

in the kinetics, this analysis is somewhat more tenuous.

If the era of testing this scheme is closing, one of incorporating it into a larger paradigm is just beginning. The oxygen reduced to H_2O_2 must be balanced by equivalent oxidation elsewhere. But where, how and by how much? Most of the recent work related to the larger aspects of the problem^{6,9} can be accommodated by the heuristic scheme shown in the figure. This diagram adapts the classical chemical auto-oxidation/photo-oxidation mechanism to the situation in the ocean. Such pathways were elucidated for other complex reactions such as smog formation and the low-temperature or light-induced reactions of many materials containing organic components or reduced transition metals (for example, cellular lipids, foods, plastics, paints and corrodable metals) in contact with air¹⁰. Photo-oxidations characteristically involve reactive free-radical intermediates (O_2^- is one), and often involve cyclic oxidation-reduction of transition metals.

Oceanic conditions differ so markedly from those of well-studied photo-oxidation/auto-oxidation environments that applying the paradigm to the oceans, far from being straightforward, will provide a challenge. A solute molecule travelling with the water, for example, experiences more than a decade of exposure to sunlight in the upper 40 metres per global oceanic 'stir'. The interpretive challenge is perhaps illustrated by noting that the side reactions of O_2^- reported by Petasne and Zika result in reduction, not oxidation, of unknown materials. Is the paradigm fundamentally awry, or are reductions by O_2^- (and H_2O_2) mere countercurrent eddies in a larger oxidative stream? Work in marine photochemistry, long supported in the United States by the National Science Foundation, is now a "special focus program" of the Office of Naval Research. Additionally, several European scientists have begun to work in the area. Thus, we may soon learn more about oceanic photochemistry. But it is no longer a radical solution to consider the ocean as a solution of radicals. □

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Vertebrate palaeontology

Conodonts classified at last

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CONODONTS, small tooth-like fossils found in Palaeozoic (570–245 million-year-old) rocks, were until recently a mystery. Many supposed conodont animals have been reported, but it was not until 1983 that an acceptable specimen was described¹. New findings² improve our knowledge of this conodont animal and its affinities, and a second, older, form of conodont animal has just been reported^{3,4}.

Conodonts are composed of calcium phosphate (apatite), as are the bones of vertebrates, and are useful index fossils for dating rocks. Many conodont experts have contented themselves with dissolving rock samples, extracting the conodonts, each only about 1 mm long, and using them for dating. The first crucial biological information was obtained in the 1930s with the discovery^{5,6} of a bilaterally symmetrical arrangement of three or four different types of conodonts, assumed to be some sort of feeding device. But the subsequent confirmation that conodonts all form 'feeding baskets' did not indicate what the animal was. In the past 20 years, conodonts have been described as plants, coelenterates, Aschelminthes, Gnathostomulida, molluscs^{7,8}, Tentaculata, chaetognaths and chordates.

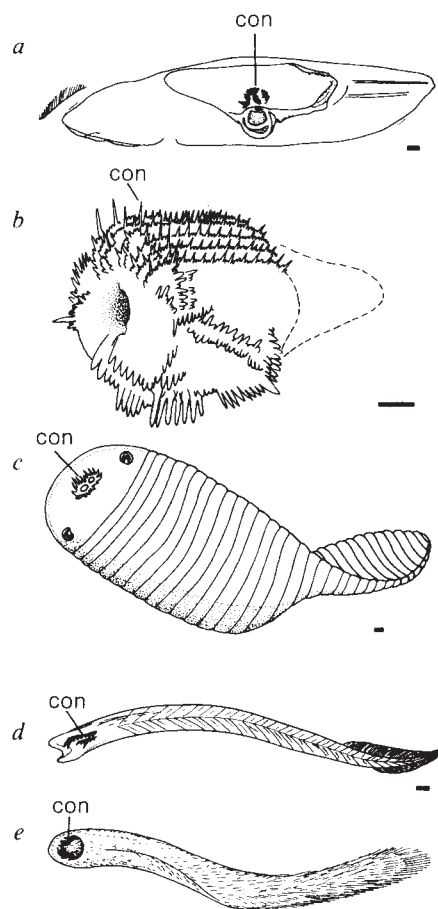
The first supposed conodont animal was described⁹ in 1973. The animals bearing the conodonts have a long flattened cigar-shaped body with a fin-like structure at the posterior end (*a* in the figure). There were several conodonts in the central part of the animal, which seemed to have a nerve cord near the front, and the animal was made the type of a new Phylum Conodontochordata, related to the chordates.

Soon after the description of this animal had been published, Lindström¹⁰ and Conway Morris¹¹ suggested that it had merely ingested the conodonts, which were in the stomach region, not the head: it turned out that the guts of some specimens contained mixtures of different conodont apparatuses.

As well as debunking one conodont animal, these authors described two more. Lindström illustrated a hypothetical conodont animal in which the conodont elements faced outwards on a body shaped like a toilet roll (*b* in the figure). Conway Morris described, on the basis of fossils, a wide, flat animal about 6 cm long with ring-like structures around its body (*c* in the figure). There is an opening ringed by impressions of curved tooth-like elements in the head region underneath. This animal, named *Odontogriphus*, comes from the Middle Cambrian (about 540 million years ago) of western Canada, and

the tooth-like elements are rather like some fossils identified as ancestral to true conodonts. The preservation of *Odontogriphus* is not good enough, and the ancestry of conodonts is too uncertain, for it to be clear whether or not this is a conodont animal.

In 1983 the 'real' conodont animal was described¹ from the Carboniferous of Edinburgh and was discussed in a News and Views article¹². This 4-cm-long, worm-shaped animal had a conodont apparatus in its head region, traces of muscle blocks in the trunk and some kind of tail fin. It seemed to have affinities to both the chordates and to the chaetognaths (arrow worms), but it was placed in a separate, intermediate, Phylum Conodontata. This conodont animal has since



The conodont animal. *a*, A Carboniferous fossil from North America; *b*, a hypothetical animal with the conodonts facing outwards; *c*, *Odontogriphus*, a Cambrian fossil from western Canada; *d*, the Carboniferous fossil from Scotland interpreted as a chordate; and *e*, interpreted as an aplousophoran mollusc. Scale bar, 1 mm; con, conodonts. (After refs 9, 10, 11, 2 and 8, respectively; drafted by L. Lawson.)

been assigned^{7,8} to all three of these groups and also to the Mollusca.

The molluscan interpretation seems the most unusual. In general outline the Scottish conodont animal resembles living shell-less molluscs called Aplacophora. Tillier and colleagues^{7,8} believe the conodonts to be equivalent to the molluscan radula (the rasping feeding structure) because of morphology, and because both are made of calcium phosphate. The chevron-shaped 'muscle blocks' in the conodont animal are interpreted as the spicules that occur over the body surface of aplacophoran molluscs, and the tail fin is seen as the elongated spicules on the back (*e* in the figure). However, this molluscan interpretation is weakened by the new fossil discoveries² from Scotland, which reveal further anatomical details (*d* in the figure) and strengthen the view that the conodont animal was a true chordate with V-shaped muscle blocks, a laterally flattened body and unequal tail fins. In particular, the Edinburgh conodont animal has close affinities with the living myxinooids (the jawless hagfishes), which have similar feeding apparatus consisting of several rows of teeth that can be turned

outwards for parasitic feeding. The new Silurian conodont animal^{3,4}, although less well known, appears to confirm the chordate affinities of the conodonts.

The conodonts seem to have found a home at last, and a long-standing palaeontological puzzle has been largely solved. The interesting questions now concern the exact placing of the conodonts in relation to the various primitive chordate groups, for which more well-preserved specimens will be needed. □

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Cultural evolution

Why do animals specialize?

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ECOLOGISTS have tended to consider all individuals within a single population as being equivalents; that is, having the same ecology and behaviour. But a closer look at any population reveals that individuals can be very different and that these differences change the dynamics or behaviour of the population as a whole. Why do individuals in the same population, and thus exposed to the same environment, exhibit different behaviours? Are the causes of these differences genetic, cultural or learnt¹? Detailed studies of the oystercatcher *Haematopus ostralegus* show that these birds exhibit a remarkable diversity of feeding specializations and their feeding behaviour has become a classic example of culturally determined behaviour in birds². Recent work helps to unravel the causes of these specializations and shows that the role of culture may have been greatly exaggerated. It may be more useful to look for ecological explanations for this specialization.

By marking birds with individual combinations of colour rings, it can be shown that an oystercatcher can feed almost entirely on one species, for example mussels or cockles, throughout the winter³.

Among the individuals that specialize on mussels some, called stabbers, push their bill between the valves of the mussel whereas others, hammerers, use violent blows of the beak against one valve until it cracks and then insert their bill through



Hammerer (above) and worm-feeder (below).

the break and chisel out the flesh³. There are even more specializations among the hammerers⁴: some birds consistently break into the dorsal side and others break into the ventral surface. Individuals may specialize further by attacking either the left-hand or the right-hand valve⁵. No doubt there are yet more undiscovered specializations.

Why should oystercatchers show such

extreme individual specializations? A long-term field study on the Exe estuary, United Kingdom, by Goss-Custard and colleagues^{4,6-8} helps to answer this question. One likely explanation is that bivalves are a difficult prey to tackle. Oystercatchers might have to exploit different weaknesses in different mussels and practise using one technique for maximum profit. Dorsally hammering oystercatchers thus pick out those mussels whose dorsal shell has worn thin from abrasion by sand carried over it by the tide. In any one patch of mussels, only a few individuals have shells thin enough for the birds to break into. The oystercatchers find these vulnerable prey by tapping the shells with the tip of their beaks⁶. Ventral hammerers also seek out mussels with thin shells, though on the ventral side. They cannot tell the thickness of the shell underneath from its thickness on the dorsal side because the two measures are unrelated, and therefore they need another cue. The colour of the shell, and perhaps the presence of barnacles, give the bird a clue⁶. Young mussels that grow fast tend to have thinner shells on the underside than do the older and slower-growing ones. The fast-growing ones are blacker and often covered in barnacles, so the birds could use the general appearance of the mussel to gauge the thickness of the shell underneath. Even so, they often make mistakes and give up trying to hammer into a significant proportion of the mussels they tear off the mussel bed⁶. The defences of the mussels mean that it pays an individual bird to stick to one method of attack.

The specialization is reflected in bill shape, which is generally correlated with the feeding technique and diet. By marking the bill, J. Hulscher¹⁰ and C. Swennen and co-workers¹¹ in Holland discovered that oystercatcher bills replace themselves once every six months. This rapid turnover of the bill allows the bill shape to adjust quite quickly to a change in feeding technique. Hulscher¹⁰ showed that when oystercatchers move from their coastal wintering areas to breeding areas inland, their bill shape changes within two weeks from the blunt shape of a hammering mussel specialist to the pointed bill of a worm specialist.

The shape that wear imposes on the bill might restrict the options for flexibility. The case for this hypothesis seems strongest when considering mussel and worm specialists. To catch a worm, the bird must force its bill tip into the ground and a pointed beak may be more efficient for this than one with a flattened tip¹¹. It is not so clear, however, that the different bill shapes attained by members of the oystercatcher community that open mussels in different