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RESEARCH NOTES

Mid-Cretaceous heteromorph ammonite shell damage

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Ammonites were a widespread and important part of Cretaceous marine communities. However, descriptions of interactions between ammonites and other parts of the biota are relatively scarce. This is most probably because the majority of studies on ammonites concentrate on their biostratigraphic utility rather than their palaeobiology. Important evidence of interactions between ammonites and their contemporaries comes from shell damage and subsequent repair. The best known examples of this are the bite-marks caused by a mosasaur on a specimen of the Late Cretaceous ammonite *Placenticeras*.[1] Not all damage to ammonite shells was as dramatic—or as fatal—as that example. In many cases the ammonite recovered and the damage was more or less fully repaired. Hengsbach[2] has recently summarised the variety of pathologies expressed in fossil ammonite shells. Shell repair is of course good evidence of the experiences of a living ammonite, since it could not have taken place *post mortem*.

A particularly rich source of well preserved ammonites is the Lower Cretaceous (Middle and Late Albian) Gault Clay Formation of Southern England. In excess of one hundred species of ammonites are known from the Gault, of which about one quarter are 'heteromorphs', the peculiar uncoiled ammonites so characteristic of the Cretaceous (Casey in Smart *et al*.[3]). The Gault Clay is a shelf deposit presumed to have been laid down under about 50 to 100 metres of water (A. S. Gale, pers. comm.). It has a high organic content and is rich in pyrite, promoting the preservation of the aragonitic shells of ammonites.[4]

While collecting material from the Gault Clay for my PhD thesis, I came across a specimen of *Hamites intermedius* J. Sowerby, 1814 with an unusual example of shell repair (Figure 1A; area of shell repair magnified ×2, 1B). The specimen is oriented with the aperture end downwards. Because the aragonitic shell was preserved, it was possible to observe the fine structure of the repair, including the growth lines. Using the ornamentation to deduce the direction of the aperture relative to the fragment, it was clear that the repair had progressed from the aperture backwards. The shell had been broken in such a way that a short, broad slot parallel to the long axis of the animal had been formed, with the slot lying on the dorsal surface of the shell. The rib immediately before the repair, and presumably the damage, is intact. The next three ribs were clearly extensively damaged, and the repaired ribs are imperfect, being less strongly defined and sweeping backwards over the dorsum to a greater degree than normal. Finally, a portion of a rib laid down after the damage was inflicted is preserved. This rib is well defined and clearly does not follow the same arc over the dorsum as the preceding ones, but is similar to the normal, undamaged ribs.

Following a brief examination of the Gault Clay heteromorphs in the collections of the Department of Palaeontology at the Natural History Museum, London, ten specimens with comparable shell damage were found (from a collection of about two hundred specimens). A few are figured here. Unfortunately, the aragonitic shell layers had decomposed, as is usual with Gault Clay fossils once exposed to air and moisture. Three specimens exhibited repair similar to that seen in the new specimen, with only a small number of ribs damaged (Figures 1C, D, and E). Figure 1C is a specimen of *Hamites maximus* J. Sowerby, 1814 oriented with the aperture end of the fragment towards the bottom. Figure 1D is from the *Protanisoceras raulinianum* (Orbigny, 1842). This specimen is oriented with the aperture end upwards; in this specimen damage is slight and confined to the first two ribs at the bottom of the fragment. There are a large number of normal ribs after the repaired part of the shell in these two examples; clearly the damage inflicted did not affect the ability of the ammonite to produce normal shell. The next specimen (Figure E) is oriented with the aperture end upwards. The ribs anterior to the repair, i.e. before the shell was damaged, are clearly normal.

Two other specimens had a very different level of shell repair (Figures F, G). In these specimens the distorted ribs persist for extensive lengths of the shell. Although it is possible the damage itself was a very long, narrow slit, it seems unlikely. It is more probable that the damage was confined to a relatively small area, but damaged the mantle itself so extensively that not just repair but all subsequent growth was imperfect. In Figure 1G there are ribs of normal form before the distorted ones, so that at least in that specimen and in the one shown in Figure 1E, genetic ontogenetic abnormality can probably be discounted.

A key question is of course what caused the damage. Shell breakage post mortem is very common among ammonites, through the action of scavengers

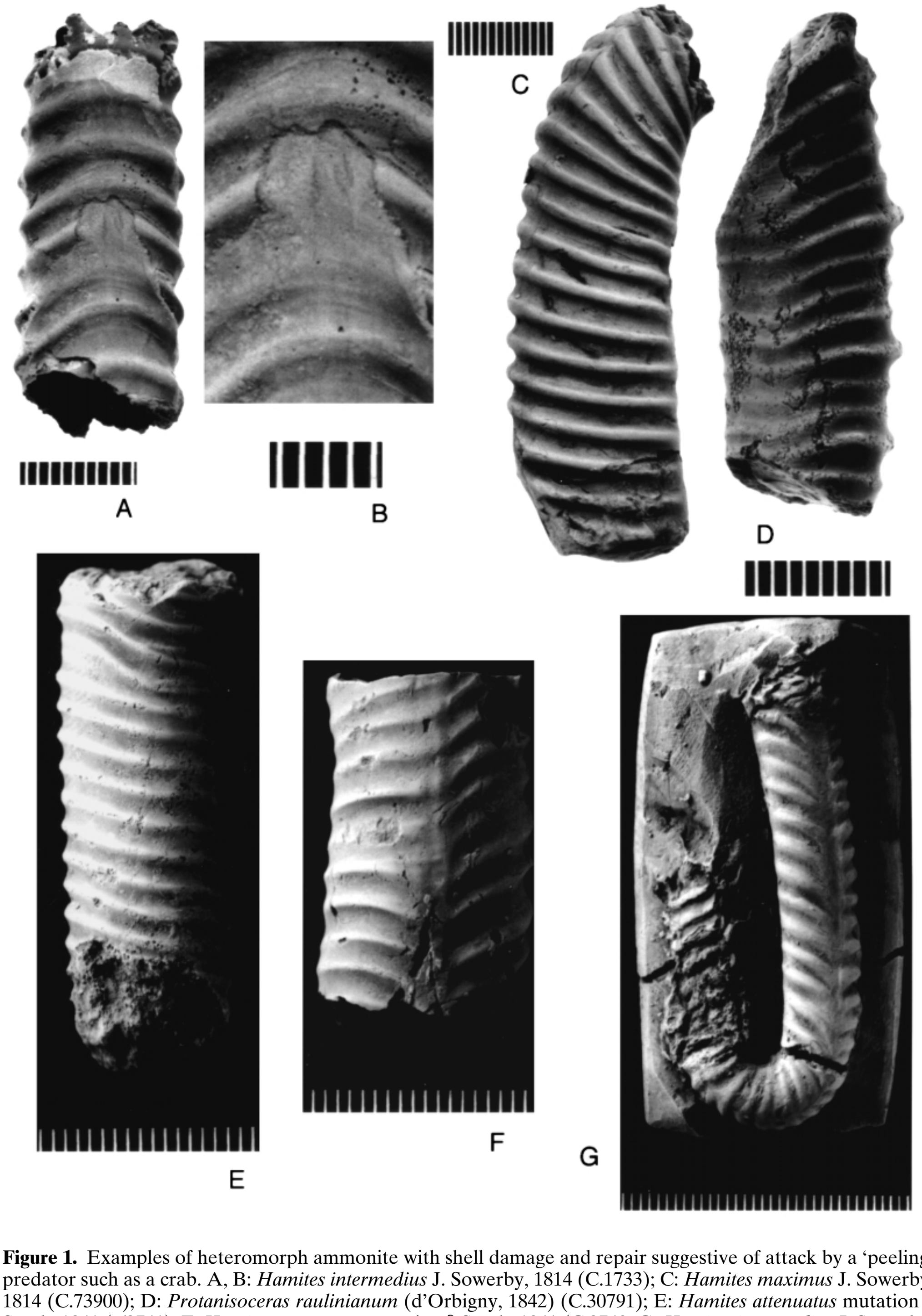

Figure 1. Examples of heteromorph ammonite with shell damage and repair suggestive of attack by a 'peeling' predator such as a crab. A, B: *Hamites intermedius* J. Sowerby, 1814 (C.1733); C: *Hamites maximus* J. Sowerby, 1814 (C.73900); D: *Protanisoceras raulinianum* (d'Orbigny, 1842) (C.30791); E: *Hamites attenuatus* mutation ∂ Spath, 1941 (c/2741); F: *Hamites attenuatus* mutation ∂ Spath, 1941 (C.2740; G: *Hamites intermedius* J. Sowerby, 1814 (C 886). In all cases the scale bars are in millimetres.

or other taphonomic processes. Such damage is not accompanied by shell repair. The pieces of heteromorph amonite shown here exhibit both repair and extensive, subsequent growth. One possible cause of the damage is predation. There are striking similarities between the elongate wounds of these ammonites and the damage caused by 'peeling predators' such as crabs when attacking marine snails.[8] Crabs are diverse in the Lower Cretaceous and the Gault Clay is especially rich in their fossils.[9] Crabs, as well as a number of other crustaceans, use their claws to manipulate snails and peel the shell back from the aperture until the flesh is exposed. Is it possible that ammonites fell prey to crabs?

If this is the case, it has important implications for reconstructing the ecology of heteromorph ammonites. Because these ammonites had shells which were uncoiled, they would have been clumsy swimmers. Furthermore, the 'paper club' coiling mode of genera such as *Hamites* would probably have made swimming very difficult indeed, since such shells produce a lot of drag. It is difficult to visualise such ammonites employing the mode of locomotion used by the extant *Nautilus*. Most ammonite workers have assumed that these ammonites must have been planktonic, perhaps rather passive feeders, analogous with modern cranchid squids.[10] The buoyancy provided by the chambered shell would be enough to keep the ammonite in midwater, and swimming would be limited perhaps to diurnal vertical migrations.

An alternative view is that they were benthic, and that the shell was buoyant only enough to keep it clear of the sea bed; otherwise the animal crawled about like an octopus.[10] One possible danger in the life of a benthic ammonite would be predators such as crabs, which hunt on the sea floor. While there are midwater crabs in today's oceans, these have elongate, delicate claws from snapping at fish rather than processing shells.[11] The crustaceans capable of peeling shells are all benthic, where their prey are, and it is probable that this was the case in the Early Cretaceous. Are the scars exhibited by the heteromorph ammonites shown here examples of ones which encountered hunting crustaceans, escaped or otherwise survived, and repaired their damaged shells? If this is the case, then it has to be more probable that these ammonites were benthonic, and so could fall prey to crustaceans, and not midwater animals, living tens or hundreds of metres off the sea floor.

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