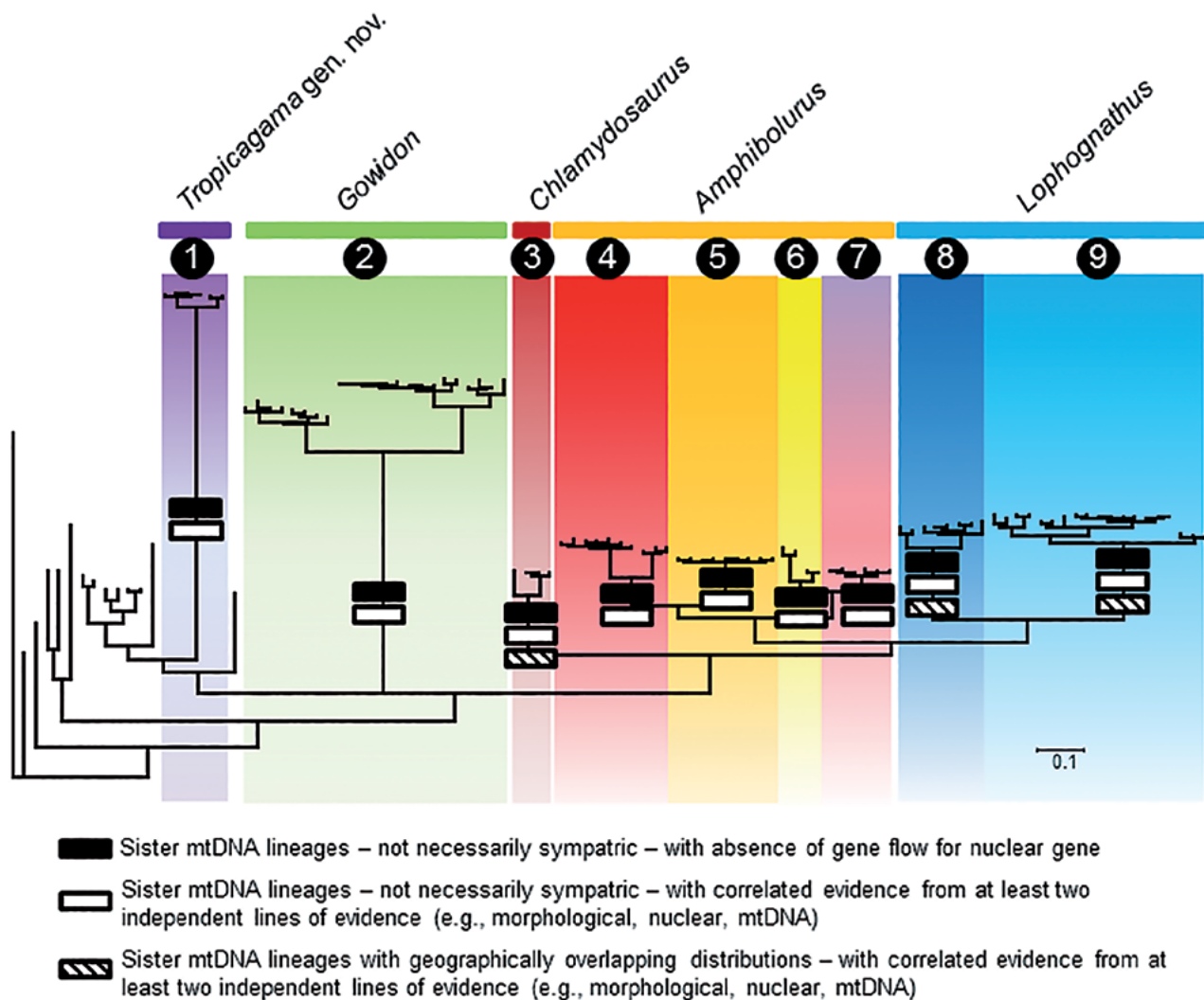


Figure 3. Results from the integrative taxonomic approach to species delimitation. Genera are designated by a multicoloured horizontal bars at the top of the figure, and species within genera are designated by a number in black above a coloured vertical segment. Segment colours and species numbers correspond to those in fig.1.

### *Amphibolurus centralis*

(Figs. 5 & 8)

*Physignathus gilberti centralis* Loveridge, A. 1933. New agamid lizards of the genera *Amphibolurus* and *Physignathus* from Australia. *Proceedings of the New England Zoological Club*, Boston 13: 69–72 [71]. Designation that of Wells, R.W. and Wellington, C.R., 1983. A synopsis of the Class Reptilia in Australia. *Australian Journal of Herpetology* 1: 73–129 [80].

*Holotype*. MCZ 35207, Anningie 30 mi[les] W of Teatree Well, Northern Territory.

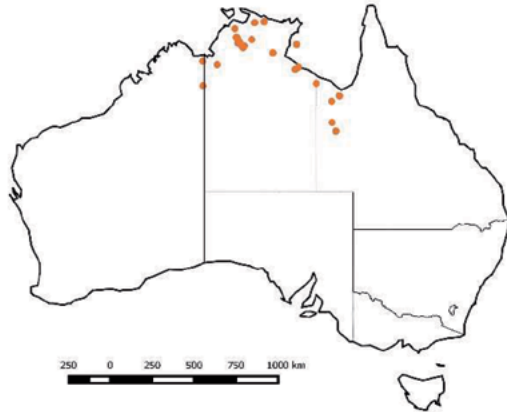
*Paratype*. AM R10993 (formerly MCZ 35208), Australia, Northern Territory, Tea Tree Well, (22° 8' S, 133° 24' E). Juvenile. Note: Original MCZ catalogue lists locality information identical to MCZ 35207.

*Diagnosis*. Large robust member of the *Amphibolurus* genus. Large wide head in proportion to body size. Well-developed spinose nuchal and vertebral crest. Scallation on back heterogeneous. Scales on thighs relatively homogeneous, lacking row of large spinose scales. Shades of light to dark brown and grey. Two broad pale dorsolateral stripes running from ear or neck to hip, discontinuous with pale lip scales. Dorsolateral stripes intersected by multiple wedges of brown or grey along their length. Most individuals have a broad pale or white stripe running along extent of the lower lip. Femoral pores 2–6; preanal pores 3–6.

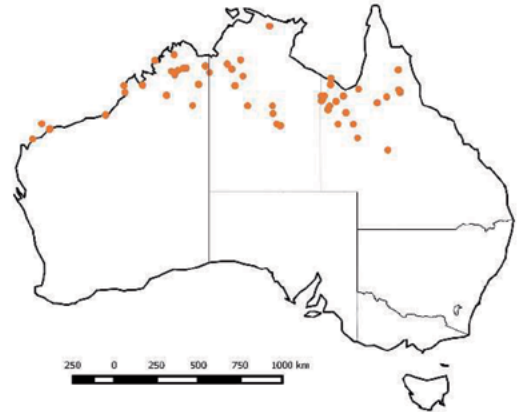
*Description of holotype*. Adult male. Large robust lizard with large wide head in proportion to body size and well-developed spinose nuchal crest comprising a row of eight enlarged scales.



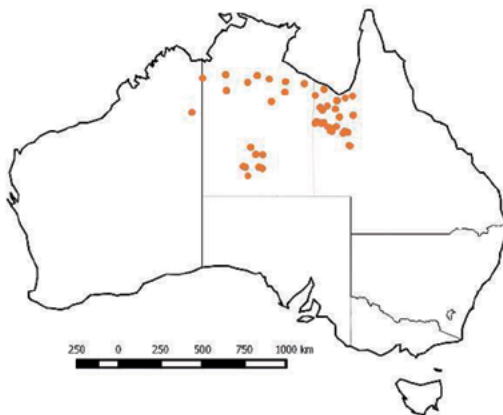
a. *L. gilberti*



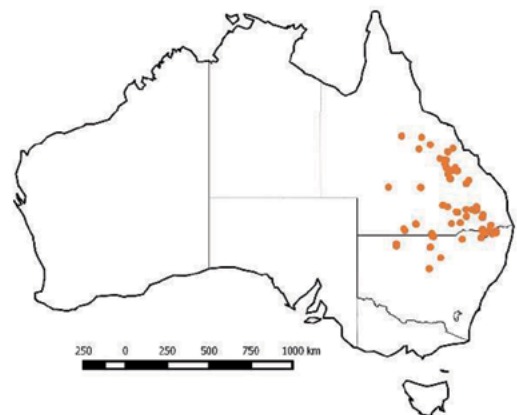
b. *L. horneri* sp. nov.



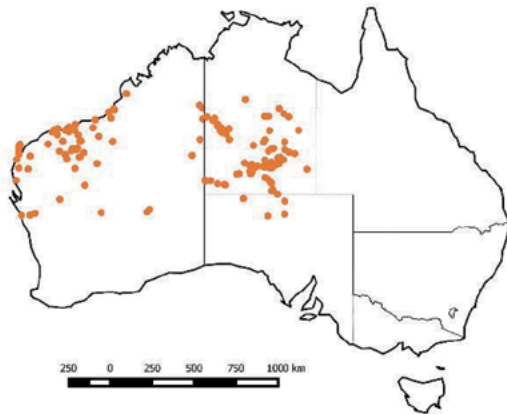
c. *A. centralis*



d. *A. burnsi*



e. *G. longirostris*



f. *T. temporalis*

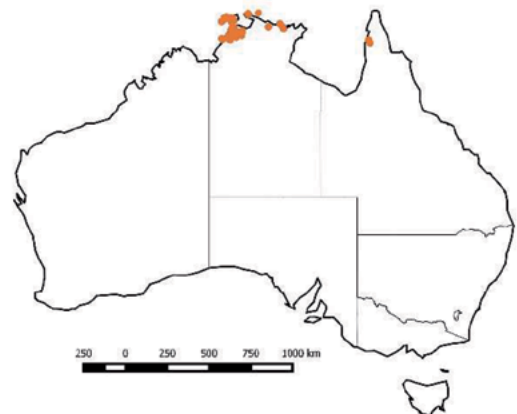


Figure 4. Distribution of study species included in this study, compiled from museum records.

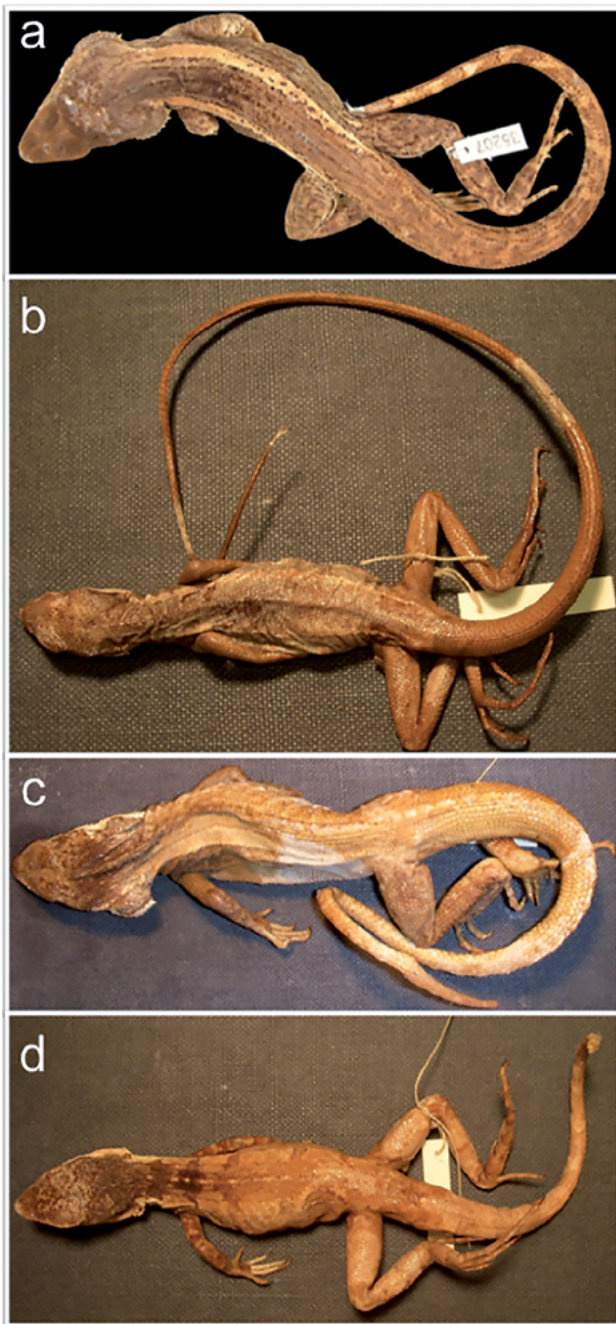


Figure 5. Primary type specimens: a, *Amphibolurus centralis* (MCZ 35207); b, *Gowidon longirostris* (BMNH 1946.8.28.73); c, *Lophognathus gilberti* (BMNH 1946.8.28.69); d, *Tropicagama temporalis* (BMNH 1946.8.28.72).

Additional (4–6) enlarged spinose scale protruding from rear of head, posterior to the jaw. Scales on thighs relatively homogeneous, lacking row of large spinose scales. Distinct neck, limbs long and robust; canthus well defined; nasal scale below canthal ridge, nare slightly to the posterior–dorsal section of the nasal scale; visible tympanum. Infralabials 13,

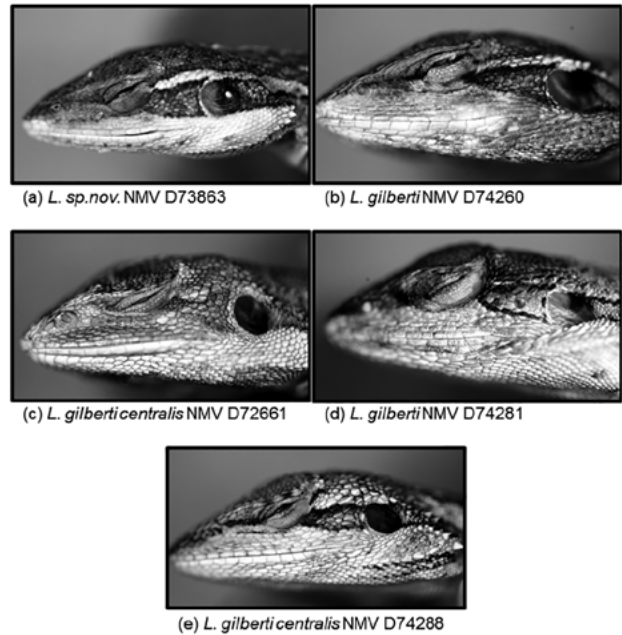


Figure 6. Colour pattern variation in the lateral head views of *Amphibolurus centralis*, *Lophognathus gilberti* and *L. horneri* sp. nov. Museum registration numbers for the individual lizards photographed are provided.

supralabials 14. Labials elongate without obvious keels. Scales on dorsal surface of head heterogenous and strongly keeled. Scattered enlarged, keeled mucronate scales present on side of head posterior to the eye. Scales on the dorsal surface of body and tail are strongly keeled and scales on the ventral surface are weakly keeled. Tail long, robust at base, tapering distinctly from approximately one-third along its length to a fine tip. Shades of cream, light to dark brown and grey. Two broad pale dorsolateral stripes running from rear of head to back of rear legs; pale stripes bordered by narrow discontinuous dark brown stripes along entire length and flecks of dark brown within the posterior two-thirds of the pale stripes. Irregular dark brown colouration between the pale dorsolateral stripes on the anterior one-third of the torso. Lacking pale stripe running along the extent of the lower lip.

**Variation.** Marked variation in colour pattern between individuals. Broad white lip stripe occurs along the upper lip in some individuals, mostly adult males. Alternatively, some individuals do not have a white stripe on either the upper or the lower lips. Diffuse pale stripe between eye and ear in some individuals, but it is not a well-defined stripe bordered dorsally and ventrally by a row of darker scales extending the full span of eye–ear.

**Distribution and ecology.** Arid northern-central and central Australia, particularly associated with mulga woodlands but also occurring in eucalypt woodlands. Western Queensland, Northern Territory and Western Australia.

Table 4. Summary of morphometric measurements (mm) for the primary types of *Amphibolurus burnsi*, *A. centralis*, *Gowidon longirostris*, *Lophognathus gilbert*, *L. horneri* sp. nov. and *Tropicagama temporalis*

	<i>Amphibolurus burnsi</i>	<i>Amphibolurus centralis</i>	<i>Gowidon longirostris</i>	<i>Lophognathus gilberti</i>	<i>Lophognathus horneri</i> sp. nov.	<i>Tropicagama temporalis</i>
	AM R116981 Holotype	MCZ 35207 Holotype	BMNH 1946.8.28.73 Lectotype	BMNH 1946.8.28.69 Holotype	NTM R16472 Holotype	BMNH 1946.8.28.72 Lectotype
SVL	105.2	99.6	88.8	112.9	102	102.7
HL	39.4	38.3	29.1	40.2	36.1	31.3
HW	31.0	29.6	18.9	27.5	23.2	19.5
HD	13.3	12.2	12.8	14.5	14.4	13.2
LegL	88.6	85.2	83.9	105.6	102.0	87.1

Note: SVL, snout–vent length; HL, head length; HW, head width at widest point; HD, head depth; LegL, hindlimb length.

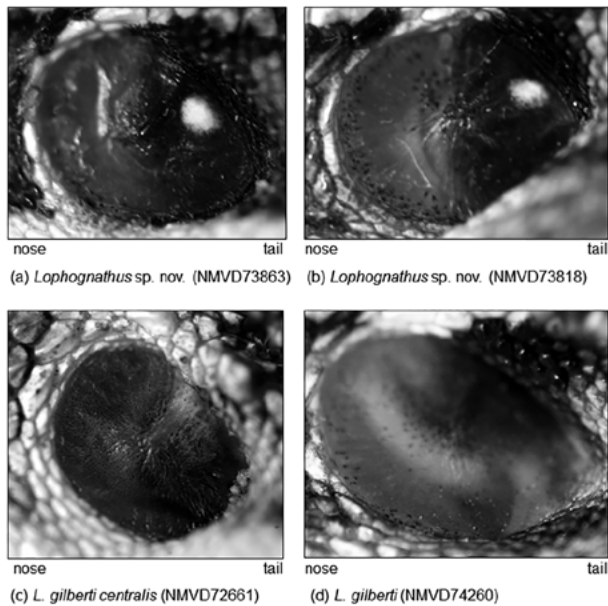


Figure 7. Variation in white pigmentation on tympanums of *Lophognathus* sp. nov., *L. gilberti* and *L. gilberti centralis*. Orientation of the tympanums is provided under images. Museum registration numbers for the individual lizards photographed are also provided.

**Remarks.** As detailed above, the distribution of *Amphibolurus centralis* potentially overlaps with *A. burnsi* Wells and Wellington, 1985, *Gowidon longirostris* Boulenger, 1883, *Lophognathus gilbert* Gray, 1842 and *L. horneri* sp. nov. DNA sequencing has confirmed that *Amphibolurus centralis* is unrelated to the *Gowidon* and *Lophognathus* species and demonstrates a clear sister-species relationship with *A. burnsi*. Morphologically, *A. centralis* can be distinguished from *A. burnsi* by having mostly homogeneous scales on the thighs,

lacking spinous scales on the thigh and having no enlarged spinous scales along the rear of the thigh.

#### Genus *Gowidon* Wells and Wellington, 1984.

*Gowidon* Wells, R.W. and Wellington, C.R., 1983. A synopsis of the Class Reptilia in Australia. *Australian Journal of Herpetology* 1: 73–129. Type-species *Gowidon longirostris* Boulenger, G.A., 1883 by monotypy.

**Diagnosis.** A monotypic genus consisting of a large agamid lizard in the subfamily Amphibolurinae with exposed tympanum, gular scales smooth to weakly keeled, ventral scales smooth to weakly keeled. Long-limbed, very long tail, long snout and distinct nuchal crest. Head narrow and shallow in depth compared with length of snout. Dorsal scales uniform, with keels converging posteriorly toward midline. Prominent pale dorsolateral stripes and pale stripe along lower jaw. One to three small white spots on a black background positioned directly posterior to the ear. Preanal pores 4–7; femoral pores range 11–22.

**Included species.** *Gowidon longirostris* Boulenger, G.A., 1883.

**Distribution.** Arid western interior of Australia. Semi-arboreal, occurring in a broad range of habitats across arid and semi-arid habitats, particularly associated with inland arid watercourses, gorges and river beds.

#### *Gowidon longirostris*

(Figs. 5 & 8)

*Gowidon longirostris* Boulenger, G.A., 1883. Remarks of the lizards of the genus *Lophognathus*. *Annals and Magazine of Natural History* 12(5): 225–226 [225].

*Physignathus eraduensis* Werner, F., 1909. Reptilia exkl. Geckonidae and Scincidae. In Michaelsen, W. and Hartmeyer, R. (eds.) *Die fauna südwest-Australiens*. Jena: Gustav Fischer 2: 251–278 [275]. Type data. holotype, status unknown, from Eradu, Western Australia.

*Physignathus longirostris quattuorfaciatus* Sternfeld, R., 1924. Beiträge zur herpetologie inner-Australiens. *Abhandlungen der*



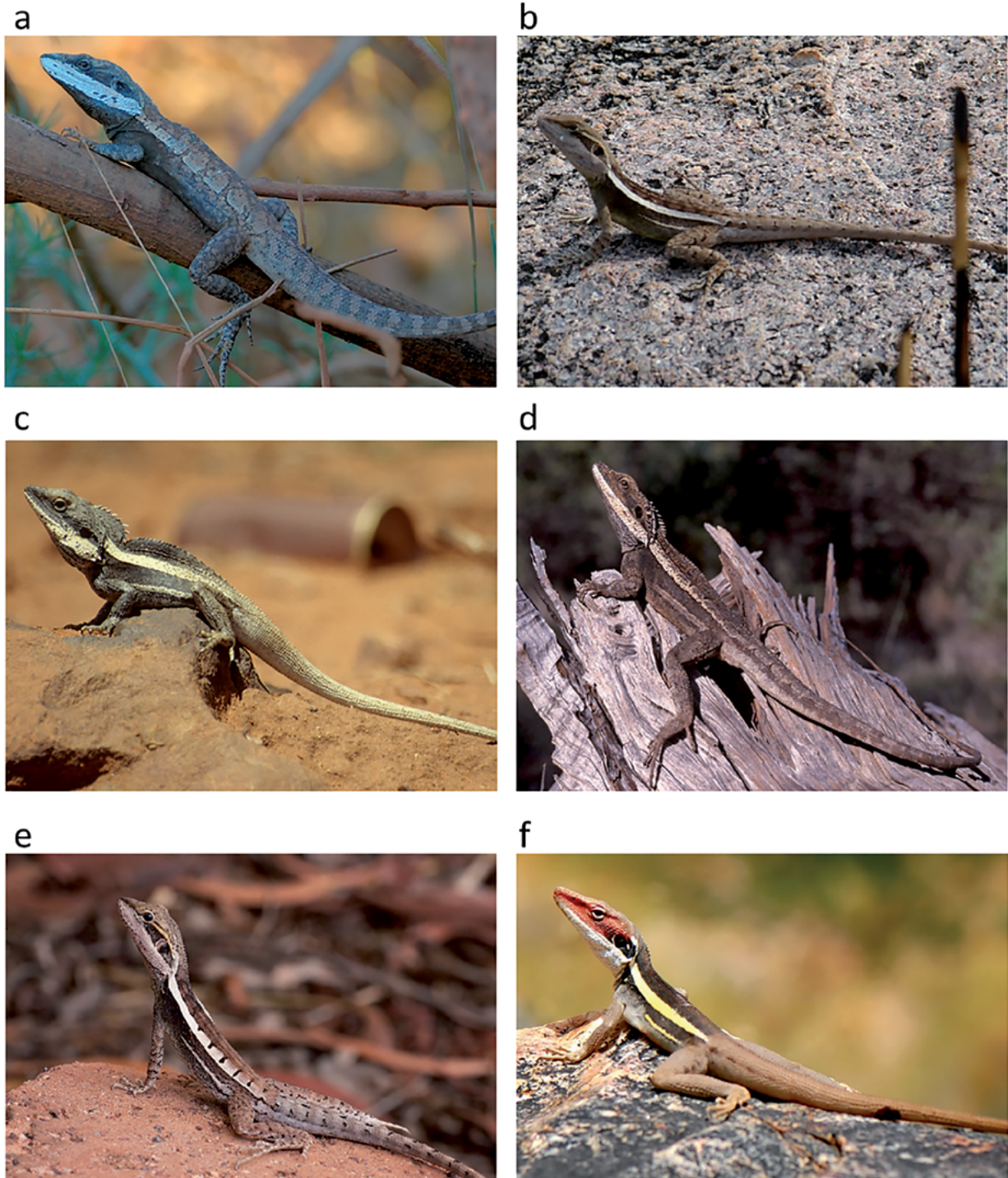


Figure 8. Photos in life of species under revision: a, *Lophognathus horneri* sp. nov., adult male with breeding colouration, 80 mile beach, Western Australia (photo: R. Glor); b, *Lophognathus gilberti*, Katherine, Northern Territory (photo: R. Glor); c, *Amphibolurus centralis*, adult male with breeding colouration, West MacDonnell Ranges, Northern Territory (photo: J. Melville); d, *Amphibolurus burnsi*, adult male with breeding colouration, Westmar, Queensland (photo: S. Wilson); e, *Tropicagama temporalis*, Jabiru, Northern Territory (photo: S. Wilson); f, *Gowidon longirostris*, adult male with breeding colouration, Ormiston Gorge, Northern Territory (photo: R. Glor).

*Senckenbergischen Naturforschenden Gesellschaft* 38: 221–251 [236]. Type data. lectotype SMF 10366, from Hermannsburg Mission, Northern Territory. Designation by Mertens, R., 1967. Die Herpetologische Section des Natur-Museums und Forschungs-Institutes Senckenberg in Frankfurt-a-M. nebst einem Verzeichnis ihrer Typen. 1. *Senckenberg Biology* 48: 1–106.

Synonymy that of: Melville, J., this work; Cogger, H.G., 1983, in Cogger, H.G., Cameron, E.E., and Cogger, H.M. Amphibia and Reptiles. Pp. 121–122 in: Walton, D.W. (ed.) *Zoological catalogue of Australia*. Vol. 1. Netley, South Australia: Griffin Press Ltd. vi 313 pp. [122].

*Lectotype*. BMNH 1946.8.28.73, Champion Bay, Western Australia. Designation by Wells, R.W. and Wellington, C.R., 1985. A classification of the Amphibia and Reptilia of Australia. *Australian Journal of Herpetology Supplementary Series* 1: 1–61. Paralectotypes BMNH 1946.8.12.64–65, Nickol Bay, Western Australia.

*Diagnosis*. As for genus.

*Description of Lectotype*. Adult. Moderately sized slender agamid lizard with relatively long snout and dorsoventrally compressed head. A distinct neck, very long limbs and very long whip-like tail; canthus well defined; nasal scale below canthal ridge, nare slightly to the posterior–dorsal section of the nasal scale; visible tympanum. Infralabials 13; supralabials 15. Labials elongate unkeeled. Scales on dorsal surface of head moderately heterogeneous and weakly to moderately keeled. Low nuchal crest of slightly enlarged scales, extending as a row of enlarged vertebral scales down the back to base of tail. Lacking enlarged spinose scales on head or torso. Dorsal scales on body and tail mostly homogeneous and moderately keeled. Scales on thighs homogeneous and strongly keeled. Scales on ventral surface of head strongly keeled and weakly keeled on the body. Colour dorsally is light to dark brown and grey. Broad white lip stripe, widest on lower jaw and narrow on upper lip, extends below ear and as two broad white dorsoventral stripes extending to mid-way down the back. A dark diffuse area of pigmentation behind ear with diffuse pale spot immediately behind the tympanum but the characteristic well-defined white spot or spots on a black background behind the ear is not apparent. Ventral surface of head, throat and upper chest darkly pigmented with the dark pigmentation extending to the lateral surfaces of the throat and up over the shoulders, bordering the white dorsolateral stripes.

*Variation*. A few specimens examined lack the broad dorsolateral stripes and are a pale grey colour, with a few rust-brown coloured markings between the shoulders. An example of this colour-morph is NMVD74317 collected on the Great Northern Highway, 1 km E of Roebuck Roadhouse, Western Australia (17° 48' 57"S, 122° 40' 44" E). However, these pale colour morphs still retain the white spot or spots on a black background behind the ear.

*Distribution and ecology*. Arid western interior of Australia. Semi-arboreal, occurring in a broad range of habitats across arid and semi-arid habitats, particularly associated with inland arid watercourses, gorges and river beds.

**Remarks**. The distribution of *Gowidon longirostris* overlaps with *Amphibolurus centralis* and *Lophognathus horneri* sp. nov. but can be distinguished morphologically by having more

than 10 femoral pores,  $\geq 1$  white spot on a black background behind the ear, a relatively long snout and dorsoventrally compressed head, and a very long whip-like tail.

### Genus *Lophognathus* Gray, 1842

*Lophognathus* Gray, J.E., 1842. Description of some hitherto unrecorded species of Australian reptiles and batrachians. Pp. 51–57 in: Gray, J.E. (ed.). *The zoological miscellany*. London: Treuttel, Würz & Co. [53]. Type-species *Lophognathus gilberti* Gray, 1842 by monotypy.

*Redtenbacheria* Steindachner, F., 1867. *Redtenbacheria fasciata* Steindachner, F., 1867. Reptilien. Pp. 1–98 in: *Reise der Österreichischen Fregatte Novara um die Erde in den Jahren 1857, 1858, 1859 unter den Befehlen des Commodore B. von Wüllerstorff-Urbair*. Zoologie 1(3). Vienna: State Printer. [1869 on title page] [31]. [junior homonym of *Redtenbacheria* Schiner, 1861]. Type species. *Redtenbacheria fasciata* Steindachner, 1867 by monotypy.

Synonymy that of: Cogger, H.G. 1983, in Cogger, H.G., Cameron, E.E., and Cogger, H.M. Amphibia and Reptiles. Pp. 121–122 in: Walton, D.W. (ed.) *Zoological catalogue of Australia*. Vol. 1. Netley, South Australia: Griffin Press Ltd. vi 313 pp. [121]

*Diagnosis*. A genus consisting of large agamid lizards in the subfamily Amphibolurinae, with exposed tympanum, gular scales smooth to weakly keeled, ventral scales weakly to strongly keeled. Stoutly built with moderately long legs and tail. Broad white stripe on the upper and lower lips, extending along the full extent of the jaw, pale stripe from behind the eye to the top of the ear, which is cream, white, grey or yellow in life. This pale stripe is well defined ventrally and dorsally by a row of darkly pigmented scales (fig. 6). Heterogenous scales on the back both at the midline and dorso-laterally, associated with a weak to prominent row of enlarged, strongly keeled scales. Colour patterns of grey, brown, rust-brown and black. Well-developed nuchal crest continuous with the enlarged row of vertebral scales. Broad pale dorsolateral stripes, which may extend from top of ear or back of head to hips. Dorsolateral stripes are not continuous with the pale lip stripes. On the back, dorsolateral stripes may be intersected by wedges of brown or grey. Preanal pores 3–6; femoral pores 2–8.

*Included species*. *Lophognathus gilberti* Gray, J.E., 1842; *Lophognathus horneri* sp. nov.

*Distribution*. Northern Australia, extending from northern-central and western Queensland, through the northern regions of the Northern Territory and across northern Western Australia. Occurs in woodlands and river courses.

### *Lophognathus gilberti*

(fig. 5)

*Lophognathus gilberti* Gray, J.E., 1842. Description of some hitherto unrecorded species of Australian reptiles and batrachians. Pp. 51–57 in: Gray, J.E. (ed.). *The zoological miscellany*. London: Treuttel, Würz & Co. [53].

*Redtenbacheria fasciata* Steindachner, F. 1867. Reptilien. Pp. 1–98 in: *Reise der Österreichischen Fregatte Novara um die Erde in den Jahren 1857, 1858, 1859 unter den Befehlen des Commodore B. von Wüllerstorff-Urbair*. Zoologie 1(3). Vienna: State Printer. [1869 on title page] [31]. Type data. Holotype whereabouts unknown (not found), Australia.

*Physignathus incognitus* Ahl, E. 1926. Neue Eidechsen und Amphibien. *Zoologischer Anzeiger* 67: 186-192 [190]. Type data. Holotype ZMB 30086, Australia.

Synonymy that of: Melville, J., this work; Cogger, H.G. 1983, in Cogger, H.G., Cameron, E.E., and Cogger, H.M. Amphibia and Reptiles. Pp. 121-122 in: Walton, D.W. (ed.) *Zoological catalogue of Australia*. Vol. 1. Netley, South Australia: Griffin Press Ltd. vi 313 pp. [121].

*Holotype*. BMNH 1946.8.28.69 from Port Essington, NT.

*Diagnosis*. As for genus. *Lophognathus gilberti* is distinguished from *Lophognathus horneri* sp. nov. by lacking a distinct white spot on the tympanum (fig. 7) that is surrounded by or adjacent to black pigmentation.

*Description of Holotype*. A large robust male dragon lizard with large robust limbs and tail. Large head in comparison with body size, prominent nuchal crest of 18 enlarged spinose scales, extending from anterior of ear to shoulders. Small nasal scale and nares, below canthal ridge. Supralabials 13; anterior point of lower jaw damaged. Head scales heterogeneous and strongly keeled; 3-5 enlarged white spinose scales protruding from rear of head, posterior to the jaw. Dorsal scales on body and tail strongly keeled and heterogeneous. Gulars smooth and ventrals weakly to strongly keeled. Scales on thighs heterogeneous and strongly keeled. Very broad white lip stripes, extending under jaw and up to anterior border of ear. Broad pale dorsolateral stripes, continuous from neck to hips, bordered and well defined by row of darker scales. Dorsolateral stripes discontinuous with lip stripes. Poorly defined and discontinuous pale stripe between eye and top of ear, bordered dorsally and ventrally by darker scales. No clearly defined white spot on a dark background on the tympanum, although there is a patch of pale pigment in the upper-back quadrant of the tympanum. Colour dorsally is light to dark brown and grey. Ventral surface of head, throat and upper chest darkly pigmented with the dark pigmentation extending to the lateral surfaces of the throat and up over the shoulders, bordering the white dorsolateral stripes. Femoral pores 6; preanal pores 4.

*Variation*. Some specimens of *L. gilberti* do have white areas on the tympanum but they are not a well-defined spot surrounded by the black pigmented area (fig. 7); instead, they are a diffuse white or off-white smear or patch of pale pigment without the associated black pigmentation. An example of this is specimen NMVD74026 collected from Mt Wells Road, near Grove Hill in the Northern Territory (13° 28' 47" S, 13° 132' 41" E), which has a smear of white pigmentation across the posterior half of the tympanum.

*Distribution and ecology*. Far northern Australia in woodlands and tropical savannahs. In the Northern Territory north of Katherine, in Arnhem Land, and across coastal areas into Western Australia and western Queensland. In Western Australia, occurs north of Kununurra and extending up into the eastern coastal Kimberley.

*Remarks*. *Lophognathus gilberti* shares similar body proportions and meristic characters with *L. horneri* sp. nov., with extensive distributional overlap (fig. 4) but is readily separated by the lack of a well-defined white spot on the tympanum. *Lophognathus gilberti* is also superficially similar

to *Amphibolurus centralis* and potentially has distributional overlap, but it differs in mostly having a well-defined white or pale stripe extending the full length between the ear and the eye, and a broad white stripe running the extent of the upper lip being mostly present.

#### *Lophognathus horneri* sp. nov.

ZooBank LSID: urn:lsid:zoobank.org:act: 4E027CDD-F9B2-451B-B08E-26D6A0B8A8ED.

(Figs. 8 & 9)

*Grammatophora temporalis* (part.) Günther, A., 1867. Additions to the knowledge of Australian reptiles and fishes. *Annals and Magazine of Natural History* 20(3): 45-68 [52].

Synonymy that of: Melville, J., this work.

*Holotype*. NTM R16472 Sambo Bore, Wave Hill Station, Northern Territory (18° 52' 48" S, 130° 40' 12" E).

*Paratypes*. NMV D72658 Wave Hill Homestead, Northern Territory (17° 23' 08" S, 131° 06' 44" E); NMV D73846 King Edward River Camp, Mitchell Plateau, Kimberley, Western Australia (14° 52' 57" S, 126° 12' 10" E); NMV D74687 road to Davenport Ranges National Park, Northern Territory (20° 37' 34" S, 134° 47' 14" E); WAM R131990 Kununurra, Kimberley, NE Western Australia (15° 48' 0.00" S, 128° 43' 0.12" E); WAM R108806 Mabel Downs Station, Calico Springs, NE Western Australia (17° 16' 59.88" S, 128° 10' 59.88" E); WAM R132850 Kununurra, NE Western Australia (5° 47' 37.68" S, 128° 43' 10.92" E); BMNH 1946.8.12.73 Nickol Bay, Western Australia [paralectotype *Grammatophora temporalis* (part.) Günther, 1867].

*Diagnosis*. A member of the Australian genus *Lophognathus* Gray, 1842, characterised by broad white stripe on the upper and lower lips, extending along the full extent of the jaw, a pale stripe from behind the eye to the top of the ear, which is cream, white, grey or yellow in life. This pale stripe is well defined ventrally and dorsally by a row of darkly pigmented scales (fig. 6). It is a large robust dragon with long head and well-built moderately long limbs. It has heterogeneous scales on the back, both at the midline and dorsolaterally, associated with a weak to prominent row of enlarged strongly keeled scales. *Lophognathus horneri* is distinguished from *Lophognathus gilberti* by the presence of a distinct white spot on the tympanum (fig. 7). This well-defined white spot is wholly surrounded or bordered dorsally and to the anterior by an area of black pigmentation that is positioned on the upper posterior quarter of the tympanum. This area of black pigmentation also runs along a raised ridge that extends from the outer dorsoposterior edge of the tympanum towards its centre (fig. 9).

*Description of holotype*. A large robust male dragon lizard (snout-vent length: 102 mm; head length: 36.1 mm; head width at widest point: 23.2 mm; head depth: 14.4 mm; hindlimb length: 102 mm). Head moderately long and wide, slightly rounded profile of snout and slightly dorsolaterally compressed. Nuchal crest low, extending from anterior of ear to shoulders and composed of enlarged strongly keeled scales. Gulars smooth and ventrals weakly to strongly keeled. Dorsal scales strongly keeled and heterogeneous in size. Broad pale dorsolateral stripes, continuous from neck to the hips, bordered and well-defined by row of darker scales. Dorsolateral stripes discontinuous with lip stripes. Well-defined pale stripe between eye and top of ear,





Figure 9. Holotype of *Lophognathus horneri* sp. nov. (NTM R16472).

bordered dorsally and ventrally by row of darker scales. Well-defined white spot on the tympanum, which is adjacent to an area of black pigmentation that runs along a raised ridge that extends from the outer dorsoposterior edge of the tympanum towards its centre. Femoral pores 2L/3R; preanal pores 4.

**Variation.** The white stripe on the lower lip and the white spot on the tympanum are always present. The white stripe between the eye and the ear is almost always present. The broad white stripe on the upper lip can be pale and not prominent in a few individuals. The pale dorsolateral stripes are not continuous

with the white lip stripes. Dorsolateral stripes are often absent between the ear and neck or are intersected by wedges of darker scales along the back. Three specimens collected from 80 Mile Beach (fig. 8), Western Australia (NMV D74362–D74364), lacked a distinct stripe between the eye and the ear – superficially similar to *Amphibolurus centralis* – but they still had the white spot on the tympanum. A range of specimens were examined from large adult males, females, juveniles and hatchlings. All these specimens had a white stripe on the lower lip and the white spot on the tympanum.

*Coloration in alcohol.* Specimens retain key diagnostic characters in preservative. For example, the paralectotype *Grammatophora temporalis* (part.) BMNH1946.8.12.73 from Nickol Bay, Western Australia, which has also been designated as a paratype for *L. horneri* sp. nov., was collected before 1867. This specimen, which has been in preservative for over 150 years, still retains diagnostic characters: broad white stripe on upper and lower lips, white spot on the tympanum and a pale stripe between eye and ear, which is bordered ventrally and dorsally by a row of darkly pigmented scales.

*Distribution and ecology.* Arid and semi-arid eucalypt woodlands and tropical savannahs of the central and western portions of northern Australia. Specimens were collected in 2009 as far south as the Davenport Ranges in the Northern Territory, which are south-east of Tennant Creek. This species extends north of Threeways but south of Katherine, west through Timber Creek and Wave Hill and into Western Australia. They have been collected in the Kununurra area, along the Gibb River Rd and in the Mitchell Plateau area. In Western Australia they extend south of Halls Creek and down to the northern Pilbara coast, south-west to Coral Bay and offshore islands.

*Comparison with other species.* *Lophognathus horneri* shares similar body proportions and meristic characters with *L. gilberti* with extensive overlap (Tables 2 and 3; fig. 4). It is readily separated from this species by the presence of a well-defined white spot on the tympanum (fig. 7), which is wholly surrounded or bordered by an area of black pigmentation. *Lophognathus horneri* is also superficially similar to *Amphibolurus centralis*, but it differs in having proportionally shorter tail, hindlimbs and head. Additionally, *L. horneri* has a well-defined white spot on the tympanum and a well-defined stripe between the eye and the ear (figs 6 and 7), which are lacking in *A. centralis*. Some specimens of *L. gilberti* and *A. centralis* do have white areas on the tympanum but they are not a well-defined spot surrounded or adjoining the black pigmented area; instead, they are a diffuse white or off-white smear or a patch of pale pigment without the associated black pigmentation. *Lophognathus horneri* can be distinguished from *Tropicagama temporalis* gen. nov. by having a well-defined stripe between the eye and the ear and heterogeneous dorsolateral scales along the back. In addition, *Lophognathus* has > 2 preanal pores, whereas *Tropicagama temporalis* gen. nov. has only two. *Gowidon longirostris* differs from *L. horneri* by having very long limbs and tail, being dorsoventrally compressed, having 1–3 white spots on a black background behind the ear and having > 10 femoral pores.

*Etymology.* This species is named in honour of Paul Horner, the Curator of Terrestrial Vertebrates at the Museum and Art Gallery of the Northern Territory, in recognition of his contributions to the knowledge of the tropical lizard fauna of Australia and his instrumental role in the taxonomic review of agamid lizards from this region.

### Genus *Tropicagama* gen. nov.

ZooBank LSID: urn:lsid:zoobank.org:act: F534B4D5-CBD7-41E0-950A-B95B14F1D858.

*Type-species.* *Grammatophora temporalis* (part.) Günther, A., 1867. Additions to the knowledge of Australian reptiles and fishes. *Annals and Magazine of Natural History* 20(3): 45–68 [52] [one of the original syntype series, BMNH 1946.8.12.73 (Nickol Bay), represents *Lophognathus horneri* sp. nov.].

*Diagnosis.* A monotypic genus consisting of a large agamid lizard in the subfamily Amphibolurinae, with exposed tympanum, gular scales smooth to weakly keeled, ventral scales smooth to weakly keeled. Very long-limbed, prominent erectable nuchal crest. Long tail and head relatively narrow for length. Dorsal scales uniform, with keels converging posteriorly toward midline. Prominent pale dorsolateral stripes that are broadly continuous with wide pale stripe along upper and lower jaw. Lacks well-defined pale stripe between eye and ear. Upper portion of head usually dark grey or black and uniformly coloured. Under the head, on the chin, gular and neck areas, there is dark grey or black uniform pigmentation in adult males, with two narrow white stripes extending from the back of the jaw anteriorly under the chin, parallel to the jaw, ending approximately half way along the jaw. Femoral pores 1–6; preanal pores 2 (range 1–3).

*Included species.* *Grammatophora temporalis* (part.) Günther, A., 1867.

*Distribution.* Far northern Australian coastal regions in the Northern Territory and western Cape York. Also occurs on northern offshore islands, including Indonesian islands close to Australian waters and southern Papua New Guinea.

### *Tropicagama temporalis* (Figs. 5 & 8)

*Grammatophora temporalis* (part.) Günther, A., 1867. Additions to the knowledge of Australian reptiles and fishes. *Annals and Magazine of Natural History* 20(3): 45–68 [52] [one of the original syntype series, BMNH 1946.8.12.73 (Nickol Bay), represents *Lophognathus horneri* sp. nov.].

*Lophognathus lateralis* Macleay, W., 1877. The lizards of the Chevert Expedition. Second paper. *Proceedings of the Linnean Society of New South Wales* 2: 97–104 [1878 on title page] [103]. Type data. Holotype AM R31882, Mawatta, Binaturi River (as Katow), Papua New Guinea.

*Lophognathus labialis* Boulenger, G. A., 1883. Remarks on the lizards of the genus *Lophognathus*. *Annals and Magazine of Natural History* 5 12: 225–226 [225]. Type data. Syntype(s) BMNH 1946.8.12.72, Port Essington, NT; BMNH 1946.8.12.63.

*Lophognathus maculilabris* Boulenger, G. A., 1883. Remarks on the lizards of the genus *Lophognathus*. *Annals and Magazine of Natural History* 12(5): 225–226 [226]. Type data. Syntypes: BMNH 1946.8.28.70–71 (BMNH 1919.8.26.13–14), Timor Laut Islands, Indonesia.

Synonymy that of: Melville, J., this work; Cogger, H.G. 1983, in Cogger, H.G., Cameron, E.E., and Cogger, H.M. Amphibia and Reptiles. Pp. 121–122 in: Walton, D.W. (ed.) *Zoological catalogue of Australia*. Vol. 1. Netley, South Australia: Griffin Press Ltd. vi 313 pp. [122].

*Lectotype.* BMNH 1946.8.28.72, Port Essington, Northern Territory. Designation by Cogger, H.G., 1983, in Cogger, H.G., Cameron, E.E., and Cogger, H.M. Amphibia and Reptiles. Pp. 121–122 in: Walton, D.W. (ed.) *Zoological catalogue of Australia*. Vol. 1.



Netley, South Australia: Griffin Press Ltd. vi 313 pp. [122].  
*Paralectotype*. BMNH 1946.8.12.63, Nickol Bay, WA.

*Diagnosis*. As for genus.

*Description of Lectotype*. Adult. Moderately sized slender agamid lizard with relatively short rounded snout; head narrow and moderately elongated. Prominent canthal ridge consisting of row of enlarged heavily keeled scales. Small nasal scale and nares below ridge. Visible tympanum. A distinct neck, long limbs, long and slender tail, which is damaged and missing its end. Infralabials 11; supralabials 12. Labials elongate unkeeled. Scales on dorsal surface of head moderately heterogeneous, strongly keeled. Prominent nuchal crest of 10 enlarged scales, from ear to shoulder and extending along the back as a row of enlarge scales to base of tail. Head scales heterogeneous and strongly keeled; 4–5 enlarged white spinose scales protruding from rear of head, posterior to the jaw. Dorsal scales on body and tail mostly homogeneous and weakly to moderately keeled. Scales on thighs homogeneous and strongly keeled. Scales on the ventral surface of head strongly keeled and are weakly keeled on the body. Upper portion of head dark grey-brown and uniformly coloured. Under the head, on the chin, gular and neck dark grey pigmentation, with two pale stripes extending from back of the jaw anteriorly under chin, parallel to jaw, ending approximately half way along jaw. Broad white lip stripe, equally wide on lower and narrow upper lip, extends below ear and continues as two broad white dorsoventral stripes, extending to shoulder. Broad dorsoventral stripes intersected by three dark bands at neck, shoulders and upper back.

*Variation*. Adult males have dark grey to black uniform colour on top of head and below chin, onto neck and ventral surface of shoulders. However, females and juveniles often lack this uniform colour and instead have brown and black patterning on top of the head and only have flecks of grey, brown or black on their ventral surface. However, they still have two continuous dorsolateral stripes from the jaw onto the back and lack a well-defined pale stripe between the eye and the ear. Also, it is common for *Tropicagama temporalis* to have one or more broad dark lateral bands across the back at the shoulders. Commonly, the white lower lip stripe does not extend the full length of the jaw; instead, it is only present on the posterior section of the lower jaw.

*Distribution and ecology*. Far northern Australian coastal regions in the Northern Territory and western Cape York. Also occurs on northern offshore islands, including Indonesian islands close to Australian waters and southern Papua New Guinea. Semi-arboreal, occurring in dry tropical woodland habitats, particularly associated with coastal pandanus and paperbark watercourses. Genetic data has not yet found evidence of this species occurring on the Western Australian mainland. However, future work may find this species occurring in coastal Kimberley regions.

*Remarks*. *Tropicagama temporalis* is superficially similar to, and has extensive distributional overlap with, *Lophognathus gilberti* (fig. 4). *T. temporalis* is readily separated from this

species on body proportions (fig. 2) and by having two or fewer preanal pores, uniform dorsal scales with keels converging posteriorly toward midline, a prominent pale dorsolateral stripe that is broadly continuous with stripe along jaw, and lacking a well-defined pale stripe between the eye and the ear.

#### Identification key for *Amphibolurus*, *Chlamydosaurus* and *Lophognathus*

1. No large “frill” of skin around neck ..... 2  
 A large, loose “frill” of skin around neck .....  
*Chlamydosaurus kingii*
2. Fewer than 10 femoral pores, no white spots on a black background behind the ear ..... 3  
 More than 10 femoral pores,  $\geq 1$  white spot on a black background behind the ear, relatively long snout and dorsoventrally compressed head, very long whip-like tail .....  
*Gowidon longirostris*
3. More than 2 preanal pores, dorsal scales heterogeneous, dorsolateral stripes discontinuous with wide pale stripe along upper or lower jaw (if present) ..... 4  
 Two or fewer preanal pores, dorsal scales uniform, with keels converging posteriorly toward midline. Prominent pale dorsolateral stripes that are broadly continuous with wide pale stripe along upper and/or lower jaw. Lacks well-defined pale stripe between eye and ear. ....  
*Tropicagama temporalis*
4. Lacks well-defined white or pale stripe extending full length between ear and eye (fig. 6), which is defined dorsally and ventrally by darker scales. Broad white stripe running extent of upper lip mostly absent ..... 5  
 Well-defined white or pale stripe extending full length between ear and eye present (fig. 6). Broad white stripe running extent of upper lip mostly present ..... 6
5. Scales on thighs strongly heterogeneous, with scattered spinous scales and a row of small to large spinous scales running along rear of thigh ..... 7  
 Scales on thighs mostly homogeneous, lacking spinous scales on the thigh and row of enlarged spinous scales running along rear of thigh absent .....  
*Amphibolurus centralis*
6. Well-defined white spot on tympanum is present (fig. 7). It is wholly surrounded or bordered by an area of black pigmentation that runs along a raised ridge, which extends from the outer dorsoposterior edge of the tympanum towards its centre .....  
*Lophognathus horneri*  
 Well-defined white spot on tympanum absent (fig. 7). If white or pale pigmentation is present on the tympanum, it is not a well-define spot or not wholly surrounded or bordered by an area of black pigmentation that runs along a raised ridge, which extends from the outer dorsoposterior edge of the tympanum towards its centre ....  
*Lophognathus gilberti*

7. Prominent spinose nuchal and vertebral crest, and two or more additional dorsal crests. A row of large spinose scales running along rear of thigh ..... *Amphibolurus burnsi*  
Lacking multiple additional dorsal crests and row of only small spinose scales running along rear of thigh ..... 8
8. Dark strip between nostril and eye .. *Amphibolurus norrisi*  
Dark stripe between nostril and eye absent .....  
*Amphibolurus muricatus*

## Discussion

Molecular work, incorporating both mitochondrial and nuclear gene regions, provided compelling evidence that taxonomic revision of the genera *Amphibolurus*, *Gowidon* and *Lophognathus* was required (Melville et al., 2011). This molecular work also provided a starting point for morphological analyses, allowing us to determine diagnostic characters for each species. Until now, without the aid of molecular data, it has been difficult for taxonomists to determine which morphological characteristics were diagnostic. These past difficulties and our current study have shown that there is significant morphological homoplasy across these agamid species, with significant overlap in morphometrics, colour, patterning and scalation.

We have determined that there are four independent evolutionary lineages in the former genus *Lophognathus* (now *Gowidon*, *Lophognathus*, *Amphibolurus* and *Tropicagama*). Despite the deep divergences between the four lineages, there are extensive morphological similarities in the constituent species. In addition, the fact that we have found that the junior synonym of one *Lophognathus* species was an unrelated species, now *Amphibolurus centralis*, demonstrates the extent of homoplasy in these dragons.

It seems that most of the difficulties in determining species in these genera have occurred in northern Australia, with *Amphibolurus centralis*, *Gowidon longirostris*, *Tropicagama temporalis*, *Lophognathus gilberti* and *Lophognathus horneri* all occurring in northern and north-western Australia. This geographic concentration of taxonomic problems may result from several reasons. A lack of dedicated taxonomic research into the genera *Lophognathus* and *Amphibolurus* in northern Australia may be an important factor. There has been a paucity of taxonomic research undertaken on the Australian agamid lizards, particularly those of the Northern Territory and western Queensland. Glenn Storr from the Western Australian Museum provided much of the foundational work on the taxonomy of dragons in the arid and semi-arid regions of Australia but his taxonomic work did not include *Amphibolurus* and *Lophognathus*, except for his taxonomic review of bearded dragons and the dismemberment of the *Amphibolurus* genus (Storr, 1982). Since Storr, there has been little taxonomic work conducted on northern Australian agamids. Similar taxonomic problems have arisen in dragons occurring in the eastern states of Australia, where more research is focused. For example, Witten (1972)

described *Amphibolurus nobbi* from Queensland, New South Wales and Victoria, but more recent work has demonstrated that this species is in the genus *Diporiphora* (Edwards and Melville, 2011). Following Witten's taxonomic placement of the nobbi dragon into *Amphibolurus*, Greer (1989) noted that the colour patterns of the nobbi dragon were similar to other species of *Diporiphora*, rather than *Amphibolurus*, with a pink or rose flush to the base of the tail and yellowish sides. Thus, it appears that Witten (1972) selected characters that were not correlated with evolutionary relatedness when placing the nobbi dragon into *Amphibolurus*. Consequently, the problems with the taxonomic resolution in *Amphibolurus* and *Lophognathus* have probably resulted from a combination of little research and difficulties in morphological taxonomic research into these genera.

There is a reoccurring theme of non-diagnostic characters and morphological homoplasy in the taxonomy of Australian agamids. The use of molecular tools in the taxonomy of Amphibolurinae has greatly improved resolution and nomenclatural stability that has not been possible with morphology alone. In addition, these molecular data allow insight into evolutionary patterns in this diverse group of lizards, where there is both a high degree of morphological diversity and homoplasy across the subfamily. Our study has demonstrated the high level of morphological homoplasy across independent evolutionary lineages. Our results provide significant scope for future research into the evolutionary processes underlying the morphological convergence or parallelism in Australian agamid lizards.

## Supporting information

### Supplementary Appendix S1 List of museum specimens examined morphologically.

(PDF)

## Acknowledgments

JM examined specimens for morphological review at the Australian Museum, Western Australian Museum, British Museum of Natural History, Museum Victoria, Museum of Comparative Zoology (Harvard University), Senckenberg Naturmuseum (Frankfurt-am-Main) and Zoological Research Museum Alexander Koenig (Bonn, Germany). JM would like to thank staff and researchers from these institutions for their help and assistance, including W. Longmore, R. O'Brien, D. Bray, P. Doughty, R. Sadlier, J. Rosado, C. McCarthy and, in particular, P. Wagner for organising type loans from other museums within Germany to be examined at the Zoological Research Museum Alexander Koenig (Bonn, Germany). We thank S. Wilson for use of images. We thank G. Shea for advice on nomenclature and discussions regarding synonymies. Research funding provided to JM by Australian Research Council and to JM, RG and JS by the Australian Biological Resources Study.

## References

- Bowman, D.M.J.S., Brown, G.K., Braby, M.F., Brown, J.R., Cook, L.G., Crisp, M.D., Ford, F., Haberle, S., Hughes, J., Isagi, Y., Joseph, L., McBride, J., Nelson, G., and Ladiges, P.Y. 2010. Biogeography of the Australian monsoon tropics. *Journal of Biogeography* 37: 210–216.
- Department of the Environment and Energy. 2014. *Agamidae. Australian Faunal Directory. Australian Biological Resources Study*. Viewed 8 November 2017. <http://www.environment.gov.au/biodiversity/abrs/online-resources/fauna/afd/taxa/AGAMIDAE>
- Edwards, D.L., and Melville, J. 2011. Extensive phylogeographic and morphological diversity in *Diporiphora nobbi* (Agamidae) leads to a taxonomic review and a new species description. *Journal of Herpetology* 45: 530–546.
- Greer, A.E. 1989. *The biology and evolution of Australian lizards*. Surrey Beaty & Sons: Chipping Norton, NSW.
- Hugall, A.F., Foster, R., Hutchinson, M., and Lee, M.S.Y. 2008. Phylogeny of Australasian agamid lizards based on nuclear and mitochondrial genes: Implications for morphological evolution and biogeography. *Biological Journal of the Linnean Society* 93: 343–358.
- Melville, J.E., Richie, G., Chapple, S.N.J., Glor, R.E., and Schulte, II, J.A. 2011. Evolutionary origins and diversification of dragon lizards in Australia's tropical savannas. *Molecular Phylogenetic and Evolution* 58: 257–270.
- Melville, J., Smith, K., Hobson, R., Hunjan, S., and Shoo, L. (2014). The role of integrative taxonomy in the conservation management of cryptic species: the taxonomic status of endangered earless dragons (Agamidae: *Tympanocryptis*) in the grasslands of Queensland, Australia. *PLoS One* 9: e101847.
- Miralles, A., and Vences, M. 2013. New metrics for comparison of taxonomies reveal striking discrepancies among species delimitation methods in *madascincus* lizards. *PLoS One* 8: e68242.
- Moritz, C., Fujita, M.K., Rosauer, D., Agudo, R., Bourke, G., Doughty, P., Palmer, R., Pepper, M., Potter, S., Pratt, R., and Scott, M. 2016. Multilocus phylogeography reveals nested endemism in a gecko across the monsoonal tropics of Australia. *Molecular Ecology* 25: 1354–1366.
- Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B., and Kent, J. 2000. Biodiversity hotspots for conservation priorities. *Nature* 403: 853–858.
- Oliver, P.M., Smith, K.L., Laver, R.J., Doughty, P., and Adams, M. 2014. Contrasting patterns of persistence and diversification in vicars of a widespread Australian lizard lineage (the *Oedura marmorata* complex). *Journal of Biogeography* 41: 2068–2079.
- Potter, S., Bragg, J.G., Peter, B.M., Bi, K., and Moritz, C. 2016. Phylogenomics at the tips: inferring lineages and their demographic history in a tropical lizard *Carlia amax*. *Molecular Ecology* 25: 1367–1380.
- Schulte, II, J.A., Melville, J., and Larson, A. 2003. Molecular phylogenetic evidence for ancient divergence of lizard taxa on either side of Wallace's Line. *Proceedings of the Royal Society of London B* 270: 597–603.
- Smith, K.L., Harmon, L.J., Shoo, L.P., and Melville, J. 2011. Evidence of constrained phenotypic evolution in a cryptic species complex of agamid lizards. *Evolution* 65: 976–992.
- Storr, G.M. 1982. Revision of the bearded dragons (Lacertilia: Agamidae) of Western Australia with notes on the dismemberment of the genus *Amphibolurus*. *Records of the Western Australian Museum* 10: 61–66.
- Witten, G.J. 1972. A new species of *Amphibolurus* from eastern Australia. *Herpetologica* 28: 191–195.
- Woinarski, J.C.Z., Mackey, B., Nix, H.A., and Traill, B. 2007. *The nature of northern Australia: its natural values ecological processes and future prospects*. ANU E Press: Canberra, ACT.
- Wilson, S., and Swan, G. 2017. *A complete guide to reptiles of Australia*. 5th edition. New Holland Publishers: Sydney, Australia.

## Supplementary Appendix S1.

### Voucher specimens examined

Museum abbreviations are: AM for Australian Museum Sydney, NMV for Museum Victoria Melbourne, WAM for Western Australian Museum.

### *Amphibolurus burnsi*

NMV D52082, 8 km E of Surat, Queensland, 27° 09' S, 149° 05' E; NMV D56415, St George, Queensland, 28° 03' S, 148° 35' E; NMV D56416, St George, Queensland, 28° 03' S, 148° 35' E; NMV D74134, 10 km N of Chinchilla, Queensland, 26° 40' 23" S, 150° 35' 52" E; NMV D74135, 15 km W of Cecil Plains, Queensland, 27° 33' 29" S, 151° 03' 04" E; NMV D74137, 15 km W of Cecil Plains, Queensland, 27° 32' 44" S, 151° 04' 55" E; AM R151557, Gingham Floodplain, Te Mona, 3 km N of Allombie Bridge over Gwydir River, New South Wales, 29° 19' S, 149° 27' E; AM R151838, Kwiambal National Park, New South Wales, 29° 11' 13" S, 150° 57' 51" E; AM R155887, Brewarrina, Barwon River at West Brewarrina, New South Wales, 29° 58' S, 146° 52' E; AM R166772, Nocoleche Nature Reserve, New South Wales, 29° 51' 15" S, 144° 8' 8" E; AM R166873, AM R166874, Wanaaring township, New South Wales; AM R166910, Nocoleche Nature Reserve, New South Wales, 29° 51' 26" S, 144° 8' 9" E; AM R137612, Byerawering Property, Site 1, Banks of Culgoa River, 30 km from Goodooga Road, New South Wales, 29° 5' S, 147° 8' E; AM R148373, Macquarie Marches, Sandy Camp Property, 8 km N of Homestead on Carinda River, New South Wales, 30° 49' S, 147° 43' E; AM R153324 Yuleba State Forest (South of Condamine Hwy.), Coup 105, Queensland, 26° 54' 13" S, 149° 44' 18" E.

### *Amphibolurus centralis*

NMV D11166, Attack Creek, Northern Territory, 18° 18' S, 134° 35' E; NMV D175, NMV D176, NMV D182, NMV D184, NMV D189, NMV D196, Alice Springs, Northern Territory, 23° 42' S, 133° 52' E; NMV D492, Illamurta, Northern Territory, 24° 18' S, 132° 41' E; NMV D72659, Buntine Highway, 20 km E of Kalkaringa, Northern Territory, 17° 24' 08" S, 130° 56' 56" E; NMV D72661, NMV D72680, Buchanan Highway, 101 km E of Top Springs, Northern Territory, 16° 45' 25" S, 132° 40' 20" E; NMV D72709, 108 km S of Cape Crawford on Tablelands Highway, Northern Territory, 17° 32' 24" S, 135° 41' 17" E; NMV D72710, 3 km S of Heartbreak Inn on Tablelands Highway, Northern Territory, 16° 42' 14" S, 135° 43' 46" E; NMV D73981, Kimberley, Duncan Road, N of Spring Creek Station, Western Australia, 16° 25' 02" S, 129° 02' 54" E; NMV D73988, Buchanan Highway S of Jasper Creek, Northern Territory, 16° 06' 55" S, 130° 53' 23" E; NMV D74005, Nutwood Road, 3 km SE, N of Daly Waters, near Scarlet Hill, Northern Territory, 16° 11' 03" S, 133° 26' 28" E; NMV D74021, Carpentaria Highway, W of Northern Territory–Queensland border, SE of Robinson River Aerodrome, Northern Territory, 16° 51' 43" S, 137° 14' 39" E; NMV D74023, Carpentaria Highway, 125 km E of Hi Way Inn, Northern Territory, 16° 28' 59" S, 134° 25' 26" E; NMV D74052, Lawn Hill Road via Gregory Downs Station, Queensland, 18° 38' 28" S, 139° 05' 55" E; NMV D74283, road to Hamilton Station Youth Camp, off Tanami Track, Northern Territory,

23° 36' 07" S, 133° 34' 36" E; NMV D74288, Red Bluff Gorge, Northern Territory, 23° 36' 07" S, 132° 30' 38" E; NMV D74673, Hodgson River Road, near Tennant Creek, 2 km E of Stuart Highway, Northern Territory, 16° 12' 18" S, 133° 25' 50" E; NMV D74695, West MacDonnell Ranges, Haast Bluff Road, Northern Territory, 23° 33' 14" S, 132° 18' 21" E.

### *Lophognathus gilberti*

NMV D290, Arnhem Land, Oenpelli, East Alligator River, Northern Territory, 12° 19' S, 133° 03' E; NMV D34178, NMV D34179, NMV D34180, Ord River Dam area, Western Australia, 17° 24' S, 128° 52' E; NMV D5096, NMV D5123, Borroloola, Northern Territory, 16° 04' S, 136 18' E; NMV D5150, Arnhem Land, Upper Roper River, Northern Territory, 14° 44' S, 134° 31' E; NMV D5222, Arnhem Land, Oenpelli, Northern Territory, 12° 19' S, 133° 03' E; NMV D72579, West Arnhem Land, Yirrkakak, Northern Territory, 12° 12' 14" S, 133° 48' 04" E; NMV D72590, West Arnhem Land, Gubjekbinj, Northern Territory, 12° 15' 09" S, 133° 48' 07" E; NMV D74026, Mt Wells Road, near Grove Hill, Northern Territory, 13° 28' 47" S, 131° 32' 41" E; NMV D74027, Wells Road, near Grove Hill Station, Northern Territory, 13° 28' 42" S, 131° 32' 13" E; NMV D74258, 20 km N of Katherine, Stuart Highway, Northern Territory, 14° 18' 57" S, 132° 06' 18" E; NMV D74260, Mount Wells, Northern Territory, 13° 40' 25" S, 132° 48' 26" E; NMV D74263, road to Umbarrumba Gorge, S of Pine Creek, Northern Territory, 13° 51' 19" S, 131° 49' 14" E; NMV D74280, Mount Wells Road, Northern Territory, 13° 29' 31" S, 131° 34' 25" E; NMV D74281, NMV D74282, Mount Wells Road, Northern Territory, 13° 29' 33" S, 131° 36' 44" E; NMV D74286, off Stuart Highway, 42 km N of Katherine, Northern Territory, 14° 11' 12" S, 132° 01' 52" E; NMV D74289, NMV D74293, Umbrawarra Gorge, Northern Territory, 13° 57' 14" S, 131° 41' 39" E; NMV D74298, Marrakai Road, about 8 km SW of Arnhem Highway, Northern Territory, 12° 47' 59" S, 131° 26' 38" E. WAM R126027, WAM R126029, WAM R126031, 4 km SW of Point Spring Yard, Western Australia, 15° 25' 35" S, 128° 51' 09" E; WAM R163559, Anjo Peninsula, Western Australia, 14° 04' 19" S, 126° 24' 27" E.

### *Gowidon longirostris*

NMV D222, NMV D224, NMV D231, NMV D235, Central Australia, Dalhousie (original label in Spencer's writing "Dalhousie"), Northern Territory, 26° 30' S, 135° 28' E; NMV D2336, NMV D3481, Finke River, Northern Territory, 25° 02' S, 134° 24' E; NMV D239, Derwent Creek, Northern Territory, 17° 34' S, 145° 13' E; NMV D4945, NMV D4946, Central Australia, Barrow Creek, Northern Territory, 21° 32' S, 133° 53' E; NMV D50509, NMV D50510, NMV D50511, Todd River, Alice Springs, Northern Territory, 23° 48' S, 134° 25' E; NMV D50537, Emily Gap, MacDonnell Ranges, Northern Territory, 23° 45' S, 133° 57' E; NMV D509, NMV D510, NMV D511, Charlotte Waters, Northern Territory, 25° 56' S, 134° 53' E; NMV D5383, NMV D5384, no data; NMV D56308, Alice Springs, Northern Territory, 23° 42' S, 133° 52' E; NMV D67487, Finke River, Northern Territory, 25° 02' S, 134° 24' E; NMV D67644, Simpsons Gap, Northern Territory, 23° 42' 07" S, 133° 43' 05" E; NMV D67663, NMV D67665, NMV D67668, Ellery Creek, Northern Territory, 23° 47' 10" S, 133° 04' 07" E; NMV D67669, NMV D67670, NMV D67671, NMV D67672, NMV D67703,

Serpentine Gorge, Northern Territory, 23° 45' 25" S, 132° 58' 24" E; NMV D67713, NMV D67714, Ormiston Pound, near creek, Northern Territory, 23° 37' S, 132° 48' E; NMV D67758, Finke River, Palm Valley, old rangers' station, Northern Territory, 24° 03' 21" S, 132° 45' 22" E; NMV D67764, NMV D67765, NMV D67766, Palm Valley, Finke River, Northern Territory, 24° 02' 33" S, 132° 42' 22" E; NMV D67777, NMV D67778, Finke River, Palm Valley, Red Gum site near old rangers' station, Northern Territory, 24° 03' 06" S, 132° 45' 18" E; NMV D67786, Central Australia, waterhole, 3.4 km from Boggy Hole, Northern Territory, 24° 08' 07" S, 132° 50' 07" E; NMV D69, NMV D70, Tennant Creek, Northern Territory, 19° 39' S, 134° 11' E; NMV D72733, Todd River, East MacDonnell Ranges, Northern Territory, 23° 47' 45" S, 134° 18' 42" E; NMV D74269, Ormiston Gorge, Northern Territory, 23° 37' 56" S, 132° 43' 39" E; NMV D74317, Great Northern Highway, 1 km E of Roebuck Roadhouse at entrance to Kilty Station, Western Australia, 17° 48' 57" S, 122° 40' 44" E; NMV D74368, NMV D74370, NMV D74371, Great Northern Highway, N of Sandfire Roadhouse, Stanley picnic stop, Western Australia, 19° 02' 35" S, 121° 39' 57" E; NMV D74391, Pilbara, Ingee Station, off Great Northern Highway, Western Australia, 20° 46' 42" S, 118° 31' 33" E; NMV D74407, Great Northern Highway, South Gascoyne River, 64 km S of Kumarina Roadhouse, Western Australia, 25° 12' 09" S, 119° 20' 05" E; NMV D74408, Great Northern Highway, South Gascoyne River, 64 km S of Kumarina Roadhouse, Western Australia, 25° 12' 09" S, 119° 20' 05" E; NMV D74426, Tjukayirria Roadhouse, about 3 km W, Warburton Hwy, Western Australia, 27° 09' 57" S, 124° 32' 54" E; NMV D95, NMV D96, NMV D97, Oodnadatta, South Australia, 27° 33' S, 135° 27' E.

***Lophognathus horneri* sp. nov.**

NMV D10440, NMV D10441, NMV D10442, NMV D10443, NMV D10444, NMV D10838, NMV D10887, Timber Creek, Northern Territory, 15° 39' S, 130° 29' E; NMV D2360, NMV D2365, Port George IV, Western Australia, 15° 22' S, 124° 39' E; NMV D2934, NMV D5630, Tennant Creek, Northern Territory, 19° 39' S, 134° 11' E; NMV D72638, NMV D72652, Montejinni Creek, Buntine Highway, Northern Territory, 16° 38' 06" S, 131° 45' 20" E; NMV D72643, Willaroo Station, Top Springs, track off Victoria Highway, Northern Territory, 15° 18' 55" S, 131° 34' 10" E; NMV D72658, Kelly Creek, Wave Hill Homestead, Northern Territory, 17° 23' 08" S, 131° 06' 44" E; NMV D73807, NMV D73809, NMV D73810, NMV D73811, Kimberley, Gibb River Road crossing of the Durack River, Western Australia, 15° 58' 26" S, 127° 09' 13" E; NMV D73818, Kimberley, Gibb River Road, 10 km W of Ellenbrae Station, Western Australia, 15° 59' 27" S, 126° 57' 10" E; NMV D73820, Kimberley, Gibb River Road, 8 km W of Ellenbrae Station, Western Australia, 15° 59' 24" S, 127° 00' 16" E; NMV D73845, NMV D73846, Kimberley, Mitchell Plateau, King Edward River Camp, Western Australia, 14° 52' 57" S, 126° 12' 10" E; NMV D73851, Kimberley, Gibb River Road, 1 km W of the Kalumburu turn-off, Western Australia, 16° 09' 19" S, 126° 30' 10" E; NMV D73863, Kimberley, Mt Elizabeth, Western Australia, 16° 13' 59" S, 125° 59' 21" E; NMV D73867, Kimberley, Gibb River Road, W of Snake Creek, Western Australia, 16° 32' 15" S, 126° 15' 29" E; NMV D73886, Kimberley, Derby Caravan Park, Western Australia, 17° 18' 30" S, 123° 37' 44" E; NMV D73967,

Kimberley, Duncan Road, N of Spring Creek Station, Western Australia, 16° 19' 43" S, 129° 03' 33" E; NMV D73984, Buchanan Highway S of Jasper Creek, Northern Territory, 16° 02' 45" S, 130° 51' 59" E; NMV D74259, Stuart Memorial, Stuart Highway, Northern Territory, 19° 01' 24" S, 132° 08' 30" E; NMV D74271, Stuart Memorial, 48 km N of Three Ways, Stuart Highway, Northern Territory, 19° 01' 24" S, 134° 08' 30" E; NMV D74309, NMV D74312, Wolfe Creek, Tanami Road, Western Australia, 18° 59' 44" S, 127° 41' 52" E; NMV D74334, Derby, road to Prison Boab Tree, Western Australia, 17° 21' 04" S, 123° 40' 09" E; NMV D74362, NMV D74363, NMV D74364, 80 Mile Beach Caravan Park, 50 km S of Sandfire, Western Australia, 19° 45' 16" S, 120° 40' 20" E; NMV D74683, road to Karundi, 35 km E of Stuart Highway, Northern Territory, 20° 28' 22" S, 134° 28' 51" E; NMV D74687, road to Davenport Ranges National Park, near Tennant Creek, Northern Territory, 20° 37' 34" S, 134° 47' 14" E; NMV D74690, road to Davenport Ranges National Park, near Tennant Creek, Northern Territory, 20° 38' 28" S, 134° 46' 42" E; WAM R102296, WAM R102307, Hermite Island (South), Montebello Islands, Western Australia, 20° 28' 00" S, 115° 31' 00" E; WAM R102321, Ah Chong Island, Montebello Islands, Western Australia, 20° 31' 00" S, 115° 33' 00" E; WAM R108806, Calico Springs, Western Australia, 17° 17' 00" S, 128° 11' 00" E; WAM R113222, South Muiron Island, Western Australia, 21° 42' 00" S, 114° 48' 00" E; WAM R113987, King Edward River, Western Australia, 14° 55' 00" S, 126° 12' 00" E; WAM R114385, Coulomb Point Nature Reserve, Western Australia, 17° 22' 00" S, 122° 09' 00" E; WAM R131275, Fitzroy Crossing, Western Australia, 18° 10' 58" S, 125° 36' 00" E; WAM R131990, Kununurra, Western Australia, 15° 48' 00" S, 128° 43' 00" E; WAM R132850, Kununurra, Western Australia, 15° 47' 38" S, 128° 43' 11" E; WAM R132851, Kununurra, Western Australia, 15° 47' 38" S, 128° 43' 11" E; WAM R139477, WAM R139481, Potter Island, Western Australia, 20° 56' 15" S, 116° 09' 10" E; WAM R141302, Cape Preston Area, Western Australia, 20° 52' 59" S, 116° 11' 41" E.

***Tropicagama temporalis***

NMV D14455, NMV D14456, NMV D14457, NMV D14458, NMV D14459, NMV D14460, NMV D14461, Gulf Province, Balimo, Papua New Guinea, 08° 00' S, 142° 55' E; NMV D2289, NMV D2293, NMV D3732, NMV D3733, NMV D5924, NMV D5925, Borebada (as "Bora Bada, New Guinea"), 09° 28' S, 147° 12' E; NMV D4551, Northern Territory; NMV D49838, NMV D49839, NMV D49840, NMV D49841, NMV D49842, NMV D49889, NMV D50083, NMV D50084, NMV D50085, NMV D50086, NMV D50087, NMV D50088, NMV D50089, Gulf Province, Aramia River, Awaba, Papua New Guinea, 08° 01' S, 142° 45' E; NMV D5234, Melville Island, Northern Territory, 11° 27' S, 130° 47' E; NMV D5517, Darwin, Northern Territory, 12° 27' S, 130° 50' E; NMV D6655; NMV D74299, Marrakai Road near Heather Lagoon, Northern Territory, 12° 54' 40" S, 131° 12' 24" E; NMV D74306, NMV D74307, Darwin, Malack, Wescombe Court, Northern Territory, 12° 23' 26" S, 130° 54' 24" E; NMV D74311, NMV D74313, NMV D74314, NMV D74318, NMV D74319, Darwin, gardens at Museum and Art Gallery of the Northern Territory, Northern Territory, 12° 26' 16" S, 130° 50' 03" E.