

metabolic pathway. More generally, to have an impact on cell or organism function, a gene product involved in metabolism needs a substrate, a transcription regulator needs a target, and a protein involved in signal transduction needs interacting partners. If these conditions are not met, a transferred gene might have no, or only negligible, impact on the recipient organism. Even if these conditions are met, the impact of a transferred gene might be selectively neutral or deleterious.

So what happens to products of HGT? It is reasonable to expect standard population genetic principles to apply. At one end of the spectrum, strongly deleterious genes will be eliminated from populations through purifying selection. While at the other extreme, advantageous genes will become fixed through positive selection. Neutral and nearly neutral genes occupy the middle ground and will have a probability of fixation or elimination determined by genetic drift. The frequency with which HGT occurs, and where transferred genes fall on the spectrum of potential adaptive impact, remains an open question. However, examples of adaptive HGT suggest the likely occurrence of a larger number of non-adaptive HGT events. Furthermore, this suggests the hypothesis that eukaryote genomes are littered with horizontally transferred DNA. This hypothesis is being actively investigated and genome-scale analyses are already finding support for relatively frequent HGT into eukaryotes (e.g. [9,10]).

The remarkable impact that HGT appears to have had on the evolutionary trajectory of ferns suggests an exciting, albeit highly speculative, solution to a classic problem in evolutionary biology. Sister lineages often have significantly different numbers of species. Commonly referred to as the phylogenetic imbalance problem, this enigmatic pattern was famously highlighted by the geneticist J.B.S. Haldane, who suggested that, a creator, if one exists, must have had "an inordinate fondness for beetles" [11]. Indeed, why are there so many species of beetles (Coleoptera) and so few of, for example, velvet worms (Onychophora). Or amongst plants, why are there so many daisies (Asteraceae) and only one *Ginkgo*? Could it be that the acquisition of

adaptive genes via HGT is responsible for accelerating diversification in some lineages?

The Li *et al.* report is likely to inspire biologists to search for further cases. But I would like to offer a small word of caution: in seeking evidence for HGT, it is important to recognise that the assumptions of standard phylogenetic methods will often be violated in cases of suspected HGT. For an accessible discussion of phylogenetic models and their assumptions, see [12]. The severity of such violations will vary, and in many cases will not produce incorrect results, but it is important to realise that phylogenetic analysis will not necessarily yield reliable trees. The reliably of phylogenetic methods in identifying the correct origin of horizontally transferred genes will decrease with increasing age of the putative HGT event and different approaches can produce dramatically different results for ancient HGT (e.g. [13,14]). Nevertheless, with increased interest in HGT we can expect additional cases to be identified, and the impact of HGT in macroevolution will become better known.

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Evolution: How a Barnacle Came to Parasitise a Shark

A new study on a parasitic barnacle that lives on a deep sea shark found that its closest living relatives are rocky shore barnacles. The findings provide insight into barnacle phylogeny and raise new questions about the evolution of parasitism.

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Parasitism is one of the most common modes of life on this planet [1]. It has independently evolved several times in

all domains of life, and many animal phyla have parasitic species [2]. But for most parasite groups, very little is known about how they made the evolutionary transition from a

free-living to a parasitic mode of life. This is mainly due to two reasons. First, many parasites have such derived morphology that they bear little resemblance to their free-living relatives. For example, *Enteroxenos oestergreni* is a parasitic snail that lives inside holothurians (sea cucumbers), yet the adult snail is nothing more than a long string of gonads [3]. Secondly, parasites in general have a very poor fossil record [4] because they tend to be small, soft-bodied organisms and are rarely preserved as fossils. Thus, there is a lack of transitional forms available that can inform us of how the evolution from free-living to a parasitic lifestyle might have occurred, aside from comparing parasites with their closest living relatives.

In this issue of *Current Biology*, Rees *et al.* [5] report on a study into *Anelasma squalicola*, a peculiar stalked barnacle that parasitises deep-sea squaloid sharks such as the velvet belly lantern shark (*Etmopterus spinax*). They examined the phylogenetic position of *Anelasma* within the stalked barnacle clade and their analysis placed a group of rocky shore stalked barnacles as being the closest living relatives of *Anelasma*.

Parasitism has evolved multiple times within Crustacea and while some parasitic crustaceans resemble their free-living relatives, the morphology of many species has become so derived that they are completely unrecognisable as arthropods. Among Cirripedia (barnacles), a well-known parasitic species is *Sacculina carcini* — a crab-infecting parasite that not only castrates its decapod host but is also capable of altering its morphology and behaviour so that the host cares for the parasite's brood as if it was its own [6]. *Sacculina carcini* belongs to a superorder of endoparasites called Rhizocephala. These barnacles have lost almost all traces of their arthropod ancestry; the adult body plan consists of a branching mass of fine rootlets that extends throughout the interior of the host's body, and a bulbous female reproductive organ that protrudes from the host's abdomen [6].

Aside from rhizocephalans, there are only two other genera of parasitic barnacles: *Rhizolepas*, which infects polychaete worms [7], and *Anelasma*, which was the subject of Rees *et al.*'s study [5]. Unlike other stalked

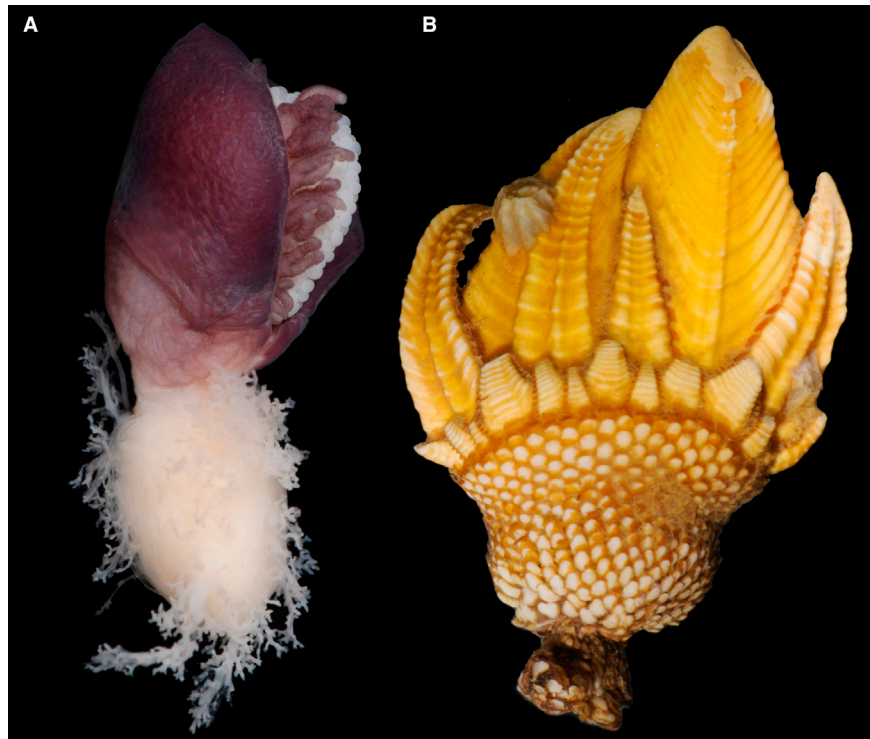


Figure 1. Parasitic and non-parasitic barnacles.

(A) A specimen of *Anelasma squalicola* in full. (B) *Capitulum mitellam*, an intertidal stalked barnacle which has been found to be the closest living relative of *A. squalicola*. (Photo from [5].)

barnacles that obtain their food by filtering the water column with their limbs, *Anelasma* draws nutrition directly from its shark host through the peduncle — a bulbous structure covered in fine, root-like filaments which is deeply embedded in the shark's body (Figure 1A). But unlike *Sacculina* and other rhizocephalans, *Anelasma* still has some of the morphological characteristics of its non-parasitic ancestry in the form of vestigial feeding limbs which are wholly non-functional.

Apart from those species, all barnacles are strictly filter-feeders, though many of them do live as epibionts attached to the surface of other animals. One group, the Coronuloidea, is a superfamily of cirripeds that specialise in attaching to various mobile marine animals, including cetaceans, sirenians, sea turtles, sea snakes, and crustaceans [8]. While some coronuloids form relatively superficial attachments, others are deeply embedded in their host's tissue and have structures or physiological adaptations for anchoring themselves securely to the host's body [9].

Unlike *Anelasma*, the coronuloids remain nutritionally independent of their host and are strictly filter-feeders. But given that they are already somewhat invasive and have at least some degree of interaction with host physiology, they do seem to be in a prime position to evolve into true parasites. So did *Anelasma* evolve from or share a common ancestry with this group of barnacles? This scenario is certainly appealing; both *Anelasma* and coronuloids embed themselves into the body of marine animals, and one can therefore envision *Anelasma* as being a heavily-derived coronuloid that has gradually abandoned filter feeding in favour of drawing nourishment from the host to which it is attached.

But the analysis by Rees and colleagues challenges that scenario. They found the closest living relatives of *Anelasma* are actually intertidal barnacles that attach to non-living substrates (Figure 1B), which means both *Anelasma* and the coronuloids have independently evolved their respective associations with marine animals.

Given the stark contrast in lifestyle and habitat between *Anelasma* and its closest living relatives, this suggests there is a gap of currently unknown and extinct species that might be transitional forms between *Anelasma* and other stalked barnacles. Furthermore, Rees *et al.*'s analysis [5] points to an origin for *Anelasma*'s lineage that dates back to 120 million years ago in the Cretaceous period. They suggested that *Anelasma* may actually be a remnant species from a clade that was far more speciose in the past. Though *Anelasma* is only found on a few species of deep-water sharks, it might have once been part of a more diverse group of parasitic stalked barnacles that infected a wider range of marine animals.

But what of the coronuloids and other barnacles that live as epibionts? Given the lineage that led to *Anelasma* had successfully evolved to be parasitic from an ancestor which was most likely a rock-clinging filter-feeder, why have none of the coronuloids evolved to be parasitic since some

species are already deeply embedded in the body of various animals?

The results from Rees *et al.*'s study provide us with an additional perspective on what it takes for an organism to evolve from a free-living to a parasite lifestyle. It also raises more questions about why certain groups (such as the coronuloid barnacles) have not evolved to be parasitic, even though they seem to be in a prime position to do so. The discovery that *Anelasma*'s closest living relatives are intertidal rather than epibiont barnacles also reminds us that the most likely or plausible evolutionary scenarios we can come up with may not necessarily correspond with what actually happened. The evolutionary history of any organism is convoluted and complex, and does not always conform to our own expectations.

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Sensory Biology: It Takes Piezo2 to Tango

A trio of papers has resolved an outstanding controversy regarding the function of Merkel cells and their afferent nerve fiber partners. Merkel cells sense mechanical stimuli (through Piezo2), fire action potentials, and are sufficient to activate downstream sensory neurons.

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Effective tactile communication is crucial for the exquisite beauty and breathtaking dynamics embodied in dance and depends on sensory neurons embedded in the skin that vary in their size, shape, and sensitivity [1–3]. Mammals, including humans, have skin domains enriched in Merkel cell–neurite complexes needed for the discrimination of fine textures [4]. Merkel's description of specialized cells associated with nerve endings in the skin in 1875 launched more than a century of speculation and investigation about the nature of the dance they might perform together with their sensory endings. Until now, researchers have been unable to

decipher whether the Merkel cell, its sensory afferent, or both were responsible for touch sensation. A trio of recent papers [5–7] exploit the discovery of the Piezo proteins [8] and provide unprecedented clarity: Merkel cells rely on Piezo2 to transduce mild skin indentation and whisker deflection into electrical signals. Confirming speculation regarding the potential for a synapse-like connection between Merkel cells and their afferents, optical stimulation of Merkel cells engineered to express light-gated cation channels is sufficient to activate downstream sensory neurons [6].

Nestled at the inside border of both glabrous and hairy skin (Figure 1), Merkel cells aggregate in touch domes and are closely apposed to myelinated sensory nerves. In rodents, Merkel cells

additionally cluster around guard hairs of the pelage and sinus hairs (i.e. vibrissae, whiskers) in facial skin. Though the cells and their nerves have been known since the 1880s, it was not clear that Merkel cells and their nerves were separate cells until the invention of the electron microscope (reviewed in [9]). Iggo and Muir [10] established that tactile stimulation elicits action potentials (spikes) from nerves associated with Merkel cells and classified such nerve fibers as slowly adapting type I (SAI) A β mechanosensory afferents according to their slow conduction velocity (A β fibers) and the observation that spike frequency adapted slowly during touch stimulation.

While this work established that the Merkel cell–A β afferent complex detects touch, it remained unclear which of the cell partners leads the dance. Over the years, evidence accumulated to both support and refute the idea that Merkel cells are like hair cells in the inner ear — non-neuronal cells that detect mechanical stimuli and signal to neurons. The alternative idea that tactile stimuli are sensed solely by the