Macroevolution

Predation by drilling gastropods

from Michael J. Benton

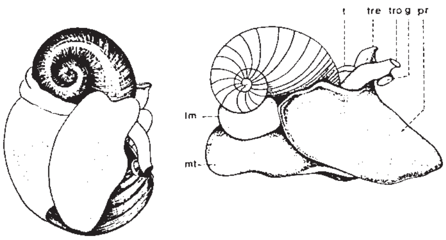
PREDATION is an important agent of natural selection, and it is regarded by many as an important driving force of evolution[1]. There is growing evidence that the fossil record can offer unique information on the history of particular predator–prey systems, and thus complement the work of ecologists on living forms. Gastropod molluscs (limpets, winkles and other molluscs with 'coiled' shells) are major marine predators on other shelled animals, and they use various mechanical and chemical means to drill or bore through the shell (see figure). Evidence of this activity has been found in the fossil record, although until recently, the oldest precisely identified gastropod borings dated from the early Cretaceous Blackdown Sands of Southern England — about 100 million years (Myr) ago. But new evidence shows that drilling by gastropods occured much earlier and suggests that these early gastropods had a different form from their present-day counterparts[2].

Gastropod drill holes are readily identifiable in fossils or recent specimens of shells. They are round, perpendicular to the shell surface, cylindrical or conical in cross-section, generally pass right through the shell at its thinnest point[3] and are produced by the mechanical action of tooth-like structures on the gastropod radula and by the chemical action of acids.

Certain families of gastropods produce quite distinctive holes. For example, naticid gastropod drill holes are tapered inwards, forming a broad parabolic section on the outside (countersunk) and are 0.2–3.1 mm in diameter; there is a central boss in incomplete holes where the animal has stopped before reaching the flesh inside.

The fauna from the early Cretaceous Blackdown Sands of Southern England[3,4] contains naticid gastropods and other boring forms, as well as various bivalve species. Of the 83 species of bivalves, 43 show gastropod borings, 11 of which account for 73 per cent of the attacks. One species, *Corbula elegans*, accounts for 28 per cent of the attacks. The naticids also bored into the shells of other gastropods. In general, for the Blackdown fauna, prey preference tends to vary with the relative abundance of the prey species, although some particularly thick-shelled oysters (which were quite common) were not drilled very much and some quite rare gastropod prey species were heavily attacked. The naticids selectively attacked medium-sized shells, avoiding very small ones (not enough meat inside) and very large ones (too thick to make the effort worthwhile)[5]. The siting of drill holes is also fairly constant — there seem to be preferred locations that depend on the way the predator grasps the prey shell in its fleshy foot, and on the size, shape, ornamentation and behaviour of the prey species[4,5].

The Blackdown Sands fauna, with its evidence of extensive naticid gastropod predation, forms part of the Mesozoic marine revolution[6], a phase marked by the simultaneous evolution, from the early Cretaceous onwards, of powerful, relatively small, shell-destroying predators such as teleost fishes, stomatopods, decapod crustaceans and drilling gastropods. In response, prey animals took to burrowing and evolved stronger, thicker shells that often had heavy sculpture, spines and narrow apertures[1,4–6]. After the Cretaceous, the shell-drilling gastropods became more efficient — in the Blackdown fauna, about 4 per cent of all bivalve specimens contain drill holes, and this rose to 5–26 per cent afterwards. The numbers of drilled gastropod prey rose from 5 per cent in the Cretaceous to 11–26 per cent afterwards[4].



Right, *Natica josephina*. Feeding apparatus: g, 'foraging gland' secreting acid; t, tentacle) tre, respiratory tube; tro, proboscis containing radula system. pr, lm, mt comprise the hinged foot. (From Ankel, W.E. *Veh. dt. zool. Ges.* **40**, 223; 1938.) Left, *N. josephina* eating a bivalve.

There are several examples of predation by naticid gastropods before the Cretaceous. Newton[7] reported examples from the late Triassic of North America (about 220 Myr ago) and Fürsich and Jablonski[8] described some slightly older late Triassic cases from Italy (about 225 Myr ago). The latter bore holes show all the typical naticid characteristics, and coincide in age with the oldest known naticid gastropods. It had been assumed previously that these gastropods were initially non-drillers, and that they acquired this skill only 125 Myr later in the early Cretaceous.

Fürsich and Jablonski[8] argue that naticid drilling ability evolved twice but became successfully established only the second time. The evidence for this assumption is the absence of naticid bore holes in the intervening Jurassic period. In evolutionary terms, Fürsich and Jablonski view the late Triassic drillers as well enough adapted, but afflicted by bad luck — they may have had low speciation rates, or may have been wiped out in a chance extinction event. When the drilling habit was reinvented by their close relatives in the Cretaceous, it was associated with high rates of diversification, and the habit persisted to the present day in a wide range of naticid species.

But Smith and colleagues now report an even older occurrence of drilling[2] from the middle Devonian of North America (about 380 Myr ago). The holes are indistinguishable from those made by naticid gastropods, but they pre-date the oldest known naticid shells by 155 Myr. The bore holes were made in articulate brachiopods, and the predators show all the features of modern naticid behaviour: the drill holes are highly prey-specific in all localities sampled; they are concentrated over the 'meaty' part of the shell; and the brachiopods were attacked while still alive. As many as 44 per cent of preferred prey species were drilled, but the predators were relatively inefficient — in one locality nearly half of the drill holes were incomplete. This case forms part of the mid-Palaeozoic revolution[9] during which several groups of predators became adapted to shell-crushing and boring (placoderm and chondrichthyan fishes, shrimp-like arthropods and possibly naticid gastropods) and the prey species evolved stronger shells with ribbing and spines in tandem.

In evolutionary terms Smith and colleagues propose that their sample documents a third origin of the naticid-like drilling habit in the Devonian, but they argue that is was not chance that terminated the first attempt at drilling. In the Devonian, there are no known naticids, nor are there any relatives that are fossilized. Smith *et al.* argue that the Devonian driller was a shell-less form (thus not fossilizable) that had evolved the physical and chemical means of drilling. Drilling is a slow process, and the predator was vulnerable itself while going about its business (hence the high number of abandoned drill holes which indicate that the predator may have been disturbed, or

1. Stanley, S.M. *Macroevolution* (Freeman, San Francisco, 1979).
2. Smith, S.A., Thayer, C.W. & Brett, C.E. *Science* **230**, 1033 (1985).
3. Bromley, R.G. *Acta Geol. Hispan.* **16**, 55 (1981).
4. Taylor, J.D., Cleevely, R.J. & Morris, N.J. *Palaeontology* **26**, 521 (1983).
5. Kitchell, J.A., Boggs, C.H., Kitchell, J.F. & Rice, J.A. *Paleobiology* **7**, 533 (1981).
6. Vermeij, G.J. *Paleobiology* **3**, 1977).
7. Newton, C.R. *Geol. Soc. Am. Abstr. Prog.* **15**, 652 (1983).
8. Fürsich, F.T. & Jablonski, D. *Science* **224**, 78 (1984).
9. Signor, P.W., III & Brett, C.E. *Paleobiology* **10**, 229 (1984).
10. Miller, R.H. & Sundberg, R.H. *Lethaia* **17**, 185 (1984).
11. Liljedahl, L. *Lethaia* **18**, 53 (1985).
12. Stridsberg, S. *Fossils Strata* **18**, 1 (1985).
13. Sheehan, P.M. & Lesperance, P.J. *J. Paleont.* **52**, 812 (1978).

indeed eaten, before it could withdraw its drilling equipment). In either case, Smith *et al.* argue that the two 'failures' of the naticid-like shell-drilling habit in the Devonian and the Triassic were the result of poor adaptation. Only in the Cretaceous did the naticids evolve the necessary drilling techniques and the means of self-protection.

Many older examples of predatory bore holes in shells are known — for example from the late Cambrian of the United States (about 510 Myr ago)[10], from the Silurian of Sweden (about 420 Myr ago)[11,12] and from the early Devonian of Canada (about 400 Myr ago)[13]. The predators could have been gastropods in some of these cases[12,13] but the holes are either much smaller than those produced by living naticids[10,11] or they lack the central boss and the inwards taper[12,13]. The holes could have been produced by cephalopods[3,11,12], or by unknown forms[3,11]. Whatever the answer, these studies offer much scope for further work on the history of marine predation, on the modelling of predator–prey interactions[5] and on establishing the role of predation in macroevolution. □

Michael J. Benton is in the Department of Biology, The Queen's University of Belfast, Belfast BT7 1NN, Northern Ireland.

Astrophysics

Unravelling fates of black holes

from Don N. Page

EVER since S.W. Hawking's remarkable theoretical discovery of thermal radiation emitted from black holes[1,2], it has been clear that these objects cannot be the stable final states of gravitational collapse they were once believed to be. But what happens during the last stages of black-hole evaporation has remained uncertain, leaving unanswered several important conceptual issues such as the fundamental predictability of the ensuing state[3-5]. Now M.J. Bowick, L. Smolin and L.C.R. Wijewardhana argue[6] that superstring theories[7,8] can help unravel the answer.

Black holes allow nothing to escape, according to classical (that is, non-quantum) physics in which each particle has a definite position and a definite velocity, which must not exceed *c*, the speed of light. However, in quantum physics the uncertainty principle prevents a particle from definitely being confined to the space inside the hole and simultaneously definitely having a velocity $\leqslant c$. In this way quantum mechanics allows a particle to tunnel out from a black hole. Hawking[1,2] calculated this black-hole emission process in a semiclassical approximation in which quantum mechanics was applied to the particles being emitted, but not to the black hole itself, which was instead assumed to have a definite classical gravitational field.

Conservation of energy requires the black hole to lose mass, and hence shrink, as particles carry away its energy. Eventually it evaporates to such a small size that the semiclassical approximation becomes invalid, and quantum mechanics must be applied to the gravitational field of the black hole itself. It is not known how to do this in a completely consistent manner, hence the uncertainty of what happens in the last stages of black-hole evaporation. It has been variously suggested that a black hole stops radiating and shrinking when it reaches a positive-mass stable remnant; that it continues radiating until its mass becomes negative; or that it completely disappears.

There is also the question of whether the quantum evolution of the state is deterministic, or whether there is a new breakdown of predictability beyond the ordinary limitations of the uncertainty principle[3-5]. If the black-hole emission is precisely thermal, with no correlations between different modes (as is predicted by the semiclassical approximation), then its evaporation results in a loss of information or an increase in entropy even without any coarse graining of the final state. Furthermore, in a classical description of the gravitational field, the disappearance of a black hole would be accompanied by a so-called naked singularity (a visible edge to space-time), at which unpredictable information might enter the Universe.

Bowick, Smolin and Wijewardhana[6] now offer a preliminary analysis of these questions in the context of superstring theories[7,8], exciting new candidates for a consistent quantum 'theory of everything' (unification of the fundamental forces, including gravity; see ref. 9 for review). If one of these theories is indeed correct, it should in principle be able to explain what happens when a black hole evaporates. Unfortunately for our curiosity (but perhaps fortunately for the continuation of our careers), our understanding of superstring theories is still far too meagre to say definitely what they imply about black-hole evaporation. Bowick *et al.* readily admit this limitation, but investigate what can be said from our present knowledge of superstring theories.

By a thermodynamic analysis of perturbative (linearized) string modes, Bowick *et al.* conclude that it is statistically probable for a black hole to turn into a massive string when it gets sufficiently small. The string itself then decays into ordinary radiation (massless particles). The authors suggest that this allows the black hole to disappear completely (yet without the accompaniment of a naked singularity) because the gravitational field is only part of the superstring field.

This conclusion is eminently reasonable, although it must be admitted that the paper of Bowick *et al.*[6] is hardly a rigorous derivation of the result. Even before superstring theories, one could have postulated that a sufficiently small black hole turns into a suitable spectrum of massive particles without having a classical gravitational field that would lead to a naked singularity. Superstring theories give hints as to how this could conceivably happen, but so far they are just hints.

On the question of whether there is a breakdown of predictability in black-hole evaporation, Bowick *et al.* admit that they do not see how superstring theory will resolve the problem. Indeed, one would need a method for correctly calculating the enormous number of multi-particle correlations between the different black-hole emission modes. Each one of these correlations is likely to be very small and hence individually close to the semiclassical approximation that it is zero, but cumulatively it is conceivable that the correlations could gradually restore to the exterior all the information that enters the hole during its formation and evaporation process. It is still too early to say whether or not superstring theory will show this possibility to be the case. □

1. Hawking, S.W. *Nature* **248**, 30 (1974).
2. Hawking, S.W. *Commun. Math. Phys.* **43**, 199 (1975).
3. Hawking, S.W. *Phys. Rev.* D**14**, 2460 (1976).
4. Page, D.N. *Phys. Rev. Lett.* **44**, 301 (1980).
5. Wald, R.M. *Phys. Rev.* D**21**, 2742 (1980).
6. Bowick, M.J., Smolin, L. & Wijewardhana, L.C.R. *Phys. Rev. Lett.* **56**, 424 (1986).
7. Green, M.B. & Schwarz, J.H. *Phys. Lett.* **B149**, 117 (1984).
8. Green, M.B. & Schwarz, J.H. *Phys. Lett.* **B151**, 21 (1985).
9. Green, M.B. *Nature* **314**, 409 (1985).

Don N. Page is Associate Professor of Physics at The Pennsylvania State University, University Park, Pennsylvania 16802, USA.

Erratum

Consensus sequence		Lys–Gly–fob–Gly–Thr–Asp–Glu–var–var–Leu–Ilu–fil – Ilu–Leu–Ala – fil–Arg
Lipocortin residues	56-72	Met–Val–Lys–Gly–Val–Asp–Glu–Ala–Thr – Ilu – Ilu–Asp–Ilu–Leu–Thr–Lys–Arg
Lipocortin residues	128-144	Lys–Gly–Leu–Gly–Thr–Asp–Glu–Asp–Thr–Leu–Ilu–Glu– Ilu–Leu–Ala–Ser–Arg
Lipocortin residues	287-303	Lys–Gly–Val–Gly–Thr–Arg–His–Lys–Ala–Leu–Ilu–Arg–Ilu–Met–Val–Ser–Arg

In the article by Robert H. Kretsinger and Carl E. Creutz "Consensus in exocytosis" (*Nature News and Views* 17 April, page 573), two of the amino-acid residues that should have been included in the figure were omitted. The correct figure is shown above.