PLANT EVOLUTION

Did pollination exist before plants?

Research shows that seaweeds depend on crustaceans for fertilization.

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The sexual reproduction of seed plants involves the transfer of male gametes--in pollen--to their female gametes. In flowering plants (i.e. angiosperms), this is the stigma of flowers, while the gymnosperms (e.g. conifers, cycads, etc.) produce a diversity of structures on their reproductive axes to accomplish the same task. This transfer of male gametes is generally known as "pollination" and it can be mediated by animals, wind, or water. Animal pollination, principally by insects, is the dominant strategy for angiosperms but also occurs in the extant gymnosperms, as well as some species of mosses. Outside of these plants, no other group of organisms has been demonstrated to interact with animals in this way, until now. On page XXX of this issue, Lavaut *et al*. (*1*) demonstrate that a living species of red seaweed, *Gracilaria gracilis,* employs the isopod crustacean *Idotea balthica* to transfer its male gametes, substantially extending the phylogenetic scope of species that use animals as pollinators.

Although they photosynthesize, seaweeds are a type of algae and therefore are only very distantly related to what are considered true plants. The group to which the red seaweed *Gracilaria gracilis* belongs is thought to have evolved around one billion years ago, long before plants appeared (*2*). The isopods are not as old, but nonetheless there has been at least 300 million years for relationships to have developed with the seaweed. It is possible that prior to this, red seaweeds relied on some other now extinct marine invertebrates as pollinators, but the earliest unambiguous arthropods only appear about 600 million years ago. How these seaweeds were reproducing prior to this is a mystery, but Lavaut *et al*. suggest that reproduction in the seaweed is "ambophilous" -- that is, its male gametes can be transported by the isopods or by water currents. This finding is worth noting, as extant seed plants that rely on both wind and animal pollination are widespread and the strategy is assumed to be under-reported (*3, 4*).

What distinguishes the 6,750 described species of Florideophyceae--of which *Gracilaria gracilis* is a member --from most other seaweeds is that their male gametes lack a flagellum to provide movement. It was previously thought that they could reach the female reproductive structures passively via water currents, a common strategy used by other aquatic flowering plants (*5*). However, Lavaut *et al.* demonstrate that isopod crustaceans may be attracted to these seaweeds because they provide a habitat in which to shelter from predators and to feed on small algae that colonize the surface of the seaweed. In addition to pollinating, grazing by the isopods removes these algae, and may increase the growth rate of the seaweed. In this way, the isopods are engaged in a "double mutualism" (*6*) with the seaweed.

Interactions between different species are the engine that make ecosystems function effectively. Herbivores grazing on plants, predators consuming animals, decomposers breaking down organic matter and recycling it all contribute to the ultimate circular economy of the planet. Ecologists consider the outcomes of these interactions in terms of which species benefit, which are negatively affected, and which have a neutral outcome with respect to their evolutionary fitness, i.e. the ability to reproduce. Mutualistic interactions in which both species benefit are often responsible for maintaining populations because of their positive effects on individual reproductive success. Mutualism plays a crucial role in ecology, from gut microbes that facilitate digestion of cellulose in herbivores, to fish and sea anemones that protect each other from their respective predators, to plant-pollinator relationships (*7*).

Relying on a third party to facilitate reproduction is obviously a vital way for organisms that cannot move around to find mates. Although it was once considered the hallmark of flowering plants, researchers are discovering that this kind of interaction, in which animals bring together different gametes or mating types of sedentary organisms, may be found in taxa that evolved long before angiosperms and gymnosperms such as mosses (*8*) and fungi (*9,10*). The study by Lavaut et al. has broadened both the variety and the history of animal-mediated male gamete transfer, taking the concept of pollination from plants to algae and potentially pushing it back to the earliest evolution of marine invertebrates.

The reliance on an animal to ensure reproduction is not without its risks, especially in a world of rapid anthropogenic change. As Lavaut *et al*. point out, most reproduction in this seaweed occurs in the relatively still waters found in coastal rock pools at low tide. These habitats are threatened by factors such as water pollution, invasive species, physical modification of the coastline, and changing climate and sea level (*11*). In addition, crustaceans in general are susceptible to the increasing ocean acidification related to rising atmospheric CO_2 concentration. Ocean acidity can weaken their exoskeletons by decalcification, although this effect has yet-to-be thoroughly examined for isopods (*12*). Seaweeds, including *Gracilaria gracilis*, are also ecologically important for the ecosystems in which they occur and are increasingly being touted as a sustainable food source (*13, 14*). Marine environments are under huge anthropogenic pressure, however, and Lavaut et al. demonstrate the importance of preserving not just species within ecosystems, but also the interaction networks among different species. There is so much work still to be done in this area of ecology and new discoveries to be made. Despite being the most extensively studied group of plants, recent estimates suggest that only 10% of the more than 300,000 known species of animal-pollinated flowering plants have had their pollinators documented (*15*). There are no doubt many more revelations awaiting the careful observer of species interactions.

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FIGURE CAPTION: The complex interactions, and their outcomes, between the seaweed (*Gracilaria gracilis*), the isopods (*Idotea balthica*) which fertilise it and graze on the diatoms that colonise the seaweed's fronds. Positive interactions (+) increase the fitness of a partner whilst negative interactions (-) decrease their fitness. Isopod and diatom images from Lavaut et al. (*1*). *Gracilaria* image by Emoody26 at English Wikipedia, CC BY 3.0, https://commons.wikimedia.org/w/index.php?curid=3455016