



Hidden species diversity of Australian burrowing snakes (*Ramphotyphlops*)

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Julie Marin, Stephen C. Donnellan, S. Blair Hedges, Nicolas Puillandre, Ken P. Aplin, et al.. Hidden species diversity of Australian burrowing snakes (*Ramphotyphlops*). *Biological Journal of the Linnean Society*, 2013, 110 (2), pp.427-441. 10.1111/bij.12132 . hal-03922762

HAL Id: hal-03922762

<https://hal.science/hal-03922762>

Submitted on 4 Jan 2023

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Journal:	<i>Biological Journal of the Linnean Society</i>
Manuscript ID:	BJLS-2731.R1
Manuscript Type:	Research Article
Date Submitted by the Author:	n/a
Complete List of Authors:	Marin, Julie; Museum National d'Histoire Naturelle, Systematique et Evolution Donnellan, Steve; South Australian Museum, Hedges, S Blair; Penn State, Biology Puillandre, Nicolas; MNHN, Systematique & Evolution; Aplin, Ken; Australian National Wildlife Collection CSIRO Ecosystem Sciences, Doughty, Paul; Western Australian Museum, Hutchinson, Mark; South Australian Museum, Vertebrates Couloux, Arnaud Vidal, Nicolas; MNHN, Systematique & Evolution
Keywords:	cryptic species , evolution, hidden species , <i>Ramphotyphlops</i> , <i>Scolecophidia</i> , speciation

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1 1 **Running head:** Australian blindsnake diversity.
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13 9 **Title: Hidden species diversity of Australian burrowing snakes (*Ramphotyphlops*).**
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35 **ABSTRACT**

36 The worm-like snakes (Scolecophidia, ~400 nominal extant species) have a conservative
37 morphology and are among the most poorly-known terrestrial vertebrates. Although
38 molecular evidence has helped elucidate their higher-level relationships, such data have rarely
39 been used to discriminate among species. We generated a molecular data set for the
40 continental Australian blindsnakes (genus *Ramphotyphlops*) to determine the concordance of
41 molecular and morphological information in the taxonomic recognition of species. Our dataset
42 included 741 specimens morphologically attributed to 27 nominal *Ramphotyphlops* species.
43 We proposed species hypotheses (SHs) after analysis of sequences from a variable
44 mitochondrial gene (*cytochrome b*) and examined these SHs with additional evidence from a
45 nuclear gene (*prolactin receptor*) and geographic data. Although the nuclear marker was not
46 as fast-evolving and discriminating as the mitochondrial marker, there was congruence among
47 the mitochondrial, nuclear, and geographic data, suggesting that the actual number of species
48 is at least two times the current number of recognized, nominal species. Several biogeographic
49 barriers and complex phytogeographic and geologic patterns appeared to be involved in the
50 division of some burrowing snake populations, and by consequence in their diversification
51 and speciation through isolation.

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53 **Additional keywords:** cryptic species – evolution – hidden species – *Ramphotyphlops* –
54 Scolecophidia – speciation

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2 69 INTRODUCTION
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5 70 Species inventory and delineation are essential for assessing biodiversity, conservation
6 or biological control projects and more generally understanding the natural world (Wheeler *et*
7 *al.*, 2004). However, it is well known that the number of described species on earth is far less
8 than the total (Trontelj & Fišer 2009). Most of the species yet to be described are thought to
9 be fungi and ‘invertebrate’ animals, and particularly those living in tropical environments
10 (Pfenninger & Schwenk 2007) Over the last 12 years, the total number of nominal extant
11 species of squamates increased by 1.7 % each year (Pincheira-Donoso *et al.*, 2013) and this
12 value is much lower for mammals and birds (0.1–0.2%) (Uetz, Goll & Hallerman 2013;
13 Lepage 2012; Wilson & Reeder 2005). Cryptic species, two or more distinct species that were
14 classified as a single species due to their morphological similarity,, are almost evenly
15 distributed among major metazoan taxa and biogeographical regions (Pfenninger & Schwenk
16 2007). Therefore, the diversity of many vertebrate groups has yet to be explored (Oliver *et al.*,
17 2009).
18

19 83 Here we focus on Australian blindsnakes of the genus *Ramphotyphlops* (Scolecophidia,
20 Typhlopidae), whose systematics was little studied until recently (Aplin & Donnellan 1993;
21 Rabosky *et al.*, 2004; Vidal *et al.*, 2010). Blindsnakes typically are small (~10–30 cm),
22 burrowing species, and feed on social insects (Vidal & Hedges 2009). They comprise 402
23 named species segregated in five families: Anomalepididae, Leptotyphlopidae, Typhlopidae,
24 Xenotyphlopidae, and Gerrhopilidae (Vidal *et al.*, 2010; Uetz *et al.*, 2013). The 42 currently
25 recognized Australian scolecophidian species all belong to *Ramphotyphlops*, a genus of 66
26 species distributed across South and Southeast Asia, Australasia and Melanesia (as far east as
27 Fiji, and across the Caroline Islands from Palau to Pohnpei), and comprise one of the least-
28 known elements of the Australian herpetofauna (Rabosky *et al.*, 2004; Wynn *et al.*, 2012).
29 Previous molecular genetic studies on scolecophidian snakes, including members of the
30 families Typhlopidae and Leptotyphlopidae, have suggested a high level of hidden diversity,
31 as indicated by several recognized species being paraphyletic and polyphyletic, and
32 harbouring deep divergences (Hedges & Thomas 1991; Aplin & Donnellan 1993; Rabosky *et*
33 *al.*, 2004; Hedges 2008; Adalsteinsson *et al.*, 2009; Marin *et al.*, 2012; Korniliou *et al.*, 2013).
34

35 98 Strong selection associated with a fossorial lifestyle has led to miniaturisation, cranial
36 consolidation, and body elongation, all common features in burrowing reptile (Gauthier *et al.*,
37 2012). Moreover, there are limited characters for which inter- *versus* intraspecific variations
38 are adequately understood, partly due to the lack of interest in scolecophidians (Adalsteinsson
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2 102 *et al.*, 2009).. Here, we focus on testing and refining species boundaries within the Australian
3 radiation of *Ramphotyphlops* in light of new molecular genetic data.
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6 104 Although many theoretical species concepts have been discussed over the years, there is
7 general agreement, supported by genetic data, that species are reproductively isolated from
8 one another (Coyne & Orr 2004). It is then a practical matter how to identify and delimit
9 species. If two species occur together in sympatry and are not exchanging genes, then
10 identifying concordance of two or more characters (coded by unlinked genes) will usually
11 suffice in demonstrating reproductive isolation and delimitation of species. However, whether
12 or not to recognize allopatric populations as full species is a more subjective decision, often
13 requiring additional case-specific information. Padial *et al.*, (2010) discuss two different
14 approaches to distinguish species: (1) "cumulation", where only one character set (e.g.,
15 mitochondrial DNA sequences) is used, and (2) "congruence", where multiple data sets (e.g.,
16 DNA sequences and morphology) are used. Rather than alternative approaches, they could
17 also be viewed as a continuum concerning level of evidence (stringency), especially because a
18 single study might diagnose some species using one character set and other species using
19 multiple sets, depending on availability.
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22 118 In our study, we have explored species limits in Australian *Ramphotyphlops* using data
23 from only one character set (mitochondrial DNA) and multiple sets (mitochondrial DNA,
24 nuclear DNA, and geography). We took the general approach of defining preliminary species
25 hypotheses (SHs) using the low stringency approach (mitochondrial DNA data set) and then
26 comparing the SHs with additional character sets (Padial *et al.*, 2010; Goldstein & DeSalle
27 2011; Yeates *et al.*, 2011; Puillandre *et al.*, 2012b). By adding more specimens (634) to our
28 previous molecular genetic dataset (Marin *et al.*, 2012) we built a new dataset. The ABGD
29 (Automatic Barcode Gap Discovery) method (Puillandre *et al.*, 2012a) was used with
30 mitochondrial gene (*cytochrome b*) sequences, and resulting SHs were then compared with
31 variation from a nuclear gene (*prolactin receptor*), and geography. Genetic divergent
32 population in sympatry or divided by recognized barriers was used as additional evidence.
33 The goal was to test the following hypothesis: is the number of nominal species a reasonably
34 accurate reflexion of true species diversity?. This represents an initial step that could assist a
35 morphology-based taxonomic revision, providing a better delimitation of some Australian
36 *Ramphotyphlops* species.
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40 134 **MATERIALS AND METHODS**
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2 136 **Taxon sampling**

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4 137 Ingroup sampling included 741 individuals belonging to 27 nominal Australian
5 138 *Ramphotyphlops* species (as identified using morphology). Appendix 1 lists the taxa,
6 139 localities, and GenBank accession numbers of specimens used in the study. Three typhlopids
7 140 snakes were used as outgroups: *Acutotyphlops subocularis* (Vuovo Camp, West New Britain,
8 141 Papua New Guinea, *cyt b*: JQ910524, *PRLR*: JQ910414), *Ramphotyphlops acuticaudus*
9 142 (Palau, *cyt b*: JQ910543, *PRLR*: JQ910412), and *R. braminus* (Florida, United States, *cyt b*:
10 143 JQ910548, *PRLR*: JQ910434).

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14 145 **Molecular genetic markers**

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16 146 A mitochondrial protein coding gene and one nuclear protein coding gene were used.
17 147 The mitochondrial marker, *cytochrome b* (*cyt b*), is highly variable (intraspecific variation)
18 148 and thus potentially useful to identify recent speciation events (Burbrink, Lawson &
19 149 Slowinski 2000; Adalsteinsson *et al.*, 2009). Among the nuclear genes available for squamate
20 150 phylogenies (Townsend *et al.*, 2008) we selected one of the most variable, the *prolactin*
21 151 *receptor* (*PRLR*). For this work, 83.9 % of the sequences were newly determined; 943
22 152 sequences were deposited in GenBank under accession numbers KC489799–KC490909 and
23 153 KC493653.

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27 155 **DNA extraction, amplification, and sequencing.**

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29 156 DNA extraction was performed with the DNeasy Tissue Kit from Qiagen.

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31 157 Amplification and sequencing was performed using primers listed in Table 1.

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33 158 For the two markers, DNA amplification was performed by PCR in a final 21 µL
34 159 volume containing 1 µL DMSO, 0.8 µL of dNTP 6.6 mM, 0.12 µL of Taq DNA polymerase
35 160 (MP Biomedicals or Qiagen), using 2.5 µL of the buffer provided by the manufacturer, 100
36 161 uml⁻¹ and 0.32 µL of each of the two primers at 10 pM; 1 µL of DNA extract was added.

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38 162 The PCR reactions were performed with the following conditions: an initial denaturation
39 163 at 94°C for 3 min followed by 40 cycles (3 min at 94°C, 40 s at 50°C, 1 min at 72°C) and a
40 164 final elongation at 72°C for 10 min, using a PCR System 2700 thermocycler (Applied
41 165 Biosystems). Amplification products were visualised on ethidium-bromide stained agarose
42 166 gels. Sequencing was performed by the National Centre for Sequencing (Genoscope, Evry,
43 167 France) using the same primers.

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45 168 The two strands obtained for each sequence were combined using the Sequencher 4.9
46 169 software (GeneCodes, Ann Arbor, Michigan). Sequence alignment was performed with

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3 170 ClustalW2 (default parameters) (Larkin *et al.*, 2007) implemented in BioEdit (Hall, 1999) and
4 then manually refined with MEGA 5 (Tamura *et al.*, 2011), using amino acid translations. The
5 absence of stop codons was checked.
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174 **Phylogenetic analysis**

11 175 *Cyt b* analyses were performed on all the obtained sequences; *PRLR* analyses were
12 performed on haplotypes only to reduce computation time. We built phylogenies using
13 Bayesian and Maximum Likelihood (ML) methods of inference. Bayesian analyses were
14 performed with MrBayes 3.1.2 (Ronquist & Huelsenbeck 2003) and ML analyses were
15 performed with RAxML 7.2.8 (Stamatakis, 2006; Stamatakis, Hoover & Rougemont 2008).
16
17 180 For both *cyt b* and LRPR, the three-partition strategy (by codon position) was preferred to the
18 one partition strategy (by gene) using standard Bayes factors (Nylander *et al.*, 2004). Bayesian
19 analyses were performed by running 50,000,000 generations in four chains, saving the current
20 tree every 1000 generations (until convergence), with GTR+I+G model, applied to each
21 partition (best-fit model inferred by Modeltest (Posada & Carndall 1998)). Convergence of
22 ESS values were checked with Tracer 1.4.1 (Rambaut & Drummond 2009) using the default
23 burning (10%). The last 45,000 trees were used to construct a 50% majority rule consensus
24 tree. For the ML analysis, we defined the same partitions and performed 1000 bootstrap
25 replicates to obtain a bootstrap majority rule consensus tree. Trees were visualised with
26 FigTree 1.3.1 (<http://tree.bio.ed.ac.uk/software/figtree/>).
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38 191 **Species delimitation**

39 192 The ABGD method (Puillandre *et al.*, 2012a) was employed to statistically detect a
40 barcode gap (i.e. a gap in the pairwise genetic distance distribution, presumably between
41 intraspecific and interspecific distances) from the *cyt b* data set, which is then used to partition
42 the data set (initial partition) into species hypotheses. The resulting inferences are then
43 recursively applied to yield finer partitions (recursive partitions) until no further partitioning is
44 possible. We used the online version
45
46 (<http://wwwabi.snv.jussieu.fr/public/abgd/abgdweb.html>) to analyse the pairwise distance
47 matrix calculated for each dataset with PAUP (Swofford, 2003) under a GTR+I+G model, as
48 inferred by Modeltest (Posada & Carndall 1998) using the AIC criterion as the best-fitting
49 model of nucleotide substitution for the entire data set. ABGD default parameters were used,
50 with the exception that the relative gap width (X) was set to 1 (except for *Ramphotyphlops*
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2 203 *nigrescens* (Gray): 0.9), and Pmin (minimal prior intraspecific divergence) was set to 0.01 to
3 204 avoid the capture of intraspecific gaps due to weak sampling.
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6 205 The number of putative species (species hypotheses, SHs) was first determined using
7 206 *cyt b*. Then, those *cyt b* SHs were compared with the nuclear gene data to assess concordance
8 207 or discordance. Major geographic features which can be barriers to gene flow (rivers,
9 208 mountains, climatic zones) for well-sampled groups were identified and used in further
10 209 comparisons of the SHs.
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13 211 **LRPR haplotypes**
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16 212 The software DnaSP v5 (Librado & Rozas 2009) was used to determine the haplotypes.
17 213 For generating the haplotypes data files, invariables sites were included and sites with gaps or
18 214 missing data were not considered.
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21 216 **RESULTS**
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24 217 For the *cyt b* gene, the alignment comprised 678 sites, with 386 variable sites among the
25 218 741 specimens successfully sequenced (4.6% of missing data). For the *PRLR* gene, the
26 219 alignment comprised 483 sites, of which 197 were variable among the 583 specimens (0.38%
27 220 of missing data), 158 specimens were unsuccessfully amplified. The alignments were
28 221 straightforward for both genes.
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31 223 **Phylogenetic analyses**
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34 224 Based on the *cyt b* analysis, 17 of the 27 nominal species are monophyletic in the *cyt b*
35 225 tree with moderate support using both methods (ML bootstrap > 75% / PP > 95) except
36 226 *Ramphotyphlops diversus* (Waite) (ML bootstrap = 71 / PP = 1) (see Appendix 1), and five
37 227 species, *R. affinis* (Boulenger), *R. howi* (Storr), *R. longissimus* (Aplin), *R. silvia* (Ingram &
38 228 Covacevich) and *R. troglodytes* (Storr), have one representative only. *Ramphotyphlops*
39 229 *ligatus* (Peters) is polyphyletic in the *cyt b* phylogram (Fig. 1), and *R. kimberleyensis* (Storr),
40 230 *R. leptosoma* Robb, *R. grypus* (Waite) and *R. guentheri* (Peters) are polyphyletic in both the
41 231 mtDNA and nDNA phylogenograms (Figs 1, 2).
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44 233 **Species delineation**
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47 234 *Molecular genetic data*
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50 235 The ABGD method was applied independently to 21 monophyletic groups defined from
51 236 the *cyt b* phylogeny (Fig. 1), because groups including a limited number of lineages allowed
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us to avoid problems linked to the heterogeneity of evolution times between lineages. This phenomenon may lead to inter- and intraspecific pairwise distributions overlapping and by consequence may prevent the barcode gap detection. These groups corresponded to 17 nominal species that are represented by at least two specimens (16 nominal species and *Ramphotyphlops guentheri* lineage 1) plus three *cyt b* clades with non-monophyletic nominal species (clade 1: *R. grypus* lineage 1, *R. leptosoma* and *R. longissimus*; clade 2: *R. kimberleyensis* and *R. troglodytes*; clade 3: *R. ganei* (Aplin) and *R. ligatus*) and *R. grypus* lineage 2. Three nominal species and the *R. guentheri* lineage 2 were represented each by only one specimen and were not analysed with ABGD. Based on the distribution of pairwise genetic distances, ABGD proposed several partitions that varied according to the different *a priori* thresholds. Apart from the two extreme *a priori* threshold values ($p = 0.009$ and $p = 0.013$), for which aberrant number of species hypotheses were obtained for some groups (almost every haplotype was considered as a different species hypothesis for $p = 0.009$ and, conversely, all the haplotypes were combined in a single species hypothesis for $p = 0.013$, as described in Puillandre et al. 2011), all the tested *a priori* thresholds lead to the same splitting. The only exception is for five groups (*R. ammodytes*, *R. bituberculatus*, *R. ganei*, *R. hamatus* and *R. ligatus*), for which ABGD proposed two different partitions. We only used initial partitions because they were stable on a wide range of values contrary to the recursive partitions (results not shown); the initial partitions are also supposed to more closely match the groups described by taxonomists (Puillandre et al., 2012a).

Considering all possible initial partitions allowed the delineation of 92 partitions or *cyt b* SHs (Table 2). SHs containing more than one specimens are monophyletic and highly supported with three exceptions: SH 55 (ML bootstrap = 70 / PP = 0.93), SH 90 (ML bootstrap = 43 / PP = 0.79) and SH 91 (ML bootstrap = 61 / PP = 0.53) (Appendix 2). SH 15 and SH 11 are polyphyletic (Figure 1).

In a few cases, when ABGD splits one nominal species into several *cyt b* SHs, the divergence between these SHs is similar to the divergence between pairs of nominal species. For example, the genetic distance (p-distance) between *Ramphotyphlops guentheri* lineage 2 (SH 54) and *R. howi* (SH 62) is 0.10, whereas it is 0.12 among SHs 86–89 within the group of specimens identified morphologically as *R. unguirostris* (Peters).

The 92 *cyt b* SHs displayed 121 different *PRLR* haplotypes. Among them, 55 SHs are defined by their own haplotypes, i.e. their haplotypes are not shared with any other *cyt b* SHs (Table 2, Fig. 2): *Ramphotyphlops affinis* (SH 1), *R. ammodytes* (SH 3, 7), *R. australis* (Gray) (SH 12–13), *R. bicolor* (Peters) (SH 14–15), *R. bituberculatus* (SH 16–18), *R. diversus* (SH

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3 271 24–26, 30–31), *R. grypus* (SH 40–48), *R. guentheri* (SH 49–54), *R. hamatus* (SH 61), *R. howi*
4 272 (SH 62), *R. kimberleyensis* (SH 65–66), *R. leptosoma* (SH 67–68), *R. ligatus* (SH 71–72), *R.*
5 273 *longissimus* (SH 73), *R. nigrescens* (SH 74–78), *R. pilbarensis* (Aplin & Donnellan) (SH 79),
6 274 *R. pinguis* (Waite) (SH 80), *R. polygrammicus* (Schlegel) (SH 81–82), *R. proximus* (Waite)
7 275 (SH 83), *R. silvia* (SH 84), *R. troglodytes* (SH 85), *R. unguirostris* (SH 86–89) and *R. wiedii*
8 276 (Peters) (SH 92). Among them, SH 15 (*R. bicolor*) was the only non-monophyletic SH in the
9 277 *cyt b* ABGD analysis; however, it is represented by unique *PRLR* haplotypes. Five species
10 278 include only one sample. The 33 remaining *cyt b* SHs share *PRLR* haplotypes, the SHs within
11 279 a nominal species that are sharing haplotypes are phylogenetically closely related.
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280 281 *Geographic data*

282 Geographic distributions of mtDNA clades for several well sampled species are
283 congruent with landscape features (Fig. 3). Three main climatic zones are recognized across
284 the Australian continent (Fig. 4). The monsoon tropic zone in northern Australia receives
285 heavy rainfall during the summer and dates from the Late Eocene/Early Oligocene
286 (Greenwood 1996; Pole & Bowman 1996; Alexandre *et al.*, 2004). The mesic zone, which
287 includes the Wet Tropics rainforest in the far northeast, extends south along the Great
288 Dividing Range of the eastern coast, with an isolated region in the southwest. It is the oldest
289 Australian biome, originating from the forests of the Mesozoic that were widespread until the
290 Early Miocene (Hill, 1994; Schodde, 2006). The arid zone in central and western Australia is
291 much younger, with origins from the Early Pliocene (Fujioka *et al.*, 2005; Byrne *et al.*, 2008;
292 Fujioka *et al.*, 2009).

293 In the monsoon tropic zone of northern Australia four major phylogeographic barriers
294 have been identified: the Daly River Drainage Barrier (Ford 1978), the Victoria River
295 Drainage Barrier (Joseph & Omland 2009), the Ord Arid Intrusion (Ford & Blair 2005;
296 Bowman *et al.*, 2010) and the East-West Kimberley Divide (Potter *et al.*, 2012). These
297 barriers are congruent with the distributions of *Ramphotyphlops guentheri*, *R. kimberleyensis*
298 and *R. unguirostris* (Fig. 3), with SHs restricted to each side of the barriers. The geographical
299 repartition of mitochondrial lineages of *R. diversus* can be partly explained by these
300 geographic barriers, and by the boundary between the arid and monsoon regions (Fig. 3). For
301 *R. waitii* (Boulenger), the boundary between the south-west mesic zone and the arid zone is
302 congruent with distributions of SHs 90 and 91 respectively (Fig. 3). Further south, two rivers
303 (Darling River, River Murray) and the Flinders Ranges are congruent with the three major
304 mtDNA lineages of *R. bituberculatus* (SHs 16, 19 and 20; Fig. 3) and to a lesser degree with

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3 305 those of *R. bicolor* (not shown). SH 14 and SH 15 (*R. bicolor*) are distributed on each side of
4 the Flinders Ranges except three specimens of the SH 15 located within the eastern SH 14
5 geographic zone. The separation by recognized barriers of allopatric SHs is additional
6 evidence for SHs 19 and 20 (*R. bituberculatus*; separated by Darling River and River
7 Murray), SHs 63–64 (*R. kimberleyensis*; separated by four major phylogeographic barriers:
8 the Daly River Drainage Barrier, the Victoria River Drainage Barrier, the Ord Arid Intrusion
9 and the East-West Kimberley Divide) and SHs 69–70 (*R. ligatus*; separated by the Victoria
10 River Drainage Barrier and also a huge distance (~2600 kilometers)) (Fig. 3).

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13 312 Other species display different distribution patterns. Instead of observing geographically
14 restricted mtDNA lineages, some species harbour deep genetic divergences (0.73 between
15 SHs 7 and 8 (*R. ammodytes*) and 0.137 between SHs 40 and 45 (*R. grypus*)) among
16 geographically close and/or sympatric clades. This pattern is clearly observable for
17 *Ramphotyphlops ammodytes* and *R. grypus*, each with many SHs in the rocky Pilbara region,
18 and to a lesser degree for *R. australis* and *R. leptosoma* that are restricted to the west central
19 coast and for *R. nigrescens* on the east coast. Divergent genetic lineages (a SH with distinct
20 nuclear haplotype) found in sympatry reinforce SHs, because despite geographical proximity
21 there is no evidence of gene flow. But as many PRLR haplotypes are shared among the SHs
22 of *R. ammodytes*, is it more parsimonious to consider these SHs (2,4-6 and 8-11) as a single
23 species than a complex of several species with incomplete lineage sorting or hybridization.

24
25 324 Conversely, the four *R. endoterus* (Waite) SHs occur across the arid zone in four
26 allopatic mtDNA lineages but without recognized barriers between them. In this case, as with
27 the seven *R. hamatus* SHs (distributed across the rocky Pilbara zone and the eastern part of
28 the arid zone), geographic data do not suggest consolidation of SHs.

29
30 328 In several cases, there is strong congruence among mitochondrial, nuclear, and
31 geographic data, leading us to recognize 55 robust putative species using *cyt b* and *PRLR*
32 haplotypes and 61 putative species when adding geographic (sympatry or allopatry with
33 barriers) data only (Table 2). In the least conservative scheme (*cyt b* only), there are 92
34 putative species (Table 2).

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334 DISCUSSION

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336 335 The concordance of independent genes (nuclear and mitochondrial) is generally
337 considered valuable evidence for species delimitation (Knowlton, 2000; Barberousse &
338 Samadi 2010). In our data set, 55 of the 92 *cyt b* SHs are robustly defined by an independent
339 nuclear gene. The other *cyt b* SHs shared nuclear haplotypes, but the fact that these SHs
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remain closely related in the *cyt b* phylogram suggests a lack of variability of the *PRLR* gene at this scale, or a nuclear gene flow. To clarify this situation the use of other more variable nuclear markers is needed in the future. Analyzing more specimens per nominal species should be useful as well. Indeed the probability to find rare and shared haplotypes is higher for species that are densely sampled (several localities and several specimens per localities) even if some nominal species appear to be genetically uniform. For example, the 9 SHs of the nominal species *Ramphotyphlops grypus* are defined by specific haplotypes over the 59 species analyses with the nuclear marker. Concerning *R. pilbarensis*, even when the number of nuclear sequences was relatively high (29), only 2 different haplotypes were found. If we analyse the *cyt b* SHs on an individual basis, the number supported by different independent sources of information increases to 61 when geographical data are considered. Therefore, from the 27 nominal species of Australian blindsnakes studied here, our results support at least 55 (most conservative) and up to 92 (least conservative) species. Nine nominal species were not subdivided. The identification of new morphological characters should also help to discriminate among the different hypotheses proposed here. The visceral anatomy traits may be useful as they allowed the discrimination of some leptotyphlopidae species (Adalsteinsson *et al.*, 2009).

The early diversification of Australian *Ramphotyphlops* was probably driven by the development of the arid zone ~20 Ma (Marin *et al.*, 2012). As the arid zone expanded in central Australia, mesic-adapted lineages were confined to the east coast and southwest, to the northern monsoonal tropics, and also to Pilbara in the arid zone which likely served as refugia (Martin 2006; Byrne *et al.*, 2008, 2011). Occupation of areas like the Pilbara and Kimberley (northern monsoonal tropics), that have humid refugia but are seasonally very arid may have allowed time for this lineage of snakes that has a wet-tropical origin to acquire adaptations to resist seasonally dry conditions which then pre-adapted them for the truly arid conditions further inland (Fujita *et al.*, 2010).

Several biogeographic barriers within these refugia seem to be involved in a later, younger than eight Ma (Marin *et al.*, 2012), allopatric diversification of species (*R. bicolor*, *R. bituberculatus*, *R. diversus*, *R. guentheri*, *R. kimberleyensis*, *R. ligatus* and *R. unguirostris*) (Fig. 3). They are more subject to isolation due to their fossorial lifestyle (Vidal *et al.*, 2010). Similar patterns of diversification were recently found for rock wallabies in the monsoon tropic zone (Potter *et al.*, 2012) and for beaked geckos in the eastern arid zone and southeast mesic zone (Pepper *et al.*, 2011). Some other SHs of our *Ramphotyphlops* dataset display close and/or sympatric geographic distributions in the rocky Pilbara region. This region is

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373 characterized by geological heterogeneity, complex phytogeography and long-term geological
374 stability (Pepper, Doughty & Keogh 2006) leading to a mosaic of habitat types (Doughty *et*
375 *al.*, 2011). This may explain the sympatric distribution observed for *R. ammodytes*, *R. grypus*
376 and *R. hamatus*. Assuming that each SH may be restricted to a particular habitat, they should
377 have evolved independently through ecological diversification. But contrary to the results for
378 *R. grypus* and *R. hamatus*, nuclear haplotypes of *R. ammodytes* are shared between SHs. This
379 could reflect a more recent speciation event or more probably could be linked to the fact that
380 *R. ammodytes* is one species. One other interesting geographic pattern concerns *R. endoturus*,
381 which is consistent with a sandy desert expansion out of the west. Several different genetic
382 groups (SHs 33–35) have differentiated in the west, but only a single lineage (SH 32) has
383 expanded eastward into the younger central and eastern desert areas, a pattern seen in other
384 arid zone non-snake taxa (Moritz & Heideman 1993; Kearney *et al.*, 2006). *Ramphotyphlops*
385 *hamatus* shows a similar though less expansive pattern. SHs of *R. endoturus* share a common
386 nuclear haplotype, reflecting a recent speciation event or a single species with a polymorphic
387 mitochondrial marker.

388 Overall, our results suggest that the current complement of nominal Australian
389 *Ramphotyphlops* species is less than the total, with the true species diversity ranging between
390 210–340% of the currently described species. However, even though our dataset is large
391 (~740 specimens), the sampling is limited for some taxa, and adding more specimens—
392 especially for species with a single sequenced specimen—may help to more accurately
393 delimitate the current species. On a larger taxonomic scale, these new species (55–96)
394 represent an increase of 7–16% of the entire scolecophidian species diversity. Currently 402
395 scolecophidian species are described, while acknowledging that extrapolations of hidden
396 biodiversity from limited surveys are subject to sampling errors (Gray, 2002), taken at face
397 value our results suggest that up to 1200 scolecophidian species may exist, mostly hidden
398 from current taxonomy. If true, that would be an exceptional increase in the number of reptile
399 or vertebrate species.

400 The morphological conservativeness of blindsnakes may be responsible for this hidden
401 diversity, as potentially informative characters have been reduced or eliminated as an outcome
402 of their burrowing lifestyle (Hedges & Thomas 1991; Thomas & Hedges 2007). The limited
403 knowledge on the morphological characters useful for the discrimination of blindsnakes is
404 also likely responsible. Fortunately, in other cases where genetic analysis has revealed hidden
405 species of scolecophidians, non-traditional morphological characters always have been found
406 and used to diagnose the species (Hedges & Thomas 1991; Aplin & Donnellan 1993; Rabosky

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2 407 *et al.*, 2004; Thomas & Hedges 2007). For this reason, we suspect that most of all of the
3 408 putative new species revealed here will be diagnosed morphologically and named.
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6 409 These results also have implications for conservation, because accurate taxonomic data
7 410 are critical for determining basic parameters of protection such as distributions and threat
8 411 levels (Rondinini *et al.*, 2006). Also, nominal species already considered endangered or
9 412 threatened may be composed of several species, each of which are often rarer than their
10 413 "parent species," making them more susceptible to extinction (Hedges & Conn, 2012). For
11 414 these species, taxonomic revisions are urgent. Without published descriptions, these species
12 415 are essentially "off the conservation radar" and therefore cannot be considered in conservation
13 416 plans (Hedges & Conn, 2012).
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18 418 **CONCLUSION**
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20 419 Morphological conservativeness and the limited knowledge of useful morphological
21 420 discriminant characters seem to have prevented the recognition of numerous Australian
22 421 blindsnake species (*Ramphotyphlops*). Using several lines of independent evidence, including
23 422 mtDNA, nuclear DNA, and geography, we found that at least 55 species exist, which is twice
24 423 the currently recognized number of species. This is consistent with the results of previous
25 424 smaller-scale studies of scolecophidians elsewhere in the world, suggesting that the proportion
26 425 of species of these burrowing snakes yet to be described is greater than is typical in terrestrial
27 426 vertebrates.
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32 428 **ACKNOWLEDGEMENTS**
33

34 429 We thank three anonymous reviewers for their helpful comments. This work was
35 430 supported by the 'Consortium National de Recherche en Génomique', and the 'Service de
36 431 Systématique Moléculaire' of the Muséum National d'Histoire Naturelle (UMS 2700; OMSI).
37 432 It is part of the agreement number 2005/67 between the Genoscope and the Muséum National
38 433 d'Histoire Naturelle on the project 'Macrophylogeny of life' directed by Guillaume Lecointre.
39 434 We thank Kyle Armstrong, Chris Austin, Patrick Couper, Karim Daoues, Paul Horner, Yuki
40 435 Konishi, Robert Palmer, Olivier Pauwels, Luke Price, Steve Richards, Ross Sadlier and
41 436 Miguel Vences for specimen collection or access to tissue samples in their care. The project
42 437 was supported by the Australian Department for the Environment, Water, Heritage and the
43 438 Arts' CERF programme to K.P.A. and S.C.D., and by the U.S. National Science Foundation
44 439 to S.B.H.
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FIGURE LEGENDS

Figure 1. Bayesian inference phylogenetic tree of Australian *Ramphotyphlops* based on analysis of sequences of a mitochondrial protein-coding gene, *cytochrome b*, showing species hypotheses (SHs) obtained with the ABGD method. Framed clades share common PRLR haplotypes. Dashed lines join SH when they shared a PRLR haplotype. Nodes with black circles are supported by posterior probabilities > 95% and ML bootstrap probabilities > 75%. Nodes with white circles are supported by posterior probabilities > 90% and ML bootstrap probabilities > 70%. The first set of vertical bars (Mt: mitochondrial data) corresponds to the 56 SHs supported by mitochondrial DNA. The second set of vertical bars (Mt & N: mitochondrial and nuclear data) corresponds to the 92 SHs supported by nuclear and mitochondrial DNA. Asterisks (*) indicate nominal species for which SHs are found in sympatry.

Figure 2. Maximum Likelihood phylogenetic tree of Australian *Ramphotyphlops* based on the analysis of a nuclear protein-coding gene, *prolactin receptor (PRLR)*. Species hypotheses (SHs) shown here were obtained with the ABGD method using *cytochrome b*. Nodes with black circles are supported by posterior probabilities > 95% and ML bootstrap probabilities > 75%. Nodes with white circles are supported by posterior probabilities > 90% and ML bootstrap probabilities > 70%.

Figure 3. Sample locations of Australian *Ramphotyphlops* species for which geographic patterns are discussed. Recognized biogeographic barriers – 1: Daly River, 2: Victoria River, 3: Ord Arid Intrusion, 4: East-West Kimberley Divide, 5: Flinders Ranges, 6: Darling River, 7: Murray River.

Figure 4. Map of the three main climatic zones and mountainous regions of the continental Australia. Modified from Fujita *et al.*, 2010; Byrne *et al.*, 2011; Pepper *et al.*, 2011).

639 **TABLES**640 **Table 1.** List of primers used in this study.

Gene	Primer	Authors
<i>cyt b</i>	CS1L GAAAAACCGCYRTTGTWWTTCAACTA	Adalsteinsson <i>et al.</i> , 2009
	LTyph2R AGYTTGTTGGGATKGCTCGTAGRAT	Adalsteinsson <i>et al.</i> , 2009
	L14910 GACCTGTGATMTGAAAACCAYCGTTGT	Burbrink <i>et al.</i> , 2000
	H16064 CTTTGGTTACAAGAACAAATGCTTTA	Burbrink <i>et al.</i> , 2000
<i>PRLR</i>	PRLR_f1 GACARYGARGACCAGCAACTRATGCC	Townsend <i>et al.</i> , 2008
	PRLR_f2 AAGAGTCRCCCACTTAA	This study
	PRLR_r3 GACYTTGTGRACCTTCYACRTAATCCAT	Townsend <i>et al.</i> , 2008
	PRLR_r4 AAGAACYTCTCTGGAGGT	This study
	PRLR_r5 ATCCATTGGYTTGYAGACA	This study

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2 642 **Table 2.** Recapitulative table of Australian *Ramphotyphlops* (*R.*) results.
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5 N hp, number of haplotypes; Nb, number; SH, Species hypotheses.
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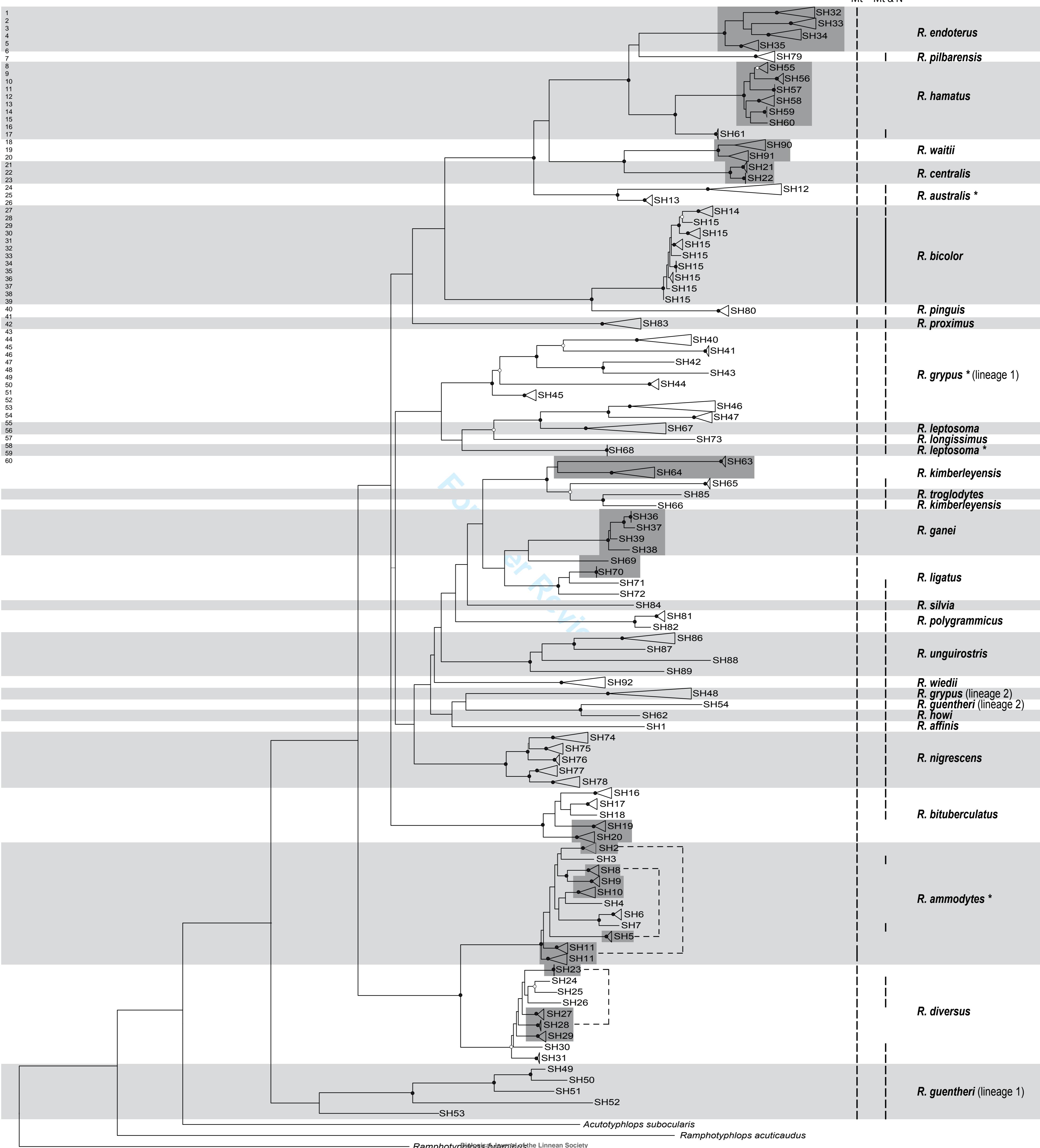
7 Geographic patterns (sympatry and allopatry) are globally and visually assessed for each
8 morphologically-defined species.
9

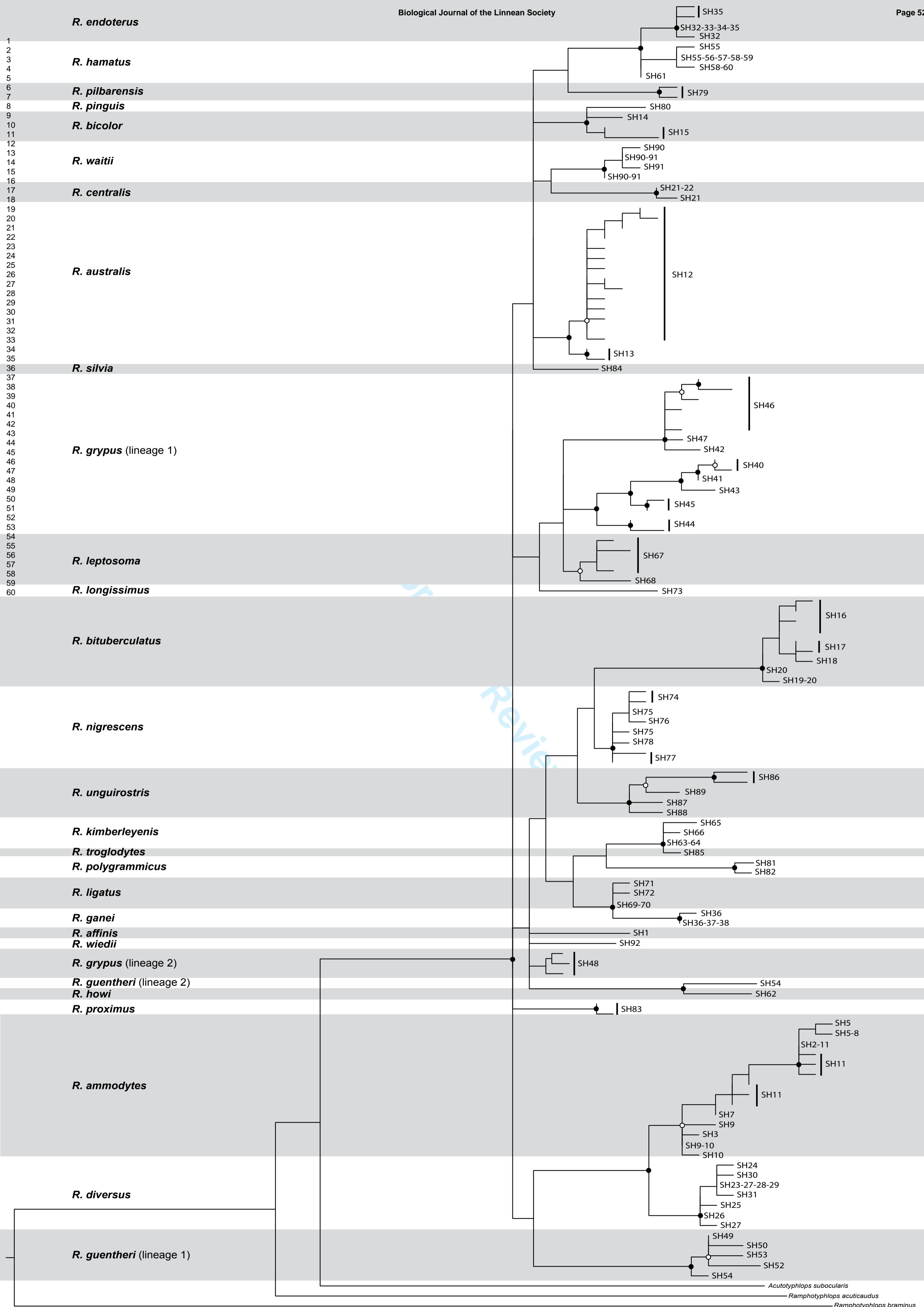
Species names	Number of sequences		SHs (cumulative approach)	First partition	Alternative partition	PRLR		SHs (congruent approach)	Geography
	cyt b	PRLR				Nb hp	Shared hp		
<i>R. affinis</i>	1	1	SH1	x		1		SH1	—
<i>R. ammodytes</i>	9	5	SH2	x	x	1	SH11	SH3	sympatry
	1	1	SH3	x	x	1			
	1	0	SH4	x	x	0			
	11	3	SH5	x	x	2	SH8		
	4	1	SH6	x		0			
	1	1	SH7	x	x	1			
	2	2	SH8	x		1	SH5		
	2	2	SH9	x		2	SH10		
	4	3	SH10	x		2	SH9		
	58	32	SH11	x		7	SH2		
<i>R. australis</i>	135	116	SH12	x		14		SH12	sympatry
	6	3	SH13	x		2			
<i>R. bicolor</i>	17	11	SH14	x		1		SH14	allopatry
	26	20	SH15	x		2			
<i>R. bituberculatus</i>	25	20	SH16	x		4		SH16	allopatry
	4	4	SH17	x	x	2			
	1	1	SH18	x		1			
	11	10	SH19	x	x	1	SH20		
	14	11	SH20	x	x	2	SH19		
<i>R. centralis</i> (Storr)	3	3	SH21	x		2	SH22	—	—
	2	2	SH22	x		1	SH21		
<i>R. diversus</i>	3	2	SH23	x		1	SH27–28–29	SH24	allopatry
	1	1	SH24	x		1			
	1	1	SH25	x		1			
	1	1	SH26	x		1			
	4	4	SH27	x		2	SH23–28–29		
	4	4	SH28	x		1	SH23–27–29		
	2	2	SH29	x		1	SH23–27–28		
	1	1	SH30	x		1			
	2	1	SH31	x		1			
	76	58	SH32	x		2	SH33–34–35	SH30	allopatry
<i>R. endoterus</i>	7	6	SH33	x		1	SH32–34–35		
	3	3	SH34	x		1	SH32–33–35		
	10	9	SH35	x		3	SH32–33–34		
	2	2	SH36	x		2	SH37–38		
<i>R. ganei</i>	1	1	SH37	x		1	SH36–38	—	—
	1	1	SH38	x	x	1	SH36–37		
	1	0	SH39	x		0			
	10	8	SH40	x		2			
<i>R. grypus</i>	4	4	SH41	x		1		SH40	sympatry
	1	1	SH42	x		1			
	1	1	SH43	x		1			
	10	5	SH44	x		2			
	21	12	SH45	x		2			
	28	22	SH46	x		6			
	2	2	SH47	x		1			
	4	4	SH48	x		2			
<i>R. guentheri</i>	1	1	SH49	x		1		SH49	allopatry

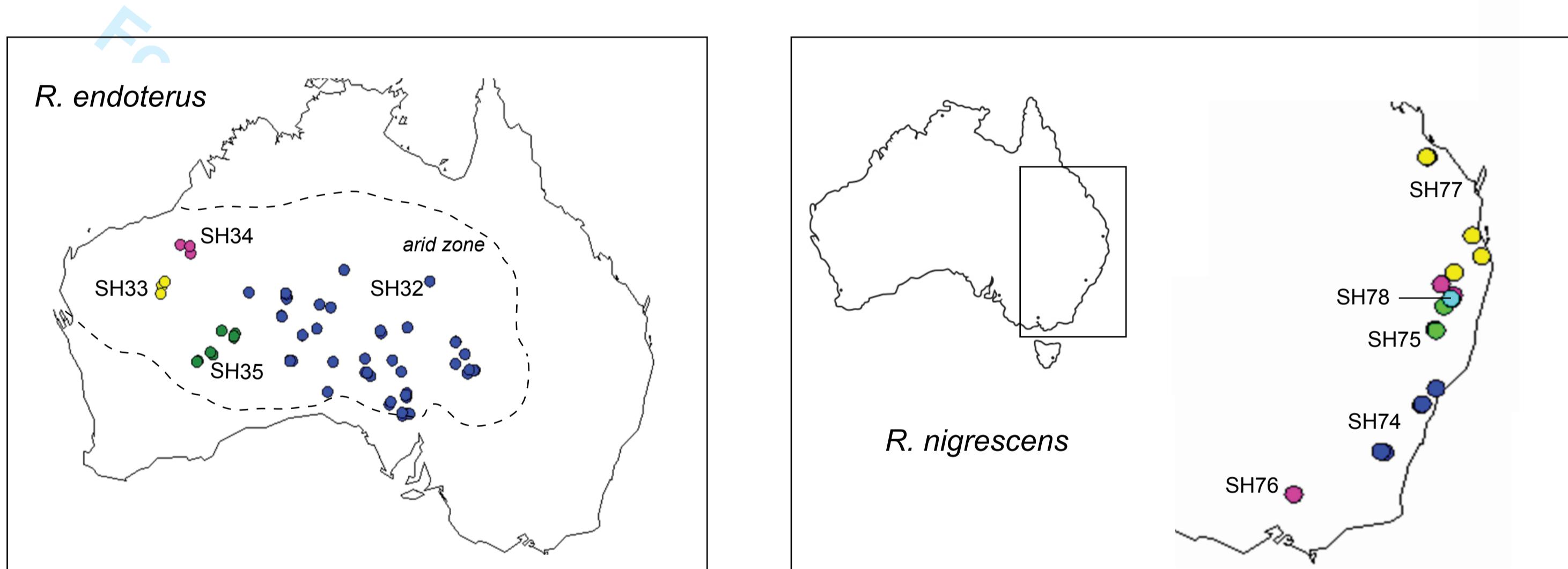
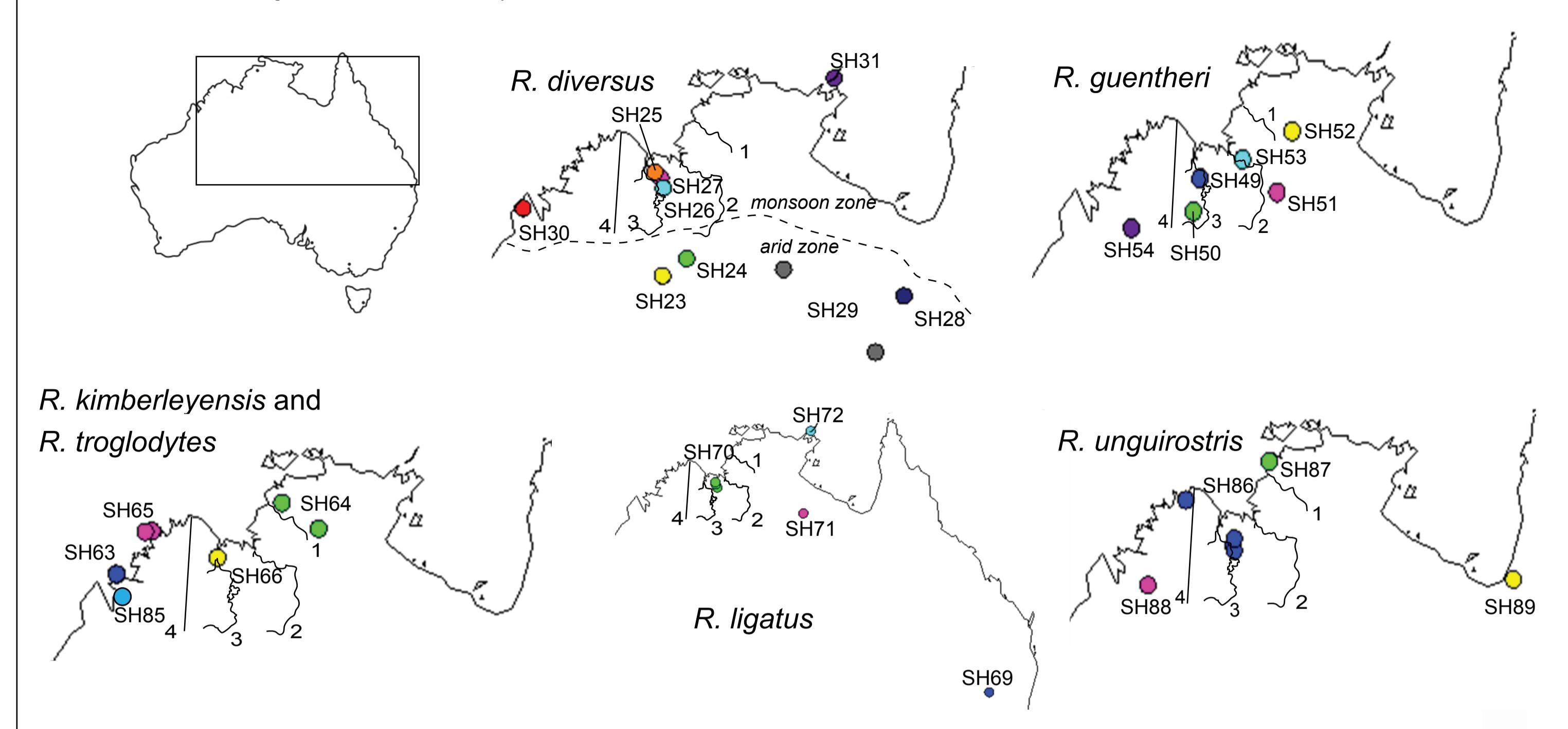
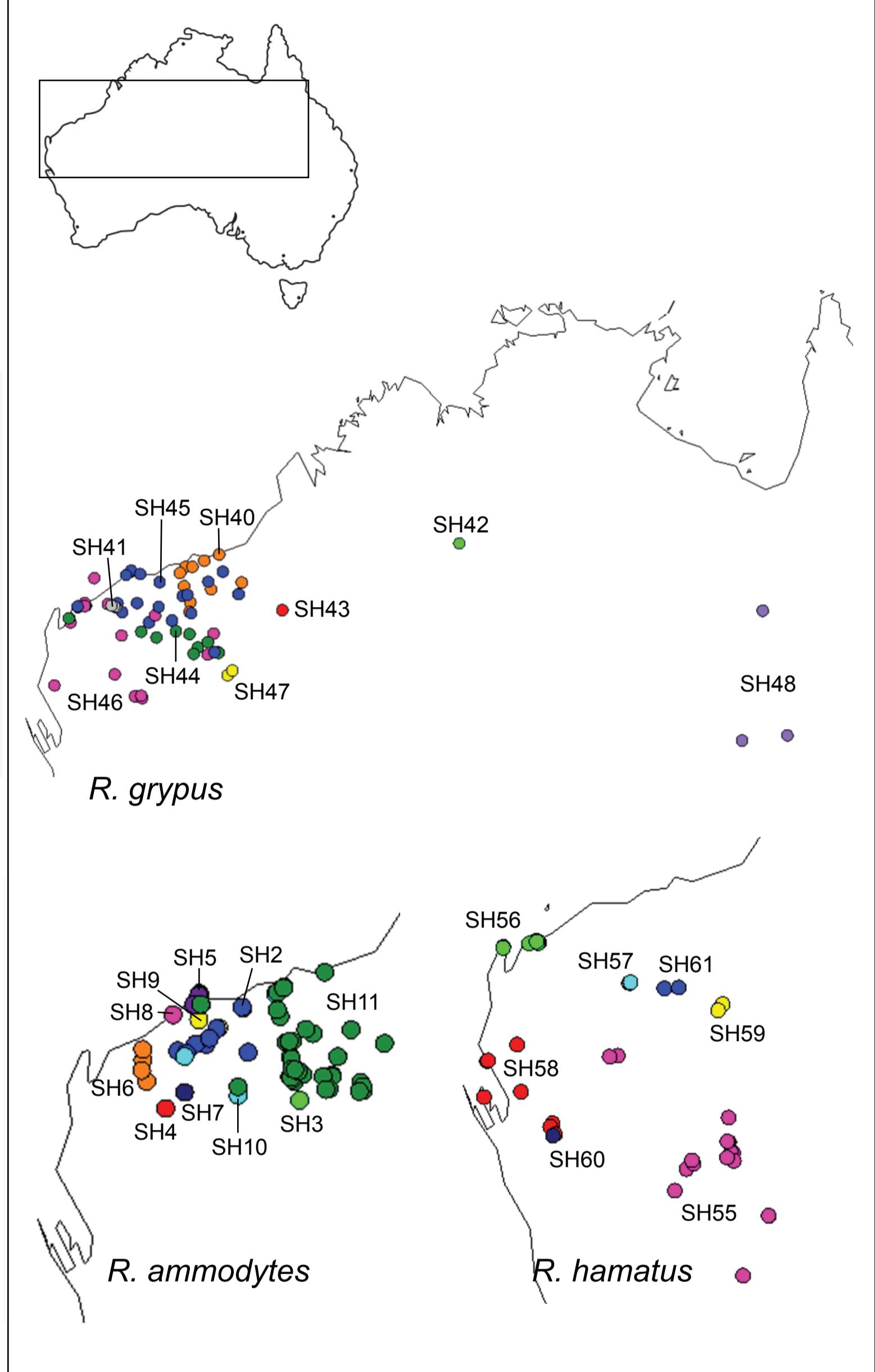
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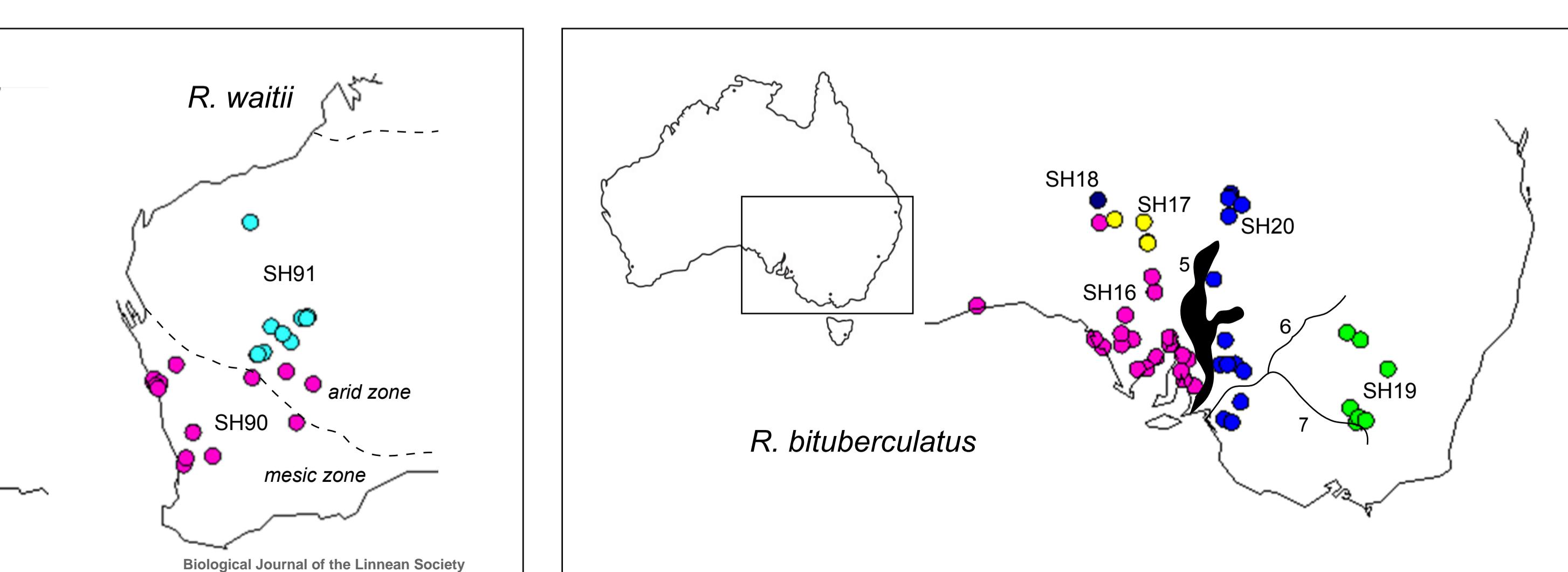
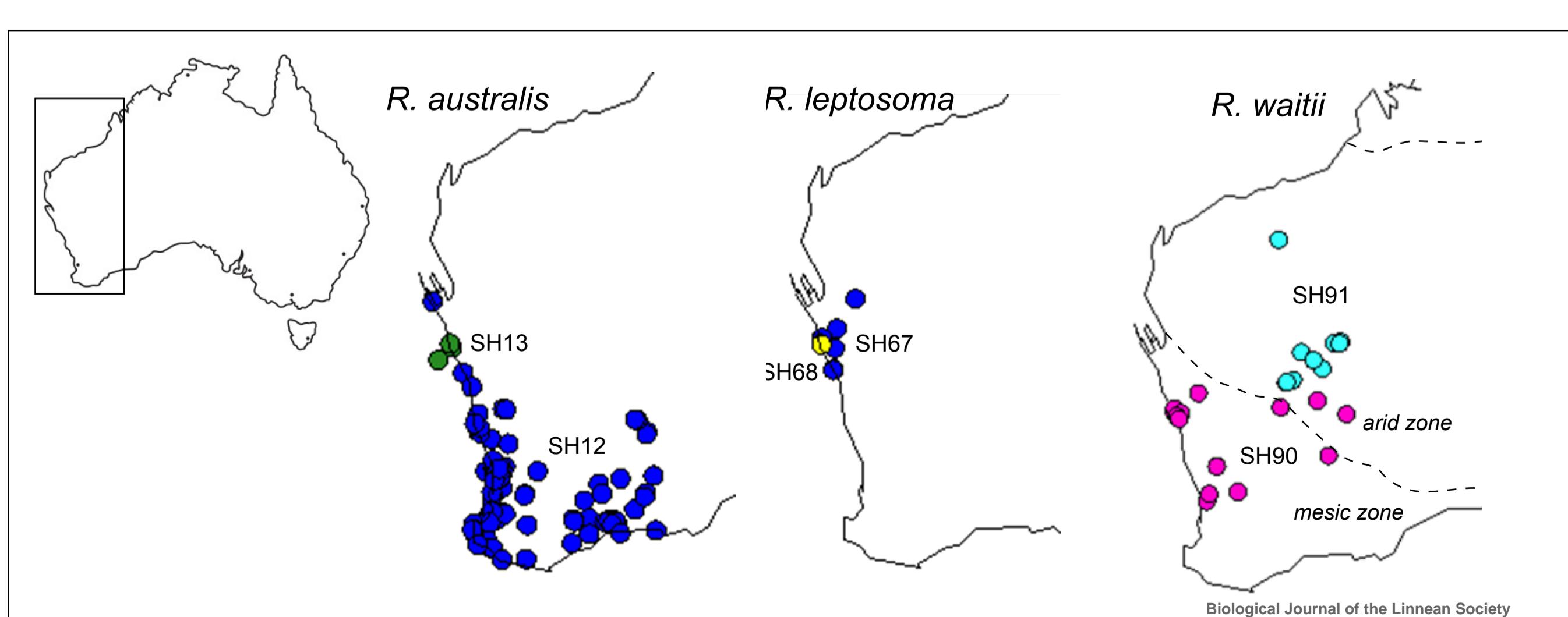
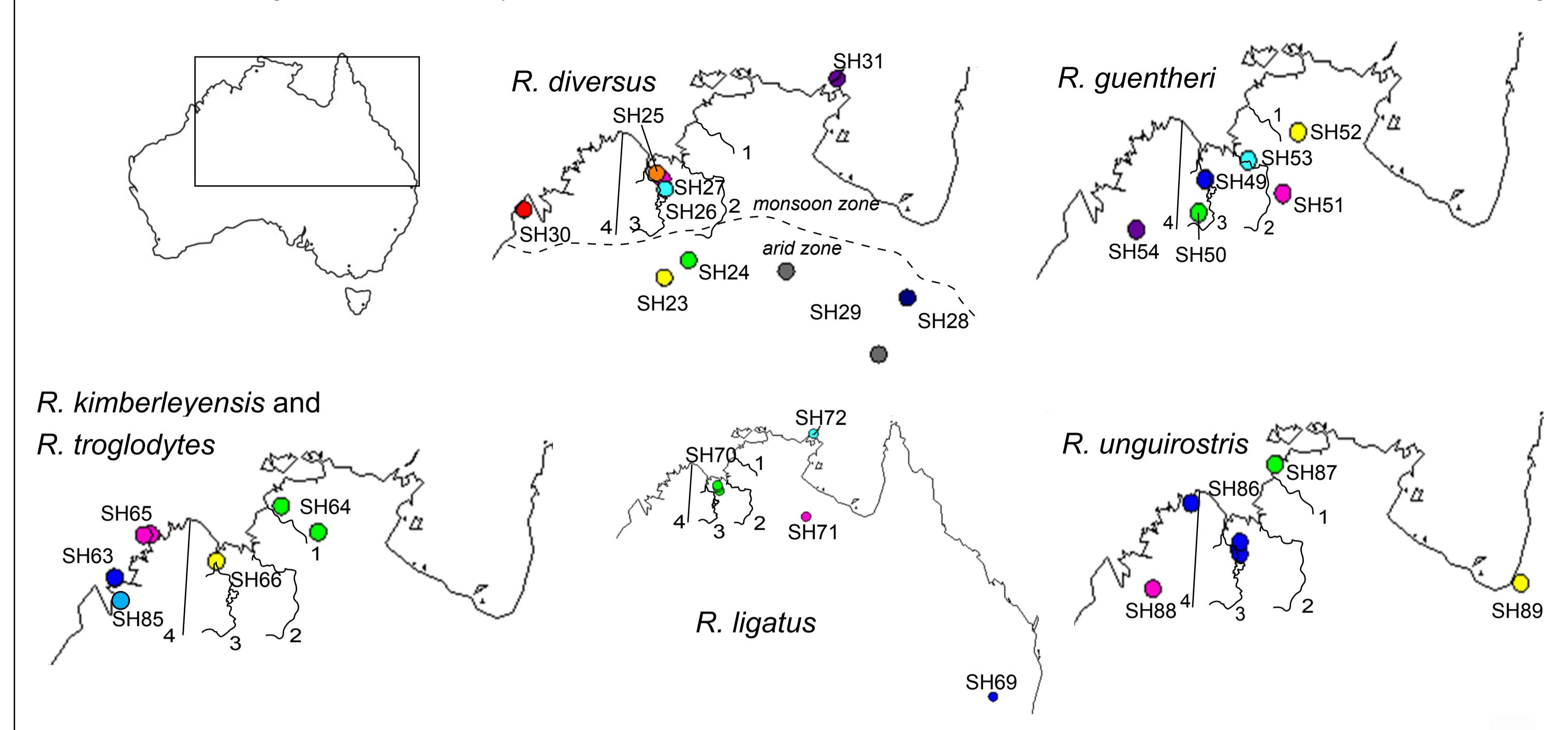
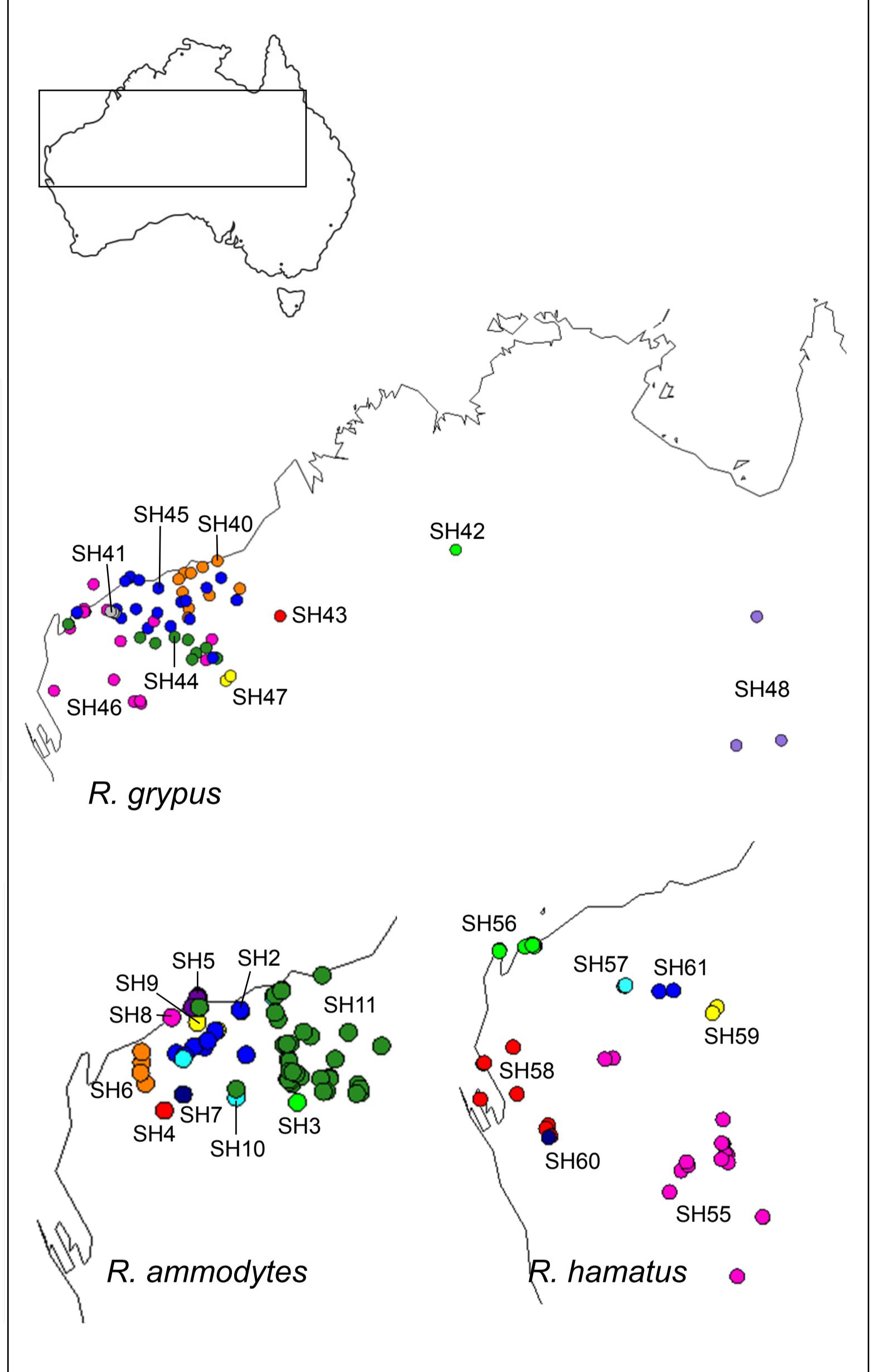
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3 653 APPENDICES
4 654 Table1_SuppInfo.xlsx
5 655 Description: Taxa, localities and accession numbers of the specimens used in the study.
6
7 656 Figure1_SuppInfo.docx
8
9 657 Description: Phylogenetic tree of Australian *Ramphotyphlops* based on the analysis of
10 sequences of *cytochrome b* (*cyt b*).
11
12 658 Figure2_SuppInfo.doc
13
14 660 Description: Phylogenetic tree of Australian *Ramphotyphlops* based on the analysis of
15 sequences of prolactine receptor (*PRLR*).
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For Peer Review









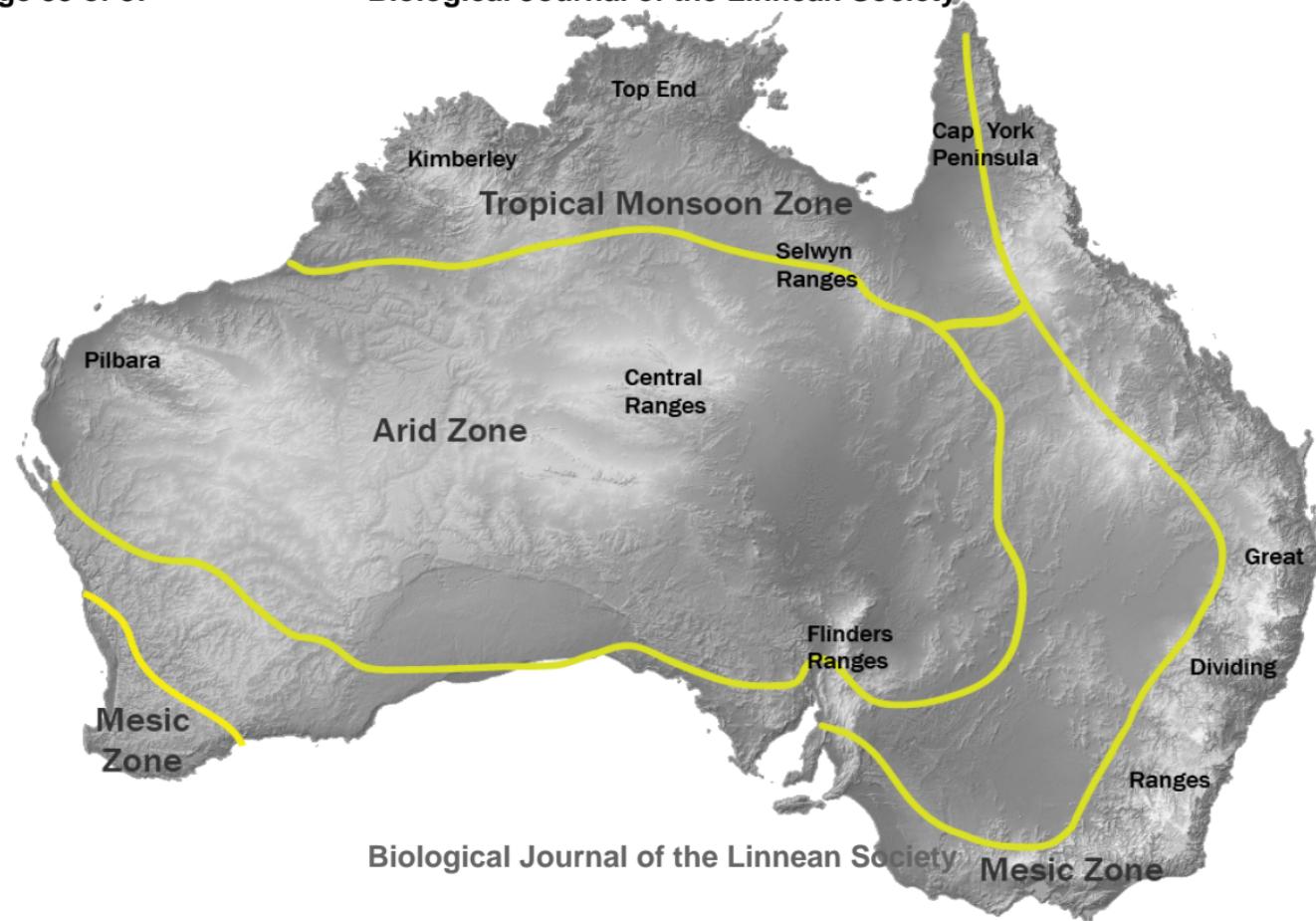


Table1_SuplInfo: Taxa, localities and accession numbers of the specimens used in the study.

Genus	species	GenBank numbers		SH	Museum catalogue
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<i>Ramphotyphlops</i>	<i>ammodytes</i>	KC489799	KC490434	11	WAMR114541
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		KC489802		11	WAMR108831
		KC489803		5	WAMR110068
		KC489804		2	WAMR110144
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		KC489806	KC490435	2	WAMR110199
		KC489807	KC490436	11	WAMR110244
		KC489808		11	WAMR110247
		KC489809		11	WAMR110279
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		KC489816	KC490440	11	WAMR111958
		KC489817		11	WAMR111969
		KC489818		11	WAMR111995
		KC489819	KC490441	11	WAMR111996
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26	<i>Ramphotyphlops</i>	<i>centralis</i>	JQ910549	JQ910435	22	ABTC24079
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30			JQ910634	JQ910521	21	SAMAR56511
31	<i>Ramphotyphlops</i>	<i>diversus</i>	KC490116	KC490665	29	QMJ85421
32			KC490117	KC490666	28	ABTC102725
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39		KC490215		35	WAMR145081	
40		KC490216	KC490744	35	WAMR156836	
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47	<i>Ramphotyphlops</i>	<i>grypus</i>	KC490221	KC490747	48	SAMAR45005
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24	<i>Ramphotyphlops</i>	<i>guentheri</i>	JQ910574	JQ910461	52	NTMR13611
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29		<i>Ramphotyphlops</i>	<i>howi</i>	JQ910587	JQ910474
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<i>Ramphotyphlops</i>	<i>ligatus</i>	JQ910597 JQ910598 JQ910599 JQ910600 KC490346 KC490347	JQ910484 JQ910485 JQ910486 JQ910487 KC490843 KC490844	69 71 70 72 70 70	SAMAR31019 NTMR35156 NTMR13753 NTMR19109 WAMR137952 WAMR137954
<i>Ramphotyphlops</i>	<i>longissimus</i>	JQ910525	JQ910416	73	WAMR120049
<i>Ramphotyphlops</i>	<i>nigrescens</i>	KC490348 KC490349 KC490350 KC490351 JQ910602 JQ910603 KC490352 JQ910604 KC490353 KC490354 KC490355 KC490356 KC490357 KC490358 KC490359 JQ910605 KC490360 JQ910606 JQ910607 JQ910601 JQ910608 KC490361 JQ910609 JQ910610 KC490362	KC490845 KC490846 KC490847 JQ910489 JQ910490 KC490851 JQ910491 KC490848 KC490849 KC490850 KC490851 KC490852 JQ910492 KC490853 JQ910493 JQ910494 JQ910488 JQ910495 KC490854 JQ910496 JQ910497 KC490855	75 77 76 76 75 77 77 77 77 77 77 76 77 77 74 77 76 74 74 74 78 78 76 78 78 78 78 74	SAMAR31020 SAMAR31022 SAMAR31023 SAMAR31024 SAMAR31025 ABTC03939 ABTC03940 ABTC100162 QMJ83805 ABTC100627 SAMAR40863 QMJ54856 SAMAR40954 SAMAR55640 AMSR145555 AMSR146228 AMSR152666 AMSR157050 AMSR157114 SAMAR31022 AMSR157200 AMSR157265 AMSR157267 ANWCR05614 ANWCR06776
<i>Ramphotyphlops</i>	<i>pilbarensis</i>	KC490363 KC490364 KC490365 KC490366 KC490367 KC490368 KC490369 KC490370 JQ910611 KC490371 KC490372 JQ910628 KC490373 KC490374 KC490375 KC490376 KC490377 KC490378 KC490379 KC490380	KC490856 KC490857 KC490858 KC490859 KC490860 KC490861 KC490862 JQ910498 KC490863 KC490864 JQ910515 KC490865 KC490866 KC490867 KC490868 KC490869 KC490870 KC490871 KC490872	79 79	WAMR90643 WAMR90864 WAMR108989 WAMR102604 WAMR108813 WAMR108989 WAMR110733 WAMR110734 WAMR110744 WAMR110860 WAMR110938 WAMR110939 WAMR110940 WAMR110942 WAMR110943 WAMR120727 WAMR124836 WAMR135459 WAMR139141 WAMR139387

1		KC490381	KC490873	79	WAMR139388	
2		KC490382	KC490874	79	WAMR139400	
3		KC490383	KC490875	79	WAMR140330	
4		KC490384	KC490876	79	WAMR141303	
5		KC490385	KC490877	79	WAMR156309	
6		KC490386	KC490878	79	WAMR156814	
7		KC490387	KC490879	79	WAMR156822	
8		KC490388	KC490880	79	WAMR160167	
9		KC490389	KC490881	79	WAMR166182	
10		KC490390	KC490882	79	WAMR166501	
11	<i>Ramphotyphlops</i>	<i>pinguis</i>	JQ910633	JQ910520	80	WAMR125664
12			JQ910627	JQ910514	80	WAMR146995
13	<i>Ramphotyphlops</i>	<i>polygrammicus</i>	JQ910612	JQ910499	82	QMJ60625
14			KC490391	KC490883	81	ABTC51251
15			JQ910613	JQ910500	81	ABTC51252
16			KC490392	KC490884	81	ABTC58999
17			KC490393	KC490885	81	ANWCR06771
18	<i>Ramphotyphlops</i>	<i>proximus</i>	KC490394		83	ABTC100639
19			KC490395	KC490886	83	SAMAR22713
20			KC490396		83	AMSR132486
21			KC490397		83	AMSR132486
22			JQ910630	JQ910517	83	AMSR151562
23			JQ910629	JQ910516	83	ANWCR06668
24	<i>Ramphotyphlops</i>	<i>silvia</i>	KC493653	JQ910501	84	QMJ46128
25	<i>Ramphotyphlops</i>	<i>troglodytes</i>	JQ910614	JQ910466	85	WAMR146048
26	<i>Ramphotyphlops</i>	<i>unguirostris</i>	JQ910615	JQ910502	87	NTMR21669
27			KC490398	KC490887	86	WAMR115861
28			JQ910616	JQ910503	88	SAMAR54430
29			JQ910617	JQ910504	86	WAMR115861
30			JQ910618	JQ910505	89	WAMR117861
31			JQ910619	JQ910506	86	WAMR146958
32			KC490399	KC490888	86	WAMR151036
33	<i>Ramphotyphlops</i>	<i>waitii</i>	KC490400	KC490889	90	WAMR97215
34			KC490401		90	WAMR104279
35			KC490402		90	WAMR120289
36			KC490403		90	WAMR104279
37			KC490404	KC490890	91	WAMR110957
38			KC490405	KC490891	90	WAMR113302
39			KC490406	KC490892	90	WAMR113321
40			KC490407		90	WAMR113392
41			KC490408	KC490893	90	WAMR114891
42			KC490409	KC490894	90	WAMR115123
43			KC490410	KC490895	90	WAMR119239
44			KC490411		90	WAMR119296
45			KC490412	KC490896	90	WAMR119299
46			KC490413		90	WAMR120289
47			JQ910620	JQ910507	90	WAMR120315
48			KC490414	KC490897	91	WAMR135251
49			KC490415	KC490898	90	WAMR136448
50			KC490416	KC490899	90	WAMR136679
51			KC490417	KC490900	91	WAMR136738
52			KC490418		91	WAMR136739

		KC490419		91	WAMR136741
		KC490420		91	WAMR136761
		KC490421	KC490901	90	WAMR136815
		KC490422	KC490902	90	WAMR140423
		KC490423	KC490903	90	WAMR144088
		KC490424	KC490904	90	WAMR144089
		KC490425	KC490905	90	WAMR145181
		KC490426	KC490906	90	WAMR145346
		KC490427		91	WAMR151432
		KC490428		91	WAMR151490
		KC490429		90	WAMR164356
		JQ910636	JQ910523	91	WAMR165022
		KC490430	KC490907	90	WAMR165623
		KC490431	KC490908	91	WAMR166685
<i>Ramphotyphlops</i>	<i>wiedii</i>	KC490432	KC490909	92	QMJ59020
		JQ910621	JQ910508	92	AMSR154152
		JQ910631	JQ910518	92	ANWCR05533

Locality	State	Latitude	Longitude
Blackdown Tableland Road, 2k S Jnctn	Qld	-23.6294444	149.1997222
28k ESE Port Headland	WA	-20.3934	118.8437
Barlee Range Nature Reserve	WA	-23.0958	116.0097
Burrup Peninsula	WA	-20.5383	116.8186
1.4k NNE Woodstock	WA	-21.6094	118.9619
8k S Karratha	WA	-20.7833	116.8500
6k S Karratha	WA	-20.7945	116.857
14.5k SE Mt Florance Homestead	WA	-21.8562	117.98
Python Pool	WA	-21.33	117.23
12.5k SW Millstream	WA	-21.6772	116.975
14k WSW Roy Hill Station	WA	-22.6757	119.841
6k SW Roy Hill Station	WA	-22.6611	119.919
14k WSW Roy Hill Station	WA	-22.6757	119.841
14k WSW Roy Hill Station	WA	-22.6757	119.841
6k SW Roy Hill Station	WA	-22.6611	119.919
6k SW Roy Hill Station	WA	-22.6611	119.919
37.9k SSE Pannawonica	WA	-21.9483	116.4636
20.6k S Pannawonica	WA	-21.8188	116.2997
18k NW Balfour Downs Homestead	WA	-22.7006	120.737
36k NW Balfour Downs Homestead	WA	-22.5181	120.678
36k NW Balfour Downs Homestead	WA	-22.5181	120.678
25k NW Balfour Downs Homestead	WA	-22.6111	120.729
23k WNW Balfour Downs Homestead	WA	-22.7183	120.646
28k ESE Port Hedland	WA	-20.5166	118.6833
Weeli Wollie Spring	WA	-22.9166	119.2167
32k N Port Hedland, Great Northern Highway	WA	-20.4166	118.8333
5k S Mount Tom Price Mine	WA	-22.8080	117.7489
5k S Mount Tom Price Mine	WA	-22.8080	117.7489
Burrup Peninsula	WA	-20.5963	116.8108
Burrup Peninsula	WA	-20.5602	116.8053
Burrup Peninsula	WA	-20.5847	116.8000
Pardoo Roadhouse	WA	-20.0666	119.8167
Meentheena	WA	-21.3511	120.4469
Mount Minnie Homestead	WA	-22.0333	115.4667
Cape Preston area	WA	-21.0152	116.1872
69k S Port Hedland	WA	-20.9100	118.6800
69k S Port Hedland	WA	-20.9100	118.6800
86k S Port Hedland	WA	-21.0600	118.7500
69k S Port Hedland	WA	-20.9100	118.6800
69k S Port Hedland	WA	-20.9100	118.6800
27k S Port Hedland	WA	-20.5400	118.6400
231k SSW Port Hedland	WA	-22.3600	119.9900
248k SSW Port Hedland	WA	-22.5000	119.0900
Munni Munni	WA	-21.1297	116.8039
235k SSW Port Hedland	WA	-22.3900	118.9800
231k SSW Port Hedland	WA	-22.3600	119.9900
235k SSW Port Hedland	WA	-22.3900	119.9900
Hesta Rail siding	WA	-22.1819	119.0214

1				
2				
3	Yule River, 7.2k WSW Woodstock	WA	-21.6341	118.8872
4	Tom Price area	WA	-22.6202	117.7436
5	Fortescue Marsh	WA	-22.2991	119.0228
6	Fortescue Marsh	WA	-22.2591	119.0264
7	Fortescue Marsh	WA	-22.4144	119.0067
8	Fortescue Marsh	WA	-22.2591	119.0264
9	Fortescue Marsh	WA	-22.3497	119.2911
10	Mulga Downs Station	WA	-22.4144	119.0067
11	Fortescue Marsh	WA	-22.4591	119.0364
12	Fortescue Marsh	WA	-21.9538	118.9958
13	Fortescue Marsh	WA	-21.9880	119.0219
14	Fortescue Marsh	WA	-22.3466	119.0100
15	Fortescue Marsh	WA	-22.4144	119.0067
16	6k N Millstream	WA	-21.5402	117.057
17	5k NNE Python Pool	WA	-21.3104	117.276
18	6k SW Roy Hill Station	WA	-22.6611	119.919
19	16k N Cowra Line Camp	WA	-22.2217	119.025
20	32.6k SE Roy Hill	WA	-22.3894	119.7753
21		WA		
22	6k S Karratha	WA	-20.7945	116.857
23	6k S Karratha	WA	-20.7945	116.857
24	14k WSW Roy Hill Station	WA	-22.6757	119.841
25	6k SE Whim Creek Hotel	WA	-20.8699	117.859
26	1k SE Mt Murray	WA	-22.4984	115.558
27	21.5k NE Mt Mary	WA	-22.2554	115.437
28	16k W Mt De Courcey	WA	-22.7402	116.461
29	Newman	WA	-22.2680	119.1892
30	Newman	WA	-22.2400	119.1031
31	Newman	WA	-22.2400	119.1031
32	20k NNW Mt Elvire	WA	-21.6728	116.725
33	16.6k ENE Karratha	WA	-20.7986	116.6814
34	13.8k ENE Karratha	WA	-20.7802	116.7019
35	16.4k ENE Karratha	WA	-20.7922	116.6806
36	16k ENE Karratha	WA	-20.7927	116.6850
37	Nullagine	WA	-21.9519	120.1317
38	Nullagine	WA	-21.9541	120.1242
39	Woodie Woodie	WA	-21.6594	121.2417
40	Whim Creek	WA	-20.8497	117.8394
41	17k WNW Peedamulla Homestead	WA	-21.7914	115.464
42	31k WSW Mt Elvire	WA	-21.8736	116.503
43	Spear Hill Mine	WA	-29.492	119.412
44	35.5k SW Marble Bar	WA	-21.4381	119.541
45	4k SE The Island Hill	WA	-21.3403	119.366
46	Woodstock	WA	-21.6169	118.9536
47	Woodstock Station	WA	-21.6111	119.0397
48	Woodstock Station	WA	-21.6097	118.9622
49		WA	-	115.5
50	Rottnest Island	WA	-32.53	115.94
51	near Dandalup	WA	-31.94	115.77
52	Bold Park	WA	-31.94	115.77
53	Bold Park	WA	-31.9709	115.9018
54	Victoria Park, Perth	WA	-31.94	115.77
55	Bold Park	WA	-	
56				
57				
58				
59				
60				

1				
2				
3	Bold Park	WA	-31.94	115.77
4	Kalgoorlie Nickel Smelter	WA	-	121.488611111111
5	Bold Park	WA	-31.94	115.77
6	Dandaragan area	WA	-30.9952	115.6958
7	Rottnest Island	WA	-32.0150	115.4750
8	Muddy Lakes	WA	-33.4208	115.6053
9	Mount Helena.	WA	-31.8666	116.2000
10	Mount McMahon, Ravensthorpe Range	WA	-33.5500	120.1000
11	Kalgoorlie Nickel Smelter, 10k S Kalgoorlie	WA	-30.8333	121.4667
12	Kalgoorlie Nickel Smelter, 10k S Kalgoorlie	WA	-30.8333	121.4667
13	Kalgoorlie Nickel Smelter, 10k S Kalgoorlie	WA	-30.8333	121.4667
14	Kalgoorlie Nickel Smelter, 10k S Kalgoorlie	WA	-30.8333	121.4667
15	10k S Kalgoorlie	WA	-30.8333	121.4667
16	Kings Park	WA	-31.9666	115.8333
17	Kings Park	WA	-31.9666	115.8333
18	Kings Park	WA	-31.9666	115.8333
19	Bold Park	WA	-31.9333	115.7667
20	11k ESE North Dandalup	WA	-32.5333	116.1000
21	11k ESE North Dandalup	WA	-32.5333	116.1000
22	11k ESE North Dandalup	WA	-32.5333	116.1000
23	Wanneroo	WA	-31.7500	115.8000
24	Byford	WA	-32.2166	116.0000
25	Edel Land	WA	-26.5000	113.5000
26	20k NE Newdegate	WA	-32.9333	119.1500
27	1k N Cape Burney	WA	-28.8500	114.6333
28	Talbot Road Reserve, Swan View	WA	-31.8736	116.0508
29	Rolystone	WA	-32.1166	116.0667
30	Talbot Road Reserve, Swan View	WA	-31.8666	116.0511
31	Bold Park, Perth	WA	-31.9538	115.7711
32	Kings Park, Perth	WA	-31.9666	115.8333
33	Bungendore, Perth	WA	-32.1911	116.0356
34	Masons Bay, 36k E Hopetoun	WA	-33.9500	120.5000
35	Bandalup Hill	WA	-33.6500	120.3667
36	Ravensthorpe	WA	-33.5833	120.0500
37	SE corner Lake Magenta Reserve	WA	-33.5000	119.3333
38	Bungendore Park	WA	-32.1833	116.0167
39	Bungendore Park	WA	-32.1833	116.0167
40	Talbot Road, Perth	WA	-31.8730	116.0461
41	Cocanarup Homestead	WA	-33.6000	119.9167
42	Corackerup	WA	-34.2666	118.7000
43	Cooliabberra Spring, Bungendore Park	WA	-32.1833	116.0333
44	Cooliabberra Spring, Bungendore Park	WA	-32.1833	116.0333
45	Cooliabberra Spring, Bungendore Park	WA	-32.1833	116.0333
46	Bungendore Park	WA	-32.1833	116.0333
47	Bungendore Park	WA	-32.1833	116.0333
48	Bungendore Park	WA	-32.1833	116.0333
49	Bungendore Park	WA	-32.1833	116.0333
50	23k N Black Point	WA	-34.1666	115.5333
51	18k SW Ravensthorpe	WA	-33.2144	121.0300
52	Lesueur National Park	WA	-30.1833	115.2000
53	Bandalup Hill	WA	-33.6819	120.3022
54	20k W Waroona	WA	-32.8666	115.7000
55	Bandalup Hill	WA	-33.6819	120.3022
56	Bandalup Hill	WA	-33.6819	120.3022
57	20k WNW Waroona	WA	-32.8166	115.7167

1	20k W Waroona	WA	-32.8666	115.7000
2	Bungendore, School Site	WA	-32.1833	116.0333
3	Brickwood Reserve	WA	-32.0638	116.0189
4	Brickwood Reserve	WA	-32.2338	116.0019
5	Brickwood Reserve	WA	-32.2311	116.0033
6	1.8k from Twertup, along Twertup Track	WA	-33.9833	119.3333
7	Bungendore Park	WA	-32.1833	116.0333
8	Hepburn Heights	WA	-31.8158	115.7808
9	8k W Esperance	WA	-33.8666	121.8333
10	16k NNW Ongerup	WA	-33.7000	117.0167
11	Lake Jasper area	WA	-34.4166	115.6833
12	8k WNW Maggie Hayes Hill	WA	-32.2500	120.5000
13	8k WNW Maggie Hayes Hill	WA	-32.2500	120.5000
14	Shannon Basin	WA	-34.7500	116.9833
15	Shannon Basin	WA	-34.7500	116.9833
16	Kalamunda	WA	-31.9666	116.0500
17	6k NE Margaret River	WA	-33.9666	115.0500
18	Lake Jasper	WA	-34.4013	115.6436
19	Ravensthorpe	WA	-33.5833	120.0500
20	Hay Park, Bunbury	WA	-33.3166	115.6333
21	5k NE Morehead	WA	-33.2969	116.0928
22	5k NW Dryandra	WA	-32.7433	116.9400
23	4k W Dryandra Settlement	WA	-32.7758	116.9211
24	Jangardup study area, Dentrecasteaux Na	WA	-34.4166	115.7500
25	2k NE Wonnerup Siding	WA	-33.6166	115.4453
26	30k W Southwest Calingiri	WA	-31.1433	116.3217
27	8k NW Norseman	WA	-32.1602	121.7417
28	Gracetown	WA	-33.8500	114.9833
29	Lake Mealup	WA	-32.6833	115.7000
30	Cervantes area	WA	-30.7508	115.2031
31	Cervantes area	WA	-30.7988	115.2708
32	Donnybrook-Collie Road	WA	-33.5500	115.8500
33	~15k WNW Cataby	WA	-30.6138	115.2508
34	~10k NE Marchagee	WA	-30.0205	116.1197
35	Ludlow Drive	WA	-33.6480	115.4164
36	Ludlow Drive	WA	-33.6480	115.4164
37	Point Douro, Australind	WA	-33.3000	115.7000
38	5k E Ora Banda	WA	-30.3788	121.1242
39	5k E Ora Banda	WA	-30.3788	121.1242
40	5k E Ora Banda	WA	-30.3788	121.1242
41	5k E Ora Banda	WA	-30.3788	121.1242
42	4k S Collie	WA	-33.3533	116.2064
43	Bandalup Hill	WA	-33.5861	120.3275
44	Lot 52, Burns Beach Road	WA	-31.7183	115.7661
45	Marchagee area	WA	-30.0500	116.2333
46	23k S Kalbarri	WA	-27.9219	114.1633
47	23k S Kalbarri	WA	-27.9219	114.1633
48	35k S Kalbarri	WA	-28.0166	114.2167
49	23k S Kalbarri	WA	-27.9000	114.1500
50	7k S Dongara	WA	-29.3138	114.9483
51	Lake Cooongoop Nature Reserve	WA	-32.3000	115.7833
52	Australind	WA	-33.2833	115.7000

1				
2				
3	Australind	WA	-33.2833	115.7000
4	Ravensthorpe area	WA	-33.6616	120.3953
5	Ravensthorpe area	WA	-33.5652	120.3175
6	Ravensthorpe area	WA	-33.5652	120.3175
7	Ravensthorpe area	WA	-33.5861	120.3275
8	Salmon Gums area	WA	-32.7000	121.4467
9	Salmon Gums area	WA	-32.8200	121.4100
10	Cervantes	WA	-30.5000	115.0667
11	Cervantes	WA	-30.5000	115.0667
12	East Wallabi Island	WA	-28.4333	113.7167
13	Kundip	WA	-33.6819	120.1989
14	Kundip	WA	-33.6800	120.1933
15	Pingrup area	WA	-33.5266	118.7422
16	Pingrup area	WA	-33.5808	118.7653
17	Australind	WA	-33.2805	115.7217
18	Australind	WA	-33.2805	115.7217
19	Australind	WA	-33.2805	115.7217
20	Canal Rocks	WA	-33.6627	115.0125
21	Quairading	WA	-32.0166	117.4000
22	Ora Banda	WA	-30.3666	121.0500
23	East Wallabi Island	WA	-28.4333	113.7167
24	Neerabup	WA	-31.6666	115.7500
25	Forrestania	WA	-32.4108	119.6950
26	Digger Rocks	WA	-32.7158	119.8017
27	Digger Rocks	WA	-32.7158	119.8017
28	Digger Rocks	WA	-32.7286	119.8081
29	Digger Rocks	WA	-32.7286	119.8081
30	3k SW Ludlow	WA	-33.6208	115.6375
31	Mount Chudalup	WA	-34.7666	116.0833
32	1k NE Augusta	WA	-34.3041	115.1708
33	Perth Airport	WA	-31.9233	115.9778
34	16.7k NNE Fig Tree Corner	SA	-31.5389	132.7144
35	Gawler Ranges	SA	-32.616667	136.35
36	Red Band Tank	SA	-	140.599444444444
37	Hideaway Hut	SA	-	140.622222222222
38	Theodolite Dam	SA	-33.4	139.936111111111
39	Theodolite Dam	SA	-33.4	139.936111111111
40	Theodolite Dam	SA	-33.4	139.936111111111
41	Burra Creek	SA	-33.8166666666	139.016666666667
42	6k SE Keyneton	SA	-34.6	139.2
43	4k NW Courtarie	SA	-	134.822222222222
44	3k E Tailem Bend	SA	-	139.480833333333
45	2.5k NW Iron Chieftain	SA	-	137.133333333333
46	17k NW Witera, Flinders Highway	SA	-	134.483333333333
47	Swan Reach	SA	-	139.6
48	W boundary track Karte CP	SA	-	140.685
49	W boundary track Karte CP	SA	-	140.685
50	Peebinga CP, Mootatunga	SA	-	140.833333333333
51	24k SW Canopus HS	SA	-	140.483333333333
52	4k NE Kalgoorlie	WA	-34.1322	146.5048
53	8.5k W Pinjarra dam	WA	-	134.704444444444
54	5k N Blanchetown	SA	-	139.6

1	14k WNW Gluepot Homestead	SA	-	139.98
2	18k NNW Barellan	NSW	-34.1322	146.5048
3	Budgerree Station	NSW	-32.8838888888	141.170833333333
4	Yathong NP	NSW	-32.59	145.4
5	JERILDERIE, McCaughee Inst./Old	NSW	-35.3474	145.5408
6	near Boolcoomata HS	SA	-31.9683	140.5451
7	5.2k E Paney shearers quarters	SA	-	135.699805555556
8	10k NE Kalbrae	SA	-	135.035333333333
9	3.7k ENE Corrobinnie Hill	SA	-	135.771944444444
10	13.4k NE Fig Tree Corner	SA	-31.6042	132.8303
11	4k NE Kalgoorlie	WA	-30.7333	121.4667
12	Kalgoorlie	WA	-30.7333	121.4667
13	Goongarrie Station	WA	-29.9833	121.0333
14	25k S Widgiemooltha	WA	-31.7000	121.5333
15	Leinster Downs Station	WA	-27.9647	120.3892
16	Leinster Downs Station	WA	-27.9647	120.3892
17	Marvel Loch	WA	-31.4830	119.5292
18	Windarling Hill	WA	-30.0130	119.2872
19	Goongarrie Station	WA	-29.8997	121.1764
20	Ora Banda	WA	-30.3972	121.1225
21	Ora Banda	WA	-30.3666	121.0500
22	Ora Banda	WA	-30.3666	121.0500
23	Welbourne Hill Station	SA	-27.55611111	134.425
24	11.5 km SSW Winninowie homestead	SA	-32.7236	137.8972
25	10.3 km SSW Winninowie homestead	SA	-32.6997	137.8511
26	6k NE Culburra	SA	-35.755	139.988888888889
27	7.5k NNW Rabbit Island Dam	SA	-	140.315833333333
28	5.2k ESE Strangways Springs	SA	-	136.596944444444
29	3.5k NW Beresford Rail Station	SA	-	136.630833333333
30	Peake Station	SA	-	136.446388888889
31	6.3k NNW Wimma Hill	SA	-	140.290555555556
32	10.3k SW Wimma Hill	SA	-	140.228888888889
33	19.6k SW Wimma Hill	SA	-	140.178055555556
34	Hideaway Hut	SA	-	140.478333333333
35	Balah Station	SA	-	139.8166666666667
36	Diamond Dam	SA	-	140.033333333333
37	Port Kenny	SA	-	134.6391666666667
38	near Arno Bay	SA	-	136.5666666666667
39	20k N Cowell	SA	-33.5	137
40	Burke's Grave, near Innamincka	SA	-27.73333333	140.7666667
41	N end Stock Route	SA	-32.85	135.95
42	SW Olympic Dam	SA	-30.5	136.8
43	Moomba	SA	-	140.183333333333
44	Wudinna	SA	-33.05	135.4666666666667
45	37.5k NE Minnipa	SA	-	135.45
46	7k E Koolunga	SA	-	138.4
47	7k S Crystal Brook	SA	-	138.15
48	7k S Crystal Brook	SA	-	138.15
49	Lake Richardson, 10k ENE Woomera	SA	-	136.933333333333
50	Kangaroo Flat, Sec 78	SA	-	138.7
51	2.9k ESE Mulga Bore	SA	-30.6	139.533333333333
52	E boundary Karte CP	SA	-35.1258333	140.7241667

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3	2k NNE Whyalla	SA	-	137.576944444444
4	3.5k W Inkerman	SA	-34.275	138.2
5	Dept of Defence Firing Range, Port	SA	-	138.2
6	1.5k ENE Gluepot HS	SA	-	140.1375
7	9.2k WNW Wharminda	SA	-	136.163888888889
8	West Wyalong	NSW	-33.93	147.2
9	Yathong NP	NSW	-32.59	145.4
10	JERILDERIE, OLD COREE STATION	NSW	-35.3474	145.5408
11	Yarra property, 35k Mt Hope on	NSW	-32.8687	145.9979
12	Yathong NP	NSW	-32.59	145.4
13	Ashleigh Park, 21k S Berrigan,	NSW	-	145.821388888889
14	BERRIGAN STATE FOREST, 11k E	NSW	-	145.923888888889
15	Pine Lodge, 18k N Mulwala, Savernake	NSW	-	146.009444444444
16	Ashleigh Park, 21k S Berrigan,	NSW	-	145.821388888889
17	Berrigan State Forest, 11k E Berrigan	NSW	-35.6883333	145.9238889
18	Fairfield 29k NE Mulwala, Savernake	NSW	-	146.221388888889
19	8.4k NE Border Village	SA	-	129.086944444444
20	Cornish Well, 22.9k WNW Moonaree	SA	-31.9414	135.6344
21	20k NE Mount Penrhyn	SA	-29.305	135.1716667
22	6.8k NNE Kulpara	SA	-34.013056	138.085
23	11.8k NE Yarnerby Hill	SA	-	134.271111111111
24	11.8k NE Yarnerby Hill	SA	-	134.271111111111
25	7.1k WNW Ant Hill	SA	-28.433889	134.500278
26	6.1k ENE Hunchee	SA	-	140.850277777778
27	30.3k N Whyalla	SA	-32.775556	137.572778
28				
29				
30	MacDonnell Ranges	NT		
31	Lawrence Gorge	NT	-23.9977	133.4291
32	Mount Barry Station	SA	-	134.7066666666667
33	9.4k SSW Granite Downs HS	SA	-	133.47
34	8k ENE Mount Chandler	SA	-26.9891667	133.4055556
35				
36	Cravens Peak property, approximately	Qld	-23.0165765	138.2344608
37	176 Camooweal Street, Mount Isa	Qld	-20.7265	139.4909
38	Mount Isa area	Qld		
39	176 Camooweal Street, Mount Isa	Qld	-20.7265	139.4909
40	176 Camooweal Street, Mount Isa	Qld	-20.7265	139.4909
41	Hidden Valley Caravan Park, Kununurra	WA	1546 S	12844 E
42	Supplejack Station, 8 Mile Bore	NT	-19.1735	129.9219
43	Guluwuru Island	NT	-11.5243	136.4231
44	Guluwuru Island	NT	-11.5243	136.4231
45	Tennant Creek	NT	-19.6269	134.191
46	117k NNW Tanami Downs Homestead	WA	-19.8894	128.8600
47	Beagle Bay Aboriginal Community	WA	-17.0597	122.7167
48	Beagle Bay Aboriginal Community	WA	-17.0766	122.7072
49	Mirima National Park	WA	-15.7833	128.7833
50	Mirima National Park	WA	-15.7833	128.7833
51	~5k S Carlton Hill Homestead	WA	-15.5386	128.5233
52	Lake Argyle	WA	-16.2166	128.9000
53	Tanami Desert	WA	-19.8986	128.8658
54	Tanami Desert	WA	-19.8891	128.8600
55	Etabuka Station	Qld	-23.8627	138.4794
56	70k E Moomba	SA	-	140.8666666666667
57	Mabel Creek HS	SA	-	134.108333333333
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1	Mabel Creek HS	SA	-	134.466666666667
2	Mabel Creek HS	SA	-	134.25
3	Yulara	NT	-	131.016666666667
4	Curtin Springs	NT	-	131.766666666667
5	4.6k N Strangways Springs	SA	-	136.545
6	86k SW Approdinna Attora Knolls	SA	-	136.953611111111
7	8.4k SW Wimma Hill	SA	-	140.245
8	11.5k SW Wimma Hill	SA	-	140.229166666667
9	Musgrave Ranges	SA	-26.65	130.816666666667
10	38k ENE Laverton	WA	-28.513	122.7621
11	4k W Mt Lindsay	SA	-	129.839166666667
12	3.1k WNW Mt Lindsay	SA	-	129.850277777778
13	N Olympic Dam	SA	-	136.916666666667
14	Olympic Dam area	SA	-30.55	136.883333333333
15	Olympic Dam Site	SA	-	136.9
16	Olympic Dam Site	SA	-	136.883333333333
17	Olympic Dam Site	SA	-30.4333333	136.85
18	near Mundibarcooloo WH	SA	-	140.216666666667
19	25k SSW Mabel Creek HS	SA	-	134.233333333333
20	Yalymboo Station	SA	-	136.625833333333
21	Mt Vivian Station	SA	-	135.821666666667
22	Glendambo near Hotel	SA	-	135.733333333333
23	near Crows Nest Bore Mt Vivian Station	SA	-	135.821666666667
24	Oakden Hills Station	SA	-	136.911388888889
25	Mt Gunson Paddock Oakden Hills Station	SA	-31.4925	137.105833333333
26	15k S Yuendemu Road	NT	-23.1823	132.6566
27	10k SSW Maralinga	SA	-	131.545833333333
28	Davenport Range	SA	-	135.941111111111
29	Wirraminna Station	SA	-	136.591944444444
30	24.4k SSE Hamilton HS	SA	-	135.196111111111
31	6.8k SE Hamilton HS	SA	-	135.118888888889
32	Yamarna Station	WA	-	123.783388888889
33	Sturt NP, Camerons Corner Road, 3.4k N	NSW	-29.0908	141.2051
34	Sturt NP, 13.5k E on Middle Road from	NSW	-29.0063	141.1436
35	Sturt NP, Camerons Corner Road, 3.4k N	NSW	-29.0908	141.2051
36	Sturt NP, 5.7k W along Whitecatch Gate	NSW	-29.1414	141.1343
37	Sturt NP, 1.8k W along Whitecatch Gate	NSW	-29.1163	141.173
38	Sturt NP, Camerons Corner Road, 3.4k N	NSW	-29.0908	141.2051
39	Sturt NP, Whitecatch Gate Road	NSW	-29.2125	141.0252
40	Sturt NP, 2.7k W Binerah Downs HS on	NSW	-29.0319	141.5249
41	Sturt NP, 9.8k W Binerah Downs HS on	NSW	-29.0317	141.4511
42	Sturt NP, 13.7k E on Middle Road from	NSW	-29.0063	141.1436
43	4.2k SSE Pungkulpirri Waterhole	WA	-24.6964	128.7628
44	5.3k SSE Pungkulpirri Waterhole	WA	-24.7072	128.7603
45	4.2k SSE Pungkulpirri Waterhole	WA	-24.6964	128.7628
46	3.2k N Pungkulpirri Waterhole, Walter	WA	-24.6286	128.7556
47	5.3k SSE Pungkulpirri Waterhole	WA	-24.7072	128.7603
48	5.6k SE Mt Ant	WA	-24.8006	128.7972
49	Kutjuntari Rockhole	WA	-24.8914	128.7692
50	3.2k N Pungkulpirri Waterhole, Walter	WA	-24.6286	128.7556
51	3.2k N Pungkulpirri Waterhole, Walter	WA	-24.6286	128.7556

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3	12.2k N Pungkulpirri Waterhole, Walter	WA	-24.5594	128.7097	
4	12.2k N Pungkulpirri Waterhole, Walter	WA	-24.5594	128.7097	
5	12.2k N Pungkulpirri Waterhole, Walter	WA	-24.5594	128.7097	
6	Morgan Range, 18.5k ENE Blackstone	WA	-25.9306	128.4525	
7	Morgan Range, 18.5k ENE Blackstone	WA	-25.9306	128.4525	
8	Morgan Range, 16.8k ENE Blackstone	WA	-25.9353	128.4378	
9	18.4k NE Blackstone	WA	-25.8917	128.4269	
10	Morgan Range, 16.8k ENE Blackstone	WA	-25.9353	128.4378	
11	Morgan Range, 17.3k ENE Blackstone	WA	-25.9325	128.4411	
12	Morgan Range, 17.3k ENE Blackstone	WA	-25.9325	128.4411	
13	Morgan Range, 17.3k ENE Blackstone	WA	-25.9325	128.4411	
14	Morgan Range, 18.5k ENE Blackstone	WA	-25.9306	128.4525	
15	Morgan Range, 18.5k ENE Blackstone	WA	-25.9306	128.4525	
16	Morgan Range, 18.5k ENE Blackstone	WA	-25.9306	128.4525	
17	Morgan Range, 16.8k ENE Blackstone	WA	-25.9353	128.4378	
18	Morgan Range, 18.5k ENE Blackstone	WA	-25.9306	128.4525	
19	179k SSW Watarru	SA	-28.46277	129.01026	
20	Anne Beadel Highway, 15.4k E SA/WA	SA	-28.5112	129.1582	
21	184k SSW Watarru	SA	-28.50788	129.00473	
22	184k SSW Watarru	SA	-28.50788	129.00473	
23	28.8k WNW Emu	SA	-	131.923333333333	
24	29.1k SSW England Hill	SA	-28.383333	134.083333	
25	29.1k SSW England Hill	SA	-28.383333	134.083333	
26	Little Sandy Desert	WA	-24.1047	120.3250	
27	Little Sandy Desert	WA	-24.1047	120.3250	
28	Little Sandy Desert	WA	-24.1047	120.3250	
29	Little Sandy Desert	WA	-23.8883	120.5217	
30	Little Sandy Desert	WA	-23.8794	120.5033	
31	Little Sandy Desert	WA	-23.8883	120.5217	
32	Willies Soak, Little Sandy Desert	WA	-24.5930	120.2500	
33	8k WSW Yamana Hs	WA	-28.0166	123.6167	
34	38k ENE Laverton	WA	-28.5500	122.7000	
35	38k ENE Laverton	WA	-28.5500	122.7000	
36	Nifty Mine	WA	-21.6666	121.5833	
37	near Telfer Dome	WA	-22.1833	122.2667	
38	Telfer	WA	-21.7611	122.2233	
39	Officer Basin area	WA	-27.1675	125.2000	
40	Officer Basin area	WA	-26.9327	125.2789	
41	Officer Basin area	WA	-26.9327	125.2789	
42	Officer Basin area	WA	-27.0750	125.2028	
43	Empress Spring	WA	-26.7666	124.3661	
44	Clutterbuck Hills	WA	-24.5172	126.2178	
45	30k W Newman, Cathedral Gorge	WA	-23.2916	119.4667	
46	Millstream	WA	-21.5833	117.0667	
47	Chichester Range	WA	-22.2302	118.9814	
48	27k ESE Mt De Courcey	WA	-22.7892	116.571	
49		WA			
50	6.4k ENE Invasion Tank	SA	-26.075	140.896667	
51	Onslow	WA	-21.6533	115.1131	
52	Phosphate Hill, Buffel site	Qld	-21.9002778	139.996944	
53	3k SSW Karrathunka Waterhole	SA	-	139.235833333333	
54	3k SSW Karrathunka Waterhole	SA	-	139.235833333333	
55	10k NW Mt Windell, Hamersley Range (Ka)	WA	-22.6027	118.4597	
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1	Withnell Bay, Burrup Peninsula	WA	-20.5750	116.7903
2	Little Sandy Desert	WA	-24.0752	120.3606
3	Little Sandy Desert	WA	-23.9233	120.5314
4	3.7k ENE Woodstock	WA	-21.6094	118.9878
5	Onslow area	WA	-21.6813	115.0942
6	8k E Yarra Bluff	WA	-21.7833	116.2500
7	8k E Yerra Bluff, ~12k SW Pannawonica	WA	-21.7833	116.2500
8	25k SE Telfer	WA	-21.8833	122.3667
9	67.5k S Fortescue River crossing	WA	-22.0592	117.693
10	5k NW Mt Florance Homestead	WA	-21.7665	117.825
11	6k SW Millstream	WA	-21.6424	117.037
12	14k WSW Roy Hill Station	WA	-22.6757	119.841
13	Brockan Mine	WA	-22.6133	117.1881
14	18.5k SW Pannawonica	WA	-21.7563	116.1964
15	37.5k W Pannawonica	WA	-21.6711	115.9622
16	25.3k WSW Pannawonica	WA	-21.7280	116.0983
17	Onslow area	WA	-21.7308	115.1569
18	Onslow area	WA	-21.7308	115.0978
19	Onslow area	WA	-21.7308	115.0978
20	10k SSE Onslow	WA	-21.7200	115.1508
21	10k SSE Onslow	WA	-21.7200	115.1508
22	Pannawonica Townsite	WA	-21.6500	116.3167
23	Wittenoom	WA	-22.2333	118.3167
24	26k ENE Port Hedland	WA	-20.4000	118.8167
25	Marble Bar	WA	-21.1666	119.7500
26	13k SW Cooralya HS	WA	-24.4166	114.0000
27	Onslow	WA	-21.6333	115.1167
28	30k E Newman	WA	-23.3166	120.0333
29	Gifford Creek Homestead	WA	-24.0500	116.2167
30	10k S Onslow	WA	-21.7333	115.0833
31	5k S Mount Tom Price Mine	WA	-22.8072	117.7500
32	Urala Station	WA	-21.7850	114.8631
33	Urala Station	WA	-21.7541	114.8508
34	Burrup Peninsula	WA	-20.5277	116.8197
35	25k WNW Abydos	WA	-21.4000	118.7061
36	Cape Lambert	WA	-20.6472	117.1522
37	Urala Station	WA	-21.7536	114.8522
38	Urala Station	WA	-21.7766	114.8719
39	36k WSW Pardoo	WA	-20.1902	119.4978
40	26k ENE Pardoo	WA	-19.9769	120.0467
41	50k E South Hedland	WA	-20.4000	119.0667
42	34k S Port Hedland	WA	-20.6100	118.6100
43	Chichester Range	WA	-21.9400	118.9608
44	Abydos Station	WA	-21.3580	118.8831
45	Brockan Ridge	WA	-23.3069	119.8767
46	Waldburg Station	WA	-24.8444	117.2236
47	Waldburg Station	WA	-24.7611	117.1903
48	Waldburg Station	WA	-24.7811	116.9589
49	Onslow area	WA	-21.7411	115.1139
50	Upper Marillana Creek	WA	-22.6927	118.9564
51	Cundaline Gap	WA	-20.5669	120.1850
52	Fortescue Marsh	WA		

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	Fortescue Marsh	WA	-21.9880	119.0219	
	Yanrey Station	WA	-22.2997	114.5931	
	Yanrey Station	WA	-22.1577	114.5286	
	Yanrey Station	WA	-22.1538	114.5508	
	Tanami Desert	WA	-19.5933	128.8611	
	Barrow Island	WA	-20.7833	115.4667	
	32.5k ESE Meentheena Outcamp	WA	-21.3337	120.752	
	35k ESE Meentheena Outcamp	WA	-21.3377	120.77	
	11k SSE Whim Creek Hotel	WA	-20.9198	117.861	
	14k WSW intersection of Coongan and Ta	WA	-20.9108	119.65	
	14k WSW intersection of Coongan and Ta	WA	-20.9108	119.65	
	20k ESE Warrawagine Homestead	WA	-20.9356	120.876	
	16k W Mt De Courcey	WA	-22.7402	116.461	
	13k SSW Giles Point	WA	-23.3611	119.112	
	11.5k SW Rhodes Ridge	WA	-23.146	119.266	
	15k NNE Wodgina	WA	-21.0636	118.761	
	55k NNW Tom Price	WA	-22.295	117.473	
	West Intercourse Island	WA	-20.6811	116.6317	
	Mount Whaleback	WA	-23.3825	119.6253	
	Mount Whaleback	WA	-23.3825	119.6253	
	Mount Whaleback	WA	-23.3283	120.0192	
	Newman	WA	-22.9680	119.6306	
	8.5k NE Mt Rica	WA	-21.9522	116.488	
	Katherine Gorge	NT	-14.31	132.46	
	Top Springs, Tanami Desert	NT	-16.5436	131.7947	
	Bradshaw Station	NT	-15.34	130.27	
	40k S Tunnel Creek Gorge	WA	-17.8275	125.37444444	
	Kingston Rest	WA	-16.0333	128.4000	
	32k N Ord River crossing	WA	-17.2286	128.0994	
	Atley Station	WA	-28.2267	119.0744	
	Onslow area	WA	-21.6777	115.0594	
	North West Cape	WA	-21.8433	114.1100	
	North West Cape	WA	-21.8513	114.1058	
	17.7k W Lake Way	WA	-26.9813	120.6417	
	44.7k NW Lake Way	WA	-27.2525	120.7578	
	14.9k W Lake Way	WA	-26.9700	120.6150	
	40.7k NW Lake Way	WA	-27.2483	120.6967	
	33.5k E Wheelarra Hill	WA	-23.3725	120.458	
	33.5k E Wheelarra Hill	WA	-23.3725	120.458	
	26k SE Wheelarra Hill	WA	-23.5356	120.326	
	Onslow area	WA	-21.7208	115.1508	
	Onslow area	WA	-21.7408	115.1139	
	Urala Station	WA	-21.7536	114.8511	
	2k W Carnarvon	WA	-24.8738	113.6369	
	6k NE Carnarvon	WA	-24.8600	113.6689	
		WA			
	6k NW Mardathuna	WA	-24.4430	114.5117	
	1.7k SSW Meedo	WA	-25.6805	114.6217	
	Jundee	WA	-26.3500	120.6333	
	5k S Mount Tom Price Mine	WA	-22.8080	117.7489	
	5k S Mount Tom Price Mine	WA	-22.8077	117.7858	
	Mount Robinson, West Angelas	WA	-22.9552	118.7706	

1	Urala Station	WA	-21.7541	114.8508
2	Muggon Station	WA	-26.5269	115.5250
3	Muggon Station	WA	-26.4888	115.5308
4	Muggon Station	WA	-26.8169	115.5439
5	Muggon Station	WA	-26.5777	115.4689
6	Muggon Station	WA	-26.7800	115.6039
7	Lake Mason Station	WA	-27.5277	119.5839
8	Lake Mason Station	WA	-27.6733	119.4086
9	Lake Mason Station	WA	-27.5413	119.6186
10	Lake Mason Station	WA	-27.4505	119.5758
11	2.5k N Peron Homestead	WA	-25.8172	113.5472
12	5k S Mount Tom Price Mine	WA	-22.7961	117.7900
13	5k S Mount Tom Price Mine	WA	-22.7961	117.7900
14	5k S Mount Tom Price Mine	WA	-22.7961	117.7900
15	Waldburg Station	WA	-24.7330	117.4186
16	Waldburg Station	WA	-24.7608	117.1903
17	Onslow area	WA	-21.7050	115.0733
18	51.2k S Leinster	WA	-27.4630	120.7825
19	North West Cape	WA	-21.8719	114.1033
20	3k SW Weeli Wollie Spring	WA	-22.9312	119.185
21	Leonora	WA	-28.8641	121.7947
22	Leonora	WA	-28.8641	121.7947
23	Leonora	WA	-28.8605	121.7906
24	Lake Way	WA	-27.3766	120.5861
25	Ora Banda	WA	-30.3666	121.0500
26	12.8k W Lake Way	WA	-26.9622	120.5956
27	12.8k W Lake Way	WA	-26.9622	120.5956
28	Kalumburu	WA	-14.3000	126.6333
29	Katherine Gorge	NT	-14.31	132.46
30	Litchfield NP	NT	-13.283	130.8752
31	Wyndham	WA	-15.4666	128.1000
32	Koolan Island	WA	-16.1272	123.7414
33	Koolan Island	WA	-16.1322	123.7633
34	Koolan Island	WA	-16.1391	123.7481
35	Prudhoe Island	WA	-14.4161	125.2722
36	Koolan Island	WA	-16.1291	123.7458
37	South Maret Island	WA	-14.4447	124.9861
38	South Maret Island	WA	-14.4363	124.9844
39	Geraldton	WA	-28.7474	114.6362
40	Geraldton	WA	-28.7666	114.6167
41	Geraldton	WA	-28.7666	114.6167
42	Geraldton	WA	-28.7666	114.6167
43	Kalbarri	WA	-27.7000	114.1667
44	Kalbarri	WA	-27.7000	114.2000
45	Kalbarri	WA	-27.7000	114.2000
46	22k S Kalbarri	WA	-27.8977	114.1669
47	31k SSE Nerren Nerren	WA	-27.3905	114.7528
48	Muggon Station	WA	-26.3827	115.4639
49	23k S Kalbarri	WA	-27.9219	114.1633
50	Binnu	WA	-28.0333	114.6667
51	Binnu	WA	-28.0333	114.6667
52	Binnu	WA	-28.0333	114.6667

1	21k E Narrabri	NSW	-30.1833333	149.9333333
2	Tableland Highway	NT	-17.705	135.696
3	Keep River NP	NT	-15.8113	129.1074
4	Raragala Island	NT	-11.61	136.26
5	~35k NNE Kununurra	WA	-15.4166	128.9500
6	~35k NNE Kununurra	WA	-15.5888	128.9833
7	Bandicoot Bay, Barrow Island	WA	-20.9000	115.3667
8	8k W Woolbrook	NSW	-	151.3
9	30k E Tenterfield	NSW	-28.8	152.08333333333
10	38k E Glen Innes	NSW	-29.65	152.05
11	38k W Glenn Innes	NSW	-29.65	152.05
12	8k W Woolbrook	NSW	-30.9666667	151.35
13	8k W McAfees Lookout	Qld	-27.4009	152.8131
14	8k W McAfees Lookout	Qld	-27.4009	152.8131
15	Kroombit Forest Drive, Kroombit Forest	Qld	-24.3757769	150.9858102
16	Kroombit Forest Drive, Kroombit Tops	Qld	-24.3597804	150.9636134
17	Egg Rock Firetrail, Lamington NP	Qld	-28.187436	153.1866493
18	Watagan SF	NSW	-	151.35
19	Kroombit Tops	Qld	-24.36	151.03
20	5k S Euroa, Mansfield Road	SA	-	145.58333333333
21	Kroombit Tops forestry hut	Qld	-	150.960555555556
22	Castlereagh SF, near Penrith	NSW	-33.68	150.75
23	Castlereagh waste depot, near Penrith	NSW	-33.68	150.75
24	WINDSOR DOWNS NATURE	NSW	-33.64	150.79
25	Llangothlin to Ben Lomond Road	NSW	-30.0707	151.6738
26	Kingsgate Road	NSW	-29.8016667	151.9825
27	30k E Tenterfield	NSW	-28.8	152.0833333
28	Torrington State Recreation area, Butler	NSW	-29.2403	151.5577
29	Red Range to Kingsgate Road	NSW	-29.7739	151.9574
30	Red Range to Kingsgate Road	NSW	-29.7739	151.9574
31	Captains Flat Road, E Queanbeyan	NSW	-35.3583333	149.2666667
32	Red Hill, Canberra	ACT	-35.325	149.116666666667
33	Woodstock Station	WA	-21.6226	118.9562
34	Woodstock Station	WA	-21.6226	118.9562
35	Lesley Salt Works	WA	-20.3432	118.6336
36	no locality data	WA		
37	20k E South Hedland	WA	-20.3833	118.8000
38	Lesley Salt Works	WA	-20.2833	118.8944
39	Brockan Mine	WA	-22.6133	117.1881
40	Brockan Mine	WA	-22.6175	117.1814
41	Brockan Mine	WA	-22.5730	117.1911
42	50.1k W Pannawonica	WA	-21.6666	115.8353
43	42.9k W Pannawonica	WA	-21.6561	115.9078
44	22.1k WSW Pannawonica	WA	-21.6938	116.1178
45	37.5k W Pannawonica	WA	-21.6711	115.9622
46	16k SW Pannawonica	WA	-21.7461	116.2200
47	29.1k WSW Pannawonica	WA	-21.6991	116.0489
48	Boodarie Hill	WA	-20.4000	118.5167
49	39k W Munjina	WA	-22.4333	118.7500
50	Mt Brockan	WA	-22.2975	117.2878
51	Meentheena	WA	-21.2038	120.4731
52	Meentheena	WA	-21.2252	120.3556

1	Meentheena	WA	-21.2902	120.4664
2	Meentheena	WA	-21.4216	120.4267
3	Millstream-Chichester Range NP	WA	-21.4619	117.1625
4	Cape Preston area	WA	-21.0163	116.1956
5	Chichester Range	WA	-22.2305	118.9794
6	Port Hedland area	WA	-20.3513	118.7186
7	Port Hedland area	WA	-20.3811	118.6853
8	52.5k N Nullagine	WA	-21.4077	120.071
9	Nullagine	WA	-21.9541	120.1219
10	Woodie Woodie	WA	-21.6847	121.2308
11	Carabooda	WA	-31.5675	115.7114
12	Helena Valley	WA	-31.9333	116.0333
13	Mt Hartley	Qld	-15.76	145.33
14	Charmillan Creek	Qld	-17.6856	145.5224
15	Charmillan Creek	Qld	-17.6856	145.5224
16	7.5k W Paluma	Qld	-19.0237	146.1395
17	Julatten	Qld	-	145.333333333333
18	Pine Creek Road, Numinbah Valley	Qld	-28.1119517	153.2441232
19	Arcadia Valley, 20k NNE Injune	Qld	-	148.833333333333
20	CLARENCE TOWN, 2.5k S - RAYMOND	NSW	-32.5937	151.7587
21	CLARENCE TOWN, 2.5k S - RAYMOND	NSW	-32.5937	151.7587
22	Goonoo SF near Dubbo	NSW	-32.08	148.9
23	Sloane Reserve, 28.5k N Mulwala,	NSW	-35.7383333	146.0483333
24	25k N Pomona	Qld	-26.1437	152.8415
25	Oobagooma Homestead	WA	-16.7500	123.9853
26	Dundee Beach, Fog Bay	NT	-12.7597	130.3553
27	Lake Argyle	WA	-16.1163	128.7303
28	Burke Development Road 10k ENE	Qld	-17.4347222	141.2763889
29	Lake Argyle	WA	-16.3000	128.8000
30	near Mount Percy	WA	-17.6630	124.9333
31	Kalumburu	WA	-14.3000	126.6333
32	10k SE Kununurra	WA	-15.8333	128.8000
33	25k N Dongara	WA	-29.033	114.8328
34	2k SE Gabalong	WA	-30.7266	116.4026
35	16k ESE Moonyoonooka	WA	-	114.916666666667
36	2k SE Gabalong	WA	-30.7500	116.4000
37	41.7k NW Lake Way	WA	-27.1894	120.7867
38	Moresby, Geraldton	WA	-28.7666	114.6167
39	Forrestfield	WA	-31.9833	115.9833
40	Geraldton	WA	-	
41	Waggrakine Pass	WA	-28.7000	114.6667
42	Tallering Peak	WA	-28.1000	115.6333
43	near Walyunga National Park	WA	-31.7333	116.0833
44	Buller River, Geraldton	WA	-28.7666	114.6167
45	Spalding Park, Geraldton	WA	-28.6500	114.6333
46	16K ESE Moonyoonooka	WA	-28.8166	114.9167
47	WA	-		
48	31k W Wiluna	WA	-26.5833	119.9167
49	Yuinmery Station	WA	-28.6166	119.0667
50	Lake Mason Station	WA	-27.6975	119.2800
51	Lorna Glen Station	WA	-26.2625	121.5108
52	Lorna Glen Station	WA	-26.2350	121.2811

1	Lorna Glen Station	WA	-26.1852	121.5644
2	Lake Mason Station	WA	-27.6133	119.5697
3	Lake Mason Station	WA	-27.6877	119.3042
4	Pinnacles Station	WA	-28.3722	120.5831
5	5k E Cunderdin	WA	-31.6500	117.2833
6	5k E Cunderdin	WA	-31.6500	117.2833
7	Greenough area	WA	-28.9333	114.7333
8		WA		
9	Lorna Glen Station	WA	-26.2702	121.4975
10	Lorna Glen Station	WA	-26.2625	121.5108
11	Leonora	WA	-28.8591	121.8036
12	1k N Mulga Downs Outcamp	WA	-22.3175	118.98
13	Ora Banda	WA	-30.3666	121.0500
14	Wiluna	WA	-26.8708	120.4167
15	Bundaburg	Qld	-24.86	152.34
16	Poison Gate road, on road to Poison	NSW	-29.5778	149.2256
17	Shoalwater Bay Army Training Reserve	Qld	-22.6491667	150.4594444

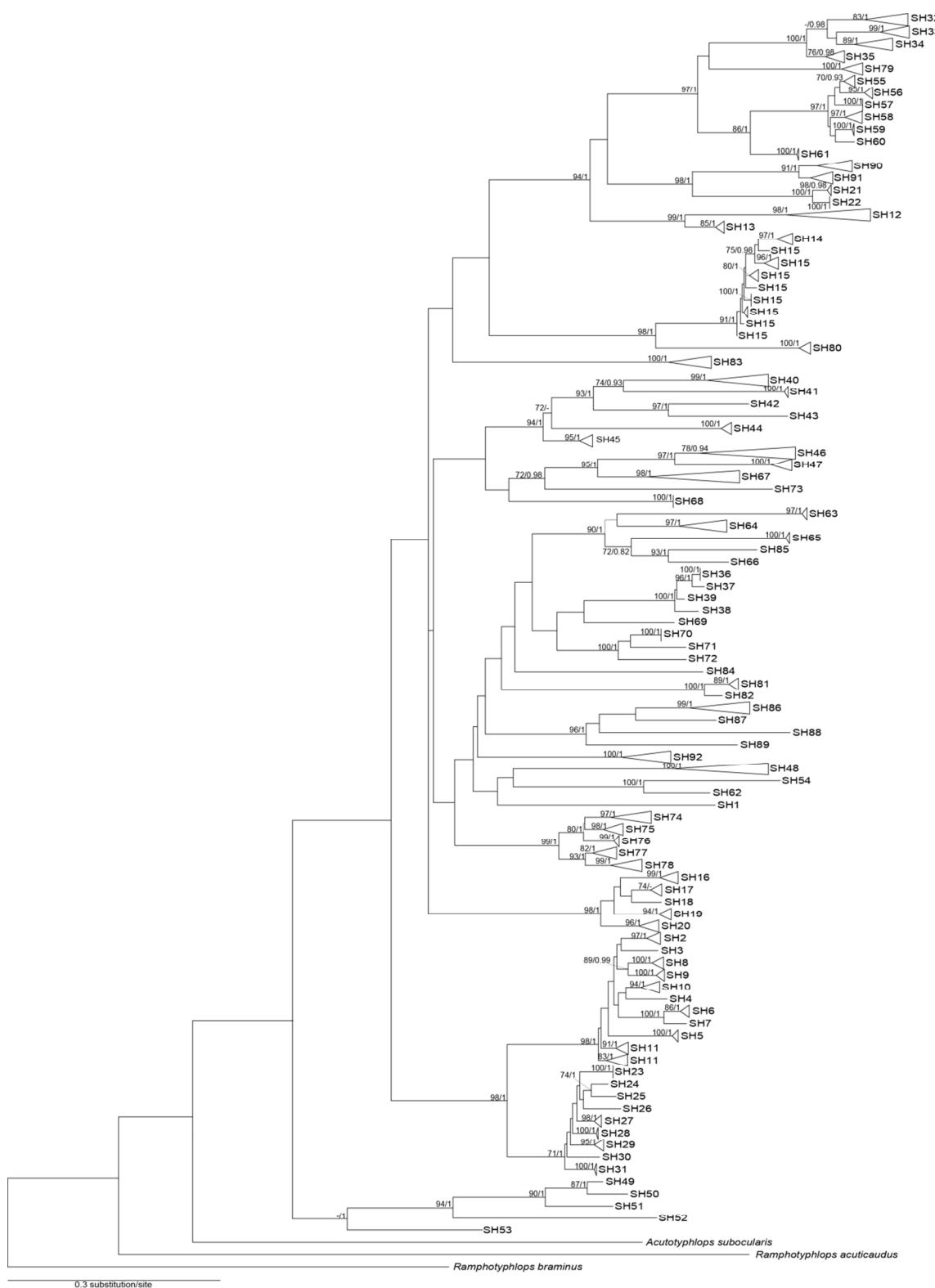


Figure 1. Bayesian inference phylogenetic tree of Australian *Ramphotyphlops* based on analysis of sequences of a mitochondrial protein-coding gene, *cytochrome b*, showing species hypotheses (SHs) obtained with the ABGD method, with bootstraps (>70) and posterior probabilities (>0.9) indicated next to each node

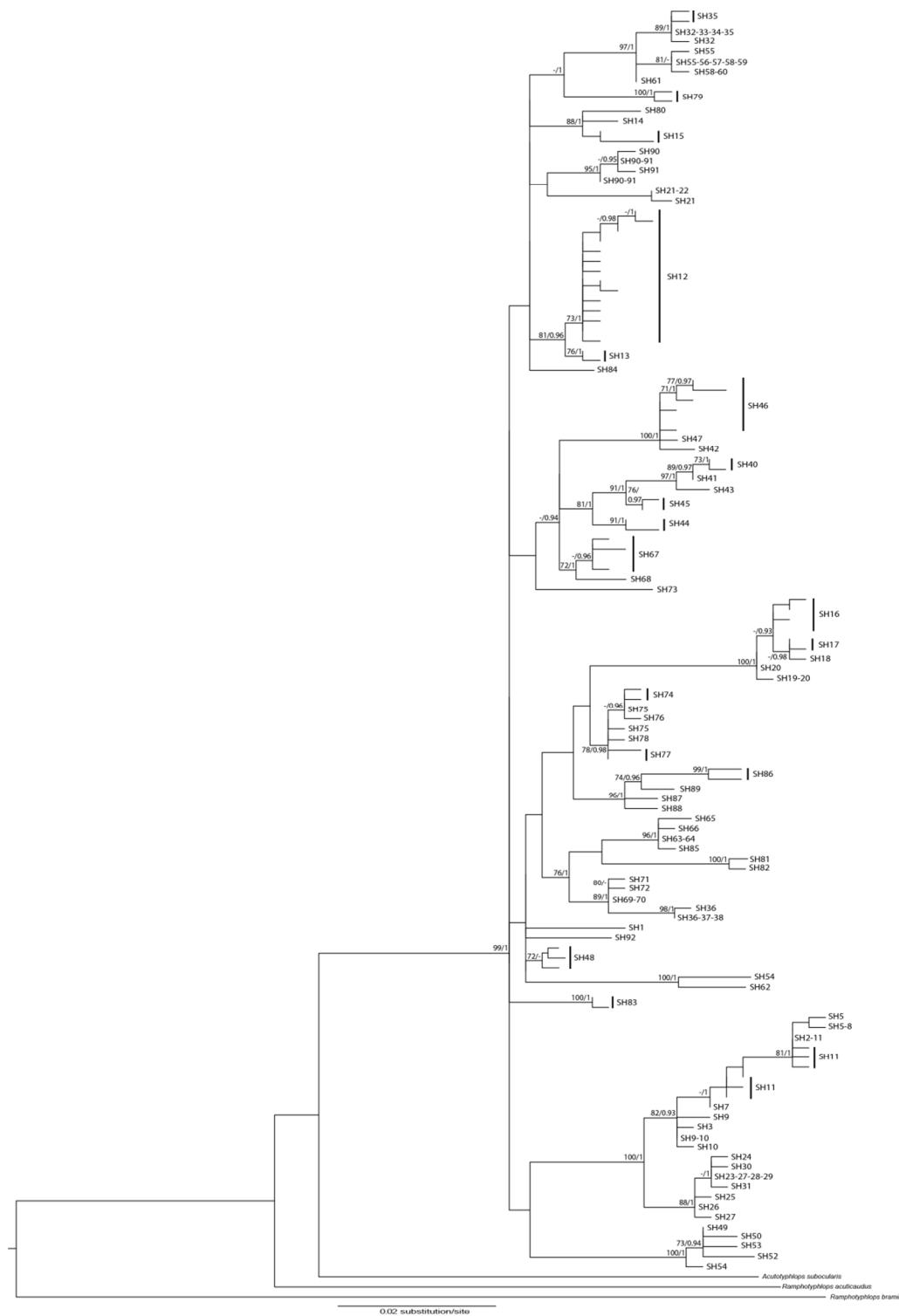


Figure 2. Maximum Likelihood phylogenetic tree of Australian *Ramphotyphlops* based on the analysis of a nuclear protein-coding gene, *prolactin receptor* (*PRLR*). Species hypotheses (SHs) reported here were obtained with the ABGD method using *cytochrome b*. Bootstraps (>70) and posterior probabilities (>0.9) are indicated next to each node.