



attention to interesting aspects of natural history. In most of my research projects I try to reserve a little bit of time for taking photographs. Our projects on waterbirds are ideal for combining data collection with a bit of photography — we observe our focal broods from floating, mobile blinds, in wetlands teeming with waterbirds. With a really good blind, it's like being invisible — we often get ridiculously close to all sorts of wildlife. In some cases we actually collect data with a camera: as coot chicks are virtually impossible to recapture within a day of hatching, I worked out a technique for obtaining accurate size measurements from photographs. I also use my photographs liberally in my teaching. The right type of photo can be used as a virtual laboratory, where students have to search for interesting patterns and come up with ecological hypotheses that can explain the patterns. As a result, I am often on the search for photographic subjects to illustrate some of the case histories I cover in class.

**Do you have a favorite paper?** Arnon Lotem's 1993 theory paper in *Nature* ('Learning to recognize nestlings is maladaptive for cuckoo *Cuculus canorus* host') is certainly one of my favorites. Cuckoo hosts can recognize non-mimetic eggs in exquisite detail but are completely clueless when it comes to recognizing foreign chicks, something that has puzzled naturalists for centuries. Lotem made the key realization that recognition cues would likely be learned through imprinting at the first breeding. As parasitized hosts raise only a cuckoo chick (the cuckoo chick evicts the host chicks), parents that are parasitized at their first breeding would imprint on the cuckoo chick and in subsequent breeding events reject their own offspring. Lotem

showed that the risk of imprinting on the cuckoo chick would make learned recognition maladaptive. Lotem's paper made me realize the insights gained from thinking about proximate mechanisms, rather than focusing exclusively on the potential adaptive basis of traits.

**What was your biggest mistake or surprise?** Completely ruling out an implausible phenomenon that in the end turned out to be true. Although I discovered that coots were really good at recognizing eggs laid by other females, I did not seriously consider that coots might be able to recognize foreign chicks. If songbirds can't recognise cuckoo chicks that differ comically from their own, how on earth should coot parents be able to discriminate between chicks of their own species? Then, a few years ago, my student Dai Shizuka swapped coot chicks among nests to synchronize hatching, and some birds appeared to recognize and reject the foreign chicks. After several unsuccessful experiments, Dai was finally able to show that coots can recognize and reject brood parasitic chicks, and he also figured out their learning mechanism: the adults imprint on the chicks that hatch on the first day of hatching, which are typically their own chicks. This project was the most enjoyable and exciting research I have ever been involved with, so I was quite happy to be proven wrong about chick recognition in coots. The work also connected back to my favorite paper by Lotem, as our research showed that learned chick recognition can evolve when learning is associated with a low risk of error, as is the case for coots.

**Any advice for someone starting a career in biology?** Natural history and science are not mutually exclusive. Natural history can be a starting point that leads you to interesting questions and experiments, but of course there are many other entry points to understanding nature as well. Notice and think about odd field observations, or failed experiments — they sometimes lead to your most exciting discoveries. And, get a camera — great for illustrating talks and for sharing your research experiences with friends and family.

Department of Ecology and Evolutionary Biology, University of California at Santa Cruz, Santa Cruz, CA 95064, USA.  
E-mail: [lyon@biology.ucsc.edu](mailto:lyon@biology.ucsc.edu)

## Quick guide

# Houses made by protists

Mike Hansell

**What kind of structures are we talking about?** Portable protective cases, known as tests, made by single-celled organisms out of collected building materials.

**What are the organisms that can do this?** There are two distinct types of single-celled eukaryotes with this ability. One group are amoebozoans with generally lobe-shaped pseudopodia; the other are the foraminifera (or forams) which are characterised by long, thread-like pseudopodia.

**Does the building behaviour of the two groups have a common evolutionary origin?** It seems not. The Protista are not a monophyletic group. The current taxonomy of them is rather fluid; however, it seems that the two case-building groups are separable at least at the Phylum level, or even at the Kingdom level in some classifications. The amoebozoans are placed in the Phylum (or Class) Lobosea, while the forams have their own Phylum (orClass), Foraminifera.

**What does one of these portable cases look like?** That of the amoeba *Diffflugia corona* is made of several hundred sand grains (Figure 1). It is almost spherical, with a single circular aperture out of which the organism can project its pseudopodia as it glides through the soil water film or across damp vegetation. The aperture itself is edged with a finely pleated collar of very tiny sand grains and from the top of the case project five or so spikes, also constructed of sand grains. The size of the case is around 200  $\mu\text{m}$  across.

**How does a single-celled organism achieve this?** *Diffflugia* multiplies by binary fission, and a new protective case is built before cell division occurs. As the amoeba moves around

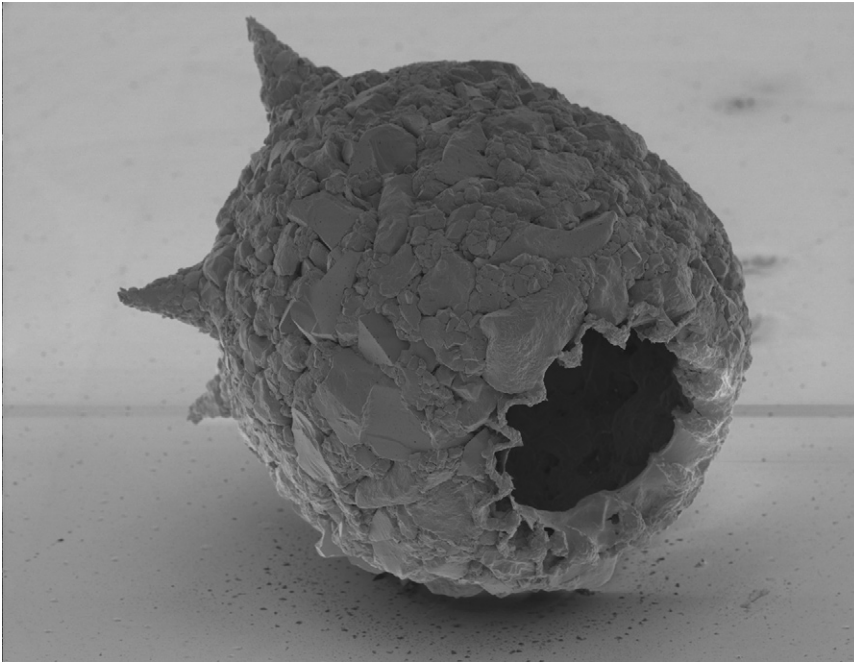


Figure 1. *Diffflugia corona* case of quartz grains (reproduced with permission from the Natural History Museum Picture Library).

over the substrate, it not only engulfs food particles, it also picks up quartz particles, which accumulate as a mass within the cell until there are enough to create a complete new case. Then, prior to cell division, the mass of building materials is extruded within a cytoplasmic bud. They then become arranged in the species-typical manner before the cytoplasm withdraws between them leaving a cement that gives rigidity to the new structure. There are now two identical cases positioned aperture to aperture, held together by a cytoplasmic bridge. The cytoplasm now divides, each daughter cell occupying one case. The two organisms move apart, carrying their sand grain cases with them.

**Can this really be described as behaviour?** The assembly process is probably best described as 'behaviour-like' as it is wholly intracellular, but what it achieves is to allocate particles of different size to particular places, creating a species-distinctive architecture. The collection of the building material is a more obviously behavioural process; the organism must have some mechanisms, however simple, to pick up the appropriate types and sizes of particles and in sufficient quantity to create a new case.

**What sort of structures do foraminifera build?** They vary in the type of material collected and the architecture created. One type of collected material used by forams is siliceous sponge spicules. *Technitella legumen* builds a portable case entirely out of these. This case was first described a hundred years ago when it attracted attention because of its elegant design coupled with apparently sophisticated engineering. It is cigar-shaped with a small aperture at one end and may be made entirely of straight rods of fragmented sponge spicules. These form two layers. In the outer layer, they are laid closely together with their long axes parallel to the long axis of the case. Those comprising the inner layer are arranged with their axes perpendicular to those of the outer layer to run round the circular section of the wall. The spicules are held together with a cement to create a rigid structure. For a single-celled organism to show such an ability was considered at the time remarkable enough to be discussed in terms of its 'purpose and intelligence', and it is still cited as evidence of a divine 'designer' in some creationist literature.

**How might this ability have evolved?** It is interesting that, in both groups, there are species that make portable

cases entirely from materials they secrete themselves. One form typical of some planktonic foraminifera is a succession of calcareous chambers of increasing size, creating the shape of a *Nautilus* shell a few hundred microns across. Each chamber is perforated by many small apertures through which the filamentous pseudopodia can project.

Among the Amoebozoa, *Arcella dentata* exemplifies species that synthesize their own building materials. It secretes within its cytoplasm large numbers of proteinaceous granules. These are extruded from the mouth of the test within a cytoplasmic bud. This bud is then enveloped by a pseudopodium under which the granules become arranged as a single layer in the shape of a new test before the protective pseudopodium withdraws. Other, related species synthesise and store within themselves siliceous particles, which are then deployed to make a new case. In *Euglypha rotunda*, the siliceous units are an extremely regular oval shape which, prior to cell division, become arranged around the newly budding organism as neatly overlapping tiles, about 120 to form an elongated dome, with a further 8 to 14 of slightly thicker, toothed ones surrounding the aperture. Some species combine collected with self-secreted materials. The case of *Diffflugia oviformis* is largely composed of self-secreted, siliceous building units of somewhat variable size, but may also include some collected elements such as diatom shells.

It does therefore seem that, in both the Amoebozoa and Foraminifera, some species have the ability to secrete their own building materials, and also the ability selectively to deploy the building units during the construction process. So, whether or not structures made with self-secreted building units evolved before or after those made of collected materials, either could make use of a system for the selective distribution and assembly of materials within the cell.

In the completed cases of some species there is evidence of sub-assembly routines as well as selective distribution. For example, the sand grains which comprise the globular cases of *Diffflugia globostoma* are of two different



sizes, smaller ones of about 1.5  $\mu\text{m}$  diameter and larger ones of about twice that, with few intermediates. The surface of the test is made up largely of 'rosettes', each made almost exclusively of small particles. The number of sand grains per rosette is about 16, arranged to create a slightly domed disc one layer thick. The spaces between the rosettes are mainly filled with large particles.

**Do these building processes share features shown by case-building invertebrates?** It is a general feature of building by metazoan animals that the acceptability of collected building materials is standardised. The selective advantage of this is that it probably simplifies the construction process and makes for a more resilient structure. Many species of both Amoebozoa and Foraminifera that build with collected materials show evidence of selection for particle size. An extreme expression of this is the use made, in a few species, of highly standardised building units manufactured by other organisms. Cases of a fossil foraminiferan resembling *Trochammina depressa* have been found to be made largely from coccoliths, the protective plates that envelop certain single-celled algae. Some cases are composed almost exclusively of the calcium carbonate coccoliths of one algal species, *Watznaueria barnesae*. These, initially elliptical, discs are laid precisely edge to edge, all with their convex faces outward and their edges modified to a hexagonal profile so that they fit tightly together (Figure 2). The *Trochammina* almost certainly collected the coccoliths as the remnants of dead algae on the ocean floor; however, the amoebozoan *Nebela collaris* seems able to obtain regular building units through predation. The small silica plates of which the domed case may be composed are apparently recycled from ingested smaller testate amoebae.

**What are these cases for?** We have almost no information on this. They are very reminiscent of the protective cases of some insect larvae, so they might similarly provide physical protection, in this instance against predators or possibly pathogens.

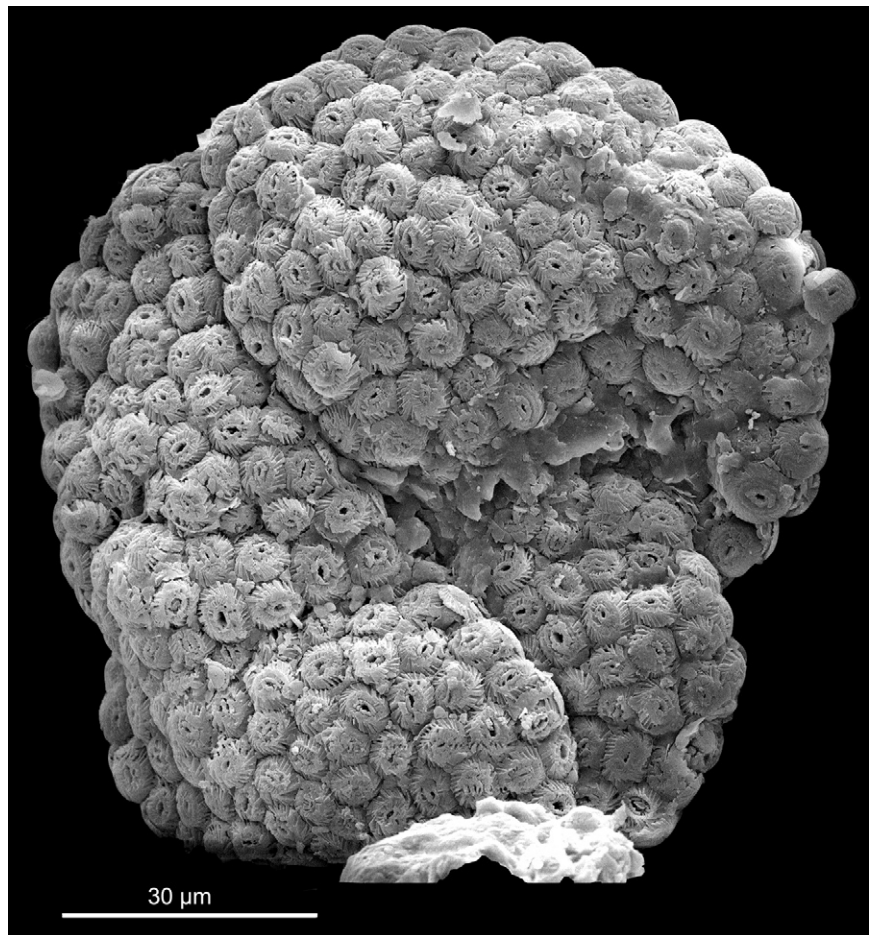


Figure 2. Case of a trochamminid foraminiferan constructed from algal coccoliths (reproduced with permission of Erik Thomsen).

**Are these cases of significance for any other biological field?** Very much so. Collectively these two groups of organisms are very widespread, found in the soil, fresh water and marine habitats, both planktonic and benthic. The structures they build or secrete are generally readily identifiable, at least to the genus level. For these reasons they have become important monitors of environmental alteration or damage. A study, for example, on the pollution caused to a marine habitat by oil-based drilling mud found that foraminifera were more sensitive indicators than benthic macro-invertebrates. The cases, whether of collected or synthesised materials, also have the merit of persisting through time and into the geological record. This allows them to be used to characterise ancient local habitats or global changes in climate. In foraminifera that secrete their own calcium carbonate tests, the ratios of

stable isotopes of oxygen and carbon also provide evidence of the oceanic or benthic temperatures at the time of their formation.

#### Where can I find out more?

- Eckert, B.S., and McGee-Russell, B. (1974). Shell structure in *Diffugia lobostoma* observed by scanning and transmission electron microscopy. *Tissue Cell* 6, 215–22.
- Hedley, R.H., and Ogden, C.G. (1974). Adhesion plaques associated with the production of a daughter cell in *Euglypha* (Testacea: Protozoa). *Cell Tissue Res.* 153, 261–268.
- Heron-Allen, E., (1915). A short statement upon the theory and the phenomena of purpose and intelligence exhibited by the Protozoa, as illustrated by selection and behaviour in Foraminifera. *J. Microscopy* 95, 486–489.
- Thomsen, E. and Rasmussen, T.L. (2008). Coccolith-agglutinating Foraminifera from the early Cretaceous and how they construct their tests. *J. Foramin. Res.* 38, 193–214.
- Zachos, J., Pagani, M., Sloan, L., Thomas, E., and Billups, K. (2001). Trends, rhythms and aberrations in global climate 65Ma to present. *Science* 292, 686–693.

Institute of Biodiversity, Animal Health and Comparative Medicine, University of Glasgow, Glasgow, UK.  
E-mail: [Mike.Hansell@glasgow.ac.uk](mailto:Mike.Hansell@glasgow.ac.uk)