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Brief report

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Late Cretaceous gastropod egg capsules from the Netherlands preserved by bioimmuration

MICHAŁ ZATOŃ, PAUL D. TAYLOR, and JOHN W.M. JAGT

Clusters of gastropod egg capsules, inferred to be of neritoids and attached to the inner shell wall of the ultimate whorl of a large volutid gastropod, are here recorded from the upper Nekum Member (Maastricht Formation; late Maastrichtian) of the ENCI-Heidelberg Cement Group quarry, St Pietersberg (Maastricht, southeast Netherlands). Because the aragonitic shell of the volutid has dissolved, the outlines of the egg capsules are now revealed on the steinkern of indurated biocalcarenite, having been subsequently overgrown by cheilostome bryozoan colonies and preserved as mould bioimmurations. This represents the first example of gastropod eggs preserved through bioimmuration, as well as the first record of gastropod eggs from the Cretaceous.

Introduction

Due to their composition and small size, invertebrate eggs are uncommon in the fossil record. Under a variety of unusual taphonomic circumstances, however, they may be preserved, even in strata as ancient as Precambrian (see e.g., Xiao et al. 1998; Xiao and Knoll 1999, 2000). Most invertebrate eggs described from the fossil record, whether isolated from or in association with their producers, belong to arthropods (Briggs and Clarkson 1985; Siveter et al. 2007; Shen and Huang 2008; Huang et al. 2008). Molluscan eggs are much rarer, particularly those of gastropods, as was recently pointed out by Zatoń et al. (2009). Eggs of Paleogene and Neogene land snails (for examples, see Cox 1960; Tompa 1976; Pierce 1993), which have calcareous capsules (eggshells), have a much better fossilisation potential and far outnumber aquatic gastropod egg capsules which have so far been recorded only from Hettangian (Lower Jurassic) deltaic deposits in Poland (Zatoń et al. 2009) and Pliensbachian (Lower Jurassic) marine strata in Germany (Kaiser and Voigt 1977, 1983). Riegraf and Schubert (1991) and Schubert et al. (2008) interpreted pyritised hemispherical structures on driftwood from the Pliensbachian of Germany as putative gastropod eggs as well. Possible gastropod egg capsules preserved on bivalve shells are also known from the Miocene of the Czech Republic (Mikuláš and Dvořák 2001).

Here we record some intriguing structures from the type area of the Maastrichtian Stage that are preserved by bioimmuration. This is a process of fossilisation through organic overgrowth, generally by cemented bivalves, serpulid worms, or bryozoans with calcified basal skeletons that produce natural moulds of any organisms they overgrew during life (see Taylor 1990; Taylor and Todd 2001). Bioimmured fossils are relatively common in the Maastricht area, and numerous examples have been recorded by the late Professor Ehrhard Voigt (Voigt 1972, 1973, 1979, 1980, 1981). However, Voigt did not consider any structures resembling those described here that, on account of their arrangement, morphology and size, are interpreted as gastropod egg capsules. This is the first example of fossilised gastropod egg capsules from the Cretaceous; it also represents the first record of bioimmuration of eggs.

Institutional abbreviations.—NHMM, Natuurhistorisch Museum Maastricht, Maastricht, the Netherlands.

Material and methods

The egg capsules studied here are preserved on the internal mould (NHMM JJ 13778) of a large volutid gastropod identified provisionally as "*Volutospina*" sp. (Fig. 1). The comparatively rich gastropod faunas from the type Maastrichtian, which include several volutid taxa (see Binkhorst van den Binkhorst 1861; Kaunhowen 1898), are in urgent need of revision. NHMM JJ 13778 comes from the indurated uppermost 0.2 m of subunit IVe-7 of the Nekum Member (Maastricht Formation) at the ENCI-Heidelberg Cement Group quarry, and is of late late Maastrichtian (*Belemnitella junior* Zone) age (Jagt and Jagt-Yazykova 2012). At this particular level, associated gastropod taxa include turritellids, cerithiids, naticids, nerineids, and neritids, all preserved as internal/external moulds with the exception of the neritid *Otostoma retzii* (Nilsson, 1827) which retains its calcitic, outer shell (see Jagt and Kiel 2008; Jagt and Severijns 2011).

The specimen of "*Volutospina*" sp. was examined in an uncoated state using a LEO 1455VP low vacuum scanning electron microscope (SEM) housed at the Natural History Museum, London, UK. Images were generated using backscattered electrons. Measurements of egg capsule length and width were taken from SEM photomicrographs.

Results

The traces of the inferred egg capsules have nearly circular to slightly oval outlines, with well-defined borders in the form of shallow grooves (Figs. 1, 2A, B). They occur in two areas on the gastropod internal mould, close to the suture with the preceding

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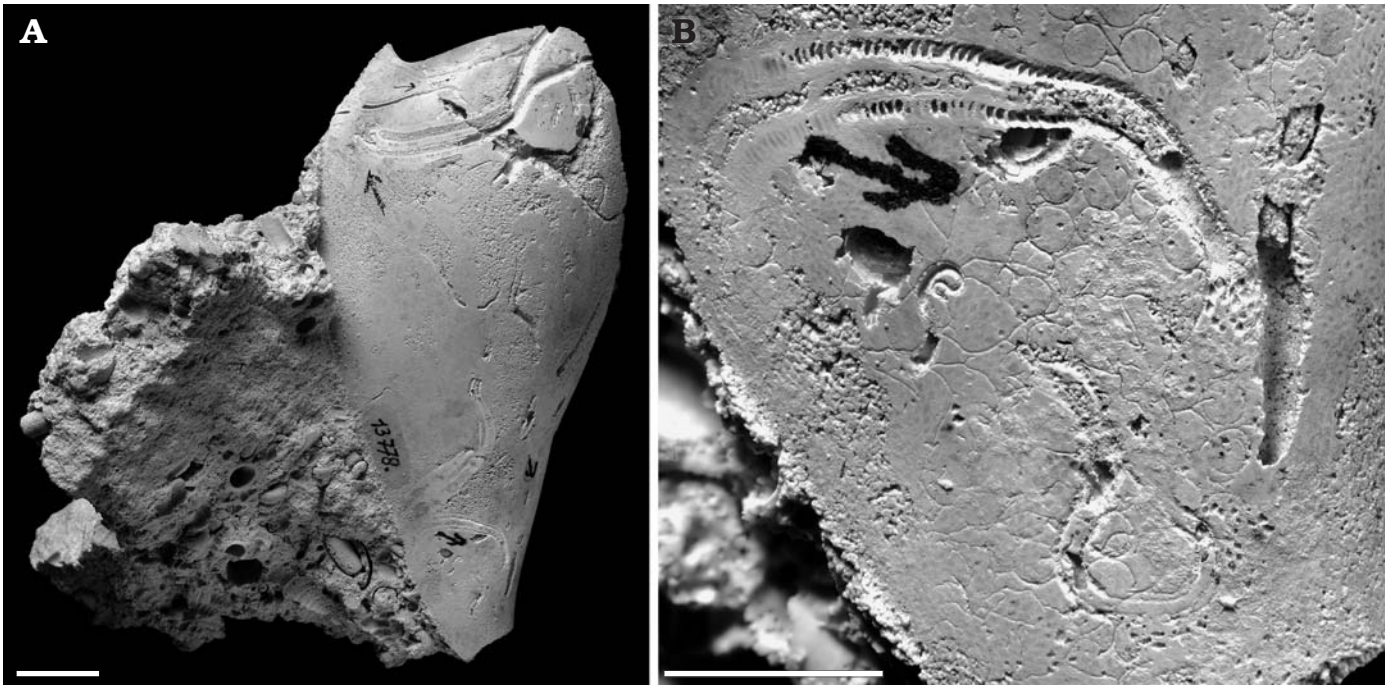


Fig. 1. **A**. The internal mould (NHMM JJ 13778) of the volutid gastropod "*Volutospina*" sp. from the late Maastrichtian (Late Cretaceous) of Maastricht, the Netherlands, with inferred egg capsules preserved by bioimmuration. Arrows drawn onto the specimen indicate the position of the preserved egg capsules. **B**. Close-up of the anterior area of the mould showing aggregated egg capsules. Scale bars: A 10 mm, B 5 mm.

whorl, one area being located more anteriorly, i.e., closer to the original apertural border of the volutid, and the second area closer to the posterior end of the mould, away from the aperture (Fig. 1). In the anterior area, the eggs form a more or less united clump consisting of about 48 capsules, whereas the posterior area seems to consist of three separate clusters comprising 10, 23, and 25 eggs. Usually, the eggs are closely spaced with contiguous borders, but some eggs are isolated and others are superimposed on one another (Figs. 1B, 2A, B). When situated close to each other, the egg capsules form variably defined rows (Fig. $2A_1$, B_1). The egg capsules are all of similar sizes, with a length of 0.95–1.2 mm (average = 1.09, SD = 0.09, N = 18) and a width of 0.85–1.15 mm (average = 0.99, SD = 0.09, N = 18).

Key to our interpretation of the preservational mode of these eggs as bioimmurations is the fact that they are visible only in parts of the internal mould that expose the undersides of sheet-like cheilostome bryozoan colonies which encrusted the internal shell surface of the volutid. Beyond these, the internal mould consists of indurated, rather coarse-grained biocalcarenite and additional eggs are not preserved. The outlines of the polygonal cheilostome zooids are clearly seen within and around those of the eggs (Fig. $2A_2$), and locally the basal walls of the zooids are abraded to reveal the interiors of the zooids (see Fig. $2A_1$, B_1). The bryozoan zooids evidently filled the interiors of the eggs, presumably after hatching, and also grew around them. However, the basal margins of the egg capsules remained intact, indenting the bryozoan zooids and forming the deep grooves that define the outlines of these bioimmured fossils.

In some places the partially sediment-filled, dome-shaped interiors of the egg capsules are preserved (Fig. $2B_1$, B_3). Here it appears that the eggs were turgid (?unhatched) and retained their shape during overgrowth by the bryozoans.

Discussion

The structures described here on the internal mould of a Late Cretaceous gastropod are interpreted as gastropod egg capsules preserved by bioimmuration. Today, egg capsules are produced by various caenogastropods and neritimorphs. Those produced by the latter group are tough, flattened capsules that are oval or spherical in shape, composed of conchiolin as well as chitin (e.g., Adegoke et al. 1969; Bandel 1982; Kaiser and Voigt 1983; Soliman 1987; Kano and Fukumori 2010). Egg capsules may be reinforced by either aragonite or calcite crystals (e.g., Bandel 1982; Kano and Fukumori 2010), increasing the likelihood of fossilisation (see Kaiser and Voigt 1977, 1983; Zatoń et al. 2009). Neritid egg capsules are laid down on various hard substrates, including mollusc shells, and are often aggregated into groups (e.g., Adegoke et al. 1969; Soliman 1987; Kano and Fukumori 2010).

The present gastropod egg capsules are circular to slightly oval in outline, aggregated in groups and preserved on a gastropod mould, indicating that the original substrate for their deposition was the inside surface of the ultimate (body) whorl of the dead gastropod shell. The arrangement of the structures resembles that of Recent neritid egg capsules (see Fig. 2C), being either closely spaced and set in rows, often abutting, or occurring as single capsules. Furthermore, the size range of the Maastrichtian structures is also quite similar to that of some Recent neritid egg capsules (see Kano and Fukumori 2010; Fig. 3 here). The shape of the Late Cretaceous egg capsule bases (circular in

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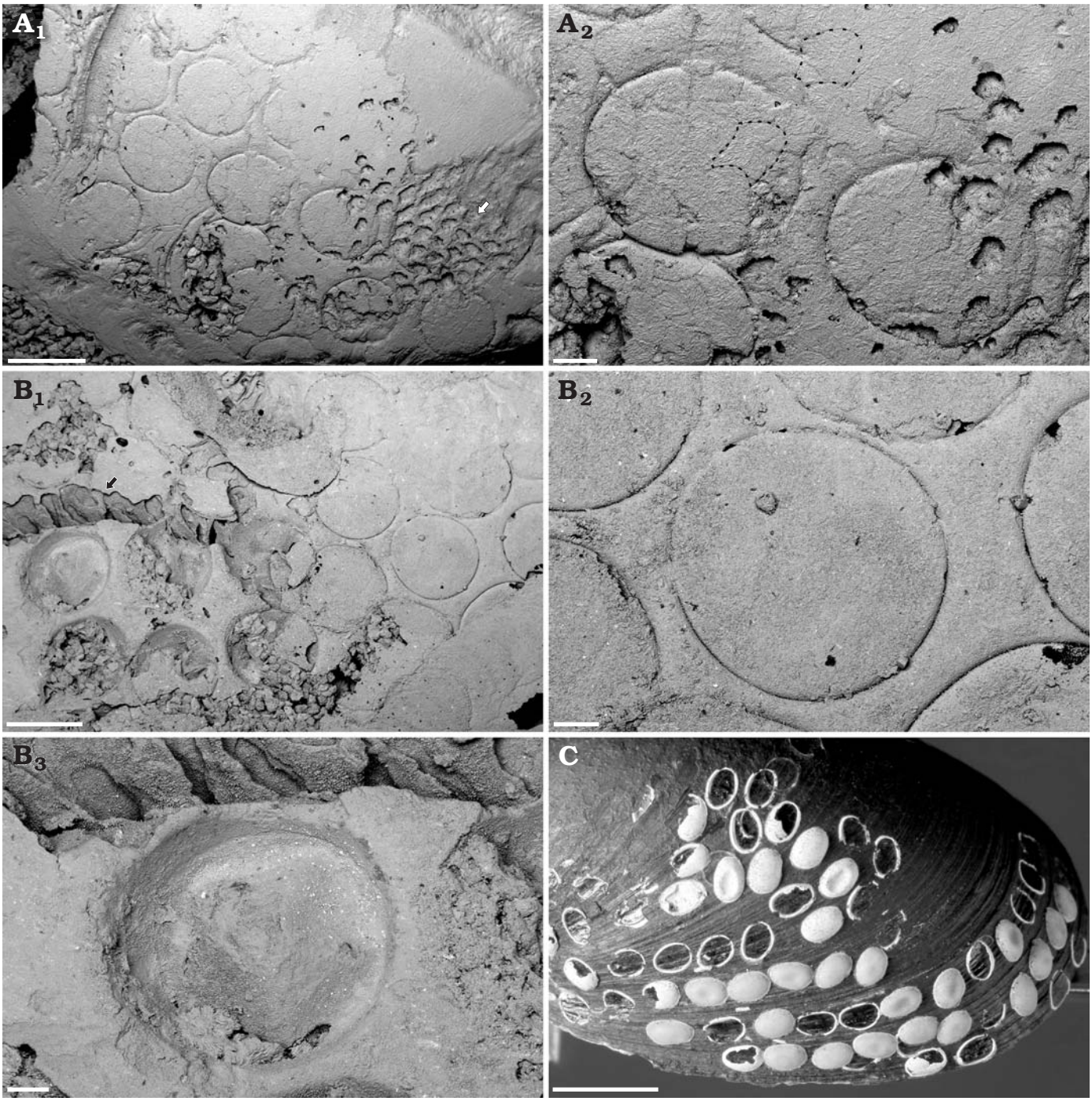


Fig. 2. **A**, **B**. Late Cretaceous gastropod egg capsules from the late Maastrichtian (Late Cretaceous) of Maastricht, the Netherlands, preserved by bioimmuration (NHMM JJ 13778). **A**. Aggregate of bioimmured egg capsules, probably the capsule bases, with an eroded basal wall of a cheilostome bryozoan colony, showing the zooid interiors (arrowed) (A_1). Close-up view of the egg capsules shown in the centre of A_1, with clearly visible outlines of cheilostome zooids within and around the egg capsules, shown by dotted lines (A_2). **B**. Aggregate of presumably unhatched (left) and hatched, in a form of bases (right), egg capsules (B_1). The arrow points to the eroded basal wall of a bioimmuring cheilostome bryozoan colony. Close-up views of presumably hatched (B_2) and unhatched (B_3) egg capsules shown in B_1. **C**. Hatched and unhatched egg capsules of the Recent neritid gastropod species *Neritina iris* Mousson, 1849, on the shell exterior of a live gastropod *Septaria porcellana* (Linné, 1758), Kagoshima Bay, Japan (photograph courtesy of Yasunori Kano). Scale bars: A_1, B_1 1 mm; A_2, B_2, B_3 200 μm; C 5 mm.

outline as opposed to more oval as in Fig. 2C) may have resulted from the substrate topography on which they were laid, or may be species specific because circular egg capsules of extant neritids are also known (e.g., Adegoke et al. 1969).

The inferred egg capsules described here are also similar in shape, size, occurrence, and arrangement to putative neritid egg capsules reported from the Lower Jurassic (see Kaiser and Voigt 1977, 1983; Zatoń et al. 2009). Their preservation, however, is

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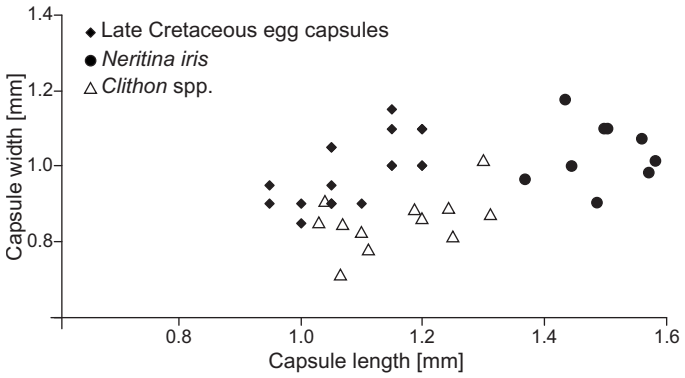


Fig. 3. Plot of measurements of Late Cretaceous and selected Recent neritid egg capsules (data from Kano and Fukumori 2010).

completely different: the Jurassic eggs are preserved as thin organic films on bivalve moulds (see Zatoń et al. 2009 for details). Many of them occur as thickened margins of the capsule bases, which are characteristic of neritid egg capsules (see e.g., Adegoke et al. 1969; Kano and Fukumori 2010). In contrast, the Late Cretaceous egg capsules studied here are preserved as natural moulds following overgrowth by cheilostome bryozoans with calcitic skeletons, a process of bioimmuration. The presence of the bioimmured egg capsules in two areas on the gastropod mould indicates that at least two colonies of cheilostomes overgrew the deposited egg capsules. The preservation of the bioimmured capsules also indicates that they were encrusted while at least some of them were still unhatched. Such a preservation of hatched and unhatched egg capsules occurring together has been reported previously by Zatoń et al. (2009).

The original deposition of the egg capsules by neritid gastropods within the empty shell is reminiscent of other fossil examples in which egg capsules were laid down in vacant body chambers of ammonites (Kaiser and Voigt 1983), or the interiors of bivalve shells (Kaiser and Voigt 1977; Zatoń et al. 2009). These cryptic locations would have provided protection for the eggs and the newly hatched gastropods.

In conclusion, the structures from the type Maastrichtian represent the first gastropod egg capsules to be described from the Cretaceous, and they add to the range of fossils preserved through the process of bioimmuration.

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