Darwin tribute

A bronze statue of Charles Darwin was unveiled on the bicentenary of his birth last month at his old Cambridge College. The sculpture portrays how he may have looked as a young undergraduate in the summer of 1831, his last year at Christ's College.

The sculptor, Anthony Smith, also a graduate of Christ's and now its artist in residence, used a range of sketches and portraits of Darwin as an older man. Smith reconstructed his features as they would have appeared in Cambridge. A watercolour by George Richmond in 1840 provided a glimpse of Darwin's jaw line, while a chalk drawing by Samuel Lawrence in 1853 revealed his prominent brow and nose in profile. And Smith met many of Darwin's descendants who also showed facial resemblances to their famous forbear.

The statue shows Darwin sitting informally on the arm of a garden bench outside the entrance to Christ's in a garden devoted to him.

"I have long been an admirer of Darwin, and studied his work as part of my degree in natural sciences in Christ's College," says Smith.

"I would like people to think about Darwin afresh when they see the statue," he says. Six months after leaving Christ's, Darwin was on board HMS Beagle on that most famous of voyages.

The statue provides a contrast to others of Darwin. "The public perception of him is as an old man with a beard, but he was, by all accounts, an energetic and life-loving student who did much of his great work in his early years," says Smith.

Nigel Williams

At ease: An informal new sculpture of Charles Darwin was unveiled at Christ's College Cambridge last month to mark the bicentenary of his birth. (Photo: Helen Mort.)

Quick guide

Scale insects

Laura Ross[1] and David M. Shuker[2]

What are scale insects? Scale insects (Hemiptera: Sternorrhyncha: Coccoidea) are a group of small, plant feeding insects closely related to aphids and whiteflies. They are characterized by their unusual shapes, so much so that it is sometimes hard to recognize them as insects or even as animals! Adult females hardly ever move, lacking wings and often even legs. Instead of being able to run away, they have evolved many other ways to protect themselves against danger, including a variety of protective secretions. For instance, the armoured scales hide under a toughened shield, whilst mealybugs cover themselves with white grains or strands of wax (Figure 1). Many felt scales on the other hand recruit the plants they infest to help protect them, forming galls on the host plant. All told, there are almost 8000 species of scales across about 32 different families, of which the mealybugs and the armoured scales are the most numerous. Scale insects are found across the world, feeding on the leaves, roots and stems of a wide variety of host plants, and even under the bark of trees.

Males don't look much like females do they? That's right, adult males and females look so completely different that it is hard to believe they are the same species! Adult males have both wings and legs, and are typically tiny (1–2 mm). However, in most species adult females are much bigger (in some species up to 3 cm) with strongly reduced (or absent) legs and antennae and no wings. The specialised wax-secreting glands and structures are also typically only found in females. In addition to these morphological differences, males and females have very different patterns of development. As juveniles, the sexes are often indistinguishable, but after the second larval stage (or 'instar') males undergo a form of metamorphosis, emerging to live but a few days as adults. Females, on the other hand, retain their larval appearance throughout their lives (through several instars), living for up to several months. However, some species of scale insect lack males altogether and reproduce asexually.

What do scale insects do? Well, at first glance, not very much. The females form dense colonies on their host plants, attaching themselves firmly to the plant and feeding on the plant sap. Adult females are usually completely sedentary and while adult males are winged, they do not disperse over great distances, because of their short lifespan and poor flight ability. In comparison to the adults, however, the young larvae ('crawlers') can be very mobile and do manage to get around, with a number of dispersal strategies, including behavioural and morphological adaptations for being carried by the wind. In an Australian species, young females even hitchhike on the back of their winged brothers. The female's sedentary lifestyle does mean that scales are incredibly fecund, with energy spent on little else apart from staying put and reproducing.

If they don't do very much, why are they important? This sitting around on plants causes millions of pounds-worth of economic damage to crops and ornamental species the world over, making scale insects a major pest to both farmers and gardeners alike. They damage plants directly by feeding on the plant sap, but they can also indirectly cause damage by transmitting plant pathogens and by their production of large quantities of honeydew. Accumulations of this sugary secretion can result in fungal growth on the plants, thereby reducing photosynthesis and promoting further pathogen attack.

They might be important, but they still just sit around — are they interesting? Yes! First, all scale insects harbour endosymbiotic bacteria (or fungi) that provide them with essential nutrients and allow them to live on the otherwise very poor diet of plant sap. Most scales have more than one species of endosymbiont, which often live together inside specialized host cells. In the case of mealybugs, these two bacteria even live inside each other — the only known case of bacterial–bacterial endosymbiosis!

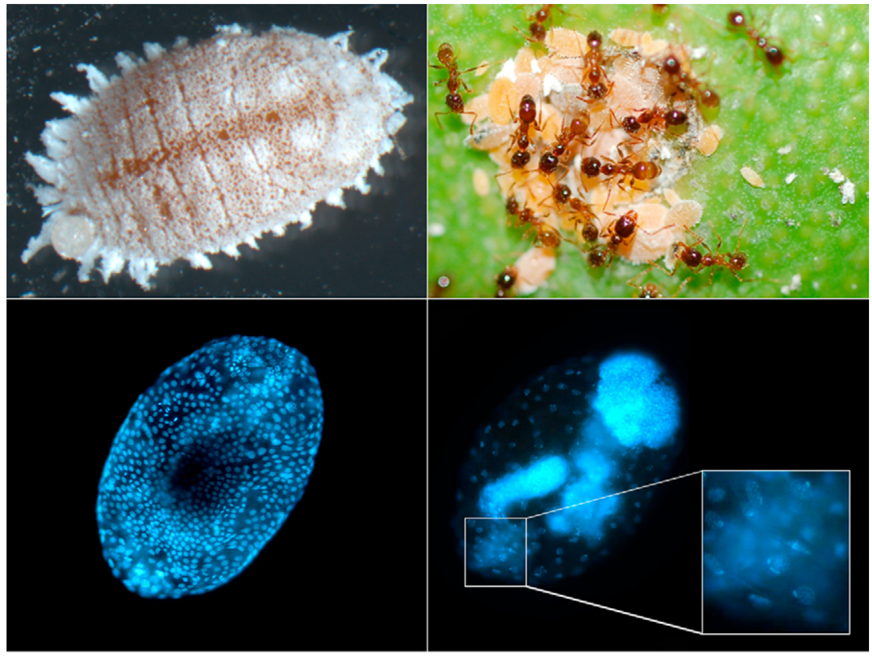

Figure 1. Mealybugs.

Clockwise from the top left hand corner: an adult female *Planococcus citri* mealybug; mealybugs being tended by mutualistic ants; a male *P. citri* DAPI-stained embryo, with the condensed paternal chromosomes visible within cell nuclei as dense dots (see inset); a female *P. citri* DAPI-stained embryo, showing normal nuclei. Pictures by Laura Ross and Alejandro Tena (mealybugs and ants).

Second, scale insects have a tremendous diversity of genetic systems, including haplodiploidy, six types of asexual reproduction and even hermaphroditism. One of the most puzzling genetic systems found in scales though is paternal genome elimination: both sexes are diploid but in males one of the parental chromosome sets is deactivated (via DNA heterochromatization) during early development. The deactivated set is always the set inherited from the father. Although the deactivated set divides faithfully in all somatic cell lines, it fails to end up in mature sperm because it is destroyed during meiosis. For an example see Figure 1.

How do they know whose chromosomes are whose? By genomic imprinting — both males and females 'tag' their genes and this affects which genes (from father or mother) are expressed in the offspring. In most taxa where imprinting is known to be important, only a small percentage of genes across the genome are involved. In scale insects, however, whole chromosomes are involved and in males only the mother's chromosomes are expressed, while the father's chromosomes are deactivated. Although the molecular mechanisms involved in the silencing of the paternal genes are fairly well understood, it is still a mystery why the silencing only happens in males and how the sex of the offspring is determined in the first place.

Are males completely helpless while their genes are destroyed? Probably not. Whilst the paternal genome is deactivated in nearly all male tissues, it is active in the cells making up the cysts in which spermatogenesis takes place. Thus, genes of paternal origin are silent except in the very place where they are prevented from gaining access to the sperm, suggesting that they might try to prevent their own destruction.

Why do scale insects have so many genetic systems? Good question! It might be because males, females and the endosymbiotic bacteria value sons and daughters differently, leading to conflict over the control of sex allocation and sex determination.

In species with paternal genome elimination, males do not pass on their genes through their sons (they do not make it into their sons' sperm) and might therefore favour daughters. The same is true for the bacteria, because these are only transmitted through the cytoplasm in scale insect eggs (and so through the maternal line of their hosts). Females, however, benefit from both male and female offspring. Therefore, all three of them have an interest in controlling sex determination, which might have led to the large diversity of unusual genetic systems through evolutionary conflicts between female-expressed genes, male-expressed genes, and the symbiotic bacteria.

Males do seem to get a bit of a rough deal, don't they? This also might have to do with their bacteria. As the endosymbionts are only transmitted through females there is no selection pressure for them to do their job that well in males. Even worse, it might be beneficial for the bacteria to kill males if this benefits their sisters, who carry the relatives of the bacteria. In order to avoid this, males appear to have been selected to depend less on their bacteria, which might explain their small size and short lifespan. There is even a scale insect where males don't have bacteria at all and do not feed. Instead they are fed by their mothers, who have evolved a placenta-like structure for this purpose.

Does the host have any means of controlling their bacteria? Perhaps. Most scale insects have a specialized organ called the bacteriome which contains their endosymbionts; this structure can take up about one third of their body. Several very peculiar mechanisms for the formation of this organ have evolved in different scale insect families. In some, it is formed from modified gut cells, whilst in mealybugs and armoured scales it is formed by the fusion of the maternal polar bodies (formed during oogenesis) and one embryonic cell, thus forming a chimera of maternal and offspring tissue. In species from the family Putoidea, the bacteriome of an individual does not contain any of its own tissue but is completely formed from maternally-derived cells! Although many of these mechanisms seem puzzling, they have in common that they make sure it is difficult for the bacteria inside these organs to infer the sex of their host from the genetic make-up of the tissue around them, perhaps helping suppress spiteful behaviour against males.

Do scales interact with any other organisms? As with many other honeydew-producing insects (such as aphids), mealybugs and other scale insects are often visited by ants that collect the honeydew (Figure 1). This is obviously good for the ants, but also for the scales because ants can offer protection from predatory insects and spiders. Indeed, although many scale species are visited by ants, some have become completely dependent on them. For example, species of the genus *Stictococcus* would drown in their own honeydew if the ants didn't remove it! In addition, species of the mealybug genus *Hippeococcus* are used as cattle by the ants, which they transport with them to new host plants and there are observations of crawlers jumping on the back of the ants and being rescued in case of danger. In several ant species, the queen even takes one of her colony's mealybugs with her on her nuptial flight. The relationship can become so close that *Hippeococcus* species have lost their endosymbiotic bacteria and are dependent on direct feeding by their host ant.

How do I find out more?

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Primer

Invertebrate solutions for sensing gravity

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Gravity is fundamental to life on Earth — plants and animals alike must compensate for the force of gravity to maintain a right-side-up posture. Accordingly, detecting gravity may be one of the first sensory capacities to have evolved in animals. Furthermore, whether running, swimming, or flying, animals that move around with coordination and direction must also account for gravity during locomotion. To estimate their orientation relative to the earth, humans and many other animals are highly reliant on vision: the sky is light, the ground is dark, the horizon is horizontal, and many environmental edges are vertical. However, we can also walk normally in the dark, yet a person who sees well but loses the ability to detect gravitational forces acting on his or her limbs becomes severely impaired.

How can an organism measure gravity? Newtonian physics provide a convenient conceptual framework. Although the force of gravity is effectively constant, its vector direction relative to an animal's body varies with any rotation of the body. There are two general strategies used for estimating the gravitational vector: integrating directional forces measured across the whole body or measuring acceleration at a single point (Figure 1). These solutions are not mutually exclusive and can be implemented in tandem. In humans, muscle spindles and Golgi organs measure tension on joints while the vestibular system senses rotational velocity and acceleration, providing complementary signals necessary to maintain the relatively unstable bipedal posture.

Just as we mammals have evolved highly acute sensory mechanisms to detect gravity acting on our bodies and appendages, so have invertebrates developed these capacities. For invertebrates, perceiving gravity's pull presents a