

RESEARCH NOTE

HITCHHIKING JUVENILES IN THE RARE NEUSTONIC GASTROPOD *RECLUZIA* CF. *JEHENNEI* (JANTHINIDAE)

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Most species in nature are rare, and their ecologies are poorly known (Lyons *et al.*, 2005). Our lack of knowledge concerning the fundamental biodiversity of rare species in natural ecosystems impairs our ability to develop effective conservation programmes and to test hypotheses of community assembly. Although the term 'rare' is qualitative, ecologists traditionally determine rarity using range and abundance, combined with guild-level comparisons (Kunin & Gaston, 1997). Ecological studies of rare marine species lag behind their terrestrial counterparts because marine species are more difficult to sample and, as a result, taxonomic ambiguities abound (Jones, Caley & Munday, 2002). In fact, we know so little about the ecological roles and contributions of rare marine species that it is not farfetched to ask "Are rare species [ecologically] boring?" (R.T. Paine in Schindler *et al.*, 2003). Here we present evidence to the contrary in a rare species of pelagic bubble-rafting snail, *Recluzia* cf. *jehennei*.

Members of the genus *Recluzia* Petit, 1853 are also known as brown janthinas, because of their close relationship to the much more common violet snails of the genus *Janthina* (Lalli & Gilmer, 1989; see *Journal of Molluscan Studies*, **77**; cover). These two genera make up the family Janthinidae and share a most unusual ecology: they drift passively in the neuston, the vast ecosystem at the surface of the planet's subtropical oceans, which occupies 40% of the Earth's surface (McClain, Signorini & Christian, 2004). They achieve floatation by a remarkable synapomorphy: using quick-setting mucus and rapid foot movements, they construct a bubble raft from which they are suspended (Lalli & Gilmer, 1989). *Recluzia* is much more poorly known than *Janthina* (Fretter & Graham, 1962) and there is a large discrepancy in publishing effort between the two genera. *Janthina* has been comprehensively revised (Laursen, 1953, synonymized 60 named species to five), has been the topic of several anatomical works (e.g. Cuvier, 1808; Graham, 1965) and has featured in several comparative morphological studies of caenogastropods (Collin, 2000; Golding, Ponder & Byrne, 2009a, b). *Recluzia*, on the other hand, has never received a formal taxonomic treatment. There are 15 nominal species, of which all but two were described in the nineteenth century and most were based on few (often single) specimens. A Web of Science search for '*Recluzia*' yields a single record (*vs* 10 for *Janthina*), reporting a beach stranding, in which the author noted that he could "now discontinue a

search [that] lasted for 25 years" (Poorman, 1980). Five years of neuston sampling by the first author in the North and South Pacific gyre systems has yielded hundreds of *Janthina* specimens, but none of *Recluzia*.

Janthinids are highly specialized predators of neustonic cnidarians: the porpitids *Velella velella* and *Porpita porpita*, the siphonophore *Physalia physalis* and the actinarian *Minyas* spp. (Abbott, 1963; Lalli & Gilmer, 1989). They are protandrous hermaphrodites (Laursen, 1953) and most adult females cement egg capsules to their floats, which develop and hatch as planktotrophic veligers. *Janthina janthina*, however, is ovoviviparous and broods preveliger stages in the gonad. Observations of *Recluzia* come from few preserved specimens (Thiele, 1928; Abbott, 1963; Poorman, 1980) and as a result their ecology has largely been inferred from that of *Janthina*. *Recluzia* is known to be oviparous (Poorman, 1980); the only record distinguishing its life history from that of *Janthina* comes from a note in the grey literature by Colman (1986; see Supplementary material). Colman observed an adult female (Australian Museum reg. no. C.145648; here tentatively identified as *R. cf. jehennei* Petit, 1853) from Bundagen Beach, New South Wales, Australia, with four conspecific individuals attached to the float. Colman hypothesized that they were dwarf males and that "they may live all their life on the float, or, after some time, make their own float and change sex to female, to complete the same sexual cycle as *Janthina*" (Colman, 1986). This proposed early life history is radically different from that of *Janthina* species. Juvenile *Janthina* float autonomously by creating a mucus stalk with a terminal bubble (Simroth, 1895) and there is no evidence that males live in association with adult females (Laursen, 1953; C.K.C.C. personal observation).

During a morphological and molecular-systematic study of Janthinidae, we obtained on loan a specimen of *R. cf. jehennei* collected stranded in the intertidal in Moreton Bay, Queensland, Australia (Field Museum of Natural History reg. no. 328104) and preserved in 95% ethanol. This represented a rare opportunity to corroborate and extend Colman's (1986) observations. In particular, Colman's samples were too decomposed to study the soft anatomy of the juveniles and look for evidence of autonomous float formation or sexual maturity. If juvenile *R. cf. jehennei* remain associated with the female until sexual maturity, it would provide an evolutionary means of achieving a functionally simultaneous hermaphroditic unit

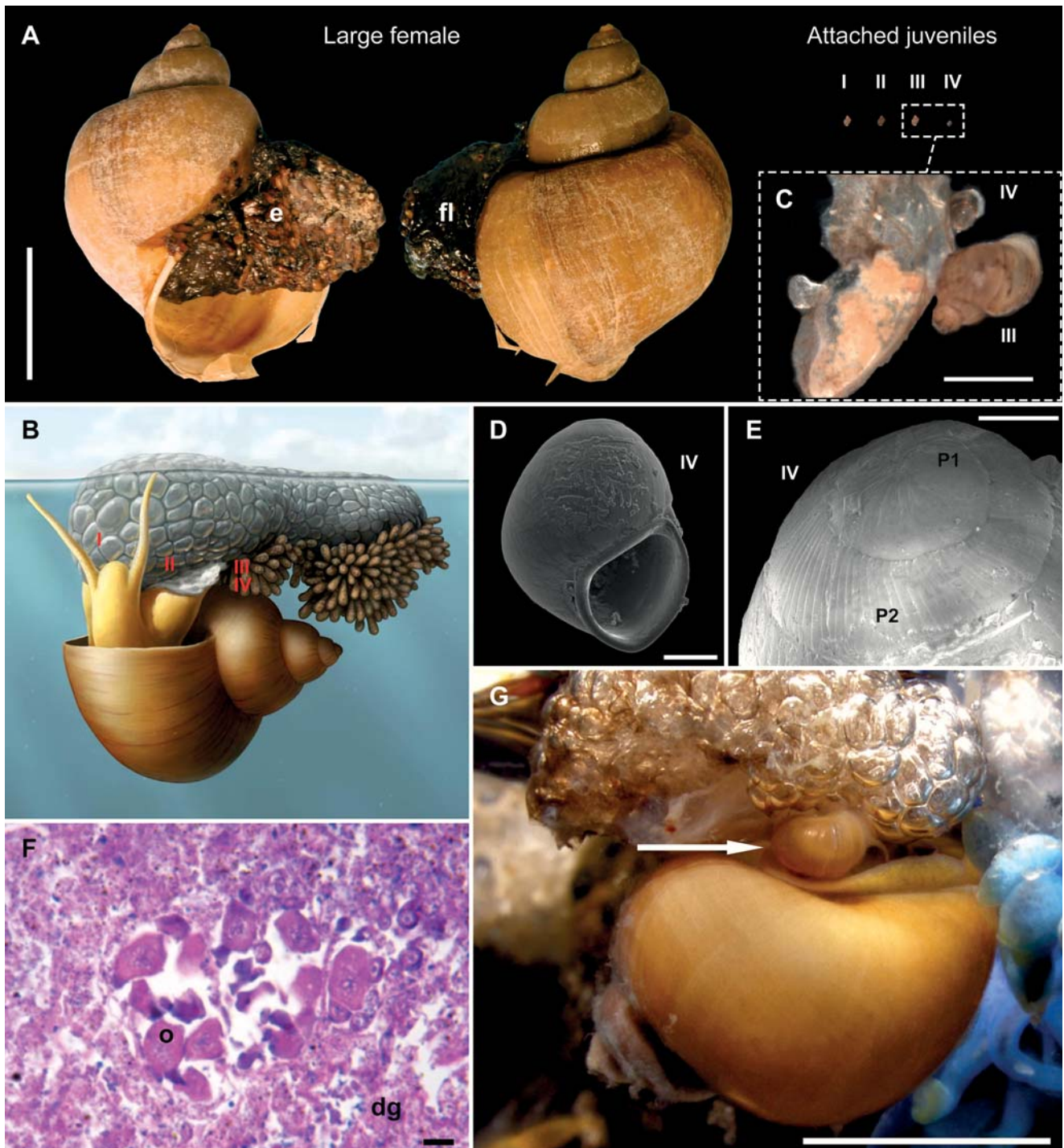


Figure 1. A–F. *Recluzia cf. jehenei*. Moreton Bay, Queensland, Australia (FMNH reg. no. 328104). **A.** Apertural and abapertural views of large female with dried float and egg capsules; abapertural views of four attached juveniles (I–IV) associated with the float (I and II) and one egg capsule (III and IV, indicated with a dashed rectangle). Abbreviations: fl, float; e, egg capsule. **B.** Artist's reconstruction of live specimen with Roman numerals indicating locations of juveniles I–IV. **C.** Egg capsule with attached juveniles III and IV. **D.** Scanning electron micrograph of individual IV, apertural view, showing a varix and no teleoconch growth. **E.** Scanning electron micrograph of individual IV, showing differences in sculpture between embryonic Protoconch 1 (P1) and postembryonic Protoconch 2 (P2). **F.** Histological section of visceral mass showing digestive gland surrounding developing oogenic follicles with oogonia. Abbreviations: dg, digestive gland; o, oogonium. **G.** *Recluzia cf. jehenei*. Live photo from Hastings Point, New South Wales, Australia. A large female, with float, is feeding on the siphonophore *Physalia physalis*. An arrow indicates a smaller associated individual with no float. Scale bars: **A, G** = 10 mm; **C** = 1 mm; **D** = 100 μ m; **E** = 50 μ m; **F** = 10 μ m.

(Ghiselin, 1969). Such unions are selectively advantageous in populations with low densities; when males have limited reproductive opportunity, remaining with one female may be the best

strategy (Charnov, 1979) and highly specialized dwarf males are known to occur in a variety of molluscan groups (Turner & Yakovlev, 1983; Warén, 1983; Ó Foighil, 1985; Voight, 1997).

Initial inspection confirmed the specimen to be a large, mature female, with associated float and egg capsules that contained early embryonic stages, although both capsules and float had partially dried prior to preservation (Fig. 1A). Close examination revealed four associated postlarval individuals (Fig. 1A). Three of these had less than one whorl of teleoconch growth (Fig. 1A: I–III) and the fourth appeared to be newly metamorphosed (Fig. 1A: IV). Each of the four small individuals was located in close proximity to the large female; two were attached to the float near the female's propodium (Fig. 1B: I, II) and two were attached to a single egg capsule near the metapodium (Fig. 1B: III, IV). The method of attachment was the same for all four individuals, achieved by means of a flat patch of mucus cemented to the shell on the side of the spire. The two individuals (I and II) attached to the float fell off as the float was removed, but the individuals on the egg capsule remained firmly attached (Fig. 1C), which is significant considering the specimen had previously been stranded, preserved and shipped. None of the small individuals showed any sign of creating an autonomous float.

Scanning electron micrographs of the smallest postlarval individual, IV (Fig. 1D, E), show a typical janthinid protoconch (see Robertson, 1971: pls V, VI). All *Janthina* spp. have obligate planktotrophic larval development (Laursen, 1953; Robertson, 1971) but their morphologies (Simroth, 1895; Laursen, 1953; Robertson, 1971) are not completely consistent with Thorson's (1950) 'shell apex theory'; they are low-spined and the line of demarcation between embryonic (P1) and post-embryonic (P2) protoconch growth may be unclear (e.g. Robertson, 1971: pl. V, fig. 20). Otherwise, janthinid protoconchs are consistent with Thorson's model: they have a small, smooth P1 and a large, multispiral P2 with increasingly prominent axial plicae (Robertson, 1971). Additionally, there is a large size difference between late-stage embryos and fully grown larvae in *Janthina* (Laursen, 1953; Wilson & Wilson, 1956; Robertson, 1971). There are no late-stage embryos present for comparison in the specimen of *R. cf. jehennei* examined here but, interestingly, the protoconch of individual IV (Fig. 1D, E) greatly resembles that of the oviparous *J. pallida* (Robertson, 1971). They have similar shell lengths (0.45 mm *vs* mean of 0.42 mm) and numbers of whorls (3.625 *vs* 3.25), a smooth P1 with faint axial plicae, an unclear line of demarcation between P1 and P2 (between 1–1.25 whorls *vs* 1 whorl) and a P2 with regular axial plicae (5–10 *vs* 3–9 μm apart) (Fig. 1E). These similarities support an inference of planktotrophic larval development in *R. cf. jehennei*.

Furthermore, the presence of a thick varix on the protoconch of individual IV (Fig. 1D) indicates that it is newly metamorphosed. Fully grown larvae of *Janthina* spp. have a continuous thickened peritreme forming a varix at the end of P2, which is further defined by a change in the axis of coiling of between 10° and 50° with the onset of teleoconch growth (Robertson, 1971). The axis of teleoconch growth appears to change in *R. cf. jehennei*, but we cannot measure the precise angle because the protoconch apex is broken in the large female and there is less than one whorl of teleoconch growth in the small individuals I–III. From the available material, it appears consistent with *Janthina*. Given that there was no evidence of float formation in any of the small *R. cf. jehennei*, the varix and lack of teleoconch on individual IV, in particular, support recruitment of larvae directly onto conspecific female floats or egg capsules, followed by a prolonged association with the host female while the teleoconch grows.

After removing the shells from the largest postlarval individuals (I and II; 2 mm shell height), there was no external evidence of gonadal tissue. Histological sections (sectioned at

5 μm , stained with haematoxylin and eosin–phloxine; Humason, 1967) show very early stages of gonadal development: developing oogenic follicles with oogonia (Fig. 1E). These are immature female reproductive structures, but because there has been no study of gonadal development in janthinids, we hesitate to identify the juveniles as female. Sections of male *Janthina* at various stages of development also show inactive female gonadal tissue (previtellogenic oocytes) (C.K.C.C., unpubl.). Our sections of *R. cf. jehennei* indicate that the female part of the reproductive system develops first, irrespective of the order of maturation. There is no evidence of male testis development or of sperm production. The pallial reproductive tract is undifferentiated and too undeveloped to be identified conclusively as male or female. In short, neither individual was sexually mature, which is not surprising given their size (2 mm).

Although there is no evidence of sexual maturity in individuals I and II, several lines of circumstantial evidence support an extended association between mature female *R. cf. jehennei* and smaller conspecifics. First, there has been no record of a free-living *R. cf. jehennei*, or of any *Recluzia*, as small as autonomously floating *Janthina* spp. (<4 mm, although this may be partially due to size bias in sampling). Second, Colman's (1986) auxiliary specimens, although too decomposed for anatomical study, were much larger than the juveniles we observed and, if growth of *Recluzia* growth is similar to that of *Janthina*, they were presumably sexually mature (as Colman supposed). Finally, a recent (2008) photograph of *R. cf. jehennei* from Hastings Point, New South Wales, taken by Denis Riek (<http://www.roboastra.com>) clearly shows a much larger auxiliary individual (shell height *c.* 5 mm) associated with the float of a large female (Fig. 1G).

Larval recruitment onto a conspecific float may be key in casting light on the evolutionary transition of ancestral janthinids from the benthos to the neuston. Interestingly, associations between mature females and smaller males are found in several species of the protandrous Epitoniidae (e.g. Robertson, 1983), the suspected sister group to the Janthinidae (Ponder *et al.*, 2008). If juvenile *R. cf. jehennei* do not build floats, then float formation is a postjuvenile trait in this species and possibly associated with the mature female phase of its life cycle. Conspecific larval recruitment and suspected dwarf/complemental males are life history traits that have likely allowed *R. cf. jehennei* to persist while remaining extremely rare. The interpretation of the latter trait could be tested directly by taking histological sections of larger hitchhiking *R. cf. jehennei*.

The results presented here not only provide ecological information about a scarcely recorded species, but will also be part of a larger study examining the evolutionary transition of Janthinidae to the neuston.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Journal of Molluscan Studies* online.

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