

The oldest *Glycymeris* individual that was confidently aged was 30.3 years. The oldest individual for *C. kingii* was 21.2 years of age and this species appears to have a shorter lifespan than *E. kingicola* and *G. grayana*.

The study was further supported by a tag and recapture study that was intended to validate the annual periodicity and time of year that the growth bands were laid down for all three species. A total of 197 individuals were tagged between 24/09/2011 and 27/12/2011. The average recovery rate was 10% or 19 individuals over a 2-year period with all three species represented by between one and five individuals. The results validated that growth bands were laid down between the time of tagging to when they were re-captured as indicated by comparison of



Fig. 3. Polished radial section of *G. grayana* individual GG039, 19.5 years of age. (I) major inner shell layer, (O) major outer shell layer, yellow arrows indicate annual growth bands or slow growth periods which appear as dark lines with reflected light. Photo: P. Beaver.

the individuals' radial lengths (Fig. 1c). These results support the assumption that a translucent band is formed annually.

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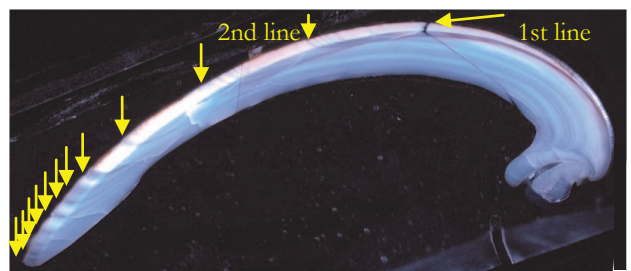


Fig. 4. Polished radial section through individual *C. kingii* NK034, 13.5 years of age. Yellow arrows indicate annual translucent bands. Photo: P. Beaver.



## Between a rock and a hard place: habitat variation drives speciation in an island snail

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Islands are widely considered the best places for relaxation and refuge. For many, mere mention of the word 'island' triggers images of tropical vegetation, foreign accents and diverse cocktail menus. When British explorer and naturalist William Dampier went ashore a small island off the west Australian coast in the year 1699, he clearly had refuge in mind. He was in search of water to resupply his ship, *HMS Roebuck*, which was on the first British scientific expedition to Australia. He found nothing, and described the landscape as, '...dry, mostly rocky and barren' (Dampier, 1703). After naming the island Rosemary after a shrub that reminded him of the herb, he set sail for greener pastures.

More than three centuries later, Rosemary Island is essentially unchanged. It is still arid, unpopulated and of little interest to those seeking creature comforts. But for those studying evolution, it deliv-

ers beyond wildest expectations. Despite its small size, only 11 km<sup>2</sup>, the island has been the site of a striking evolutionary radiation of *Rhagada* land snails (Stankowski, 2011). They are like nothing that has been seen in *Rhagada* on the mainland or on any other island. Their shells vary in size, shape, sculpture and banding pattern. The variation in shell shape really catches the eye, ranging from globose — the typical shape you see in garden snails — to a unique flat-spined form, which is only found Rosemary Island.

Despite the striking morphological differences, the *Rhagada* from Rosemary Island are very closely related (Stankowski, 2011; Johnson *et al.*, 2012). The analysis of mitochondrial DNA sequences indicates that the flat-spined form has evolved recently on the island from a globose-shelled ancestor.

Detailed studies show that the different shaped shells are the product of ecological adaptation (Stankowski, 2013). The flat-spired form has evolved on top of two isolated rocky hills, while the globose-spired populations inhabit the surrounding grassy plains. The flat and globose forms meet and mate at the narrow boundary between the rocky hilltop and low lying and grassy habitats, leading to the formation of an area of genetic mixing, commonly known as a 'hybrid zone'. The hybrid zone is kept very narrow (about 170 meters wide) by strong natural selection that stops ecologically important genes, such as those that determine shell shape, from crossing the habitat boundary. Thus, the sharp habitat transition acts as a strong barrier to gene flow, which stops the forms from merging together.

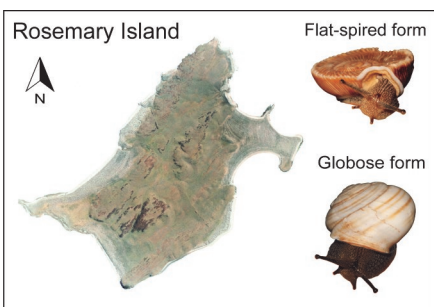
The fact that these different forms can mate and exchange genes indicates that they are part of the same biological species. Despite this, there is clear evidence that they are undergoing speciation (Stankowski, 2013). Although natural selection is only acting on genes that determine ecologically important traits (such as those that determine shells shape), it is so strong that it has started to slow the movement of other 'neutral' genes that have no biological function. Moreover, the strength of the barrier varies in different parts of the island. In some locations, it is so strong that the flat-spired and globose forms can coexist in the same location with only minimal genetic mixing; in others places, it is relatively weak, and mixing is extensive. While these snails provide a rare and striking example of ecological speciation in progress, many questions remain.

First, is the barrier to gene flow created entirely by natural selection, or have snails subsequently evolved mating preferences, so that snails with different shaped shells no longer find each other sexually attractive? Also, the transition between the habitats appears to be sharper in some places than others. Sharper transitions would mean stronger natural selection, which may explain the local variation in the strength of the barrier to gene flow. Finally, what is happening across the rest of the genome? Past research was based on a handful of neutral genes; new DNA sequencing techniques have made it possible to study tens of thousands of them.

As a naturalist, Dampier would almost certainly be surprised that Rosemary Island has become an important natural laboratory for scientific research. Future studies will deepen our understanding of the genetics of adaptation and the role that it plays in the formation of new species.

## References

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Top left: Rosemary Island with the endemic flat-spired form of *Rhagada* and the typical globose shelled form. Top right: one of the rocky hills where the flat spired form is found. Bottom: Variation in shell shape along a transect that extends up onto the rocky hill and back down onto the valley floor. The x-axis shows the distance along the transect in meters. The three colour bar shows the distribution of the two distinct habitat types, and the transition zone between them. Each black circle represents the shape score for a single shell. The change in shell shape closely matches the change in habitat. Note that the transition between the flat-spired and globose forms is much sharper of the right-hand side.

