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Lethaia Seminar
Lethaia, Vol. 28, pp. 315–316. Oslo, 1995 12 20

Limpet pits on ammonoids living in surface waters: reply

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We have presented evidence (Kase *et al.* 1994) from a limpet–ammonite bioassociation that some Late Cretaceous ammonites of the family Pachydiscidae and Puzosiidae (not Desmoceratidae; we follow Matsumoto's 1988 classification of the Desmoceratacea) were swimmers, primarily in surface waters. This conclusion strongly contradicts claims (e.g., Westermann 1990) based on sedimentary facies and shell-structure analyses that these ammonites were deep-water dwellers. This contradiction led Westermann & Hewitt (1995) to propose that the limpet home scars (depressions) we discussed were made on drifting or drifted shells of dead ammonites.

The strongest evidence for our interpretation is the presence of deeply excavated home scars that were healed with a shell blister from inside the shell. Recognition of the healed home scars, doubted by Westermann & Hewitt, is admittedly difficult, as they are mostly inferred from the presence of shallow pits in steinkerns, sometimes with a thin shell blister. Westermann & Hewitt regarded the shell blister as an original inner shell layer rather than a secondary healed surface. We address this point below.

If a shallow pit in a steinkern is positioned below a shell perforation, then it is likely to be a healing. The specimen (NSM PM8253, Kase *et al.* 1994, Fig. 4) reinvestigated here is *Pachydiscus sahekii* Matsumoto & Miyauchi from the Campanian of the Wakkanai area, Hokkaido, Japan (Fig. 1). It is a half-ammonite and has more than 130 home scars on one side of the conch. It also has many shallow depressions on the steinkern of the body chamber, suggesting the presence of healings. We here illustrate three of these depressions on the steinkern (Fig. 1A) and their counterparts on the inner shell surface (Fig. 1B). The cross section of the shell shows that there are deep perforations in the shell above the healed depressions (a, b and c in Fig. 1C). NSM PM8253 is not the only specimen to have healed home scars. We have found at least six specimens (NSM PM8254, 7569, 8272, 8273, GSJ F4890, MCM KYC561008.1) that bear healed home scars among 30 scar-bearing specimens we examined. These observations clearly suggest that the ammonites were alive when the home scars were excavated.

Large-sized puzosiid ammonites with or without limpet home scars are known to occur from strata considered to have been deposited in a wide range of water depth. They are mainly from the Turonian Saku Formation, a facies intermediate between nearshore and offshore, outer-shelf to basin-plain environments (Tanabe 1979; Hirano *et al.* 1992; Ando *et al.* 1994), but also occur in nearshore, shallow-water sediments of the Mikasa Formation in Ikushumbetsu, Hokkaido (Hirano *et al.* 1992; Ando *et al.* 1994), and of the Futaba Group of Fukushima, northern Japan (Matsumoto *et al.* 1989, 1990; Ando *et al.* 1995). Many of our *Canadoceras* and *Pachydiscus* specimens with or without limpet home scars come from the Krasnoyarka Formation in the Naiba area of southern Sakhalin and the Orannai Formation in the Wakkanai area of Hokkaido. These formations are dominated by shallow-water, clastic sediments and represent a regressive facies of the Cretaceous systems in these areas (Poyarkova 1987).

From the mechanical analyses of the siphuncle and septal structures, Westermann (1990) deduced some *Pachydiscus* and *Canadoceras* species to be outermost neritic to oceanic, deep nektobenthic and/or nektic dwellers (200–300 m). He further stated that deep-water ammonoids did not surface after death, because the high ambient pressure would have caused the camerae to become waterlogged quickly, and that surfacing is possible only when ammonoids migrated into or dwelled in shallow seas. This surfacing mechanism is further discussed in detail by Maeda & Seilacher (in press). It should be noted, however, that surface-dwelling ammonoids could not sink to the bottom soon after death; the shells therefore drifted and had the potential to be preserved in a wider variety of depositional environments than deep-water ammonoids. The common occurrence of puzosiid and pachydiscid ammonites in shallow-water deposits of Hokkaido and Sakhalin favors our pelagic bus hypothesis rather than Westermann & Hewitt's post-mortem surfacing hypothesis.

Westermann & Hewitt claimed that NSM PM8263 (Kase *et al.* 1994, Fig. 1) floated at the surface because they believed that most of the body chamber was originally missing in this specimen. However, large puzosiid and pachydiscid ammonites from Hokkaido and Sakhalin are frequently crushed by sediment compaction (Maeda 1987; our observations), so that they are difficult to excavate while keeping the body chamber intact. This is true for NSM PM8263, which we ourselves excavated during our 1993 expedition to Sakhalin. This specimen possessed, although crushed, an almost full body chamber. Usually, large *Canadoceras* and *Pachydiscus* specimens from the Krasnoyarka Formation in south Sakhalin preserve the body chamber in a similar state of preservation.

Westermann & Hewitt stated: 'The Japanese Cretaceous Patellidae are close to the time of origin of this intertidal family from these subtidal relatives. Home scars ... developed before the Patellidae exploited this adaptation by moving to an intertidal algal diet.' Kase & Shigeta (in press) recognize six species of patellogastropod limpets from the Cretaceous of Hokkaido and Sakhalin and suggest that these limpets might be responsible for the home scars documented by us. Of the six species, two evidently belong to the Patellidae and three to the Lottidae, as indicated from shell microstructure combinations. If Westermann & Hewitt's suggestion were accepted, then the Patellidae and Lottiidae were derived from the subtidal, totally blind family Lepetidae. Such an evolutionary scenario is, however, not supported by recent phylogenetic analyses (Lindberg 1988). Patellogastropoda has a long history extending to the early Paleozoic, and we can only say that diversification of the Patellogastropoda took place as early as Late Cretaceous (Kase & Shigeta, in press).

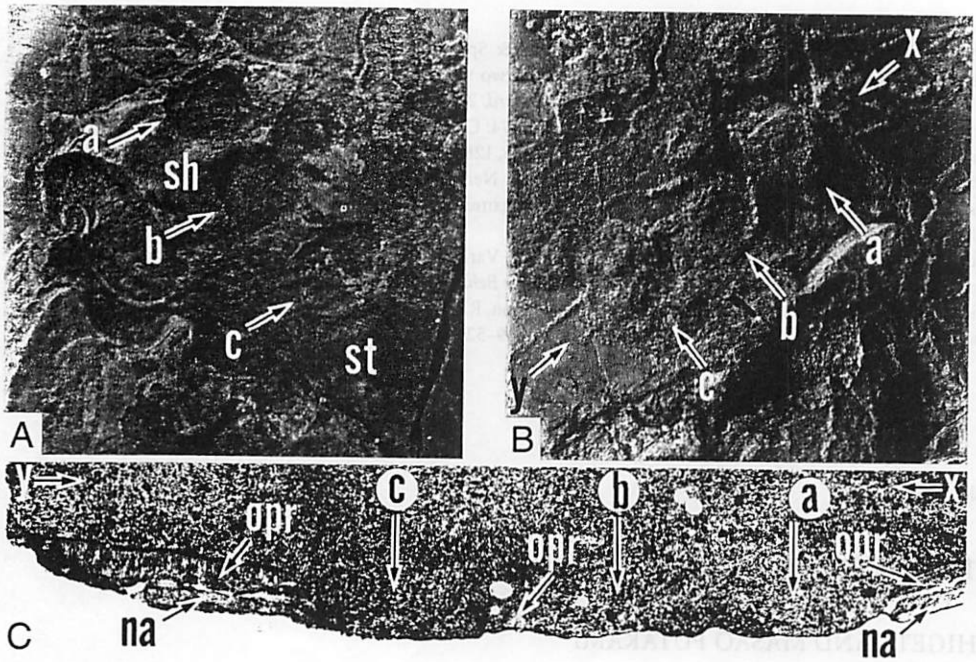

Fig. 1. Home scars in *Pachydiscus sahekii* Matsumoto & Miyauchi, NSM PM8253, Upper Campanian, Wakkanai area, Hokkaido, Japan. □A, B. Part of the steinkern of the body chamber (A) and the corresponding inner shell surface (B), showing three deep home scars, a, b and c. Note that traces of the home scars in A make a shallow penetration below the surrounding surface of the steinkern, suggesting the presence of healing. ×1.3. □C. A polished section cut along X–Y in B; neither the innermost shell layer nor the shell material between the home scars are preserved in this section but do occur in the corresponding surface of the steinkern; a, b and c correspond to those in A and B; Abbreviations: na = inner nacreous layer, opr = outer prismatic layer, sh = shell of ammonite, st = surface of steinkern. ×2.9.

Westermann & Hewitt contradict our interpretation, stating: 'Even a large ammonite shell could not have buoyed-up enough algae, or provided a large enough grazing surface, to support the large limpet populations postulated by Kase *et al.*' They are correctly assuming that the high densities documented from some of the puzosiids and pachydiscids by us imply several generations of infestation. The presence of many depressions overlapping one another clearly suggests this. They overlook, however, the fact that intertidal limpets (particularly territorial species) occur in densities much greater than we documented. Branch (1971), for example, reported a density of *Patella cochlear* of over 1400 individuals per square metre.

We do not deny Westermann & Hewitt's suggestion that home scars were produced in some port-mortem drifted ammonite shells. This idea does not contradict our conclusion that large puzosiid and pachydiscids were swimmers near the surface, as surface-dwelling ammonites would have greater potential to float than those in deep waters. We are convinced that those ammonites having healed home scars as documented by us were alive when the limpets produced the scars.

Acknowledgments. – We thank Paul A. Johnston (Royal Tyrrell Museum of Palaeontology, Alberta, Canada) for his suggestions and linguistic correction of the manuscript.

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