Notes on Two Cases of Molluscan Biogeography

by
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Alfred Russel Wallace's detailed explorations of flora and fauna of the Malay Archipelago from 1854-1862 probably mark the beginning of biogeography, the study of the geographic distributions of species. Interest has continued, culminating in a field exemplified by both journals (e.g. *Journal of Biogeography*) and organizations (e.g. International Biogeography Society). The pages of this very publication continue to expand and refine our knowledge of molluscan distributional patterns that yield insights into evolution, extinction, dispersal, and biodiversity.

Biogeography might be framed in the context of the question: "Why are not all species found everywhere?" Obviously, the answer resides in a mixture of biological limits (i.e. the giraffe cannot breathe underwater argument) and historical factors such as extinction, speciation, continental drift, volcanic eruptions, and glaciation (i.e. the stuff happens argument). Given all the reasons why an organism cannot be found everywhere, some taxonomic groups are remarkably ubiquitous. Four invertebrate phyla, Arthropoda, Polychaeta, Nematoda, and Mollusca, are found in terrestrial, freshwater, and marine biomes, with disparity in habitats from deserts to hydrothermal vents to polar icecaps. If this publication were titled *American Nematodologist* or another moniker, we would continue to muse on the non-molluscan groups. Partiality aside, however, the success of molluscs and particularly the Gastropoda is astonishing. Here, we illustrate some biogeographical questions, using as examples our own research on two mollusc species, one marine and one terrestrial.

Triumphant Molluscs

The phylum Mollusca is a remarkable group of invertebrates with a history marked by considerable alterations of the Molluscan *bauplan* [ed. note: "bauplan, n. generalized, idealized, archetypal body plan of a particular group of animals." From Lawrence, Eleanor, ed. Henderson's dictionary of biology, 13th ed. Harlow, Essex: Pearson Education Ltd., 2005, xii+748 p.]. As noted by Barnes et al. (1993), "With the possible exception of the Nematoda, the Mollusca, with almost 100,000 species (a very conservative estimate by the way), is the second largest animal phylum. Their success is probably not so much attributable to any particular special anatomical or ecological features of the group as

A female *Neptunea amianta* (Dall, 1890) in the process of laying her stalked egg case. The shell is approximately 50mm long and the finished egg case will be from 150 to 250mm high. Photo by Craig McClain, © MBARI, used with permission.

to the extreme plasticity and adaptability of the basic molluscan body plan."

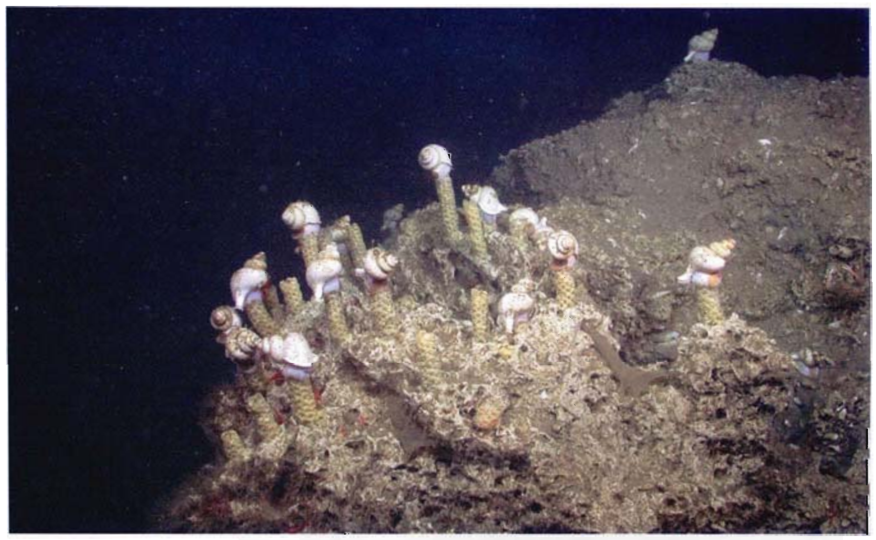
While some classes are limited to one (Cephalopoda, Scaphopoda) or two (Bivalvia) major biotic systems, the Gastropoda have diversified within all three. The radiation of the Mollusca includes the obvious addition of an exoskeleton but also subsequent major modifications by coiling, reduction, duplication, segmentation, and in multiple independent events, the ultimate loss of the shell. The phylum possesses groups with specialized neural systems and two fundamentally different respiratory systems. Body sizes vary over 12 orders of magnitude in volume from the smallest gastropods (such as *Ammonicera minortalis* at 0.0184mm^3) to the largest cephalopods (*Architeuthis dux* at 45.9m^3). Most feeding styles are known from within the group, including parasitism and symbiotic mutualisms (including coral reef zooxanthellae and hydrothermal vent chemosynthetic bacteria). Reproductive biology varies from sexual dimorphism to hermaphrodism, with uniparental mating being common in some species.

Reflections on the Biogeography of a Deep-Sea Gastropod

The buccinid *Neptunea amianta* (Dall, 1890) is a deep-water species found off the North American west coast. Typically boreal, the range extends as far south as Punta San José, Baja California, at depths usually between 300 and 1500m. In approximately 15 years of video sampling by the Monterey Bay Aquarium Research Institute with remote operated vehicles in Monterey Canyon, *N. amianta* has been documented from 100-3500m, yet dense aggregations, uncommon in deep-sea snails, seem to occur only between 200-2000m. This range extends the species into the oxygen minimum zone, where oxygen concentrations of the water column fall to such depleted levels that many species are unable to survive or require special physiological adaptations. Previous research by Craig McClain indicates that low oxygen concentrations can reduce shell size in Atlantic deep-sea gastropods; nonetheless, *N. amianta*, is a giant compared to other deep-sea gastropods, obtaining shell heights of 6cm.

Most species in the superfamily Muricoidea are carnivores, secondarily evolving to omnivory, herbivory, or deposit-feeding. Typical of its family, *N. amianta* is a scavenger, and dense aggregations in Monterey Canyon have been associated with every conceivable type of large organic matter such as dead crabs, dead whales, dead cold seep clams, kelp, and wood. The species has amazing fasting potential. In one published experiment, 5 individuals survived 12 months in

The ocean floor at approximately 1300m in Monterey Canyon. Photo by Craig McClain, © MBARI, used with permission.



Above: a closer view of one of the rock mounds with a multitude of *N. amianta* and egg stalks. This shows an unexpected level of activity for such a harsh environment.
Below: a closer look still at the activity in these cold and dark depths. Both photos by Craig McClain, © MBARI, used with permission.

aquaria without food, after which the experiment was terminated. None of the five individuals displayed clear signs of undernourishment, and one produced a large egg case with ~75 juveniles during the seventh month. The remarkable fasting potential and the ability to utilize any food resource are likely responsible for its large depth range and high density.

Buccinids have separate males and females, with fertilization occurring internally. Females can produce over 1000 eggs in a leather capsule. In *N. amianta*, egg capsules are stalked and typically 15-25cm high. Multiple stalked capsules, laid by separate females, are found grouped on a hard substrate such as a rock outcropping. The use of hard substrates may serve the dual purpose of providing a stable base and allowing the egg capsule to extend higher off the bottom into more oxygen rich water. In some *Neptunea* species, the first few juveniles to emerge from the capsule will quickly consume unhatched individuals.

So what limits the depth range of *N. amianta*? The lower depth limit of 1000-2000m possibly reflects food limitation. With increased depth and distance from productive coastal waters comes less organic material, marine snow, sinking from the ocean's surface. This marine snow drives deep-sea ecosystems, and thus increased depth corresponds to decreases in the number of individuals and total amount of biological material, i.e. less to scavenge. Because *N. amianta* is a larger deep-sea gastropod with considerable food demands, greater depths may be inaccessible. The upper depth limit of 100-300m may result from either competition with shallower species or a physiological temperature limit (~8°C).

Reflections on the Biogeography of a Terrestrial Gastropod

Prior to 2005, *Hendersonia occulta* (cherrystone drop) was known from only 2 of Pennsylvania's 67 counties. Fieldwork by Dr. Tim Pearce increased the number of known Pennsylvania counties with this rare snail from two to five. Photo courtesy of Tim Pearce of the Carnegie Museum of Natural History.

Hendersonia occulta (Say, 1831) was first observed by Thomas Say, the father of American malacology, as fossils preserved in Ice Age loess deposits along the banks of the Wabash River at New Harmony, Indiana. New Harmony was settled in 1826 when followers of the Welsh philosopher Robert Owen attempted to create a communist utopia in the hinterlands of the Midwest. The brightest minds in the New World were recruited to participate in this experiment. Riding along with Say on the "Boatload of Knowledge" to New Harmony was also biological illustrator Lucy Way Sistare, whom he secretly married a few months later. While the New Harmony experiment was an abject failure, with the settlement being disbanded in only three years due to constant quarrelling, Say and Sistare completed two monumental works (*American Entomology* and *American Conchology*) while living there.

Because he could only find fossils of *Hendersonia occulta*, Say concluded that this species had gone extinct like the mastodon and saber-tooth tiger. Living populations were soon discovered, however. By the early 1900's, Bohumil Shimek of the University of Iowa had not only located numerous colonies on wooded bluffs in northeastern Iowa and scattered other sites in the upper Midwest, but also in the southern Appalachians at places like Natural Bridge, Virginia, and Limestone Cove, Tennessee. Shimek used the habitats of these modern colonies to prove that loess deposits were formed by wind action, and not water, as many had previously believed.

Based on fossils, we now know that during the last Ice Age, *Hendersonia occulta* ranged from western Nebraska and Kansas to eastern Ohio and south to the Mississippi-Louisiana border near Baton Rouge. The bulk of these sites occurred in mixed tundra-parkland habitats a few hundred miles south of the glacial limit. Climatic reconstructions indicate that these areas had greater precipitation and decreased seasonality as compared to modern times. In particular, even though winter temperatures were comparable, summer temperatures were much cooler (perhaps up to 30-40° F). The closest modern climatic analogues are coastal habitats in the far north (e.g. Newfoundland, Labrador) and south (e.g. Tierra del Fuego, southern New Zealand).

Modern *Hendersonia occulta* populations are limited to three distinct population clusters: one centered along the Upper Mississippi river valley, one along the west shore of Lake Michigan, and one in the southern Appalachians from eastern Tennessee to southwestern Pennsylvania. In all of these areas, this species is limited to microhabitats that mimic its favored Ice-Age climate. In the southern Appalachians, populations are restricted to cool mountain coves and talus slopes. In eastern Wisconsin, populations are found only within a few dozen miles of the cool waters of Lake Michigan where summer temperatures rarely exceed 90° F, winter temperatures are moderated as compared to inland areas, and fog banks are common.

In the upper Mississippi valley, populations are limited to cool rocky bluffs and to a very special habitat termed algific talus slopes. 'Algific' is derived from the Latin word for cold (*algus*) and means 'cold-producing'. In this region algific slopes are found on steep, typically north-facing limestone slopes that shelter ice caves. The damp air exiting these caves rarely exceeds 45° F, even during the heat of summer. Coupled with winter temperatures typical for the region, the microclimate of these sites is an almost exact match to the North American Midwest regional climate of 18,000 years ago. These sites harbor not only relict populations of *Hendersonia occulta*, but a number of other species whose ranges were much more extensive during that time, including *Vertigo hubrichti* (Pilsbry, 1934), *Vallonia gracilicosta* Reinhardt, 1883, and the federally endangered *Discus macclintockii* (F.C. Baker, 1928). Algific slopes cannot, however, be considered exact miniature replicates of Ice Age habitats. Fossils of *Hendersonia occulta* are also commonly found with fossils of *Oreohelix strigosa cooperi* (W.G. Binney, 1958), *Vertigo oughtoni* Pilsbry, 1948, and *Vertigo hannai* Pilsbry, 1919. While none of these still resides in the upper Midwest, the first species still exists in mesic pine forests of the Black Hills, and the latter two in arctic tundra from Alaska to Hudson Bay. These snails tell us clearly that the Ice Age climate and habitats of the Midwest have no exact modern analogs.

Red and yellow color forms of *Hendersonia occulta* (Say, 1831) (called the cherrystone drop) from the Elk River East algific talus slope in Delaware County, Iowa. Collected July 13, 1998, Nekola collection accession #3810. Photo by Jeff Nekola.

Hendersonia occulta also helps us understand the history of ecological communities through deep time. The genus *Hendersonia* is a member of the Helicinidae, a prosobranch family that is primarily tropical in distribution, being found in both the New and Old Worlds and also on many Pacific islands. The population of *Hendersonia occulta* along the floodplain of the Escanaba River in the Upper Peninsula of Michigan is, in fact, the most northerly known for any member of this family. *Hendersonia* has a highly disjunct distribution, with species found in eastern North America, as well as in China and Japan, but not in western North America or western Eurasia. Similar distributions occur in a number of other land snail genera and families, including *Gastrocopta*, *Vallonia*, and the Strobilopsidae. Amazingly, similar distributions occur in many other groups, including trees, wildflowers, and amphibians. The cause of these convergent disjunction patterns is hinted at by the fossil record of *Hendersonia*, which also extends into 60-20 million-year-old sediments of the western USA; clearly Asian and eastern North American populations were not always so isolated. Similarly, *Strobilops* and *Gastrocopta* were found in western Eurasia and North America until about 10 million years ago. The fossil record for many broadleaf trees (maples, oaks, birches, sweet gums, sycamores, laurels, etc.), as well as many conifers (such as redwoods, cypress, and ginkgo), were also more globally continuous at that time with populations occurring throughout the northern middle latitudes. This mixed forest encircling the globe until about 15 million years ago has been termed the 'arcto-tertiary forest'. A cooling global climate and continued uplift of the Himalayas and Alps and Rocky Mountains, which decreased rainfall in some areas, brought this era of Earth's history to a close. Within each of the remaining mesic forest centers (eastern North America and Eurasia, the Caucasus and Anatolia, western North America and Eurasia), somewhat random subsets of this original forest persist. Among these relicts is *Hendersonia*. Just like the redwoods of the California coast, the laurel forests of Madeira and the Caucasus, or the maple-palm forests of China and northern Mexico, this species provides us a living glimpse of an ancient world long lost from view.

Barnes, R.S.K., Calow, P., & Olive, P.J.W. 1993. *The Invertebrates: A New Synthesis*. Oxford: Blackwell Scientific Publications.

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A closeup look at *H. occulta*, a rare snail that once ranged throughout most of the Midwest. With the loss of its Ice Age climate it has been restricted to a few specialized habitats. Photo courtesy of Tim Pearce of the Carnegie Museum of Natural History.