



## REVIEW ARTICLE

### Extreme morphological diversity in a single species of *Rhagada* (Gastropoda: Camaenidae) in the Dampier Archipelago, Western Australia: review of the evidence, revised taxonomy and changed perspective

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## ABSTRACT

In the Dampier Archipelago, Western Australia, land snails of the genus *Rhagada* are exceptional in two respects: (1) they show greater morphological diversity over distances of less than 70 km than does the rest of the genus over distances of up to 2,000 km; (2) the island morphospecies have complex, interspersed distributions, contrasting with the simple, broad-scale allopatric replacement of mainland species. Based largely on shell characteristics, this local diversity is currently recognized to encompass six species endemic to the Dampier Archipelago. We review here molecular and morphological evidence to show that almost all the diversity is attributable to a single, highly diverse species: the morphospecies are polyphyletic, are genetically very similar and do not form distinct genetic groups; furthermore, they are not morphologically distinct, but grade into one another. On this basis, we synonymize *Rhagada dampierana* Solem, 1997, *R. intermedia* Solem, 1997, *R. minima* Solem, 1997, *R. perprima* Iredale, 1939 and part of *R. angulata* Solem, 1997 (all from the Dampier Archipelago) and *R. plicata* Preston, 1914 (from Barrow Island and the Montebello and Lacepede Islands) under the earliest available name, *R. elachystoma* (Martens, 1877). Morphological variation in this inclusive *R. elachystoma* exceeds that in the rest of the genus. From this new perspective we discuss the origins and maintenance of extreme morphological diversity within a single species in the Dampier Archipelago.

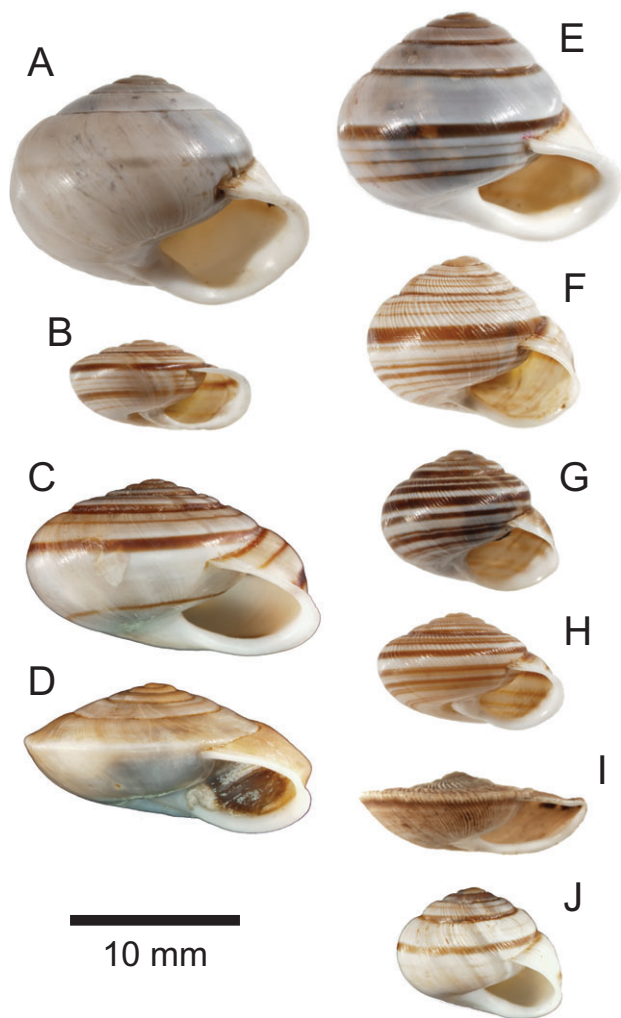
## INTRODUCTION

Taxonomic perspective is fundamental to understanding biological diversity, because taxonomy provides the framework for asking questions. For example, molecular evidence has led to an exponential increase in the discovery of morphologically cryptic species over the past 40 years, raising questions of the basis for morphological conservatism and posing problems for species conservation (Bickford *et al.*, 2006). On the other hand, recognition that what had been considered morphologically distinct species are actually conspecific changes the focus of evolutionary studies from questions of speciation to questions of mechanisms that generate and maintain diversity within species, as highlighted by recent contrasting perspectives on Darwin's finches (McKay & Zink, 2015; Cadena, Zapata & Jimenez, 2018).

These issues are widespread in snails, for which much of the taxonomy has been based on shells. For example, in the Western Australian camaenid genus *Amplirhagada*, molecular-genetic analyses have revealed eight species in what had been considered a single subspecies on the basis of shells, changing our geographic perspective of speciation and highlighting the morphological

conservatism in this group (Köhler & Johnson, 2012). In contrast, there are many examples of the evolutionary plasticity of shells, raising doubts about any taxonomy based solely on shell morphology (e.g. Gould & Woodruff, 1978; Murray & Clarke, 1980; Johnson & Black, 1999; Teshima *et al.*, 2003; Walther, Neiber & Hausdorf, 2016; Chueca *et al.*, 2017; Reijnen & van der Meij, 2017; Uit de Weerd & Velazquez, 2017).

An example of the importance of taxonomic perspective is the extreme morphological diversity in the camaenid genus *Rhagada* in the Dampier Archipelago, in Western Australia's Pilbara Region (Fig. 1). In the context of *Rhagada*, the forms in the Dampier Archipelago are exceptional in two respects (Solem, 1997; Johnson *et al.*, 2012). First, the diversity of shells in terms of size, shape and sculpture is greater in this small area, spanning 70 km, than that in the rest of the genus, distributed over 2,000 km. Second, the distributions of the shell forms are scattered across the Archipelago, without a clear allopatric pattern; this contrasts with the mainland species, which show allopatric replacement of one another, typically with distributions spanning 150 km or more (Solem, 1997).



**Figure 1.** Representatives of the described morphospecies of *Rhagada* in the Dampier Archipelago and *R. plicata* from the Montebello Islands. **A.** *R. convicta*. **B.** *R. angulata*. **C.**, **D.** *R. ngurrana*. **E.** *R. perprima*. **F.** *R. elachystoma*. **G.** *R. intermedia*. **H.** *R. minima*. **I.** *R. dampierana*. **J.** *R. plicata*.

Based largely on shells, Solem (1997) interpreted the morphological diversity in the Dampier Archipelago as representing six endemic species. This implies much more speciation than over larger distances in *Rhagada* on the mainland, as well as a more complicated history of geographic distributions. Molecular evidence, however, raises another possibility: great morphological diversity among populations within a single species (Johnson *et al.*, 2012; Stankowski & Johnson, 2014). This changes the focus from questions of speciation and complex geographic history to those about the origin and maintenance of extreme morphological diversity within a species. The purpose of this paper is to review the available molecular and morphological evidence, to re-evaluate and revise the taxonomy of *Rhagada* in the Dampier Archipelago, and to consider the implications for evolution and conservation.

## REVIEW OF EVIDENCE

### Molecular evidence

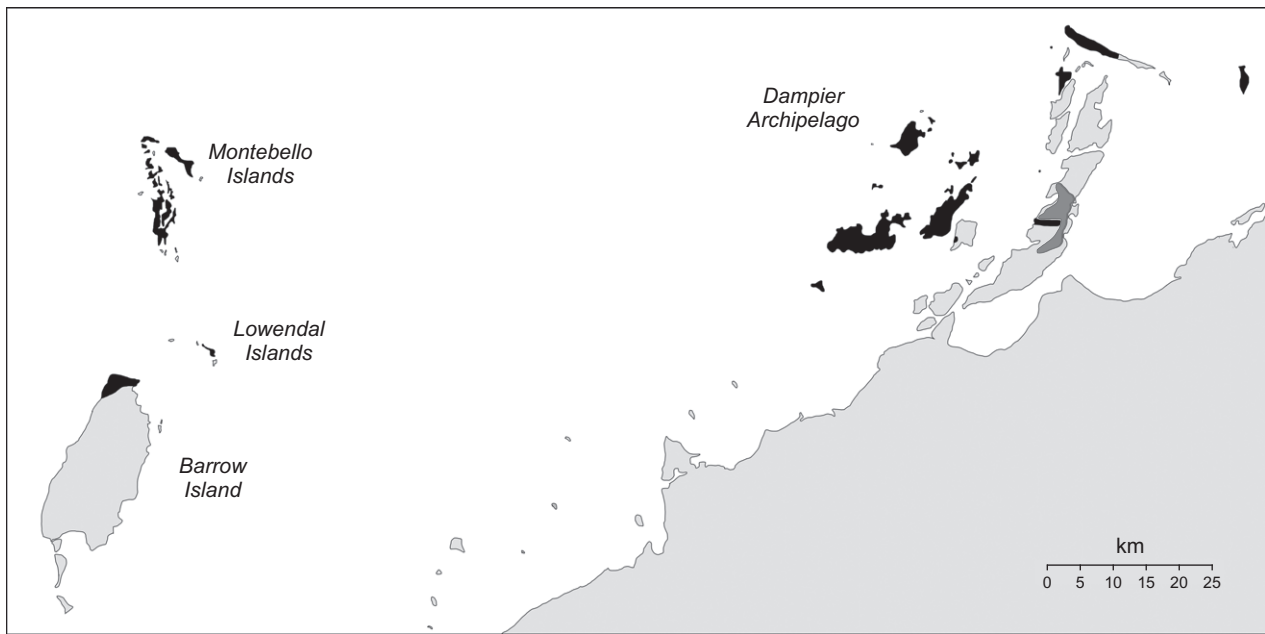
Prior to detailed work in the Dampier Archipelago, Johnson *et al.* (2012) conducted a broad-scale phylogenetic analysis of partial sequences of the mitochondrial cytochrome *c* oxidase subunit I (*COI*) and 16S rRNA (*16S*) genes, including samples of all

described species and undescribed forms of *Rhagada* from the Pilbara and adjacent southern part of its distribution. The phylogeny revealed four major clades (referred to as A–D), three of which were present in the Dampier Archipelago (DA): (1) Clade A, the large mainland clade, represented by the widespread *R. convicta* in the southern and eastern margins of the archipelago; (2) Clade C, the monospecific clade *R. angulata*, endemic to the northern DA; and (3) Clade D, a morphologically diverse clade comprising the remainder of the forms in the DA and the adjacent Burrup Peninsula, as well as *R. plicata* from the Montebello Islands, 90 km to the west (Fig. 2). This latter clade in turn includes two sister groups: *R. ngurrana* Johnson *et al.* (2016), restricted to the Burrup Peninsula, and all the remaining species of the DA plus *R. plicata* (Johnson *et al.*, 2012, 2013, 2016).

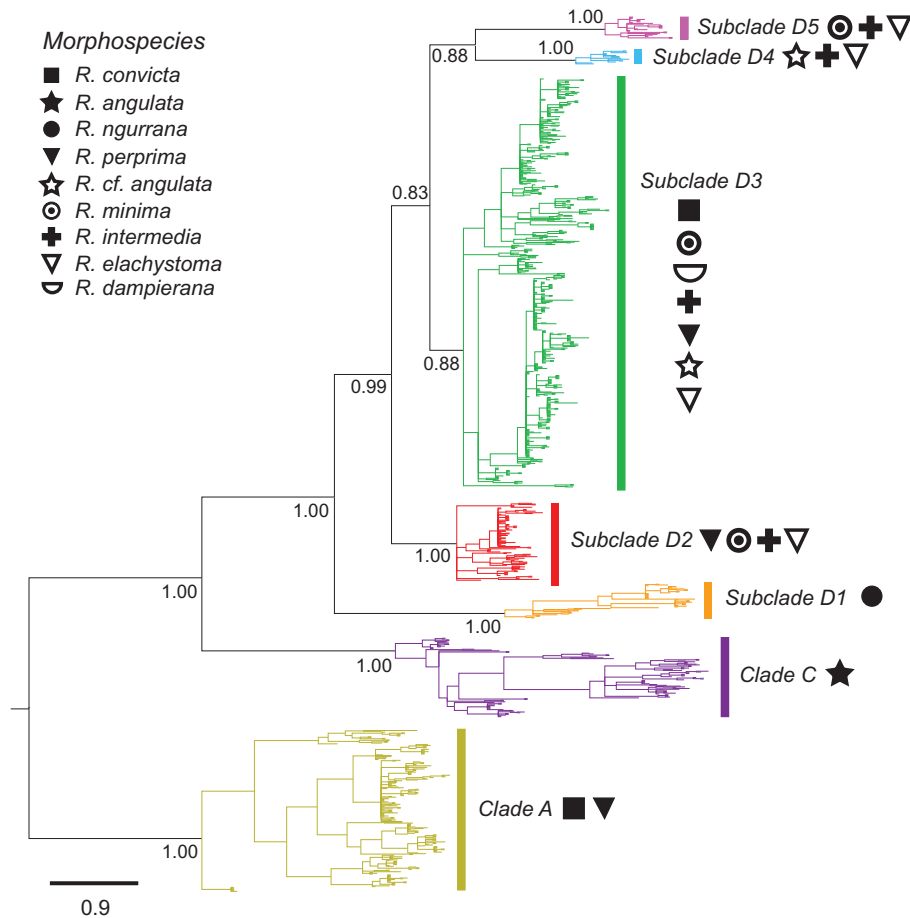
Although Johnson *et al.* (2012) included the type localities of four of the DA species (*R. angulata*, *R. dampierana*, *R. intermedia* and *R. minima*), each species was represented by only two individuals from a single island locality. To improve the geographic and taxonomic representation, Stankowski & Johnson (2014) constructed a larger *COI* phylogeny and gave a more comprehensive picture of distributions in the Dampier Archipelago, based on 1,015 individuals from 213 sites across 30 islands. While confirming the monophyly of the diverse Clade D, this detailed analysis revealed a more complex phylogenetic structure, with four major subclades (D2–D5) in the sister group of *R. ngurrana* (D1). Most importantly from a taxonomic perspective, the named morphospecies are not individually monophyletic, but instead are distributed amongst the major subclades (Fig. 3). Inconsistency between taxonomy and the mtDNA tree is evident even for *R. dampierana*, which occurs only in a small area on Rosemary Island and lies only in mtDNA Subclade D3. Detailed analysis of samples from Rosemary Island, however, showed that *R. dampierana* is in fact intermingled with the other morphospecies in the mtDNA tree (Stankowski, 2011).

The discordance between the shell-based taxonomy and the molecular phylogeny is strikingly shown by the contrasting geographic distributions of morphological and mtDNA variation. The mtDNA subclades are geographically coherent, with complementary distributions that reflect historic changes in sea level and little overlap between subclades (Fig. 4). The morphospecies are not associated with the distributions of the mtDNA subclades, but instead are broadly overlapping (Fig. 4). This lack of agreement between morphospecies and the mtDNA phylogeny extends to the widespread Subclade D3, in which major foci for mtDNA diversification are Rosemary Island and the Lewis Island group, but *R. elachystoma*, *R. intermedia* and *R. minima* are represented in both these mtDNA groups (Fig. 5). Although these three morphospecies do not occur on islands in the Lewis group, they appear separately in disparate sections of the Lewis group mtDNA network: *R. elachystoma* on Conzinc and Enderby Islands; *R. intermedia* on Legendre and Enderby; and *R. minima* on Cohen, Delambre and North Gidley. Although introgression between divergent lineages can lead to discordance between mtDNA and morphology, calculations based on dispersal rates of these snails showed that the periods of connection of the islands have been too short to allow extensive overland dispersal or neutral mitochondrial introgression (Stankowski & Johnson, 2014). Thus, instead of representing distinct lineages, the morphotypes represent either retained variation of the ancestral population of the DA Clade D or repeated evolution within that clade.

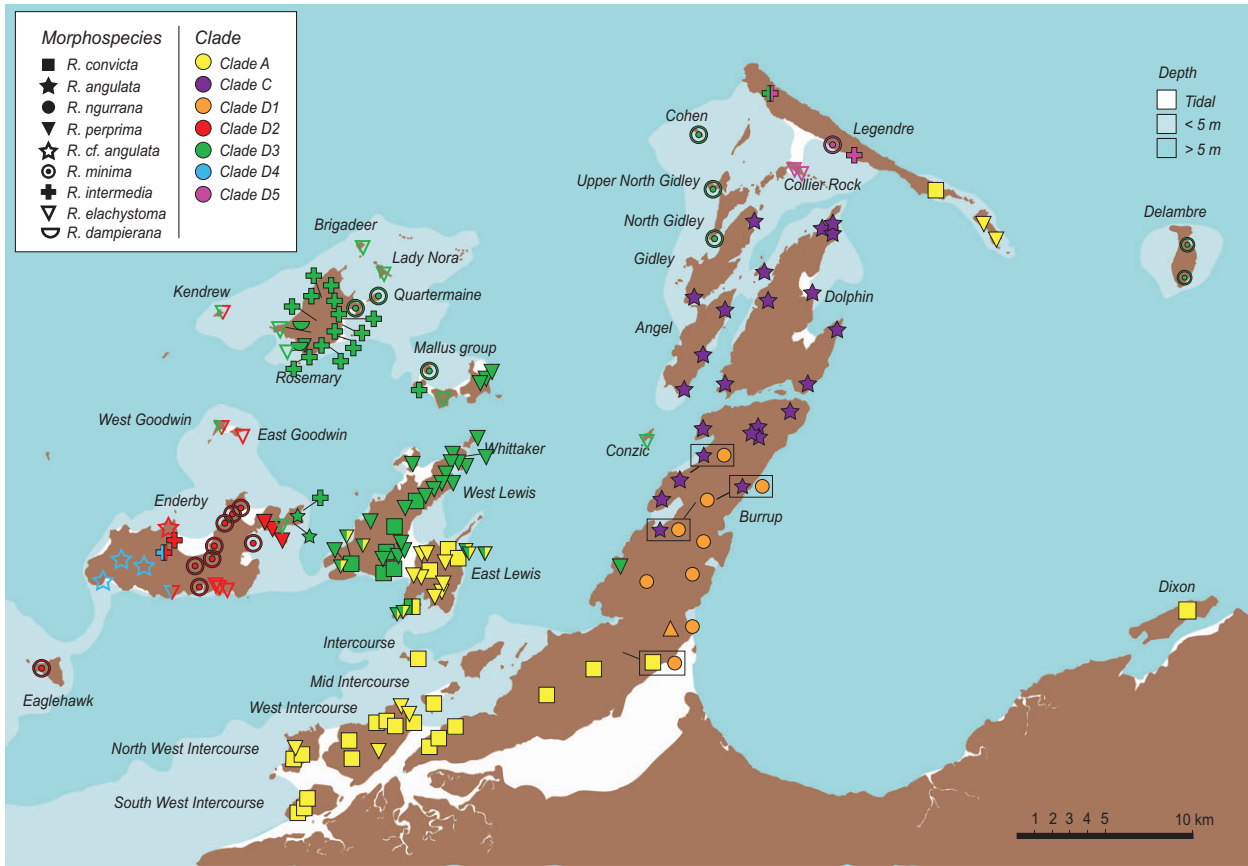
The detailed phylogenetic study of *Rhagada* in the Dampier Archipelago (Fig. 3) did not include *R. plicata*, from islands 90 km to the west, which is part of the diverse DA clade, Clade D (Johnson *et al.*, 2012, 2013, 2016). To clarify the placement of *R. plicata* within Clade D, we constructed a maximum-likelihood tree in MEGA v. 6.06 (Tamura *et al.*, 2011), based on *COI* sequences from 16 individuals of *R. plicata* from the Montebello, Barrow and Lowendal Islands (sequences from Johnson *et al.*, 2013) and 59 individuals from Clade D (sequences from Stankowski & Johnson,



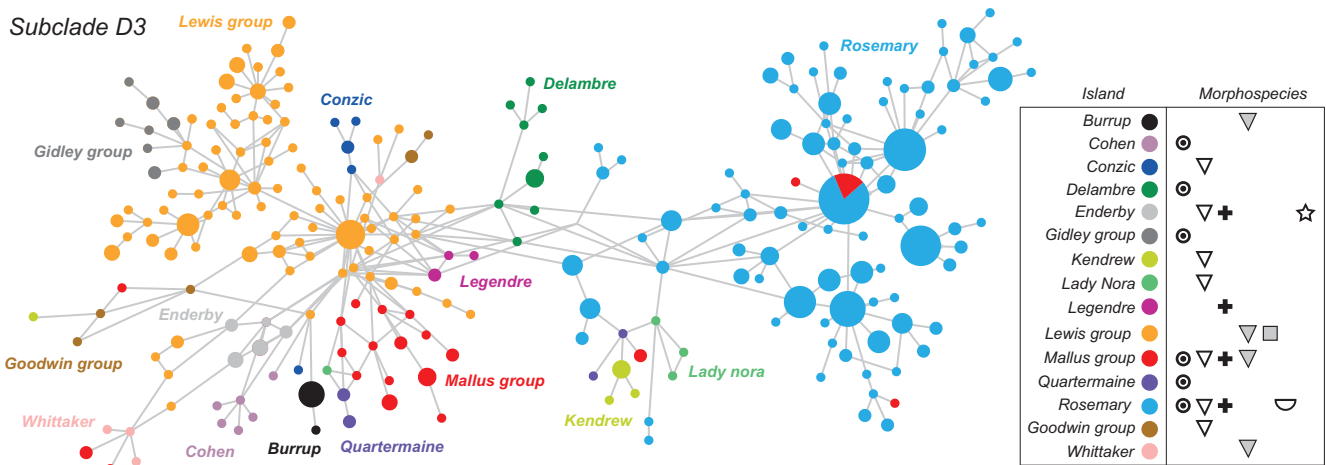
**Figure 2.** Distribution of the mtDNA Clade D, which includes all the endemic morphospecies of *Rhagada* (except *R. angulata*) from the Dampier Archipelago and *R. plicata* from the Montebello, Barrow and Lowendal Islands. Grey area indicates distribution of *R. ngurrana* (Subclade D1), which is sister group to the rest of Clade D (in black).



**Figure 3.** Bayesian tree of *COI* sequences of *Rhagada* in the Dampier Archipelago, showing distribution of morphospecies among the major clades. Based on Stankowski & Johnson (2014).



**Figure 4.** Geographic distributions of the previously described morphospecies (see Fig. 1) and major mtDNA clades (see Fig. 3) of *Rhagada* in the Dampier Archipelago. Multicoloured symbols indicate the presence of more than one clade at a location.



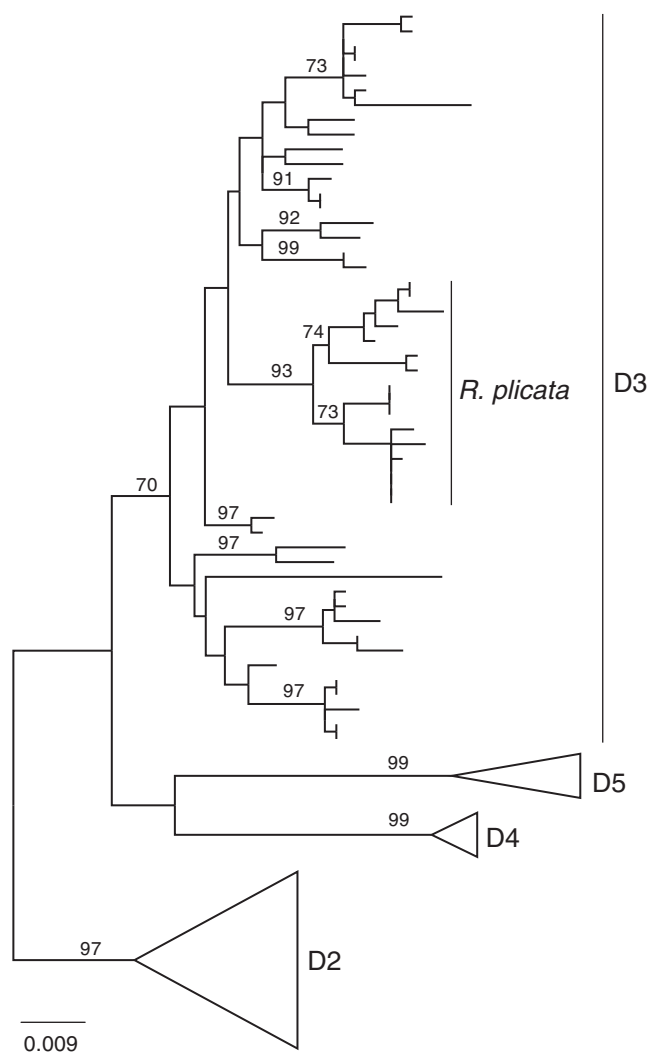
**Figure 5.** Haplotype network for the diverse Subclade D3 of *Rhagada*, showing distributions among islands of the Dampier Archipelago. Symbols for morphospecies as in Figures 3 and 4. Based on Stankowski & Johnson (2014).

2014), representing 21 islands in the Dampier Archipelago (GenBank accession nos KF151962, KF151963–4, KF151970, KF151975, KF152008–9, KF152014, KF152020, KF152058–9, KF152063–4, KF152122, KF152132, KF152137–8, KF152143–6, KF152162–3, KF152166, KF152169, KF152187–8, KF152267, KF152276–7, KF152283–4, KF152292–3, KF152298–9, KF152308–9, KF152314–5, KF152319, KF152320, KF152344, KF152345, KF152351, KF152353, KF152357, KF152359–20, KF152658, KF152668–9,

KF152674–5, KF152727–8, KF152877–8). This tree confirmed the placement of *R. plicata* as a well-supported clade within Clade D3 (Fig. 6).

The evolutionary cohesiveness of the DA Subclade D2–5 is highlighted by its young age and low genetic divergence. The split between *R. ngurrana* (Subclade D1) and the diverse Subclades D2–5 has been dated at  $730 \pm 350$  ka (95% CI) (Köhler & Criscione, 2013). Within D2–5, nearly all *COI* p-distances are less





**Figure 6.** Maximum likelihood *COI* tree of *Rhagada plicata* and representatives of *Rhagada* Clade D from the Dampier Archipelago, confirming the placement of *R. plicata* within Subclade D3. Tree rooted with *R. ngurrana* (Subclade D1, not shown) as outgroup. Bootstrap values  $\geq 70$  are shown.

than 6%, typical of values within species of *Rhagada* (Stankowski, 2015; Johnson *et al.*, 2016). The full range of shell variation occurs among populations with p-distances  $< 4\%$ , emphasizing the discordance between morphological and molecular divergence (Johnson *et al.*, 2012). Thus, the evidence from mtDNA is that the great morphological diversity in the DA has evolved within a single clade of recent origin.

#### Morphological evidence

Closer examination of the variation of shell form in the DA also indicates that the morphospecies are not separate species. Stankowski (2011) used geometric morphometrics to quantify shape variation in two sets of samples from Rosemary Island, where shell size and shape span the range of variation in the entire genus. The first set was the Western Australian Museum's specimens used by Solem (1997) in his descriptions of the morphospecies, including type material of *R. dampierana*, *R. intermedia* and *R. minima*, plus specimens of *R. elachystoma*. The second set of samples was from a grid-like configuration of 103 sites and provided a thorough coverage of the 1,100-ha island. While the museum specimens fell into discrete groups based on size and shape, the more

thorough set of samples revealed a full range of intermediate phenotypes. This clearly shows that the phenotypic clusters in the museum specimens reflect incomplete sampling rather than reproductive discontinuities.

The morphospecies with the most extreme form in the entire genus is *R. dampierana*, which has a highly compressed, heavily ribbed, keeled shell (Fig. 1I). This morphospecies is found only on Rosemary Island, where it is restricted to two rocky hills that are surrounded by low-lying grassy plains. Rather than these keeled, flat shells being a single species with a disjunct distribution, microsatellite DNA indicates that this morphotype evolved separately at each location in a striking example of parallel evolution (Stankowski, 2013). At each of these locations, transect sampling from the rocky hills to the lowland grasslands revealed continuous gradation from the flat shells to globose shells, connecting very different morphospecies over hundreds of metres (Fig. 7; Stankowski, 2011, 2013). Microsatellite DNA shows clear evidence for gene exchange along the length of the clines, confirming genetic continuity between the morphospecies (Stankowski, 2013). Cline analysis also allowed estimation of the magnitude of natural selection required to maintain the cline in shell form—only 2.5% (95% CI 1.8–4.4) against hybrids. This low rate of selection is consistent with the abundance of intermediate forms and the free gene exchange along the cline (Stankowski, 2013).

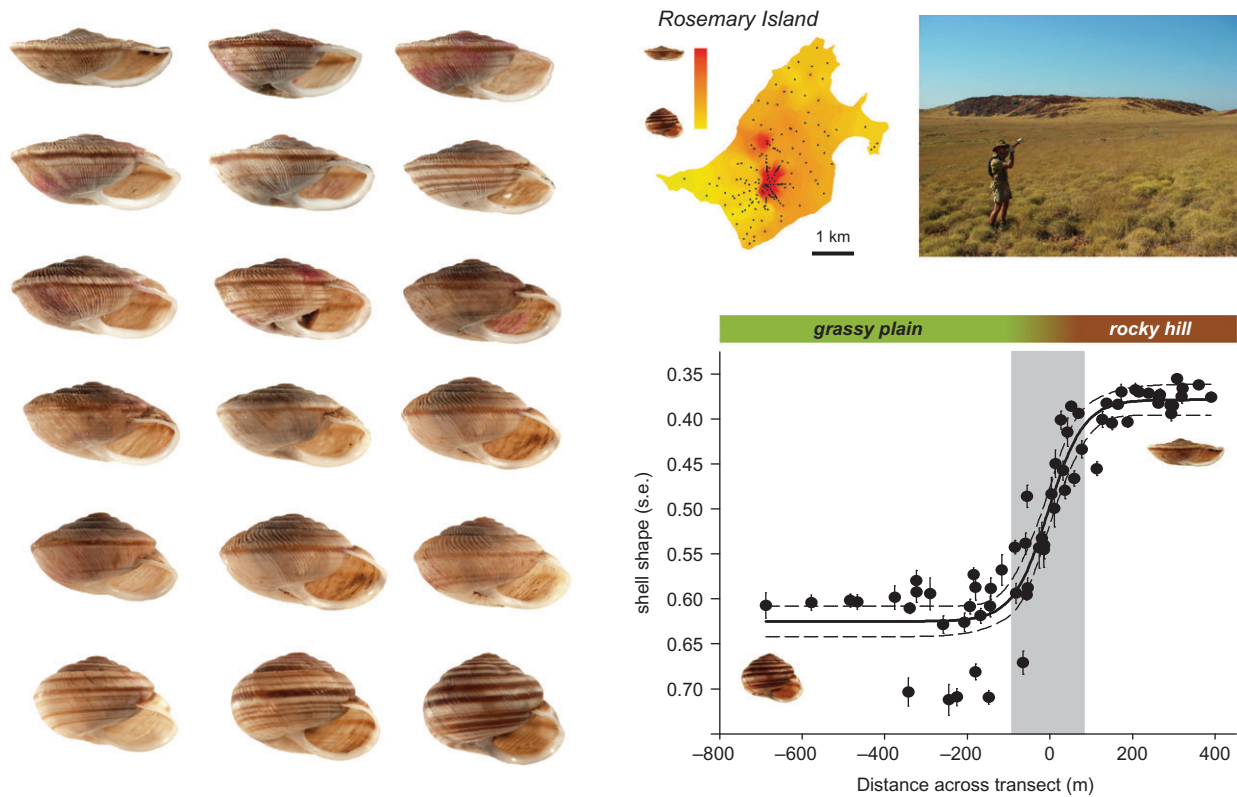
The morphological continuity and association with habitat on Rosemary are significant, because they involve four of the purported morphospecies and the type localities of three of them. The association between shell shape and habitat, despite extensive neutral gene flow, indicates that the differentiated shell forms are local adaptations rather than species-specific traits. This conclusion is supported by a similar transition in *R. ngurrana* (Subclade D1), where the relatively flat, keeled shells (Fig. 1D) on a rocky hill grade into the more globose form (Fig. 1C) on the adjacent grassland (Johnson *et al.*, 2016). As a broader test of the importance of local habitat in structuring morphological variation among populations, Stankowski (2015) examined 23 pairs of populations from Clade D from throughout the DA; each pair represented adjacent rocky and grassy habitats, and the members of each pair were genetically closely related. In all but one pair, the trend was towards lower spires in the rocky habitat, indicating that local selection underlies at least part of the morphological variation.

Although the classification of *Rhagada* in the DA was based mainly on shells, Solem (1997) described differences in reproductive anatomy among *R. dampierana*, *R. intermedia* and *R. perprima*. To test whether such differences separate the morphospecies, Stankowski (2011) did a quantitative analysis of variation in the reproductive anatomy among four groups that represented the extremes of size and shape on Rosemary Island: small flat, large flat, small globose and large globose. Despite inclusion of the traits used by Solem (1997), this analysis failed to discriminate the morphological groups. Comparisons with *R. ngurrana* also indicated conservatism of reproductive anatomy within Clade D, as no consistent features distinguish the sister groups within that clade (Johnson *et al.*, 2016). Thus, there is no anatomical support for the recognition of the morphospecies in the DA Subclades D2–5.

## TAXONOMY

#### Taxonomic implications

As shown above, the recognized species in the morphologically diverse Subclades D2–5 are not supported by either the molecular evidence or the re-examination of reproductive and shell morphology. They are paraphyletic and genetically very similar, they do not form distinct genetic groups, and the transitions between extreme morphotypes on Rosemary Island confirm interbreeding



**Figure 7.** Gradation of shell form of *Rhagada* from rocky hilltop to lowland grassy areas on Rosemary Island. Array of shells shows the continuous gradation of shell form. Map shows distribution of shell shape on the island, with transect lines. Graph summarizes the cline ( $\pm 95\%$  CI) in shell shape (spire index), which was obtained by scaling the individual clines to a common centre (based on Stankowski, 2013).

and genetic continuity, as well as showing that they are not distinct morphological groups. The anatomical evidence also provides no support for the existing taxonomy. Based on this combined evidence, these described species represent a single, morphologically highly variable species, rather than a set of morphologically distinct species. The earliest available and therefore valid name is *R. elachystoma* (Martens, 1877). A revised synonymy to reflect this change is given below. Traditional morphological description is not useful in this taxonomic context, because the variation of shell traits in this inclusive *R. elachystoma* spans that of the rest of the genus.

A complication is that some individuals on East and West Lewis Islands, Northwest and West Intercourse Islands, and the small island east of Legendre Island were keyed to *R. perprima* based on shells, but have mtDNA of the largely mainland Clade A, whereas some individuals on East and West Lewis Islands keyed to *R. convicta* have the mtDNA of Subclade D3. These discrepancies are most likely due to misidentification of shells, which are very similar for these species, as recognized by Solem (1997). Alternatively, some of the discrepancies between mtDNA and identification of shells could be due to hybridization. This is most likely on East and West Lewis Islands, where Clades A and D3 were both found together. Assessment of hybridization will require further evidence, including other genetic markers and anatomical comparisons. On its eastern boundary on the mainland *R. convicta* does hybridize with a smaller, flatter, undescribed species (Hamilton & Johnson, 2015). However, the introgression is restricted to a narrow zone, and does not affect the broader genetic and geographic cohesion of either species. Similarly, the morphological and molecular discrepancies involving *R. convicta* in the Dampier Archipelago are at the edge of its distribution, so that any hybridization has no taxonomic implications, except that possible hybrid individuals cannot be identified with certainty as either species.

#### Synonymy

#### FAMILY CAMAENIDAE Pilsbry, 1895

#### Genus *Rhagada* Albers, 1860

#### *Rhagada elachystoma* (Martens, 1877) (Fig. 1)

- Helix elachystoma* Martens, 1877: 273–274, pl. 1, figs 8–9 (syntype Museum für Naturkunde, Berlin, ZMB Moll. 26628, Mermaid Strait). Martens, 1879: 35, pl. 144, figs 1–4.
- Helix (Rhagada) elachystoma*—Pilsbry, 1890: 187.
- Theristes (Rhagada) elachystoma*—Pilsbry, 1894: 136.
- Rhagada elachystoma*—Iredale, 1938: 112. Solem, 1997: 1746–1753, Johnson *et al.*, 2004: 341–355. Johnson, Hamilton & Fitzpatrick, 2006: 45–50. Johnson *et al.*, 2012: 316–327. Köhler & Criscione, 2013: 1971–1972. Burghardt & Köhler, 2014: 37–50. Stankowski & Johnson, 2014: fig. 1.
- Helix convicta*—Martens, 1878: 272–273, pl. 1, figs 6–7 (not Cox, 1870).
- Helix (Rhagada) convicta*—Pilsbry, 1890: 187–188, pl. 30, figs 7, 11 (in part; not Cox, 1870).
- Rhagada richardsonii*—Smith, 1894: 89 (in part, not Smith, 1874). Iredale, 1939: 59–60 (in part, not Smith, 1894). Richardson, 1985: 266 (check-list; in part, not Smith, 1874).
- Rhagada plicata* Preston, 1914: 13–14, fig. (paratype Florida Museum of Natural History FMNH 41617; Montebello Islands). Hedley, 1916: 219. Solem, 1997: 1737–1741, pls 207a–d, figs 418a, b, 419a–c. Johnson *et al.*, 2012: 316–327, fig 1. Johnson *et al.*, 2013: 159–171. Köhler & Criscione, 2013: 1971–1972.
- Bellrhagada plicata*—Iredale, 1938, 114 (check-list). Iredale, 1939: 71, pl. 5, fig. 16. Richardson, 1985: 65 (check-list).

- Rhagada perprima* Iredale, 1939: 62, pl. 4, fig.13 (holotype Australian Museum AM C.64864; Rosemary Island). Solem, 1997: 1712–1718. Johnson *et al.*, 2004: 341–355. Johnson *et al.*, 2006: 45–50. Johnson *et al.*, 2012: 316–327, figs 1, 4. Johnson *et al.*, 2013: 159–171. Köhler & Criscione, 2013: 1971–1972. Burghardt & Köhler, 2014: 37–50. Stankowski & Johnson, 2014: fig 1. Johnson *et al.*, 2016: 323–334, figs 1, 8.
- Rhagada convicta perprima*—Iredale, 1939: 62, pl. 4, fig. 13.
- Rhagada angulata*—Solem, 1997: 1754, 1757, 1760 (in part, Enderby Island only; not *R. angulata* s. s. Solem, 1997: 1754–1757, 1760, type locality Dolphin Island).
- Rhagada cf. angulata*—Stankowski & Johnson, 2014: 4–7, 10, fig. 2.
- Rhagada dampierana* Solem, 1997: 1760–1764, pls 208b–d, 221e, f, figs 422d–f, 424a–c (holotype Western Australian Museum WAM 766.87; Rosemary Island). Johnson *et al.*, 2012: 316–327, figs 1, 4. Köhler & Criscione, 2013: 1971–1972. Burghardt & Köhler, 2014: 37–50. Stankowski & Johnson, 2014: fig. 1.
- Rhagada intermedia* Solem, 1997: 1743–1746, pls 207d, 222c–f, figs 420a, b, 421a–c (holotype WAM 764.87; Delambre Island). Johnson *et al.*, 2012: 316–327, fig. 1. Köhler & Criscione, 2013: 1971–1972. Burghardt & Köhler, 2014: 37–50. Stankowski & Johnson, 2014: fig. 1.
- Rhagada minima* Solem, 1997: 1741–1743, pls 207b, c, 222c–f, figs 418c–e (holotype WAM 763.87; Rosemary Island). Johnson *et al.*, 2004: 341–355, fig 2. Johnson *et al.*, 2006: 45–50. Johnson *et al.*, 2012: 316–327, figs 1, 4. Köhler & Criscione, 2013: 1971–1972. Burghardt & Köhler, 2014: 37–50. Stankowski & Johnson, 2014: fig. 1.
- Rhagada* ‘Barrow small’ Johnson *et al.*, 2006: 45–50, fig. 1. Johnson *et al.*, 2012: 316–327, fig 1. Johnson *et al.*, 2013: 159–171, fig. 1. Köhler & Criscione, 2013: 1971–1972.
- Rhagada* sp. HP, Johnson *et al.*, 2012: 316–327, fig. 1. Köhler & Criscione, 2013: 1971–1972. Burghardt & Köhler, 2014: 37–50. Stankowski & Johnson, 2014: fig. 1. Johnson *et al.*, 2016: 323–334, figs 1, 8.

## IMPLICATIONS

The revised taxonomy and synonymy change our perspective on the great morphological diversity of *Rhagada* in the DA. Instead of asking why species diversity is so high in this area, our focus is now on the evolutionary processes and factors that have shaped extreme morphological diversification within a single species. The geographical perspective is also significantly changed. Formerly, the geographically complex distributions of the morphospecies in the archipelago were in stark contrast to the geographic replacement of species of *Rhagada* on the mainland. The synonymy of the island species under a single specific name removes this discrepancy: the distribution of the inclusive *R. elachystoma*, spanning 180 km, fits the same pattern shown on the adjacent mainland, of which it was a part 8,000 years ago. Thus, the revised taxonomy highlights that what is special about *Rhagada* in the DA is its morphological diversity, not its number of species or peculiar set of distributions. This is another example of the importance of testing the validity of taxonomies based only on shell form.

Recognition of the inclusive *R. elachystoma* highlights the value of this species for studying the basis of evolutionary change. The indication is that local environment and historical contingency have determined the extent of repeated, local morphological changes in *R. elachystoma* (Stankowski, 2015), but the underlying genetic and ecological mechanisms remain to be determined. Adding to this interest is the inclusion of *R. plicata* within this inclusive *R. elachystoma*, because shell form in *R. plicata* is conserved across its distribution (Johnson *et al.*, 2012, 2013), in contrast with the DA forms of *R. elachystoma*. It is still also unclear how much of the evolutionary plasticity is due to the particular mix of habitats

in the Dampier Archipelago and how much to intrinsic potentials in this lineage. Within this population-genetic perspective, future work should focus on questions about the underlying genomics of local adaptation. Are there unique features of *R. elachystoma*? Are the same genetic changes repeated in response to local conditions, or are there different genetic solutions to similar environmental challenges?

While providing the framework for future research on the genetic basis of adaptation, the revised taxonomy is also important for conservation. Because much of the focus of conservation is at the species level, the new synonymy could be misinterpreted as justification for placing less value on the previously recognized morphospecies. The special value of *R. elachystoma*, however, is its great diversity within a single species, and it is that full range of diversity that makes this species especially important in its entirety.

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## REFERENCES

- BICKFORD, D.P., LOHMAN, D.J., SODHI, N.S., NG, P.K.L., MEIER, R. & INGRAM, K.K. 2006. Cryptic species as a window on diversity and conservation. *Trends in Ecology & Evolution*, **22**: 148–155.
- BURGHARDT, I. & KÖHLER, F. 2014. *Rhagada* revisited: on the taxonomy of species from the Kimberley and Dampierland, Western Australia (Pulmonata, Camaenidae). *Molluscan Research*, **35**: 37–50.
- CADENA, C.D., ZAPATA, F. & JIMENEZ, I. 2018. Issues and perspectives in species delimitation using phenotypic data: Atlantean evolution in Darwin’s finches. *Systematic Biology*, **67**: 181–194.
- CHUECA, L.J., GÓMEZ-MOLINER, B.J., FORÉS, M. & MAEIRA, M.J. 2017. Biogeography and radiation of the land snail genus *Xerocrassa* (Geomitridae) in the Balearic Islands. *Journal of Biogeography*, **44**: 760–772.
- COX, J.C. 1870. Descriptions of eight new species of shells from Australia and the Solomon Islands. *Proceedings of the Zoological Society of London*, **1870**: 170–172.
- GOULD, S.J. & WOODRUFF, D.S. 1978. Natural history of *Cerion* VIII: Little Bahama Bank—a revision based on genetics, morphometrics and geographic distribution. *Bulletin of the Museum of Comparative Zoology*, **148**: 371–415.
- HAMILTON, Z.R. & JOHNSON, M.S. 2015. Hybridization between genetically and morphologically divergent forms of *Rhagada* (Gastropoda: Camaenidae) snails at a zone of secondary contact. *Biological Journal of the Linnean Society*, **114**: 348–362.
- HEDLEY, C. 1916. A preliminary index of the Mollusca of Western Australia. *Journal of the Royal Society of Western Australia*, **1**: 152–226.
- IREDALE, T. 1938. A basic list of the land Mollusca of Australia—Part III. *Australian Zoologist*, **9**: 83–124.
- IREDALE, T. 1939. A review of the land Mollusca of Western Australia. *Journal of the Royal Society of Western Australia*, **25**: 1–88.
- JOHNSON, M.S. & BLACK, R. 1999. *Nodilittorina nodosa* (Gray, 1839) is a plastic morphotype of *Nodilittorina australis* (Gray, 1826). *Journal of Molluscan Studies*, **65**: 111–119.
- JOHNSON, M.S., HAMILTON, Z.R. & FITZPATRICK, J. 2006. Genetic diversity of *Rhagada* land snails on Barrow Island. *Journal of the Royal Society of Western Australia*, **89**: 45–50.
- JOHNSON, M.S., HAMILTON, Z.R., MURPHY, C.E., MACLEAY, C.A., ROBERTS, B. & KENDRICK, P.G. 2004. Evolutionary genetics of island

- and mainland species of *Rhagada* (Gastropoda: Pulmonata) in the Pilbara Region, Western Australia. *Australian Journal of Zoology*, **52**: 341–355.
- JOHNSON, M.S., HAMILTON, Z.R., TEALE, R. & KENDRICK, P.G. 2012. Endemic evolutionary radiation of *Rhagada* land snails (Pulmonata: Camaenidae) in a continental archipelago in northern Western Australia. *Biological Journal of the Linnean Society*, **106**: 316–327.
- JOHNSON, M.S., STANKOWSKI, S., KENDRICK, P.G., HAMILTON, Z.R. & TEALE, R.J. 2016. Diversity, complementary distributions and taxonomy of *Rhagada* land snails (Gastropoda: Camaenidae) on the Burrup Peninsula, Western Australia. *Invertebrate Systematics*, **30**: 323–334.
- JOHNSON, M.S., STANKOWSKI, S., WHISSON, C.S., TEALE, R.J. & HAMILTON, Z.R. 2013. Camaenid land snails on Barrow Island: distributions, molecular phylogenetics and taxonomic revision. *Records of the Western Australian Museum*, **83**: 159–171.
- KÖHLER, F. & CRISCIONE, F. 2013. Plio-Pleistocene out-of-Australia dispersal of a camaenid land snail. *Journal of Biogeography*, **40**: 1971–1982.
- KÖHLER, F. & JOHNSON, M.S. 2012. Species limits in molecular phylogenies: a cautionary tale from Australian land snails (Camaenidae: *Amphirhagada* Iredale, 1933). *Zoological Journal of the Linnean Society*, **165**: 337–362.
- MARTENS, C.E. VON. 1877. Übersicht der während der Reise um die Erde in den Jahren 1874–1876 auf S.M. Schiff Gazelle gesammelten Land- und Süßwasser-Mollusken. *Monatsberichte der Königlich Preussischen Akademie der Wissenschaften zu Berlin*, **1877**: 261–190.
- MARTENS, C.E. VON. 1879. Die *Bulimus*-Arten aus der Gruppe *Borus*. *Novitates conchologicae. Series prima. Mollusca extramarina*. In: *Beschreibung und Abbildung neuer oder kritischer Land- und Süßwasser-Mollusken*, Vol. 5 (L. Pfeiffer, ed.), pp. 1–38. T. Fischer, Cassel.
- MCKAY, B.D. & ZINK, R.M. 2015. Sisyphian evolution in Darwin's finches. *Biological Reviews*, **90**: 689–698.
- MURRAY, J. & CLARKE, B. 1980. The genus *Partula* on Moorea: speciation in progress. *Proceedings of the Royal Society of London Series B—Biological Sciences*, **211**: 83–117.
- PILSBRY, H.A. 1890–1891. *Manual of conchology*. Ser. 2. *Pulmonata*, Vol. 6. Academy of Natural Sciences of Philadelphia.
- PILSBRY, H.A. 1893–1895. *Manual of conchology*, Ser. 2. *Pulmonata*, Vol. 9. Academy of Natural Sciences of Philadelphia.
- PRESTON, H.B. 1914. Description of new species of land and marine shells from the Montebello Islands, Western Australia. *Proceedings of the Malacological Society of London*, **11**: 13–24.
- REIJNEN, B.T. & VAN DER MEIJ, S.E.T. 2017. Coat of many colours—DNA reveals polymorphism of mantle patterns and colouration in Caribbean *Cyphoma* Röding, 1798 (Gastropoda, Ovulidae). *PeerJ*, **5**: e3018.
- RICHARDSON, L. 1985. Camaenidae: catalog of species. *Tryonia*, **12**: 1–479.
- SMITH, E.A. 1874. Zoology of the Voyage of H. M. S. *Erebus & Terror*. In: *Mollusca*, Vol. 2 (J. Richardson & J.E. Gray, eds), pp. 1–7. E. W. Jackson, London.
- SMITH, E.A. 1894. On the land-shells of Western Australia. *Proceedings of the Malacological Society London*, **1**: 84–99.
- SOLEM, A. 1997. Camaenid land snails from western and central Australia (Mollusca: Pulmonata: Camaenidae). VII. Taxa from Dampierland through the Nullarbor. *Records of the Western Australian Museum*, **50**: 1461–1906.
- STANKOWSKI, S. 2011. Extreme, continuous variation in an island snail: local diversification and association of shell form with the current environment. *Biological Journal of the Linnean Society*, **104**: 756–769.
- STANKOWSKI, S. 2013. Ecological speciation in an island snail: evidence for the parallel evolution of a novel ecotype and maintenance by ecologically dependent postzygotic selection. *Molecular Ecology*, **22**: 2726–2741.
- STANKOWSKI, S. 2015. Layers of contingency shroud pervasive ecological divergence in a local radiation of land snails. *Biological Journal of the Linnean Society*, **116**: 267–276.
- STANKOWSKI, S. & JOHNSON, M.S. 2014. Biogeographic discordance of molecular phylogenetic and phenotypic variation in a continental archipelago of land snails. *BMC Evolutionary Biology*, **14**: 2.
- TAMURA, K., PETERSON, D., PETERSON, N., STECHER, G., NEI, M. & KUMAR, S. 2011. MEGA5: molecular evolutionary genetics analysis using maximum likelihood, evolutionary distance, and maximum parsimony methods. *Molecular Biology and Evolution*, **28**: 2731–2739.
- TESHIMA, H., DAVISON, A., KUWAHARA, Y., YOKOYAMA, J., CHIBA, S., FUKUDA, T., OGIMURA, H. & KAWATA, M. 2003. The evolution of extreme shell shape variation in the land snail *Ainohelix editha*: a phylogeny and hybrid zone analysis. *Molecular Ecology*, **12**: 1869–1878.
- UIT DE WEERD, D.R.U. & BELAZQUEZ, A.F. 2017. Pinning down *Tenuistemma* (Pulmonata: Urocoptidae): local evolution of an extreme shell type. *Biological Journal of the Linnean Society*, **121**: 741–752.
- WALTHER, F., NEIBER, M.T. & HAUSDORF, B. 2016. Species complex or complex species? Integrative taxonomy of the land snail genus *Rossmassleria* (Gastropoda, Helicidae) from Morocco and Gibraltar. *Systematics and Biodiversity*, **14**: 394–416.