

# Diversity, complementary distributions and taxonomy of *Rhagada* land snails (Gastropoda : Camaenidae) on the Burrup Peninsula, Western Australia

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**Abstract.** Phylogenetic diversity of *Rhagada* land snails is high on the Burrup Peninsula, Western Australia, with four distinct clades, representing three of the four major clades of the Pilbara region. Detailed sampling indicated little geographic overlap of the four clades, conforming to the general rarity of congeneric sympatry in Australian camaenids. The diversity on the Burrup Peninsula includes three previously unclassified morphotypes. One of these lies within the broad endemic clade of the adjacent Dampier Archipelago, and is provisionally assigned to the island species *R. perprima*, based on phylogenetic evidence. The two other undescribed morphotypes constitute an endemic clade that is the sister group of the broader Dampier Archipelago clade. All COI p-distances within clades are less than 6%, whereas nearly all distances between clades exceed 10%, the gap corresponding to differences among species of *Rhagada* generally. One morphotype in the Burrup Peninsula endemic clade has a low spire and a distinctive keel, and is restricted to a single rockpile. Detailed local sampling revealed gradation between this form and the more widely distributed globose morphotype. On the basis of genetic similarity and morphological continuity, we describe the morphologically variable endemic Burrup Peninsula clade as *Rhagada ngurrana*, sp. nov., which has a distribution spanning only 9 km.

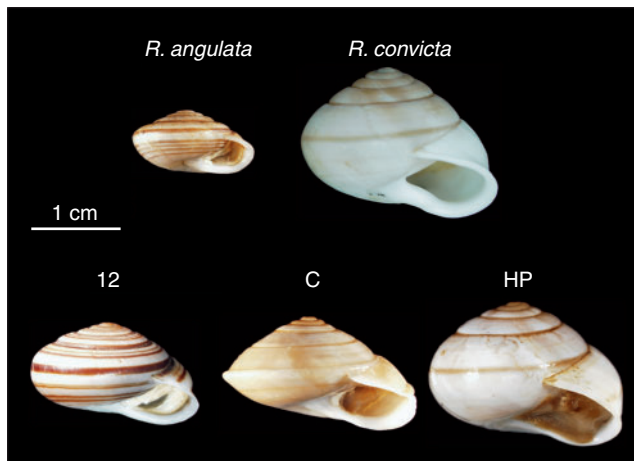
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## Introduction

The Camaenidae are the dominant land snails of northern and eastern Australia, including Western Australia's Pilbara region, where the genus *Rhagada* Albers, 1860, is the most diverse (Solem 1997). Because land snails often exhibit highly local endemism, they are vulnerable to degradation of habitat (Ponder 1997; Harvey 2002), and are a targeted group in the assessment of environmental impacts (Harvey *et al.* 2011). A case in point is on the Burrup Peninsula (20°35'S, 116°48'E), in the Pilbara region of northern Western Australia. The Burrup is an area of substantial resource development, where *Rhagada* snails are widespread, varying in shape, patterning and size of the shell (Stankowski and Johnson 2014). The Burrup was not included in Solem's (1997) major taxonomic revision of *Rhagada*, so this variation has not been formally recognised. In the absence of taxonomic description, three undescribed forms (morphotypes) have been informally recognised (Fig. 1): (1) Morph HP, which has a globose shell that is generally faintly banded, is known from near Holden Point, on the western side of the Burrup, where it aestivates under *Triodia* bushes; (2) the comparatively flat Morph C, which has a distinct peripheral keel, is known only

from near a rockpile at Hearson Cove, on the eastern side of the Burrup; and (3) Morph 12, which has a lower spire than Morph HP, is typically banded, and is widespread on the Burrup, occupying a wide range of habitats. In addition to these undescribed morphotypes, two described species of *Rhagada* are known from the Burrup Peninsula (Fig. 1): *R. angulata* Solem, 1997, which also occurs on islands just north of the Burrup in the Dampier Archipelago (Solem 1997; Stankowski and Johnson 2014), and has been collected from the northern Burrup; and *R. convicta* (Cox, 1870), which is the most widespread mainland species (Solem 1997; Johnson *et al.* 2012), and occurs in the southern Burrup, adjacent to the mainland.

Phylogenetic analysis of mtDNA sequences throughout the geographic range of the genus has revealed four major clades in the Pilbara region, three of which are on the Burrup Peninsula: Clade A is the widespread mainland clade, and is represented by *R. convicta* on the Burrup; Clade C includes only *R. angulata*, which is known from the Burrup and islands immediately to the north; and Clade D comprises all other species in the Dampier Archipelago, and is represented on the Burrup by the undescribed



**Fig. 1.** Examples of the two described species and three undescribed morphotypes of *Rhagada* on the Burrup Peninsula.

morphotypes (HP, C and 12) (Johnson *et al.* 2012; Stankowski and Johnson 2014). These morphotypes in turn represent the two sister groups that divide Clade D. All published mtDNA sequences of the HP morphotype are part of the subclade that occurs throughout most of the Dampier Archipelago. All published sequences of the other morphotypes, Morph C and Morph 12, form Clade D1, which is the sister group of the combined subclades D2, D3 (which includes Morph HP) and D4, and which is apparently restricted to the Burrup (Stankowski and Johnson 2014). In the few specimens examined in the broad-scale comparisons, mtDNA sequences of these two morphotypes (C and 12) were indistinguishable (Johnson *et al.* 2012; Stankowski and Johnson 2014).

In addition to the importance of clarifying the taxonomy of the Burrup forms, the high diversity of distinct forms within a relatively small area is unusual, given that co-occurrence of congeneric species of *Rhagada* and other Australian camaenids is rare (Solem, 1988, 1997; Solem and McKenzie 1991; Cameron *et al.* 2005; Hugall and Stanisic 2011; Gibson and Köhler 2012; O'Neill *et al.* 2014). To resolve the taxonomic status of the forms on the Burrup and to determine their distributions, we examine in greater detail the variation on the Burrup Peninsula, by including a more thorough set of samples and a combination of genetic and morphological analyses. To test the possible usefulness of DNA barcoding for these snails, we examine the frequency distributions of the pairwise sequence differences for the COI (cytochrome c oxidase subunit 1) mitochondrial gene. We also test whether Morphs 12 and C are distinct morphological groups or intergrade. On the basis of these results, we describe the local endemic *Rhagada ngurrana* sp. nov.

## Materials and methods

### Samples

To determine geographic distributions of the five forms, we used all COI sequences of *Rhagada* from the 24 sites on the Burrup Peninsula that were included in earlier genetic comparisons (Johnson *et al.* 2012; Stankowski and Johnson 2014), plus sequences from an additional 22 sites that were included in reports by Biota Environmental Sciences (2006a, 2006b,

2006c) (Table 1; Fig. 2). Previously unpublished sequences have been deposited in GenBank (Accession numbers KT933075–KT933117). In the Biota reports, sequences of the COI gene were generally shorter than those in the published studies. The comparisons here are based on 309 bp, in contrast with the 651 bp used in the broader phylogenetic analyses. The shorter sequences were adequate to assign specimens to previously detected clades.

Previous molecular comparisons indicated close alignment of the Burrup Morph HP with *R. perprima* Iredale, 1939 from nearby islands, but that was based on only two specimens of each form (Johnson *et al.* 2012). To confirm this relationship with the larger sample of Morph HP specimens examined here, we included previously published sequences of COI of *R. perprima* from West Lewis Island, which has the closest known populations of *R. perprima*, and nearby Whittaker, East Malus and Enderby Islands. To maximise sensitivity of these comparisons, we used only the 10 sequences of Morph HP with at least 632 bp. These were compared with one individual from each of the 30 island sites.

In addition to the specimens used for DNA sequencing, further samples of dead shells were collected within 500 m of site HCRP at Hearson Cove (Fig. 2, inset). These were used to determine the spatial extent of Morph C, and whether there was intergradation between Morph C and Morph 12. At each site, shells were collected within a radius of  $\leq 5$  m.

### Analyses

Maximum-likelihood phylogenetic analyses were conducted in MEGA5 (Tamura *et al.* 2011). The main analysis was based on the COI sequences of 161 specimens (Table 1), representing *R. convicta* (from Clade A), *R. angulata* (Clade C) and the undescribed morphotypes (from Clade D), with 1000 bootstrap pseudoreplicates to assess support for the nodes in the tree. The model that best described the evolution of these COI sequences was determined in MEGA as T92+G+I (Tamura 3-parameter, with gamma distribution and invariant sites).

To determine whether there was a clear threshold of genetic distances distinguishing species, the frequency distribution of p-distances was examined for gaps. For these calculations, only the 88 sequences of 651 bp were included to ensure comparability with previously published comparisons. Comparisons within *R. angulata* and *R. convicta* provided a benchmark of conspecific genetic distances, for comparisons with the values within and among the clades of the undescribed morphotypes. To place these comparisons in their broader context, we also calculated the frequency distribution of p-distances among all described species of *Rhagada* from the Pilbara region (based on Johnson *et al.* 2012).

To quantify variation in shell shape, we used the ratio of shell height (H) to shell width (W). Detailed geometric morphometric analysis of the variation of *Rhagada* confirmed that the simple measure of H/W expressed most of the variation of shape (Stankowski 2011).

## Results

Consistent with previous analyses, the maximum-likelihood tree of COI sequences separated the three major clades with

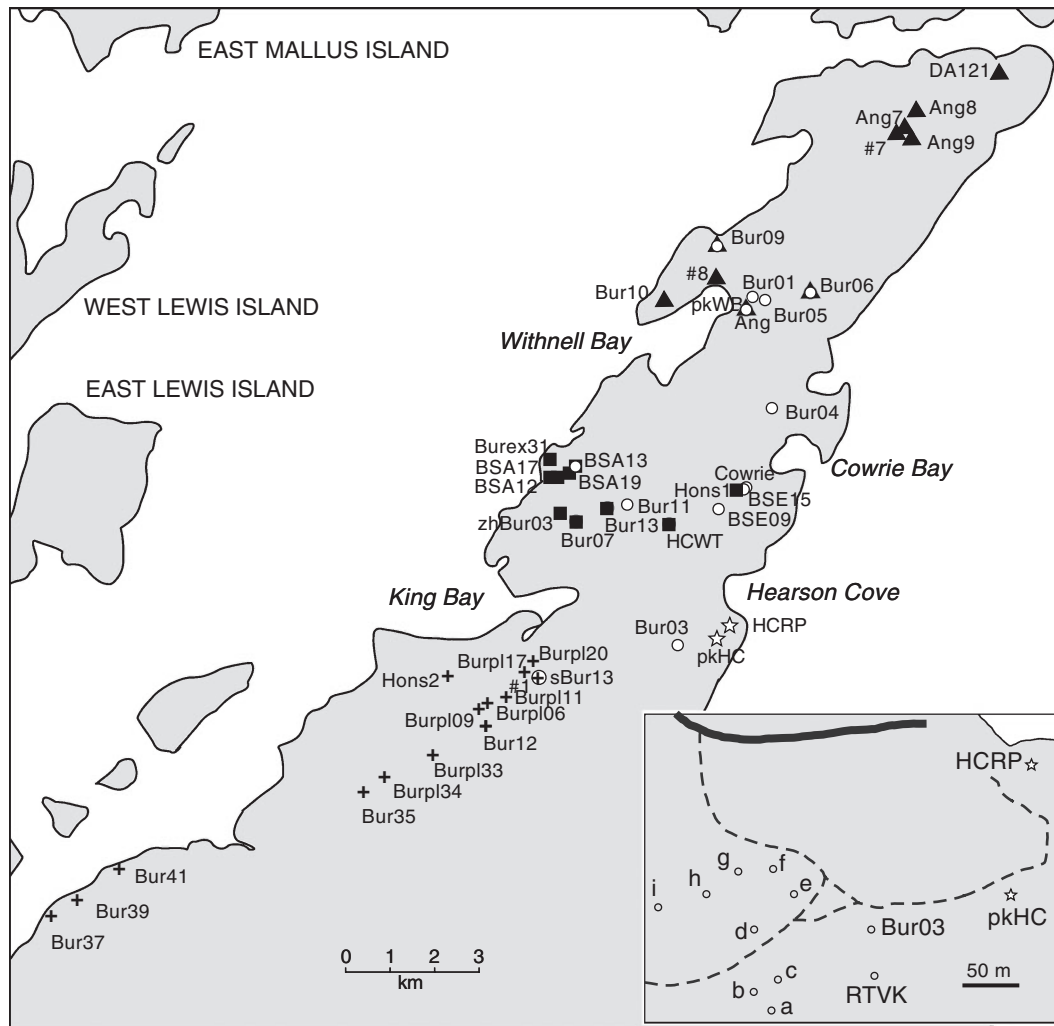
**Table 1. Samples and number of specimens examined for COI sequences**  
Site codes correspond with those in Fig. 2

Site	°S	°E	<i>angulata</i>	<i>convicta</i>	Morph 12	Morph C	Morph HP
DA121	20.52690	116.85545	7				
Ang8	20.53478	116.83781	5				
Ang7	20.53793	116.83512	4				
#7	20.53857	116.83400	2				
Ang9	20.53988	116.83687	5				
Bur09	20.56078	116.79539	3		3		
Bur06	20.57040	116.81550	3		2		
#8	20.57088	116.80112	2				
Bur01	20.57151	116.80260			5		
Bur10	20.57174	116.78403	5				
Ang	20.57206	116.80312	3		5		
Bur05	20.57254	116.80585			5		
pkWB	20.57361	116.80202	1		2		
Bur04	20.59399	116.80706			4		
Burex31	20.60477	116.75958					5
BSA13	20.60639	116.76544			2		1
BSA19	20.60705	116.76407					1
BSA17	20.60766	116.75978					10
BSA12	20.60843	116.76142					1
Cowie	20.61011	116.80077			4		
BSE15	20.61013	116.80073			2		
Hons1	20.61067	116.79972					1
Bur11	20.61360	116.77620			1		
Bur13	20.61418	116.77200					1
BSE09	20.61443	116.79567			1		
zhBur3	20.61548	116.76172					1
Bur07	20.61683	116.76515					2
HCWT	20.61742	116.78523					2
HCRP	20.63456	116.79867				6	
pkHC	20.63622	116.79797				2	
Bur03	20.63849	116.78840			5		
Burpl20	20.64480	116.75625		1			
Burpl17	20.64692	116.75458		1			
Hons2	20.64744	116.73789		2			
#1	20.64833	116.75722			2		
sBur13	20.64835	116.75729		1	4		
Burpl11	20.65185	116.75035		2			
Burpl06	20.65352	116.74635		2			
Burpl09	20.65423	116.74457		1			
Bur12	20.65762	116.74640		5			
Burpl33	20.66312	116.73485		2			
Burpl34	20.66800	116.72460		2			
Bur35	20.67075	116.71979		6			
Bur41	20.68610	116.66756		5			
Bur39	20.69237	116.65863		5			
Bur37	20.69566	116.65329		5			
Total			40	40	47	8	24

high bootstrap support (>90%), and separated the undescribed morphotypes into two clades, referred to as D1 and D3 after Stankowski and Johnson (2014) (Fig. 3). Clade D1 had 99% bootstrap support, and included Morph 12 and Morph C. The Morph C snails did not form a distinct clade, but were mixed with southern populations of Morph 12 (Fig. 3). The Morph HP clade (D3) was well separated from Clade D1, but had lower bootstrap support, at 63%. Support increased to 76% in the separate analysis of Morph HP, based on 632 bp, and that analysis confirmed that Morph HP was within the range of variation of

*R. perprima* from West Lewis, Whittaker and East Malus Islands (Fig. 4).

The average p-distance between Morph HP and *R. perprima* from West Lewis Island was 2.7%. This level of divergence was within the range seen within the four clades on the Burrup Peninsula, in which all distances <6% were within clades (*R. angulata*, *R. convicta*, D1 and D3) (Fig. 5). These within-clade values included comparisons between Morph 12 and Morph C. The frequency distribution of the p-distances on the Burrup showed a gap between 7% and 10% divergence, with a



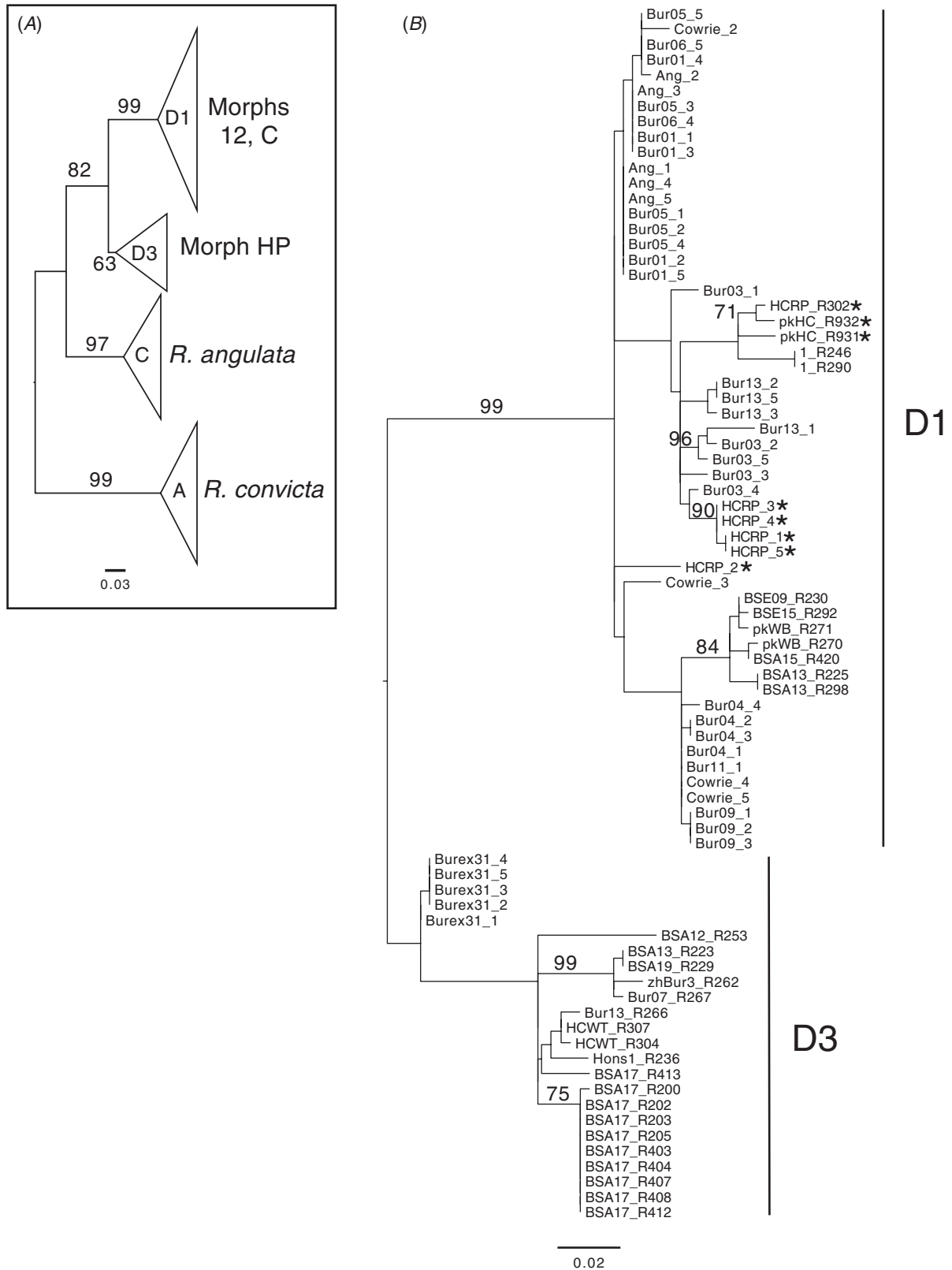
**Fig. 2.** Locations of sample sites on the Burrup Peninsula. Sites are coded by species or morphotype: +, *R. convicta*; triangles, *R. angulata*; squares, Morph HP; circles, Morph 12; star, Morph C. Inset shows sites within 500 m of site HCRP, used for analysis of local variation in shell shape, with the sealed road and unsealed vehicle tracks included for reference.

similar gap centred around 7% in the Pilbara-wide comparisons. On the Burrup, comparisons between the Clades D1 and D3 formed a distinct peak around 11–12% divergence, while higher values were between the three major clades (A, C and D) (Fig. 5).

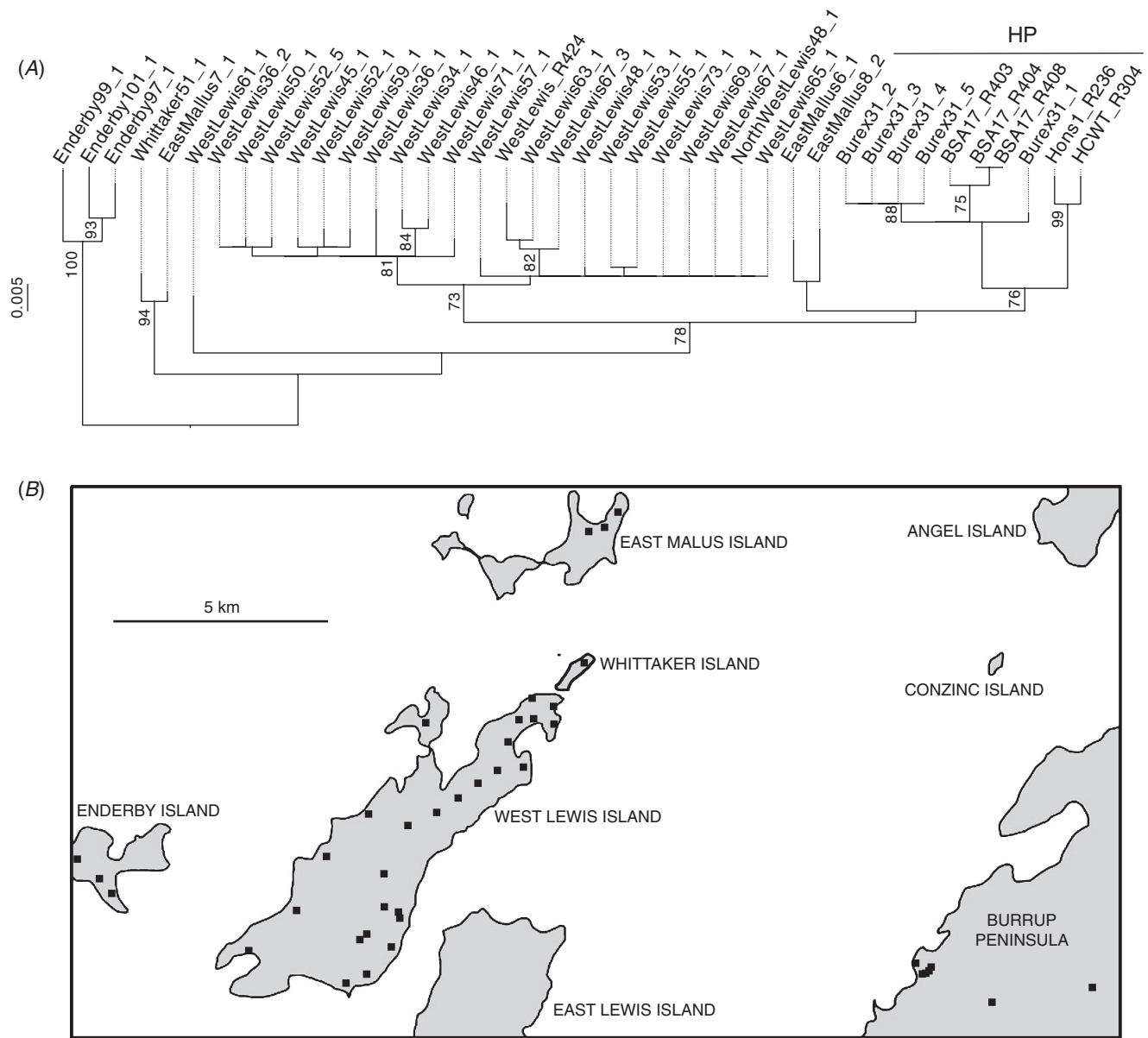
The four clades on the Burrup Peninsula had complementary geographic distributions (Fig. 2). *R. angulata* was found only in the northern portion of the Burrup, from the top of the peninsula to Withnell Bay, whereas the mainland species *R. convicta* was restricted to the southern section, south of King Bay. Clades D1 and D3 occupied the central area, with complementary distributions. Clade D3 extended beyond Holden Point, but was generally more western and southern than Clade D1. The two overlapped at site BSA13, and were found 120 m apart south-west of Cowrie Bay (sites Hons1 and BSE15). Clade D1 extended to north of Withnell Bay, where it was found with *R. angulata* at sites Bur09, Bur06 and Ang, and south-east to Hearson Cove, and then south-west, where it was found with

*R. convicta* at site sBur13 (Fig. 2). The relatively flat-shelled Morph C was found only on and near the rocky hill just south of Hearson Cove (sites HCRP and pkHC). Relative shell height (H/W) in Morph C averaged 0.53, compared with 0.67 in Morph 12, with little overlap in the ranges (Fig. 6A). However, in samples of shells collected 300–500 m from site HCRP, there was a large range of intermediate shells, showing continuity between the morphotypes (Fig. 6B).

On the basis of this continuity, we refer to Clade D1 as *R. ngurrana*, sp. nov. Variation in the shape of this new species spanned nearly the range of all four species on the Burrup (Figs 7, 8). It shared relatively flat shells with *R. angulata*, which was much smaller, while the taller shells overlapped with those of Morph HP and the tallest species, *R. convicta*. As detailed in the taxonomic section, a similar result was found for reproductive anatomy, for which the Morph 12 and Morph C were indistinguishable, distinct from *R. angulata* and *R. convicta*, but not distinctly different from Morph HP.



**Fig. 3.** Phylogenetic relationships among COI haplotypes in *Rhagada* from the Burrup Peninsula. (A) Relationships among *R. convicta*, *R. angulata*, D1 (Morphs 12 and C) and D3 (Morph HP); Clades A, C and D refer to major clades found in the large-scale analysis (Johnson *et al.* 2012). (B) Relationships within Clade D on the Burrup Peninsula. Site codes are as in Fig. 2 and Table 1. stars, Morph C.



**Fig. 4.** (A) Maximum-likelihood tree of COI haplotypes of Morph HP from the Burrup Peninsula and *R. perprima* from West Lewis, Whittaker, East Malus and Enderby Islands. (B) Location of sites for this analysis.

## Discussion

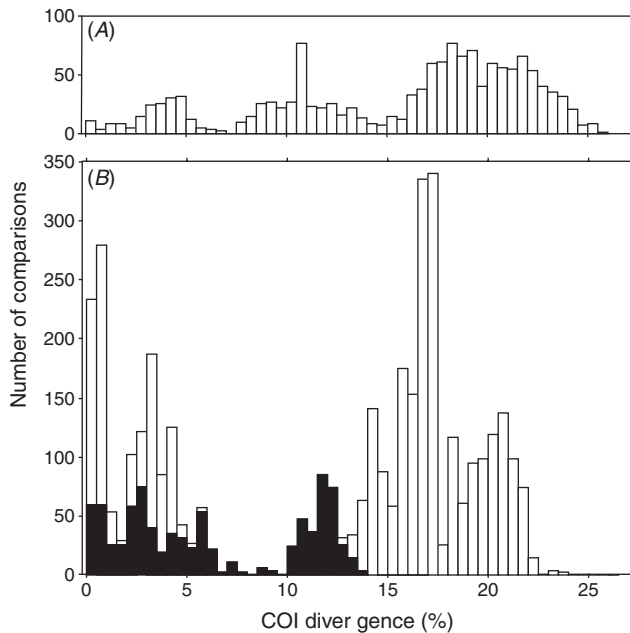
The additional samples examined here confirm that the four lineages of *Rhagada* on the Burrup Peninsula are geographically distinct, with complementary geographic distributions, as previously reported by Stankowski and Johnson (2014) based on sparser sampling. Our comparisons also illustrate the disconnection between morphological and molecular divergence that is a striking feature of *Rhagada* from the Dampier Archipelago (Johnson *et al.* 2004, 2012; Stankowski and Johnson 2014). This is evident as morphological variation within Clade D1 and its overlap with Clade D3 (Fig. 8). The inclusion of the distinctive Morph C in

the same clade as Morph 12 is an example of the evolutionary potential within a genetically tight group. Morph C is one of the flattest forms of *Rhagada*, and it and *R. dampierana* Solem, 1997, are the only forms with a distinct peripheral keel. Like *R. dampierana*, Morph C has evolved locally in a rocky habitat, from taller-spined conspecifics, which is a highly repeated pattern of flatter shells associated with rocky habitats in the Dampier Archipelago (Stankowski 2015). On the other hand, the morphological overlap of Clade D1 with Clade D3 highlights the lack of consistent differences in shell form between species. This similarity also parallels the findings in other parts of the Dampier Archipelago, in which some shells of different species are indistinguishable: snails that appear to be *R. angulata* on the

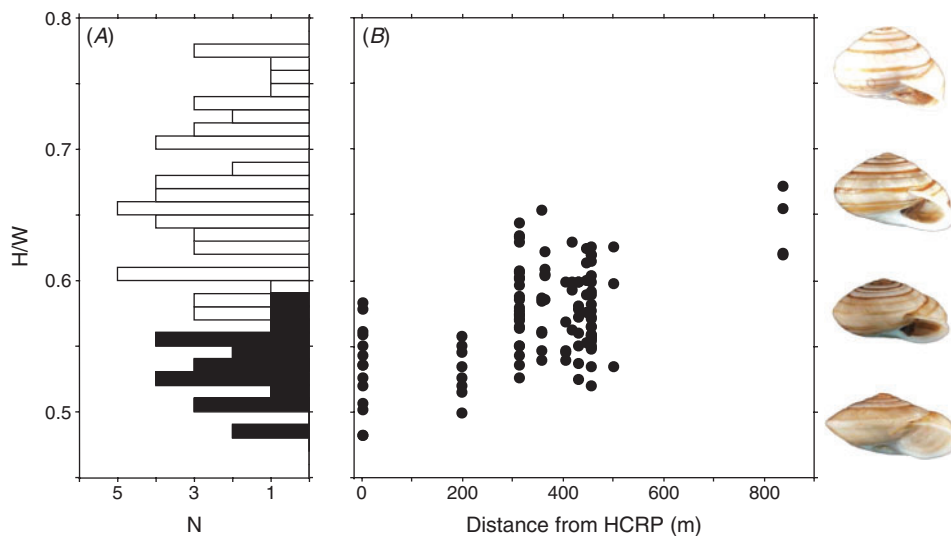
basis of shell form are split between the major Clades C (*R. angulata*) and D (the main Dampier Archipelago clade); the shell form of *R. perprima* has also evolved independently in Clades A (*R. convicta*) and D (Stankowski and Johnson 2014). Examination of genitalia also failed to reveal consistent distinctions between *R. ngurrana*, sp. nov. and Morph HP (see Taxonomy section). This similarity is not unusual, however, as reproductive anatomy is generally conservative in

*Rhagada* in the Pilbara region (Solem 1997), including among distinctive morphotypes in the Dampier Archipelago (Stankowski 2011) and even between morphologically and genetically divergent mainland species (Hamilton and Johnson 2015). In the context of the undescribed morphotypes on the Burrup, the morphological inconsistencies mean that the primary taxonomic evidence must come from the DNA sequences.

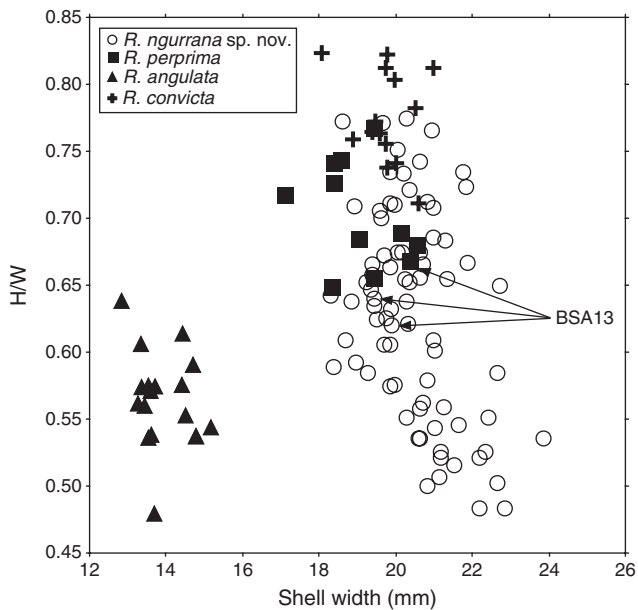
Clades D1 and D3 were found together only at site BSA13, with two and one individuals, respectively. The few individuals in that sample, combined with the otherwise mutually exclusive distributions, means that direct application of the biological species concept is not possible with the present data. Interpretations based on phylogeny and genetic distinctness, however, are clear and consistent. Although the level of COI divergence between Clades D1 and D3 is not as great as that between *R. angulata* and *R. convicta*, it is much higher than that within either of those species. This confirms the preliminary observation in the broad-scale phylogenetic study (Johnson *et al.* 2012), which included only eight snails from the Burrup, that the level of divergence between the two clades with the Burrup morphotypes was greater for the combined COI and 16S genes than between the mainland species *R. convicta*, *R. pilbarana*, *R. radleyi* and *R. richardsonii* in Clade A, between *R. capensis*, *R. globosa* and *R. torulus* in Clade B, and between *R. dominica*, *R. felicitas* and *R. primigena* from the Kimberley region. The Kimberley species *R. kessneri* and *R. primigena* also differ by 11% for COI, whereas p-distances within species were less than 5% for all five species of *Rhagada* examined by Köhler (2011). There is a similar gap in genetic distances among *Rhagada* throughout the Pilbara region (Fig. 5A). Thus, in the context of *Rhagada* broadly, the genetic evidence clearly indicates that *R. ngurrana*, sp. nov. and Morph HP are separate species (distinct phylogenetic and genetic groups), with levels of mtDNA divergence as high as between other species in the genus.



**Fig. 5.** Frequency distributions of pairwise distances among COI haplotypes. (A) Comparisons among all Pilbara species of *Rhagada* (Johnson *et al.* 2012). (B) Comparisons from the Burrup Peninsula (this study); filled segments indicate comparisons among Morphs 12, C and HP.



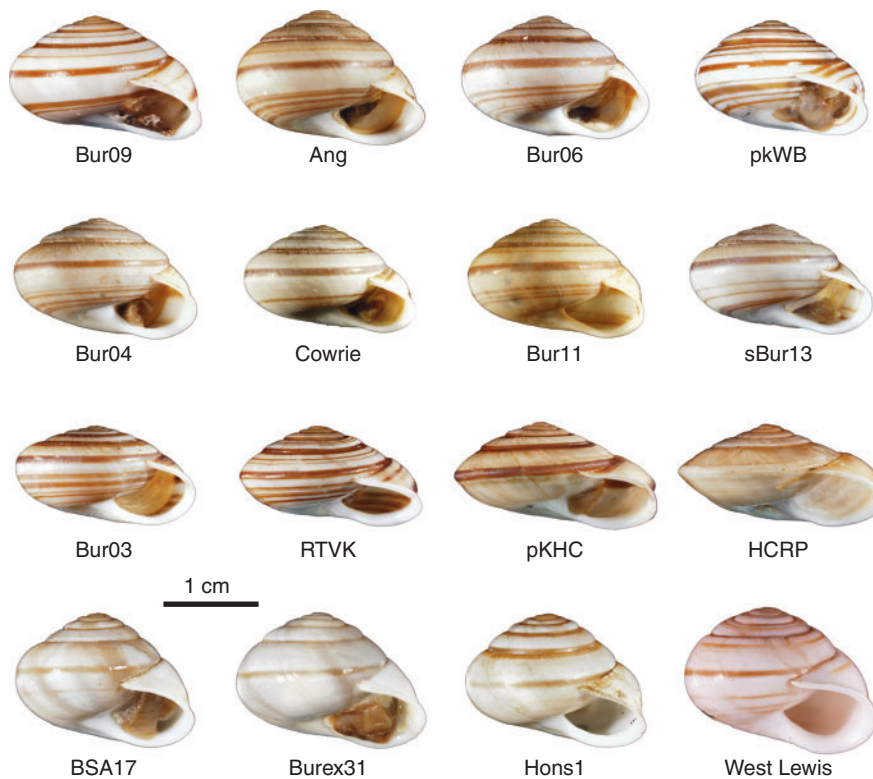
**Fig. 6.** Ratio of shell height to width in Morphs 12 and C. (A) Frequency distribution of H/W in Morph 12 (open segments) and Morph C (filled segments), excluding the extra shell-only samples near Hearson Cove (Fig. 2, inset). (B) Variation in shape within 900 m of the rockpile at site HCRP.



**Fig. 7.** Variation of shape and size of shells in the four COI clades on the Burrup Peninsula. Included are all specimens of *R. ngurrana*, sp. nov. (Morphs 12 and C) in Fig. 6A, sympatric populations of *R. angulata* (sites Ang and Bur09) and *R. convicta* (Bur 11), and Morph HP (*R. perprima*) from sites BSA13 and BSA17. Arrows indicate sympatric *R. ngurrana*, sp. nov. and *R. perprima* from BSA13.

Clade D1 (i.e. *Rhagada ngurrana*, sp. nov.) is endemic to the Burrup Peninsula. The genetic evidence, which is consistent with shell morphology (Fig. 8), indicates that Morph HP lies within *R. perprima*, a widespread species in the Dampier Archipelago. Nevertheless, this placement is provisional, pending taxonomic revision of *Rhagada* throughout the Dampier Archipelago. Substantial revision is needed, because the morphological forms that were the basis for Solem's (1997) description of six species endemic to these islands intergrade in some places, and have evolved independently multiple times (Stankowski 2011, 2013; Stankowski and Johnson 2014).

From a broader perspective, the Burrup Peninsula has the highest phylogenetic diversity of *Rhagada* of any similar area, with three of the four major clades of Pilbara species, and the two sister clades of Clade D. The Burrup endemic *R. ngurrana*, sp. nov. is the geographic complement and sister group of the rest of Clade D, but it is phylogenetically much less diverse (Stankowski and Johnson 2014). The divergence time between *R. ngurrana*, sp. nov. and the rest of Clade D was ~720 thousand years ago (95% CI=343–1092) (Köhler and Criscione 2013). During this period the Dampier Archipelago has coalesced and reformed many times, because of changes in sea level, but the major portion of the Burrup occupied by *R. ngurrana*, sp. nov. is too high to have been fragmented. This continuity, in contrast to the repeated fragmentation and fusion of much of the Dampier Archipelago, could explain the relatively low phylogenetic diversity of the Burrup endemic,



**Fig. 8.** Representative specimens of *Rhagada ngurrana*, sp. nov. (clade D1; top three rows) and *R. perprima* (clade D3; bottom row). The specimen at bottom right is *R. perprima* from West Lewis Island. All other codes are as in Fig. 2.



compared with the more widely distributed island clade within Clade D.

Despite having deep lineages in a relatively small area, *Rhagada* species on the Burrup Peninsula conform to the usual pattern of Australian camaenids, whereby congeneric species have non-overlapping geographic distributions, and are found in sympatry only at the edges of their distributions. This is despite the clear historical potential for geographic overlap. Beyond the Burrup Peninsula, the major clades have geographically complementary distributions, which meet on the Burrup (Johnson *et al.* 2012; Stankowski and Johnson 2014). The mainland species *R. convicta* (Clade A) has come from the south, and the island endemics *R. angulata* (Clade C) and *R. perprima* (Clade D) from the north and west, respectively, but they have maintained non-overlapping distributions, each

parapatric with *R. ngurrana*, sp. nov. The parapatric distributions on the Burrup add to recent evidence that the widespread lack of congeneric sympatry of camaenids is not due simply to isolation in allopatry, without secondary contact (Johnson *et al.* 2013; Hamilton and Johnson 2015; Taylor *et al.* 2015). The two species of *Rhagada* with the greatest overlap on the Burrup were locally separated by microhabitat, with *R. angulata* found on rocks and *R. ngurrana*, sp. nov. on adjacent soil. Combined with the recent finding of separation by microhabitat in *Strepsitaurus* in the Cape Range (Taylor *et al.* 2015), this local segregation indicates the importance of habitat and possibly competitive interactions in determining the parapatric boundaries of the complementary geographic distributions. Indeed, the relatively flat Morph C of *R. ngurrana*, sp. nov. occupies rocky habitat, in the absence of other species. This perspective raises the question of whether the distribution of *R. ngurrana*, sp. nov. has been restricted by the other species, which could account for its confinement to the Burrup Peninsula, despite repeated historical connections to the mainland and the rest of the Dampier Archipelago, but direct evidence is needed to test this possibility.

### Taxonomy

Family **Camaenidae** Pilsbry, 1895

Genus ***Rhagada*** Albers, 1860

*Rhagada* Albers, 1860: 108–109.

***Rhagada ngurrana***, sp. nov.

(Figs 1–3, 6–11; Tables 1, 2)

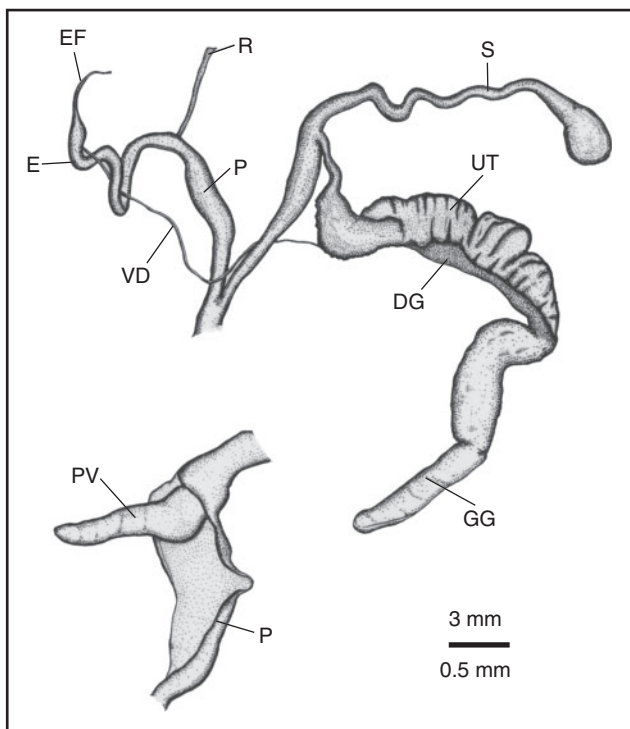
<http://zoobank.org/urn:lsid:zoobank.org:act:645D2BAF-7AA3-4B2A-8F5F-4E98DB649DBE>

*Rhagada* spp. 12, C, HC Johnson *et al.*, 2012: 319; Stankowski & Johnson, 2014: 2.

### Material examined

**Holotype.** Western Australian Museum (WAM) S67883. W = 19.9 mm, H = 12.0 mm, H/W = 0.60, Withnell Bay, site pkWB, Murujuga National Park, Burrup Peninsula, Western Australia (WA), Australia, 20°34'25.0"S, 116°48'07.3"E, P. Kendrick, 4.vi.2002.

**Paratypes.** Burrup Peninsula, WA, Australia. WAM S67896, 6 specimens (19.9–21.0 mm W, 13.9–14.9 mm H, 0.67–0.74 H/W), site Bur09, 20°33'38.8"S, 116°47'43.4"E, M. Greenham, P. Runham, 18.v.2006. WAM S67883, 6 specimens (19.1–21.8 mm W, 13.2–15.8 mm H, 0.66–0.77 H/W), site Bur06, 20°34'13.4"S, 116°48'55.8"E, M. Greenham,



**Fig. 9.** Reproductive system (top) and penial anatomy (bottom) of *Rhagada ngurrana*, sp. nov. Abbreviations: GG, albumen gland; UT, uterus; DG, prostate; UV, oviduct; S, spermatheca; V, vagina; P, penis; E, epiphalus; VD, vas deferens; EF, epiphalic flagellum; PV, penial verge.



**Fig. 10.** Holotype of *Rhagada ngurrana*, sp. nov.



**Fig. 11.** Examples of live specimens of the (A) Morph 12 and (B) Morph C forms of *Rhagada ngurrana*, sp. nov., on artificial substrates. (C) Rockpile at Hearson Cove, where Morph C was found, showing predominance of buffel grass on the adjoining flat.

P. Runham, 17.v.2006. WAM S67885, 3 specimens (18.0–19.4 mm W, 12.6–13.4 mm H, 0.65–0.77 H/W), same collection data as holotype. WAM S67886, 2 specimens (19.4–19.8 mm W, 12.3–12.4 mm H, 0.63–0.63 H/W), site BSA13, 20°35'53.3"S, 116°45'55.6"E, Z. Hamilton, P. Runham, 5.iii.2006. WAM S67887, 1 specimen (19.8 mm W, 12.4 mm H, 0.63 H/W), site BSE15, 20°36'06.8"S, 116°48'02.7"E, Z. Hamilton, P. Runham, 7.iii.2006. WAM S67888, 1 specimen (21.4 mm W, 14.1 mm H, 0.66 H/W), site BSE09, 20°36'22.3"S, 116°47'44.4"E, Z. Hamilton, P. Runham, 7.iii.2006. WAM S67889, 14 specimens (20.7–23.9 mm W, 10.7–13.2 mm H, 0.48–0.58 H/W), site HCRP, 20°38'04.4"S, 116°47'55.2"E, Z. Hamilton, 22.ix.2005. WAM S67891, 4 specimens (19.0–20.6 mm W, 10.9–13.3 mm H, 0.57–0.64 H/W), site Bur03, 20°38'11.2"S, 116°47'47.1"E, M. Johnson, P. Kendrick, R. Teale, 21.i.2006. WAM S67893, 3 specimens (19.8–20.8 mm W, 11.2–11.6 mm H, 0.54–0.57 H/W), site RTVK, 20°38'13"S, 116°47'47"E, R. Teale, V. Kessner, 15.ix.2009. WAM S67892, 1 specimen (18.9 mm W, 12.0 mm H, 0.64 H/W), site #1, 20°38'54.0"S, 116°45'26.12"E, M. Johnson, P. Kendrick, R. Teale, 21.i.2006. WAM S67890, 8 specimens (20.6–21.7 mm W, 10.4–11.8 mm H, 0.50–0.56 H/W), site pkHC, 20°38'10.4"S, 116°47'52.7"E, P. Kendrick, 4.vi.2002. WAM S67881, 2 specimens (18.7–19.3 mm W, 11.3–11.4 mm H, 0.58–0.61 H/W), site Burpl11, 20°39'06.7"S, 116°45'01.3"E, R. Teale, 14.vii.2006.

#### *Description (based on 110 measured adults)*

Shell (Figs 1, 8, 10) large, adult width 18.6–23.9 mm (mean 20.6, s.d. 1.2 mm), with  $4\frac{3}{4}$  to 6 (mean  $5\frac{1}{2}$ ) normally coiled whorls. Shell height variable, 10.4–15.8 mm (mean 12.5, s.d. 1.5 mm). Apex and spire elevated to moderately depressed, H/W ratio 0.48–0.77 (mean 0.61, s.d. 0.08). Spire and body whorl

variable in shape from rounded to sharply angled; occasionally with thickened keel at the periphery of the body whorl. Shell smooth, light in colour with a strong rust-coloured peripheral band and with 1–6 subperipheral and supraproperipheral bands; subperipheral bands unusually wider and more numerous. Umbilicus closed by a columellar callus in most specimens, but occasionally open as a narrow lateral crack. Aperture slightly to greatly expanded.

Genitalia (Fig. 9) with a short to long albumen gland and long prostate. Spermatheca unkninked, long,  $\sim 1\frac{1}{2}$  times the length of the uterus (Fig. 9). Vagina widest near centre, long,  $\sim 1\frac{1}{4}$  times the length of the penis. Epiphallus long, tapering into a long and slender epiphallic flagellum. Penial verge with smooth surface, very long ( $\frac{3}{4}$  length of the penis) and tapering. Interior penial wall smooth.

#### *Comparative remarks*

*Rhagada ngurrana*, sp. nov. is one of four congeneric species that inhabit the Burrup Peninsula. Shells of *R. ngurrana*, sp. nov. are generally flatter, with less banding than those of *R. perprima*, but the two species are not always distinguishable based on the width, height, shape (H/W), and colour and pattern of banding (Figs 7, 8). The reproductive system is also of limited use in distinguishing *Rhagada ngurrana*, sp. nov. from *R. perprima*. Although individuals of *Rhagada ngurrana*, sp. nov. tend to have a thinner epiphallic caecum and longer spermatheca than *R. perprima*, neither of these characters is diagnostic, and most traits do not vary between the species. Given that *Rhagada ngurrana*, sp. nov. and *R. perprima* occupy different areas of the Burrup Peninsula, with *R. perprima* restricted to a relatively small area near Holden Point (20°36'10.9"S, 113°54'19.6"E), sampling location can be useful for taxonomic inference. However, when the sampling location is unknown, or samples are collected close to range margins, genetic analysis is needed for confident taxonomic placement.

Although *Rhagada ngurrana*, sp. nov. and *R. convicta* cannot always be distinguished based on shell size or shape, they can be distinguished based on other phenotypic variables. First, the shells of *R. convicta* are markedly thicker and more robust than those of *R. ngurrana*, sp. nov., and tend to have fewer, fainter bands. Second, *R. ngurrana*, sp. nov. and *R. convicta* have distinct penial anatomy. *Rhagada ngurrana*, sp. nov. has a long, tapering penial verge, nearly three-quarters the length of the penis, while *R. convicta* has a small triangular verge with a corrugated surface. Third, in most cases, samples may be identified based on geography, as *R. ngurrana*, sp. nov. and *R. convicta* have largely non-overlapping distributions. The mainland species *R. convicta* is restricted to the southern Burrup (south of 20°38'54.1"S), whereas *R. ngurrana*, sp. nov. is found to the north. The two species have been found in sympatry at one location (20°38'54.1"S, 116°45'26.2"E).

The range of the fourth species of *Rhagada* on the Burrup Peninsula, *R. angulata*, has a greater overlap with that of *R. ngurrana*, sp. nov. These species occur in sympatry at several sites but are easily distinguished based on shell morphology, as *R. angulata* has much smaller shells than those of *R. ngurrana*, sp. nov. If required, the species may also be

**Table 2.** Mean ( $\pm$  s.d.) shell measurements in *Rhagada ngurrana*, sp. nov. Sites are listed from north to south, and codes correspond to those in Table 1 and Fig. 2. 'Mixed' refers to the shell-only samples near Hearson Cove (Fig. 2, inset). H, shell height; W, shell width

Site	Morph	N	W	H	H/W
Bur09	12	6	20.66 $\pm$ 0.42	14.57 $\pm$ 0.52	0.706 $\pm$ 0.024
Bur06	12	6	20.35 $\pm$ 0.85	14.39 $\pm$ 0.99	0.707 $\pm$ 0.041
Bur05	12	3	20.09 $\pm$ 0.07	14.06 $\pm$ 0.88	0.700 $\pm$ 0.045
pkWB	12	4	19.04 $\pm$ 0.36	13.27 $\pm$ 0.81	0.698 $\pm$ 0.056
BSA13	12	2	19.62 $\pm$ 0.47	12.38 $\pm$ 0.12	0.632 $\pm$ 0.009
BSE15	12	1	22.62	14.77	0.653
BSE09	12	1	21.36	14.09	0.660
Cowrie	12	8	19.43 $\pm$ 0.87	12.10 $\pm$ 0.97	0.622 $\pm$ 0.032
Bur11	12	1	20.96	16.05	0.766
HCRP	C	14	21.92 $\pm$ 0.98	11.69 $\pm$ 0.74	0.534 $\pm$ 0.032
f	Mixed	5	19.97 $\pm$ 0.89	12.09 $\pm$ 0.69	0.605 $\pm$ 0.013
g	Mixed	5	19.63 $\pm$ 0.95	10.98 $\pm$ 0.48	0.560 $\pm$ 0.024
h	Mixed	6	20.03 $\pm$ 0.91	11.90 $\pm$ 0.87	0.593 $\pm$ 0.026
e	Mixed	4	19.37 $\pm$ 0.43	11.37 $\pm$ 0.74	0.588 $\pm$ 0.047
i	Mixed	3	19.28 $\pm$ 0.77	11.30 $\pm$ 0.92	0.586 $\pm$ 0.047
pkHC	C	8	20.99 $\pm$ 0.48	11.16 $\pm$ 0.40	0.532 $\pm$ 0.020
d	Mixed	4	19.70 $\pm$ 0.86	11.75 $\pm$ 0.82	0.596 $\pm$ 0.028
Bur03	Mixed	24	19.73 $\pm$ 0.80	11.51 $\pm$ 0.63	0.584 $\pm$ 0.032
c	Mixed	9	19.55 $\pm$ 0.55	11.09 $\pm$ 0.64	0.567 $\pm$ 0.026
RTVK	Mixed	3	20.30 $\pm$ 0.53	11.39 $\pm$ 0.16	0.562 $\pm$ 0.023
b	Mixed	16	19.92 $\pm$ 0.78	11.37 $\pm$ 0.73	0.571 $\pm$ 0.028
a	Mixed	9	19.17 $\pm$ 0.94	11.11 $\pm$ 0.62	0.580 $\pm$ 0.028
#1	12	1	18.93	12.01	0.638
Bur13	12	8	20.10 $\pm$ 0.73	14.08 $\pm$ 1.99	0.700 $\pm$ 0.095
Burpl11	12	2	18.98 $\pm$ 0.57	11.32 $\pm$ 0.12	0.597 $\pm$ 0.024

distinguished based on reproductive anatomy: *Rhagada angulata* has a dome-shaped verge and sharply kinked spermatheca, which contrasts with the long, tapered verge and non-kinked spermatheca of *R. ngurrana*, sp. nov.

#### Distribution

Despite extensive surveys on the surrounding islands of the Dampier Archipelago (Stankowski and Johnson 2014), *Rhagada ngurrana*, sp. nov. has been found only on the Burrup Peninsula.

#### Conservation significance

Short-range endemism of *R. ngurrana*, sp. nov. in an area of substantial resource development highlights the need to consider its conservation. The known distribution spans only 9 km, with an area of roughly 60 km<sup>2</sup>. The large morphological variation over that small distribution indicates the significance of this species for understanding the evolution of *Rhagada* snails. Of special significance is the relatively flat Morph C, known only within 200 m of the rockpile at Hearson Cove, and any sign of that morphotype is absent beyond 500 m (Fig. 11). Our searches for *R. ngurrana*, sp. nov. indicate that it is scarce in areas dominated by the invasive buffel grass (*Cenchrus ciliaris*), which is widespread in the Hearson Cove area (Fig. 11), and which appears to have locally replaced areas of native spinifex (*Triodia*) hummock grasslands. *Rhagada* aestivates beneath *Triodia* hummocks, but not within buffel grass tussocks.

#### Etymology

After *ngurra*, the word in the language of the Ngarluma people meaning land, country or home, offered to the authors by the Murujuga Circle of Elders as an appropriate name for this species from the Murujuga area, the traditional home of the Jaburara tribe.

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