

efficiently. If this template was combined with a porphyrin pentamer in a Vernier synthesis, then the product would be a ring of 60 porphyrin units in circumference, with a molecular mass of 48 kilodaltons and a cross-section of 25 nanometres. This is the size of an average protein or nanoparticle, and is well beyond the realms of conventional chemical synthesis. A simple and efficient synthetic route to such large molecules might provide all kinds of new materials for nanotechnology. ■

Christopher Hunter is in the Department of Chemistry, University of Sheffield, Sheffield S3 7HF, UK.
e-mail: c.hunter@shef.ac.uk

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EVOLUTIONARY BIOLOGY

Catfish mimics

Mutualism can be a double-edged sword if the animals concerned also compete for food. This may explain the discovery that catfish mimics in the Amazon rarely engage in mimicry with related species. SEE LETTER P 84

JAMES MALLET & KANCHON DASMAHAPATRA

Müllerian mimicry in the warning colours of unpalatable butterflies has been well known since its discovery in the nineteenth century^{1,2}. It is beneficial because noxious prey that share warning colours also share the cost of educating predators about their unpalatability³. Müllerian mimicry is now known to occur in many other animal groups, including millipedes⁴ and poison dart frogs⁵.

Below the surface of the Amazon, on whose banks Henry Walter Bates made the first discovery of butterfly mimicry, a new example of Müllerian mimicry has just been discovered by Alexandrou *et al.* (page 84 of this issue)⁶. The authors studied armoured catfish in the sub-family Corydoradinae, which swim in multi-species shoals and are defended by retractable venomous spines and bony plates. Across the Amazon basin, it turns out that up to three unrelated species with strikingly similar colour patterns may coexist in any one locality. The bold, mimetic patterns of these fishes (Fig. 1) undoubtedly serve to warn predators away, as recently demonstrated in an unrelated African catfish genus⁷.

Bates's discovery of mimicry stemmed, in part, from his finding that local colour patterns converged, but more importantly from the fact that butterflies "are found all to change their hues and markings together, as if by the touch of an enchanter's wand, at every few hundred miles" (H. W. Bates, quoted in ref. 2). This striking and repeated phylogenetic pattern of convergence across the Amazon clinched the evolutionary hypothesis of mimicry: species differ in colour from related forms in distant areas, while at the same time mimicking unrelated species locally. A spatial pattern of local convergence and geographical divergence

is quite general in other systems of Müllerian mimicry^{4,5}, as well as in the catfish studied by Alexandrou and colleagues⁶.

However, these patterns are even stranger than they first appear. Mimicry explains why species converge, but cannot explain why species also diverge into multiple mimicry 'rings' in many Müllerian mimetic systems. Diversity is often local: in armoured catfish there may be up to six mimicry rings in some regions⁶ (although they rarely swim together), and in *Heliconius* butterflies it almost seems as if species undergo adaptive radiation⁸ into different mimicry 'niches'. Why should new mimicry rings ever evolve, given that mimicry itself should prevent divergence? Slow neutral change of pattern in geographically distant

regions might explain some of the diversity. However, although distance can prevent the swamping effect of gene flow, it cannot drive divergence directly.

Consider the diversity of mimicry in its overall ecological context. Müllerian mimicry is only one of many interactions among species. It provides an example of a positive interaction, or mutualism. To explain species coexistence, we must understand how this mutualism combines with negative interactions, such as competition. Competitively dominant species typically exclude inferior competitors. However, recent theory shows that if inferior competitors develop mutualisms with dominant species, this can allow them to invade and coexist, permitting higher diversity than without mutualism⁹. In the ithomiine butterflies, the classic group of Müllerian mimics^{1,2}, this may explain why some closely related species that use similar resources are also close mimics¹⁰.

Now imagine a superior competitor associated with multiple, mimetic mutualists. This dominant species reduces predation and enables mimics and inferior competitors to coexist, inevitably leading to some cost to itself⁹. In the first ever mathematical evolutionary theory, Müller² proved that the relative advantage of mutualistic mimicry to each species is roughly proportional to the inverse square of relative abundance: in other words, rarer mimics benefit very much more from Müllerian mimicry than commoner mimics. A more common species could suffer a considerable amount of resource competition if it is helping multiple co-mimics, while benefiting little from mimicry itself.

Therefore, a superior competitor species that escapes its ancestral mimicry could rid itself of some competitors. It could then spread at the



Figure 1 | Warning signals. The catfish *Corydoras haraldschultzi*, with its bold markings, is one of the Amazon mimetic species studied by Alexandrou and colleagues⁶.

MARTIN I. TAYLOR

expense of a less fortunate related form that continues to help competitors through mimicry. This idea cannot explain how the required speciation and mimicry divergence was initiated; but given that it did (and does) happen, it would have the consequence that dominant species would escape pesky competitors. This would stabilize the diversification of the mimicry we observe in nature.

The Amazon catfish⁶ seem to corroborate the escape idea. More than 90% of mimics differ from co-mimics in snout length and stable nitrogen isotope content, both indicators of diet: these catfish seem not to compete for resources with co-mimics. Typically, co-mimics are also unrelated. Closely related catfish, by contrast, are usually similar in terms of snout morphology and diet, and tend not to be co-mimics. Escape from mutualistic mimicry could similarly help to explain the 'adaptive radiation' of *Heliconius* butterfly mimicry⁸.

Nature is, however, full of contrasts. In unrelated venomous catfishes from Africa's Lake Tanganyika, and in ithomiine butterflies, mimics are often closely related and occupy similar habitats^{7,10}. Escape from potentially onerous mutualism has not always occurred. Perhaps resource competition is ameliorated in some other way; or perhaps the dominant species in each ring is unlucky and has

simply been unable to escape the resource pressure exerted by the mimetic mutualists that it unwittingly saves from extinction. Additional theoretical and experimental studies are needed.

Meanwhile, Alexandrou and colleagues' findings⁶ in catfish show that mimicry is still contributing fundamental ideas to ecological and evolutionary biology, 150 years after its discovery. ■

James Mallet and Kanchon Dasmahapatra are in the Galton Laboratory, University College London, 4 Stephenson Way, London NW1 2HE, UK.
e-mail: j.mallet@ucl.ac.uk

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Although it wasn't obvious at the time, a big step forward came in 1993 with the report³ of a single carbon-isotope 'excursion' — an anomalously high ¹³C/¹²C ratio ($\delta^{13}\text{C}$ value) — from a limestone sample overlying the base of one of Palmer's biomes. The beginning of the interval concerned is now dated to 499 million years ago, and it probably lasted for 2 million to 4 million years. It was characterized by biological turnover around the world, and the isotope excursion — known as the Steptoean Positive Carbon Isotope Excursion (SPICE) — has subsequently been shown to be global in extent. Increases in seawater $\delta^{13}\text{C}$ are generally believed to be the result of episodes of elevated organic-carbon burial, which can be caused by heightened ocean productivity and/or preservation of organic matter, both of which can be due to anoxia.

Sulphur in the marine environment undergoes analogous isotopic fractionation to carbon, with increased ³⁴S/³²S ratios in sea water resulting from enhanced burial of reduced sulphur in the form of pyrite (FeS₂). Gill *et al.*¹ report that parallel $\delta^{34}\text{S}$ and $\delta^{13}\text{C}$ excursions in both sulphate and sulphide $\delta^{34}\text{S}$ occurred widely across the SPICE event. This shows convincingly that organic carbon burial was accompanied by an equally spectacular rise in pyrite burial, first hinted at in an earlier, pioneering study⁴ of seawater $\delta^{34}\text{S}$. The removal of reduced carbon and sulphur into the sediments would have led to a surge in oxygen levels in the atmosphere, and so would hardly seem consistent with the spread of anoxia. But Gill *et al.*¹ marshal enough geochemical evidence, and point to a modern analogy, to convince us that this is precisely what occurred.

In the modern marine environment, parallel burial of organic matter and pyrite chiefly occurs beneath anoxic water columns that are also rich in hydrogen sulphide. Under these special conditions, anoxia restricts organic decay, while allowing soluble Fe²⁺ to build up in the water. Bacterial sulphate reduction supplies the sulphide, which, on binding with the iron, precipitates out as pyrite. Gill *et al.* suggest that the Cambrian seas during the SPICE excursion must have been rather like the modern Black Sea, with oxygen-rich waters at the surface and sulphidic waters at depth, only covering a much greater portion of the oceans and ocean margins. The SPICE interval saw a considerable change in sea level, from a high stand at the outset to lower levels. The authors propose that the result was that anoxic conditions prevailed widely in coastal areas, the same places that are normally most conducive to life.

Other predicted consequences of widespread aqueous sulphide — depletion of the molybdenum reservoir, low carbon/sulphur ratios in shales, and reduced sulphate–sulphide isotopic fractionation — are confirmed in the study¹. They all help to support the connection between biological extinction and anoxia during the Cambrian.

BIOGEOCHEMISTRY

Toxic Cambrian oceans

Isotopic evidence from carbon and sulphur points to the spread of anoxia and toxic sulphide as the chief culprits in at least one of a series of crises for marine ecosystems during the nascent stages of early animal evolution. SEE LETTER P.80

GRAHAM SHIELDS-ZHOU

By 520 million years ago, the oceans of the world were teeming with diverse forms of animal life addicted to the newly abundant, life-giving oxygen in the surface environment. Arthropods, many — like the trilobites — now extinct, ruled the seas, overshadowing the relatively few extant members of our own animal group, the chordates. But the course of this 'Cambrian explosion' of life did not run smoothly, and on page 80 of this issue Gill *et al.*¹ illuminate a likely cause.

For almost half a century it has been recognized that many of these early animal groups suffered a series of crises, or 'turnovers'. Not only did many trilobite groups diversify, only to become extinct shortly after, but they also seem to have been replaced abruptly by exotic groups taking advantage of the newly emptied ecosystem niches. The spread of anoxic sea water has long been implicated in the apparent volatility of early marine ecosystems, but evidence for

that possibility has been sparse. Gill *et al.* now present geochemical analyses and modelling of four geochemical tracers (carbon and sulphur isotopes, iron speciation and molybdenum content) from six Cambrian-age stratigraphic sections from around the world. In doing so, their work adds considerably to our appreciation of how early marine ecosystems were repeatedly devastated by highly variable levels of oxygen and sulphide.

Allison R. (Pete) Palmer was one of the first to recognize that trilobites and other Cambrian fauna suffered a series of extinctions, some of them major, between about 520 million and 490 million years ago. In 1965, he coined the term 'biomes' for such intervals of apparent stasis followed abruptly by extinction and replacement². Palmer and others put these extinctions down to changing oceanographic conditions that caused anoxic and/or cooler sea water to invade the shallow, coastal-shelf environment. But this hypothesis remained largely in the realm of speculation.