PALAEONTOLOGY

The rudists re-examined

David Jablonski

PERHAPS the most spectacular departure from the mollusc body plan in the 500-million-year history of the phylum occurs in the rudist bivalves, an extinct group of marine molluscs as fascinating and bizarre as their contemporaries, the dinosaurs. The rudists present an intriguing array of functional, ecological and evolutionary puzzles; fresh perspectives were presented on many of these last month, when most of the world's experts convened in Marseilles*.

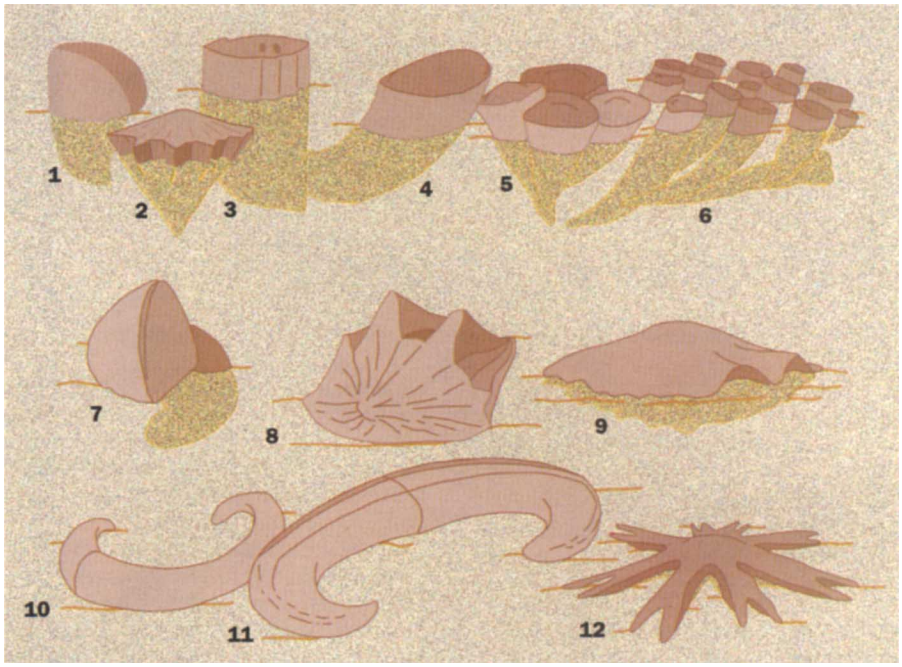
Rudists (the popular term for members of the superfamily Hippuritacea; from the Latin *rudis*, rough) abandoned the usual bivalve form, in which the paired shells or valves are essentially mirror images of one another as in scallops and cockles, to generate a conical, barrel-shaped or corkscrew-shaped lower valve and a cap-like upper valve held in place by an elaborate tooth-and-socket system; some rudist species were small and delicate, but lengths exceeding 1 m and diameters exceeding 60 cm were not uncommon. Even when they re-evolved a more symmetrical shell form, they did so in outrageous fashion, as in the Caribbean form *Titanosarcolites* (no. 11 in the figure), which is more than 2 m long and resembles "two giant, coil-toed Persian slippers placed heel-to-heel"[1].

Rudists have often been described as constructing reefs and as having outcompeted the corals that today thrive in clear tropical waters[2,3]. They certainly were overwhelmingly concentrated in shallow tropical seas from their first appearance in the Late Jurassic (about 155 million years ago) to their extinction along with the dinosaurs, ammonites and many other groups at or near the end of the Cretaceous (65 Myr ago). Further, whereas some rudist species were sparsely distributed across the entire continental shelf, others occurred in extremely dense populations within a narrow, shallow zone, forming shelly limestone bodies several metres thick and many square kilometres in extent. In fact, the enormous production of rudist limestones in the Cretaceous tropics appears to be a carbon sink so massive that no attempt to understand the carbon cycle of the Cretaceous 'greenhouse world' can afford to discount it (P. W. Skelton, Open Univ., Milton Keynes; J.-P. Masse & J. Philip, Univ. Provence, Marseilles).

Those limestone bodies are now host to many of the huge petroleum reserves of the Middle East and the Gulf of Mexico, lending rudists an economic cachet as oil companies reconstruct the geometries of dense rudist formations in order to predict profitable drilling sites.

A few rudist formations do show some of the hallmarks of a reef — a cohesive, solid structure with some topographic expression above the sea floor[1–3] (S. Götz & B. Höfling, Univ. Munich; D. Schumann, Tech. Univ. Darmstadt) — but they seem to be exceptions and a close analogy with today's reef-building corals appears to be unravelling[4,5]. Rudists are emerging as a unique evolutionary experiment in tropical seas, exploiting habitats and lifestyles that correspond only loosely, if at all, to modern reef structures. Far from producing a framework, many rudists were solitary, or formed meadows of small clusters that floated in a muddy sea floor. Flume experiments show that partially embedded shells, if inclined downstream of prevailing currents, could make use of detritus brought up from the sediment surface by eddies in the lee of the animal — a feeding strategy rare or absent in modern corals (E. Gili, Univ. Autònoma, Barcelona; M. LaBarbera, Univ. Chicago). For many species, a better modern analogue might be the Great Pearl Bank in the southern Arabian Gulf, with its dense populations of the fan mussel *Pinna* (G. W. Hughes, Saudi Aramco, Dhahran), or perhaps associations of the giant clam *Tridacna* found on Indo-Pacific reef flats and in back-reef lagoons.

Given their differences, did the rudists really out-compete and marginalize contemporary corals? We now realize that corals were diverse and abundant in the Cretaceous tropics, and in many settings even grew on and around rudists[5,6] (J.-P. Masse, Univ. Provence, Marseilles; P. Garcia-Barrera, G. Alencaster, J. Avendaño-Gil & L. Omaña, Univ. Nacional de Mexico; D. Schumann, Technische Univ., Darmstadt). Dense, monospecific rudist populations may have lacked corals, not because of competitive exclusion, but because rudists could cope with more restricted, nutrient-laden and turbid waters than could corals; again a matter of basic ecological differences rather than competition for the same resources. This is not to say that corals and rudists did not interact — space and suitable attachment sites can be at a premium in soft-bottom settings, and competition need not result in total exclusion — but a wholesale Cretaceous eclipse of the corals by rudists,



In the Cretaceous Period, rudist bivalves evolved a remarkable diversity of shell morphologies, from conical forms partly embedded in the sediment (1–6), to corkscrew-like and flattened forms (7–9), and arc-shaped and stellate creatures that reclined on the sediment (10–12). Lengths range from 15 cm (1) to 2 m (11).(From ref. 4.)

Fourth International Conference on Rudists, Marseilles, France, 9–16 September 1996.

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and their release after the rudists became extinct, now appears an oversimplification.

A more stubborn question is whether the rudists had endosymbiotic algae, such as the zooxanthellae seen in many corals and in *Tridacna*. Such a partnership has been suggested, but not proven, for those genera that have massive shells, great abundance, a preference for shallow depths, or shell margins that could have exposed tissue-bearing photosynthesizing symbionts[2,3,6,7]. But the presence of rudists in settings that must have been bathed in turbid waters, and the absence in most genera of clear-cut morphological adaptations for tissue exposure[6], suggests that zooxanthellae were not present in all rudists — perhaps not surprisingly, given the diversity of the group and the uneven distribution of symbionts among other bivalves and even among corals.

New work on oxygen and carbon isotopes may help to settle the question: rudist growth rates, estimated from what appear to be annual temperature cycles in a few well-preserved shells, can be as high as 50 mm yr^{-1}, implying calcium carbonate production rates up to 20 kg m^{-2} yr^{-1} — values that fall within the range for modern symbiont-assisted coral reefs[8] (T. Steuber, Univ. Köln). These isotopes occur in ratios far from oceanic equilibrium, and in patterns that resemble those seen in corals, but even such pronounced metabolic fractionation cannot be taken as a sure sign of symbiont activity.

Finally, the rudists suffered a number of extinction events, in the mid-Aptian (about 117 Myr ago), at the end of the Cenomanian (about 94 Myr ago), but each time re-diversified well beyond pre-extinction levels. Indeed, the rudists were at their most diverse just a few million years before their disappearance, the exact timing and cause of which remain hotly debated.

The rudists still present many enigmas, but the new burst of research, ranging from painstaking field and laboratory work in the classical mode to novel approaches in isotopic biogeochemistry and experimental biomechanics, has given us a deeper understanding, and defined the next set of questions to be tackled. □

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NEUROBIOLOGY

Memories of nicotine

Daniel S. McGehee and Lorna W. Role

THE first discussions linking the enhancement of memory with the use of tobacco almost certainly occurred long before tobacco was introduced to Western society. In 1659, Dr Giles Everard wrote:

> "...to ſtrengthen the memory the ſmoke is excellent taken by the noſtrils, for it is properly belonging to the brain, and it is eaſily conveyed into the cels of it and it cleanſeth that from all filth (for the brain is the Metropolis of flegme, as Hippocrates teacheth us...)" From *Panacea; or The Universal Medicine, Being a Discovery of the Wonderfull Vertues of Tobacco Taken in a Pipe, with its Operation and Use both in Physick and Chyrurgery*. (Fig. 1)

Although nearly all of the *"wonderfull vertues of smoke"* have now been disproved, the theory that nicotine enhances some forms of memory has remained[1]. The underlying mechanisms are still unknown, but on page 713 of this issue Gray *et al.*[2] provide evidence that nicotine increases the strength of synaptic communication between neurons in the hippocampus — a centre for learning and memory.

Many groups have examined the cellular events that control the strength of connections (synapses) between nerve cells in the hippocampus[3], and these studies have provided insight into the basic processes that are thought to underlie learning and memory. Hippocampal neurons express several classes of nicotinic acetylcholine receptors (nAChRs), and there is a differential subcellular distribution of the distinct nAChR subclasses[4]. Furthermore, nicotinic cholinergic systems are believed to be important in memory — nicotine has a memory-enhancing effect, and there is a loss of cholinergic innervation from the basal forebrain in pathologies that affect memory, such as Alzheimer's disease.

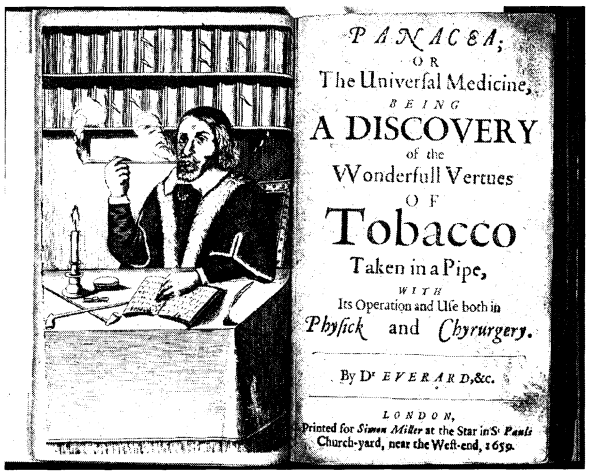

FIG. 1 As well as espousing numerous "vertues of tobacco", Dr Everard points out that abuses of "... this noble herbe ... are a great force to shorten your daies".

Gray *et al.*[2] now show that at the concentrations of nicotine detected in arterial blood during smoking, there is enhanced glutamate-mediated transmission of nerve impulses in hippocampal cultures. They also show that nicotine increases the levels of intracellular calcium measured directly from presynaptic terminals in hippocampal slices, providing the best evidence to date that the nAChRs that mediate enhanced neurotransmitter release are localized to these presynaptic terminals. Such high-resolution analysis constitutes a significant advance in our understanding of the potent effects of nicotine at an important site in the brain. The mechanism by which nAChRs are thought be involved in synaptic transmission at glutamatergic synapses is outlined in Fig. 2.

The paucity of evidence for the direct involvement of nAChRs in mediating synaptic transmission in the central nervous system is epitomized by the class of neuronal nAChRs that are blocked by α-bungarotoxin (α-BGT). Anatomical studies revealed widespread binding of α-BGT in the brain; however, the lack of evidence for α-BGT-sensitive, nicotine-gated currents branded the α-BGT-binding sites as 'nonfunctional' for decades[5]. However, the α-BGT-binding sites were resurrected by the demonstration that three of the nAChR α-subunits — α7, α8 and α9 —

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