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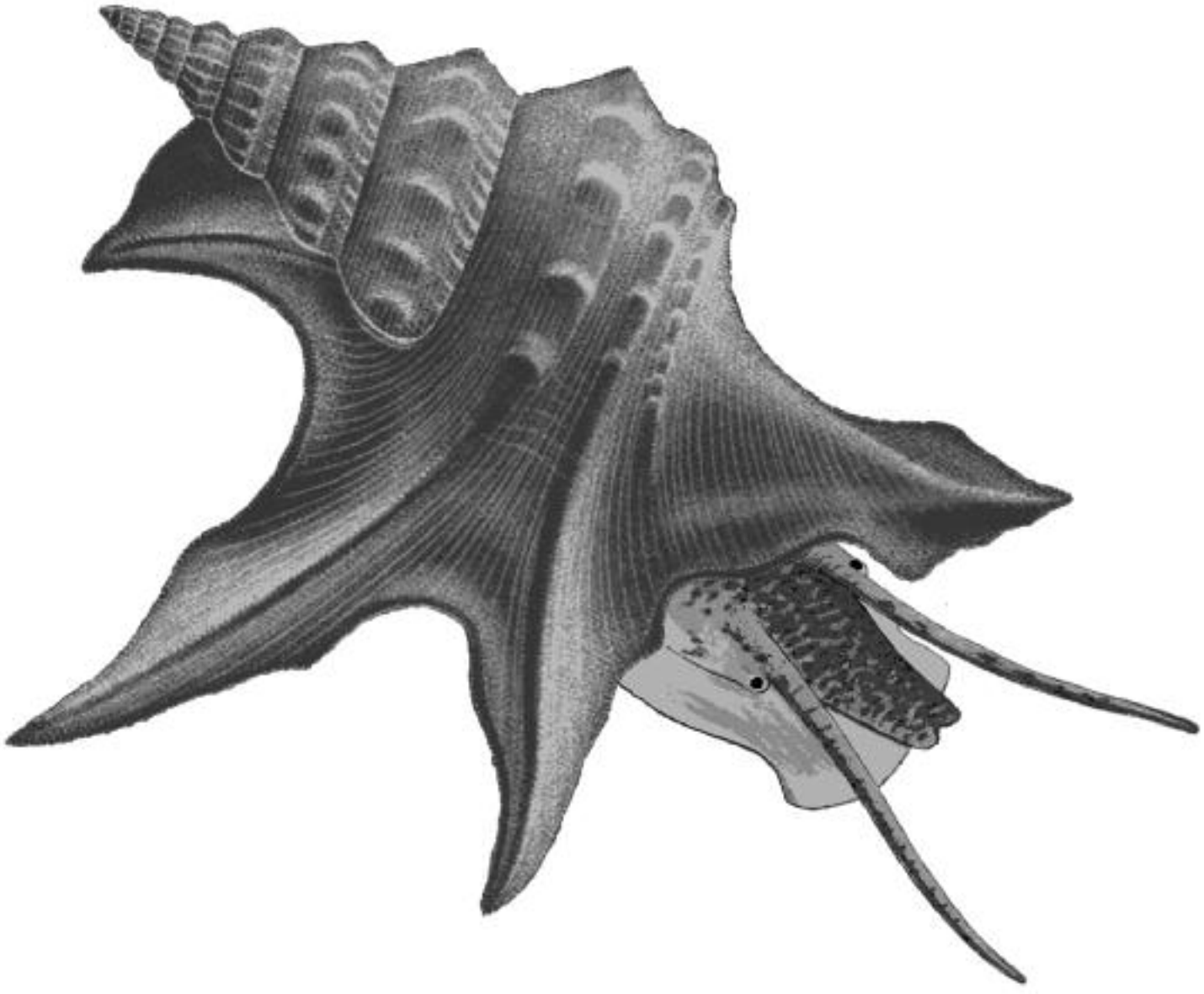

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Charles Darwin the malacologist

Aydin Örstan[1] and Robert T. Dillon, Jr.[2]

Charles Darwin, whose 200th birthday the world celebrated in February of this year, may have been the last complete biologist. His research interests spanned the entirety of the life sciences as they were known in his day, from his taxonomic studies of barnacles in *Monograph on the Subclass Cirripedia* (1851) through his Descent of Man (1871) and *The Power of Movement in Plants* (1880). Darwin's first publication[3] was a ripping-good adventure story featuring 'atmospheric dust with infusoria.' And his last publication, a four-paragraph communication appearing just two weeks before his death in 1882, was a work of freshwater malacology[4].

Darwin seems to have become interested in molluscs soon after he initiated his studies on the 'transmutation of species,' the phrase he used to describe evolution in his notebooks. One of the earliest letters in the Darwin Correspondence Project[5] was sent by the paleontologist Searles V. Wood on 5 June 1846 (Letter 983) in response to an inquiry by Darwin[6] regarding the 'variations among the Mollusca.' In that letter, Wood explained to Darwin his opinion that the shells of fossil molluscs were more variable than those of extant species.

But the focus of Darwin's malacological research rapidly turned toward the biogeography and dispersal of freshwater and terrestrial species. He had a copy of the geologist Samuel P. Woodward's *Manual of the Mollusca* (1851-1856) and corresponded with Woodward on the distributions of a variety of species (Letters 1890, 1928). He also initiated experiments with land snails to elucidate the dispersal mechanisms that may have brought them to oceanic islands.

In a letter of 23 May 1855 to his cousin William Darwin Fox (Letter 1686), Darwin intimated plans to test the survival of land snails in sea water to determine if they could withstand long transoceanic voyages: 'I am going to try land-snail shells & their eggs also. [sic] in sea-water.' Over the next two seasons, he attempted to raise snails, apparently as subjects for these experiments. On 14 July 1855, he wrote to his naturalist neighbour John Lubbock (Letter 1831): '… I got yesterday some more & enough specimens of *Helix pomatia* for my Snailery.' But his efforts at snail husbandry seem to have been less than successful. In a letter dated 9 October 1856 to an unidentified correspondent who may have offered him snails, Darwin wrote (Letter 1972): 'Next summer would not be at all too late, & if you can remember it, I shd be extremely glad to get some for my experiments. I have

been myself keeping *Helix Pomatia* in confinement all summer, but they have not laid a single egg, so that I have not at all profited by my scheme.'

His inquiry of 3 October 1856 to Fox reveals the scope of his interests when he writes about birds and molluscs together in the same paragraph, as well as his frustrations (Letter 1967): 'One other question, you used to keep Hawks, do you at all know, after eating a Bird, how soon after they throw up the pellet? No subject gives me so much trouble & doubt & difficulty, as means of dispersal of the same species of terrestrial productions on to oceanic islands.–Land Mollusca drive me mad, & I cannot anyhow get their eggs to experimentise on their power of floating & resistance to injurious action of salt-water.'

Why did land snails drive Darwin 'mad?' His 29 September 1856 letter to the American geologist James D. Dana (Letter 1964) lays out Darwin's problem plainly: 'I know that you are not a believer in the doctrine of single points of creation, in which doctrine I am strongly inclined to believe, from general arguments; but when one goes into detail there are certainly frightful difficulties. No facts seem to me so difficult as those connected with the dispersal of Land Mollusca.'

Darwin's central thesis, that all organisms have diverged from common ancestors, required that they originate at single points, and disperse throughout the world. So if a convincing case could be built for land snails, surely to be ranked among the most disadvantaged of the world's dispersers, perhaps the remainder of the worldwide biota might fall into line.

Darwin seems to have found some relief for his land snail 'madness' in 1857, perhaps by experimenting with *Helix pomatia* supplied to him by colleagues. In another letter to Fox dated 8 February 1857, he reported (Letter 2049): 'I have just had a *Helix pomatia* withstand 14 days well in Salt-water; to my very great surprise.' He revealed additional results to the geologist Charles Lyell on 11 February 1857 (Letter 2050): 'I have just had *Helix Pomatia* quite alive & hearty after 20 days under sea-water; & this same individual about six-weeks ago had a bath of 7 days.'

It was sometime during this very period that Darwin received his first letter from his fellow naturalist Alfred Russell Wallace[7]. It is thus not surprising that land snails figured prominently in his reply of 1 May 1857 (Letter 2086): 'One of the subjects on which I have been experimentising & which cost me much trouble, is the means of distribution of all organic beings found on oceanic islands & any facts on this subject would be most gratefully received: Land-Molluscs are a great perplexity to me.'

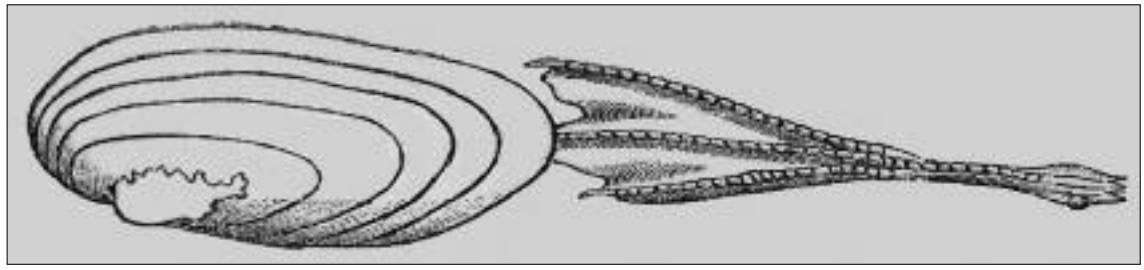
By the time the *Origin of Species* was published in November of 1859, Darwin had developed several plausible mechanisms by which land snails might be dispersed (first edition, Chapter XII): 'Now it is notorious that land-shells are very easily killed by salt; their eggs, at least such as I have tried, sink in sea-water and are killed by it. Yet there must be, on my view, some unknown, but highly efficient means for their transportal. Would the just-hatched young occasionally crawl on and adhere to the feet of birds roosting on the ground, and thus get transported? It occurred to me that land-shells, when hybernating and having a membranous diaphragm over the mouth of the shell, might be floated in chinks of drifted timber across moderately wide arms of the sea.'

He then summarized the results of his experiments: 'And I found that several species in this state [of hibernation] withstand uninjured an immersion in sea-water during seven days: one of these shells was the *Helix pomatia*, and after it had again hybernated I put it in sea-water for twenty days, and it perfectly recovered. As this species has a thick calcareous operculum, I removed it, and when it had formed a new membranous one, I immersed it for fourteen days in sea-water, and it recovered and crawled away: but more experiments are wanted on this head.'

In the same chapter, Darwin also discussed his studies in a closely related topic, the distribution and dispersal of freshwater molluscs: 'Some species of fresh-water shells have a very wide range, and allied species, which, on my theory, are descended from a common parent and must have proceeded from a single source, prevail throughout the world. Their distribution at first perplexed me much, as their ova are not likely to be transported by birds, and they are immediately killed by sea water, as are the adults.'

Darwin then went on to relay a number of anecdotes regarding the attachment of juvenile freshwater molluscs to the feet and feathers of waterfowl, concluding his lengthy paragraph with 'Sir Charles Lyell also informs me that a *Dyticus*[8] has been caught with an *Ancylus* (a fresh-water shell like a limpet) firmly adhering to it.'

Darwin's fascination with the biogeography and dispersal of molluscs brought him back to the subject of freshwater malacology in 1878 when he published in Nature9 a short note and a copy of the letter sent to him by an Arthur H.



Gray describing a surprisingly large unionid mussel attached to the toe of a duck shot in Massachusetts (Fig. 1). And it culminated in 1882, with his *On the Dispersal of Freshwater Bivalves*, also published in *Nature*[10].

Darwin opened this, the last paper he would publish before his death, with 'The wide distribution of the same species, and of closely-allied species of freshwater shells must have surprised every one who has attended to this subject.' After reviewing his observations of 1859 and 1878, Darwin wrote: 'I am now able to add, through the kindness of Mr. W. D. Crick, of Northampton, another and different case. On February 18 of the present year, he caught a female *Dytiscus marginalis*, with a shell of *Cyclas cornea*[11] clinging to the tarsus of its middle leg.' Darwin went on to relay additional data about this now most illustrious of all fingernail clams, which was large (0.45 inch), viable (dropping from the bug only after five days) and fertile (bearing two juveniles). He then added several anecdotes about other individual sphaeriids found attached to the digits of amphibians, and finished with a charming observation: 'Lastly, my son Francis, while fishing in the sea off the shores of North Wales, noticed that mussels were several times brought up by the point of the hook; and though he did not particularly attend to the subject, he and his companion thought that the shells had not been mechanically torn from the bottom, but that they had seized the point of the hook.'

Darwin laid the groundwork for the study of molluscan dispersal, which continues as an area of active research today[12]. In 1883, 16 months after Darwin's death, the island of Krakatau between Sumatra and Java was split open by a devastating volcanic eruption that also exterminated all life forms that were then present on the island. The five species of land snails that had been recorded on the island before the eruption have not recolonized it, but as of 1985, 19 other species of land snails were known from the four present day islands13. Two of them were first recorded on one of the islands in 1908, 25 years after the eruption. Wind-borne transport on leaves and rafting on floating objects have been postulated to be the most likely mechanisms that may have brought the snails to the Krakatau Islands[13]. Darwin would have been pleased.

And Darwin's research in malacology has subsequently connected him, in an interesting and unexpected way, to the life sciences of the 21st century. The 'Mr. W. D. Crick of Northampton' who sent Darwin his report of the fingernail clam pinched on the water bug leg was Walter Drawbridge Crick (1857-1903), the grandfather of Francis H. C. Crick, who (with James Watson and Maurice Wilkins) shared the 1962 Nobel Prize for elucidating the structure of DNA[14].

At the outset of this article, we characterized Charles Darwin as 'the last complete biologist.' Chief among the reasons that there can be no more such protean figures must be the 20th century explosion of molecular biology, which has expanded our discipline in directions Darwin could never have imagined. It is a source of some inspiration to us that one can trace a path from Darwin to DNA through the great man's last paper and the humble discipline of malacology.

Notes

[1]Section of Mollusks, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, USA.
pulmonate@earthlink.net

[2]Department of Biology, College of Charleston, Charleston, South Carolina, USA.
DillonR@cofc.edu

[3]Chapter 1 of Darwin's *Voyage of the Beagle* (1839) included a long paragraph about "infusoria" (primarily diatom frustules) in dust that accumulated on the Beagle while crossing the Atlantic.

[4]We've taken a bit of license with this paragraph. Darwin had a couple publishing credits prior to *Voyage* and several posthumous papers after his 6 April 1882 paper on freshwater bivalve dispersal. For Darwin's complete bibliography, including open-access pdf versions of his books and the papers mentioned here, see: http://darwin-online.org.uk/contents.html.

[5]All of the letters to and from Darwin cited here are available at the Darwin Correspondence Project: http://www.darwinproject.ac.uk. The letter numbers are those used by DCP.

[6]According to DCP, Darwin's letter to Wood is missing.

[7]According to DCP, Wallace's letter, dated 10 October 1856, is missing.

[8]*Dytiscus* is a genus of large, predatory water bugs. Although spending the majority of their lives swimming gracefully through the water column, they may on occasion take to the wing, flying like balsa-wood airplanes with rubber bands. The misspelling of the name wasn't corrected until the fourth edition of *Origin*.

[9]Darwin, C. 1878. Transplantation of shells. *Nature* 18:120-121.

[10]Darwin, C. 1882. On the dispersal of freshwater bivalves. *Nature* 25:529-530.

[11]The genus Cyclas has since been synonymized under *Sphaerium*. Today this common European "fingernail clam" is generally referred to as *Sphaerium corneum*.

[12]For more modern reviews see W. J. Rees. 1965. The Aerial Dispersal of Mollusca. *Proceedings of the Malacological Society* London 36:269–282 and Dörge, N., Walther, C., Beinlich, B. & Plachter, H. 1999. The significance of passive transport for dispersal in terrestrial snails (Gastropoda, Pulmonata). *Zeitschrift für Ökologie und Naturschutz* 8:1–10.

[13]Smith, B. J. & Djajasasmita, M. 1988. The Land Molluscs of the Krakatau Islands, Indonesia. *Philosophical Transactions of the Royal Society* B 322:379-400.

[14]Ridley, M. 2004. Crick and Darwin's shared publication in *Nature. Nature* 431:244.

Figure caption

Figure 1: The drawing from Darwin's 1878 paper showing the unionid mussel attached to the toe of a blue-winged teal (*Anas discors*). Reprinted by permission from Macmillan Publishers Ltd: *Nature* 18:120-121, copyright 1878.