

EXCEPTIONALLY PRESERVED LATE JURASSIC GASTROPOD EGG CAPSULES

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ABSTRACT: Exceptionally preserved, phosphatized gastropod egg capsules from the uppermost Jurassic (upper Volgian) in Central Russia are reported. The egg capsules were attached to the inner side of the shell wall of empty body chambers of two ammonites. Due to phosphatization, the egg capsules retained their original morphology preserving both the lower attachment base and upper hemispherical cover. Comparison with recent and fossil gastropod egg capsules indicates that these were not produced by neritimorphs, the egg capsules of which are known from the Lower Jurassic and Upper Cretaceous. Since these fossil egg capsules share many similarities with those produced by some recent rissoids and muricid neogastropods, it is evident that they were produced by some representatives of Caenogastropoda. The abundant filamentous microbial structures, as well as micron-sized apatite globules, preserved inside the egg capsules suggest that phosphatization processes were mediated by microbial consortia under anaerobic and low-pH conditions.

INTRODUCTION

In order to protect the embryos against various extrinsic factors, most recent gastropods (Caenogastropoda and Neritimorpha) lay capsule-enclosed eggs on a variety of firm and hard media (e.g., Pechenik 1982; Rawlings 1999; Przeslawski 2004; Aktipis et al. 2008; Bigatti et al. 2010; see Roche et al. 2011 for a review). These egg capsules vary widely in size and shape between different gastropod groups, especially in higher caenogastropods (Neogastropoda) where they are characterized by a variety of forms (e.g., Soliman 1987; D'Asaro 1986, 1991, 1997, 2000).

Despite the fact that gastropods were common and locally abundant in marine paleoenvironments, the fossil record of their egg capsules is extremely poor due to their low fossilization potential. Among aquatic gastropods, only representatives of Neritimorpha (Neritidae) produce tough, leathery egg capsules which, although composed of conchiolin and chitin (e.g., Adegoke et al. 1969; Bandel 1982; Kaiser and Voigt 1983; Soliman 1987; Kano and Fukumori 2010; Wysokowski et al. 2014), are additionally reinforced by calcium carbonate (aragonitic or calcitic) crystals (e.g., Bandel 1982; Kano and Fukumori 2010; Fukumori et al. 2013), which may increase their fossilization potential. The egg capsules of neogastropods are also tough; however, they are composed chiefly of proteins and carbohydrates (e.g., Tamarin and Carrier 1967; Soliman 1987; Hawkins and Hutchinson 1988; Rawlings 1999 and literature cited therein), so their potential to be fossilized is significantly lower. Those possessing strengthening calcareous covers are rare (Bigatti et al. 2010).

Thus far the great majority of known fossil egg capsules of aquatic gastropods belong to neritimorph gastropods. However, even though such egg capsules are resistant, their fossil record is sparse. Preserved as iron oxides and carbonaceous imprints on ammonite and bivalve shell molds, they were described from the Lower Jurassic of Germany (Kaiser and Voigt 1983) and Poland (Zatoń et al. 2009; Wysokowski et al. 2014). Later, preserved by bioimmuration, they were detected on a gastropod shell mold from the Upper Cretaceous of the Netherlands (Zatoń et al. 2013). Some pyritic structures resembling gastropod egg capsules were also described from the Lower Jurassic of Germany by Riegraf and Schubert (1991) and Schubert et al. (2008), and some carbonaceous

imprints resembling such capsules were also described from the Miocene of the Czech Republic by Mikuláš and Dvořák (2001). The egg capsules mentioned above, however, are preserved as compressed, two-dimensional objects, mainly representing attachment bases. Such a state of preservation limits our insight into their true geometry and structure.

Herein, we report on exceptionally preserved gastropod egg capsules from the Upper Jurassic of Russia. Due to phosphatization processes, the capsules retained their original, three-dimensional morphology, allowing for inspection of their exterior and interior sides. On the basis of detailed comparisons with modern and fossil gastropod egg capsules, we discuss their paleobiological significance and preservation.

MATERIAL AND METHODS

The egg capsules were detected in body chambers of two ammonite specimens representing two different species, *Craspedites nekrassovi* (Prigorovsky) and *C. cf. jugensis* (Prigorovsky), found in upper Volgian (=upper Tithonian, uppermost Jurassic) phosphatized sandstone nodules in black and dark-green sands outcropping along the Cheremukha River (57°58'01.7"N 38°52'22.3"E) near the village of Ivanovskoe in the Yaroslavl Region, Central Russia (Fig. 1, see also Mitta et al. 1999 for details on locality and stratigraphy). Although the ammonites were found in two different nodules, they come from the same locality and the same stratigraphic level (*Kachpurites fulgens* ammonite Zone).

In the case of the *C. nekrassovi* specimen, it was possible to separate the nacreous shell material from the internal filling. Thus two views of the preserved egg capsules are available: the original, convex structures preserved on the inner side of the shell material (Fig. 2B); and their concave counterparts preserved in the phosphatic infilling (Fig. 2A, C). In the case of *C. cf. jugensis*, the egg capsules are preserved as concave structures on the body chamber internal mold (Fig. 2D–F).

The egg capsules were investigated using a TESCAN VEGA SEM with a BSE detector at the Paleontological Institute of the Russian Academy of Sciences in Moscow. The specimens were inspected in uncoated state in low-vacuum conditions at 30 kV. Images were generated using back-scattered electrons (BSE). In order to retrieve the data on elemental

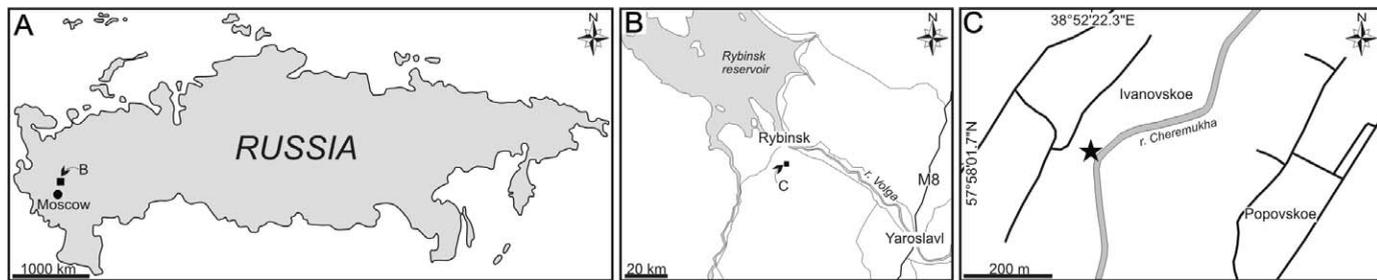


FIG. 1.—Locality of the gastropod egg capsule-bearing Upper Jurassic deposits. **A)** Map of Russia with indicated Yaroslavl region. **B)** Yaroslavl region with sampled area located south of the city of Rybinsk. **C)** The exact locality of the sampled site at the bank of the Cheremukha River at Ivanovskoe.

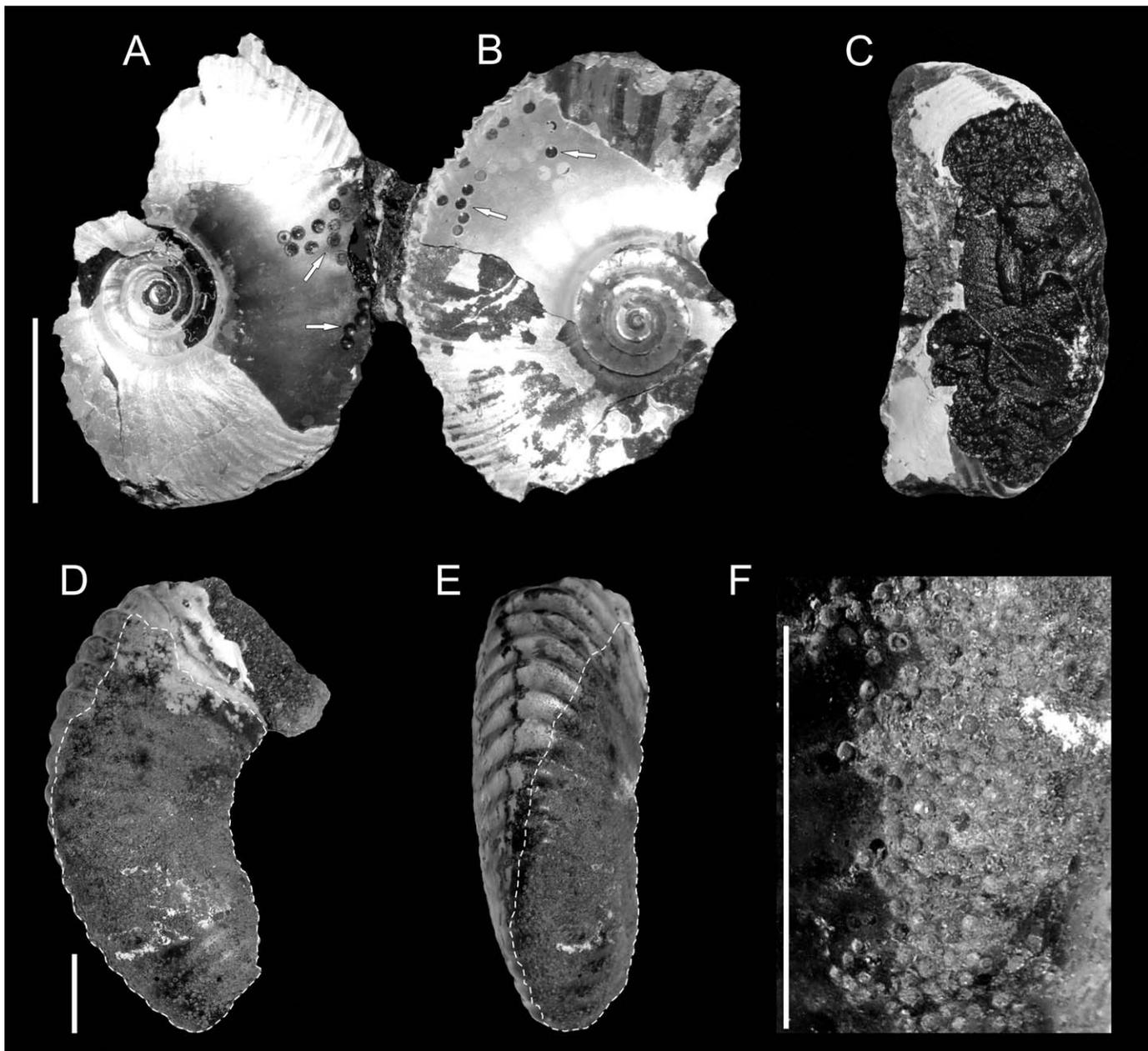


FIG. 2.—Ammonites with preserved egg capsules from the latest Jurassic of Central Russia. **A, B)** Capsules (indicated by arrows) preserved respectively in the phosphatic infilling and on the inner side of the shell material of *Craspedites nekrassovi*. **C)** Interior of the *C. nekrassovi* body chamber infilled with various organic and shelly debris. **D–F)** Numerous egg capsules (magnified in view **F**) preserved on the internal mold of *Craspedites* cf. *jugensis*. The limit of the egg capsules' occurrence is indicated by white dashed lines. Scale bars = 1 cm. **A, C)** MSU 120/1-1. **B)** MSU 120/1-2. **D–F)** MSU 120/2.

composition of the capsules and associated structures, an SEM-equipped energy-dispersive spectroscopy (EDS) detector was used.

The specimens are housed at Moscow State University Museum, Russia, abbreviated MSU 120.

RESULTS

Twenty-nine egg capsules were detected on the right lateral side of the body chamber of the specimen of *C. nekrassovi* (shell diameter 24 mm) (Fig. 2A, B). In the case of the specimen of *C. cf. jugensis* (fragment length 48 mm), more than 100 capsules occur on the left side and the ventrolateral part of the preserved body chamber (Fig. 2D, E). The better-preserved egg capsules occur in the first of the species (Fig. 3A–F). Those on *C. cf. jugensis* are in a worse state of preservation (Fig. 3G, H); however, their characteristics are quite visible on several specimens, and it is certain they are of the same type as those preserved on *C. nekrassovi*.

The preserved egg capsules are circular in outline and hemispherical in shape (Fig. 3A–H). Their diameter ranges from 457 to 600 μm (mean = 544 μm , $n = 13$). In *C. nekrassovi* all capsules are nearly the same in size and slightly larger (524 to 600 μm in diameter) than those preserved in *C. cf. jugensis* (457 to 553 μm in diameter). The egg capsules consist of a flat attachment base (Fig. 3E, F) capped by a hemisphere (Fig. 3A–D, G, H). The upper side of the hemisphere has a circular opening (Fig. 3B–D) the diameter of which ranges from 60 to 83 μm . The base, however, is not structurally separated from the hemisphere but they both form a continuous structure (Fig. 3F). The entire capsule is surrounded by an irregular rim, up to 103 μm in width, which extends beyond the base (Fig. 3B–D). Originally, the thin layer forming the rim also covered the upper hemisphere, as is shown by its remnants covering the lower part of the hemisphere (Fig. 3B, D). The capsule wall thickness is $\sim 11.8 \mu\text{m}$. Many specimens possess distinct deformation of the upper hemisphere (Fig. 3C–E), suggesting that the egg capsules were originally soft and flexible. Distinct ornamentation patterns on the exterior of the egg capsules are not visible. Inside the capsule, both on its base and inner side of its upper hemisphere, globular crystals as well as filamentous microstructures occur (Figs. 3E, F, 4), which will be further discussed below. The EDS analyses show that the egg capsules, globular crystals, and filamentous microstructures filling their interiors are composed of apatite (Fig. 5).

In *C. nekrassovi*, the inner aragonitic nacreous shell layer to which the egg capsules are attached, is covered by a dense network of thin, $\sim 2.5 \mu\text{m}$, branching filaments with occasional swellings (Fig. 3B–D), reminiscent of fungal hyphae. These filaments neither encrust nor penetrate the egg capsules, and likely represent modern microorganisms infesting the aragonitic ammonite shell. This is supported by the fact that the host deposits are located very close to the soil surface.

DISCUSSION

Identity of the Egg Capsules

Objects similar to those described here were previously noted as attached to the interior body chamber walls of the ammonite *Kachpurites fulgens* (Trautschold) collected from the same locality and horizon by Baranov (1985). The latter author, however, stated that the egg capsules were just pressed to the shell wall by sand which infilled the body chamber. As in our specimens, all his capsules are also clearly attached to one side of the shell. Baranov (1985) suggested that these objects are probably ammonite eggs or they are eggs of other invertebrate animals that used empty shells for oviposition. He did not consider gastropods as potential producers.

With respect to their morphology and mode of occurrence, the egg capsules are most similar to those produced by recent aquatic gastropods. Those produced by terrestrial snails are completely calcified spheroids and differ much from the latter (e.g., Pierce 1993). Egg capsules of neritimorph gastropods, well known from the fossil record since the Early Jurassic (Kaiser and Voigt 1983; Zatoń et al. 2009), may also be circular

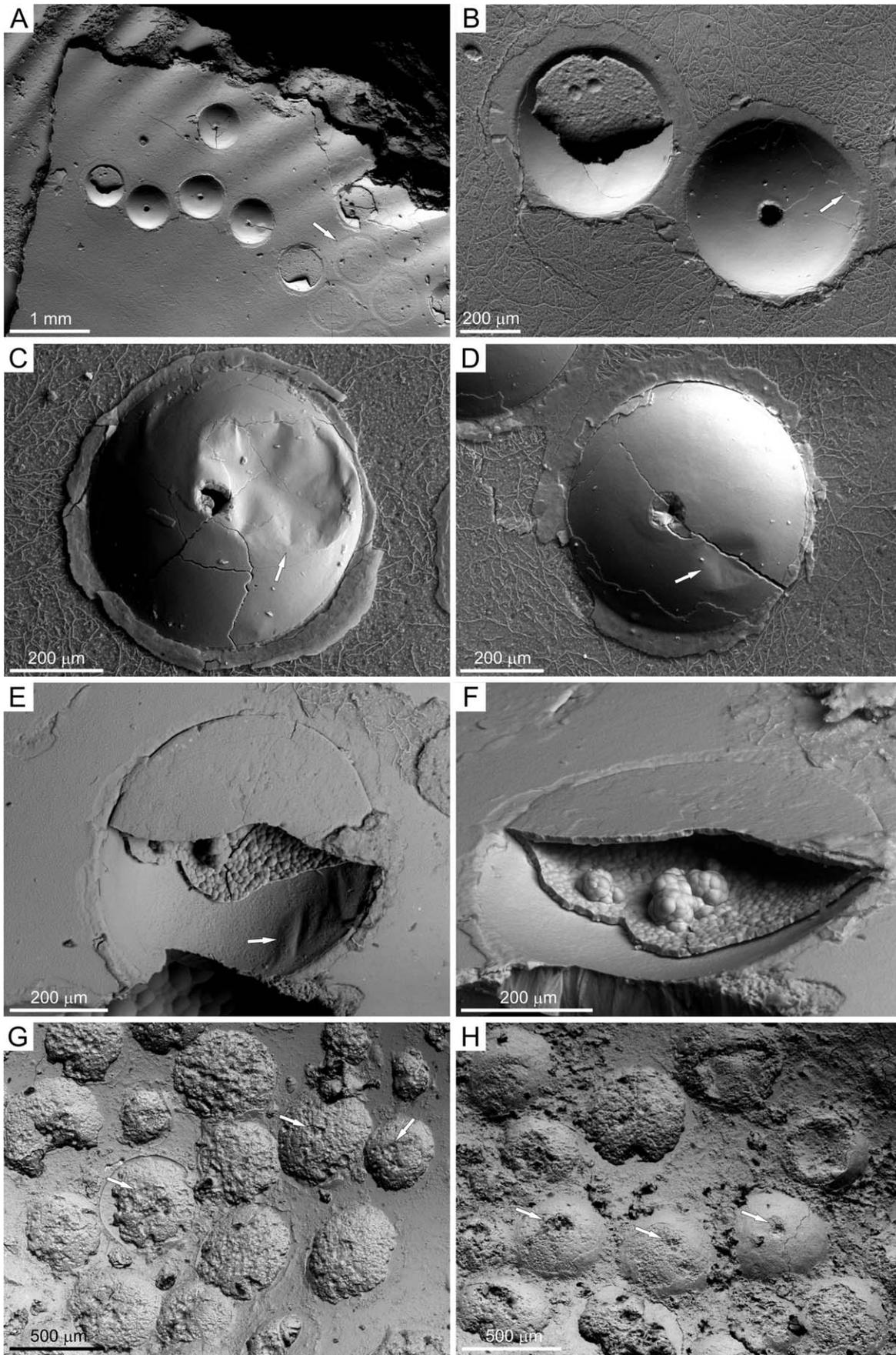
to semicircular in outline and attached to various hard media, including mollusk shells. Although neritimorph egg capsules also possess a flat attachment base, their upper lid is uniform, devoid of any smaller opening at its top (e.g., Adegoke et al. 1969; Kano and Fukumori 2010; Y. Kano, personal communication 2014). Such an opening has not been detected even in fossil neritimorph egg capsules in which some specimens, although completely flattened, preserved the remnants of the upper lid (Zatoń et al. 2009). Moreover, unlike the structures described here, in neritimorph egg capsules the attachment base is separated from its covering lid by a suture line. As a result, when hatched, the neritimorph egg capsules are preserved as distinct basal rings attached to the medium (e.g., Adegoke et al. 1969; Zatoń et al. 2009). In the capsules studied here, both the base and covering hemisphere are united by the same capsule wall (Fig. 3F). Thus, the egg capsules investigated here clearly differ from both recent and fossil neritimorph egg capsules.

It is worth noting that Kaiser and Voigt (1977, pl. 1, fig. 3, pl. 2, fig. 1; 1983, fig. 2C) also presented egg capsules preserved in the form of imprints and negative relief on the internal mold of the Early Jurassic (Pliensbachian) bivalve and ammonite, respectively. The capsules, although larger, also have hemispherical outline and some possess centrally located swellings which appear like the apical opening; however, the opening has a distinctly larger diameter and, unlike any of those present in the capsules described here, is irregular in outline, suggesting they were torn. These probably represent only a different state of preservation of neritimorph egg capsules described by the latter authors. However, any closer comparison of these structures is hampered due to the state of preservation of the Early Jurassic fossils and lack of comparative SEM documentation.

The egg capsules described in this paper can actually be compared with those produced by some representatives of recent Caenogastropoda. Morphologically similar egg capsules are produced by rissoids (Rissoiidae), as well as muricid (Muricidae) neogastropods. Rissoids are known to produce isolated, semicircular, and hemispherical egg capsules attached to a variety of firm and hard substrates (e.g., Lebour 1934; Graham 1988). Like the Jurassic egg capsules investigated, the rissoid capsules (as those produced by, e.g., *Alvania abyssicola*) may also be small sized (e.g., 0.5 mm in diameter; see Graham 1988) and have a circular (Graham 1988) or oval (Lebour 1934) opening at the top of the upper hemisphere (Fig. 6A).

The egg capsules produced by some recent muricid neogastropod species, such as *Bedevea paivae* (Crosse), *Zeatrophon ambiguus* (Philippi) described and illustrated by D'Asaro (1991) from Australia and New Zealand, or *Coronium coronatum* (Penna-Neme and Leme) from the southwestern Atlantic (Pastorino et al. 2007; Pastorino and Penchaszadeh 2009; see also Fig. 6B), are morphologically also similar to the Jurassic capsules described. The egg capsules described herein have a circular attachment base capped by a hemisphere possessing an opening that is centrally located and circular in outline, similar to *Coronium* egg capsules. As in recent forms, the opening was probably originally covered by mucoïd plug which sealed the chamber from the external environment (e.g., D'Asaro 1991; Rawlings 1999). The capsules are also surrounded by an irregular, extending rim that covered the hemisphere. The only difference is the presence of sutures on the muricid capsules mentioned above. As noted by Naegel (2004), however, this feature is not universal for all muricids. Whether the Jurassic egg capsules also had a laminated capsule wall (e.g., Tamarin and Carriker 1967; Naegel 2004) is difficult to say as phosphatization could have obliterated such a feature.

Despite the striking similarity to both rissoid and some neogastropod egg capsules, it is very difficult to say whether the Late Jurassic egg capsules described here were produced by these groups of gastropods. Rissoids appeared during the Jurassic and were a common constituent of marine, benthic paleocommunities (e.g., Conti et al. 1993; Kaim 2004). However, the egg capsules of recent representatives of this group, although similar in size and general morphology to those reported here, differ in having



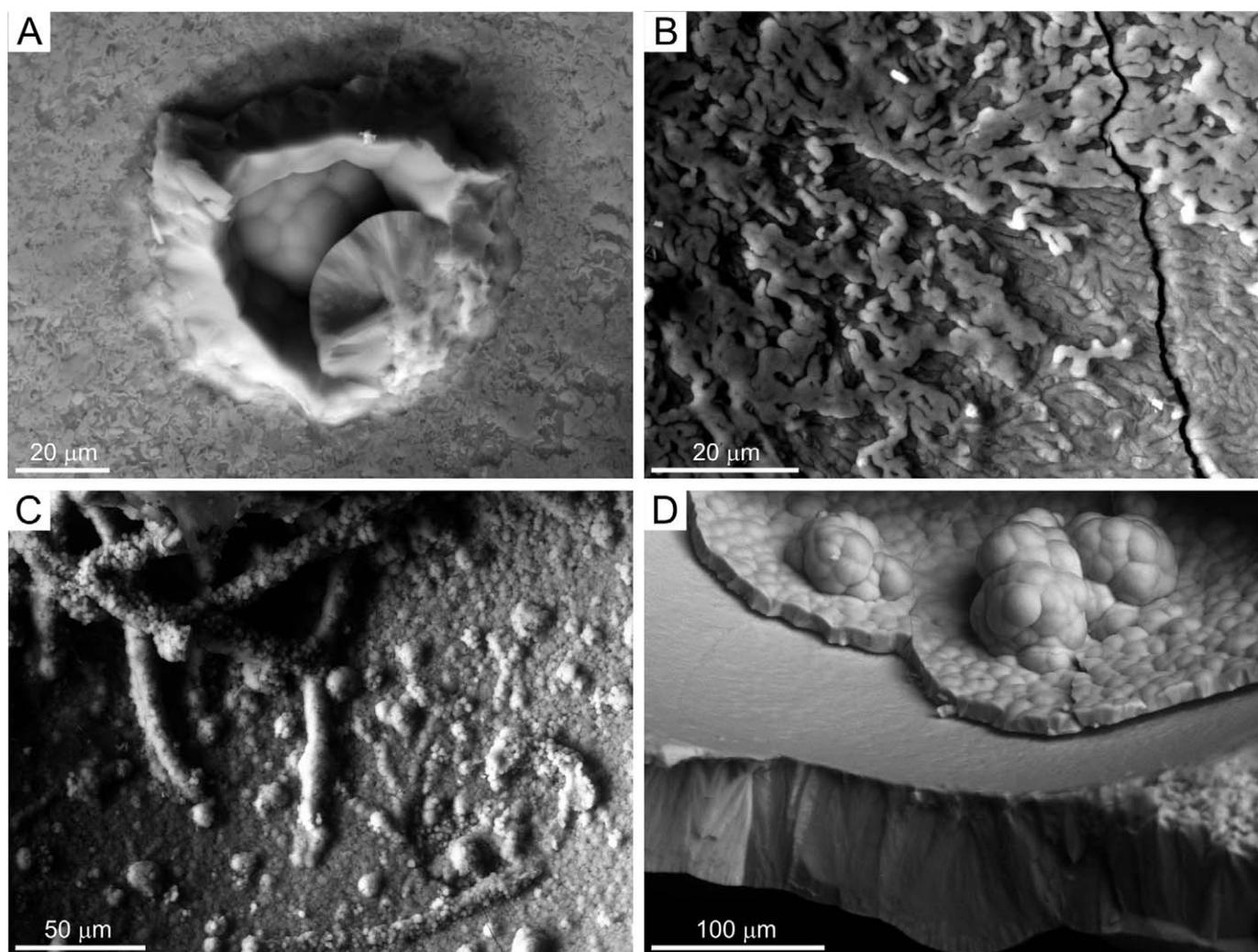


FIG. 4.—Microbial features of the egg capsules. A, B) Inner side of the thin layer covering the capsule's upper hemisphere, covered by a dense network of phosphatic, thin rodlike and bifurcating filaments. In view A, the microbial filaments are shown in lower magnification around the central opening. In view B, the microbial filaments are shown in higher magnification. C) Straight and bifurcating filaments encrusted by micron-sized apatite spherules from the inner side of the upper hemisphere. D) Cauliflowerlike apatite globules from the inside of the capsule. A, B, D) MSU 120/1-1. C) MSU 120/2.

a significantly larger apical opening (Fig. 6A), which may be even widely elliptical in outline (Lebour 1934). Additionally, rissoids have not been reported from the upper Volgian sediments of the study interval (see Guzhov 2004), although it is acknowledged that this does not prove their absence there. The egg capsules of muricid neogastropods, such as *Coronium coronatum* (Fig. 6B), are significantly larger (20 mm and more) than the Jurassic capsules (up to 0.6 mm). Moreover, neogastropods have become common and diverse since the Late Cretaceous (e.g., Kaim 2004). It must be noted, however, that the group must have appeared much earlier, which is indicated by a find of a single juvenile muricoid shell from

the Early Cretaceous (Valanginian) by Kaim (2004). Moreover, the group of gastropods called Maturifusidae (and related Purpurinidae), which are considered a stem group of modern neogastropods (see Kaim 2004; Nützel 2010), existed during the Triassic–Cretaceous. The taxon *Khetella*, a representative of that group in the European and Siberian part of Russia (e.g., Kaim and Beisel 2005), also occurs in the egg capsule-bearing deposits (Guzhov 2004). However, whether these older relatives of neogastropods were the actual producers of the egg capsules described is uncertain. The capsules are preserved in isolation from their parent gastropods, and thus affinity with other gastropod groups is also possible.

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FIG. 3.—Latest Jurassic gastropod egg capsules. A) Cluster consisting of complete hemispherical egg capsules and their basal traces (arrowed) attached to the *C. nekrassovi* ammonite shell interior. Circular central openings are clearly visible on the tops. B) Two egg capsules attached to the shell interior encrusted by recent microbial filaments infesting the aragonitic nacreous layer of the ammonite shell. Arrow indicates the remnants of the thin layer forming both the basal rim and covering of the upper hemisphere. Damaged capsule shows interior filled with apatite globules. C, D) Capsules with distinct, flexible deformation of the upper hemisphere. E, F) Capsule embedded within the apatite internal mold of *C. nekrassovi*, showing exposed base. The flexible deformation of the upper hemisphere is clearly visible as imprints in view E (arrowed) which also show dense filamentous structures (see also Fig. 4B). In view F, an interior of the upper hemisphere is encrusted by apatite globules (see also Fig. 4D). G, H) Poorly preserved clusters of hemispherical egg capsules with central openings (arrowed) from the internal mold of *Craspedites cf. jugensis*. A–D) MSU 120/1-2. E, F) MSU 120/1-1. G, H) MSU 120/2.

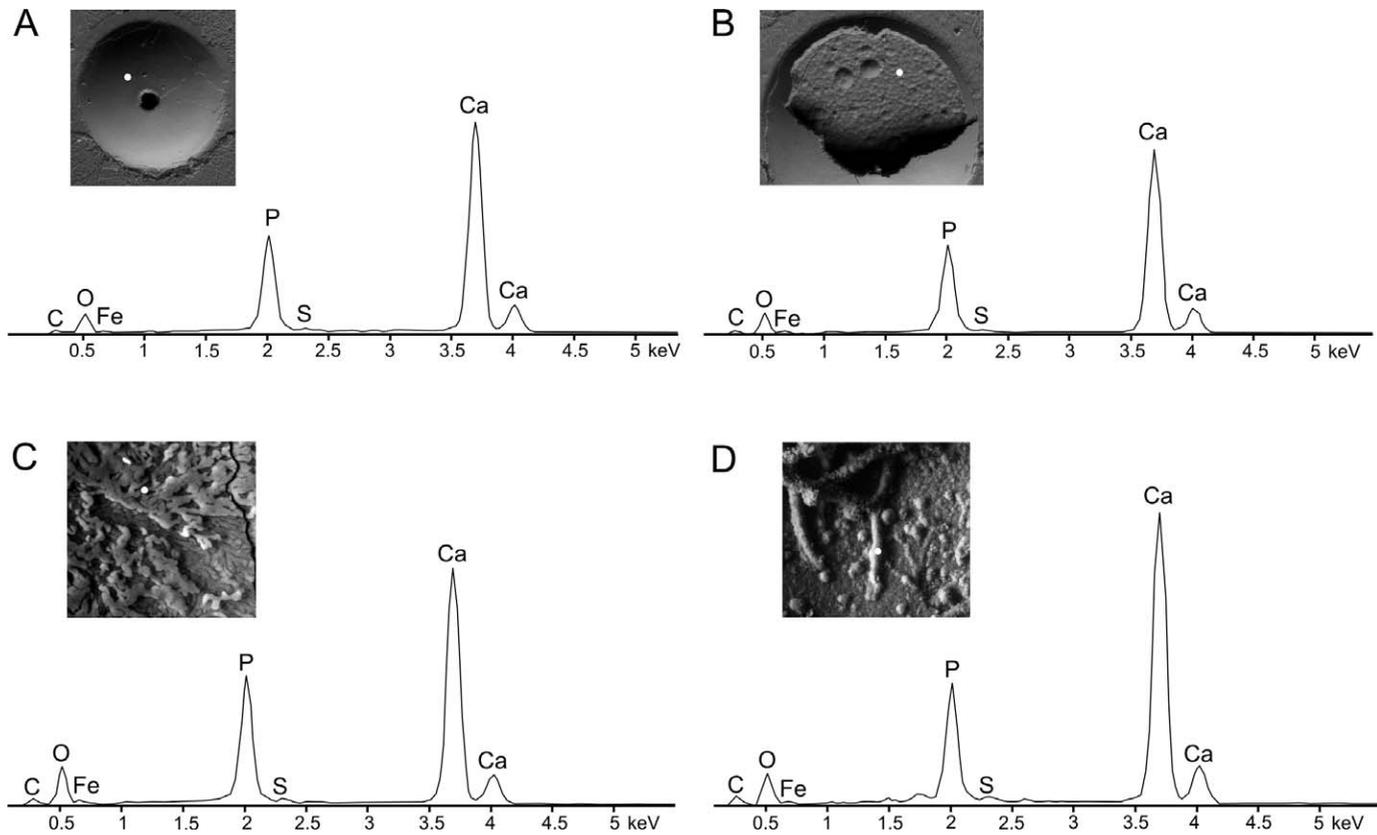


FIG. 5.—EDS spectra of egg capsules and associated structures. **A)** EDS of egg capsule hemisphere. **B)** EDS of apatite globules. **C)** EDS of dense, bifurcating filaments. **D)** EDS of straight filaments encrusted by micron-sized spherules from the interior of the capsules. The white points on the SEM photographs indicate the analyzed spots. All structures are distinctly phosphatized. A, B) MSU 120/1-2. C) MSU 120/1-1. D) MSU 120/2.

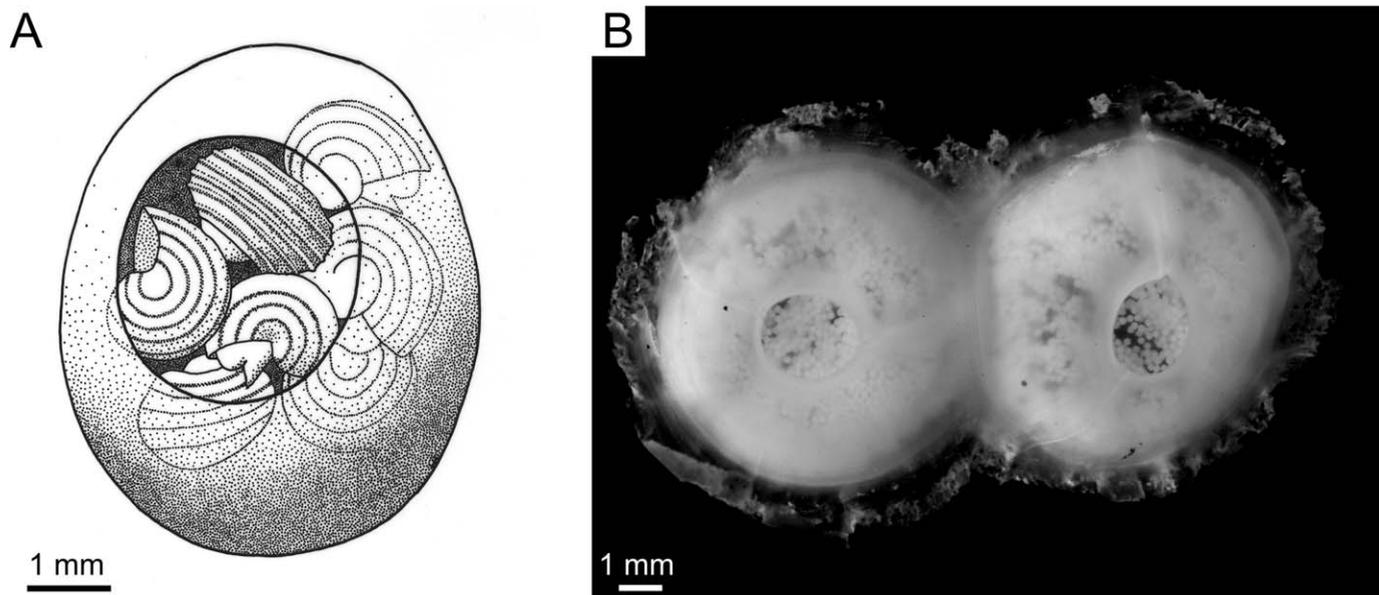


FIG. 6.—Recent examples of caenogastropod egg capsules. **A)** Schematic drawing of a rissoid (*Alvania abyssicola*) egg capsule with hatchlings inside (drawing based on Graham 1988). **B)** Egg capsules with embryos inside of the recent muricid neogastropod species *Coronium coronatum* from southwestern Atlantic (photo courtesy of Guido Pastorino).

A similar problem concerns the netlike and honeycomb-shaped egg capsules described by Kaiser and Voigt (1983, figs. 1B, C, 2D), who compared them with those produced by representatives of the recent neogastropod family Columbellidae (see Scheltema 1968).

However, although the affinities of the egg capsules described are uncertain, it is clear, based on many similarities shared with egg capsules produced by recent rissoids and muricids, that they were produced by representatives of Caenogastropoda. The egg capsules were laid down by

a small-sized species, as indicated by both the small diameter of the ammonite shell and the tiny size of the egg capsules preserved. In the present case it is also possible that the egg capsules were produced by two different gastropod species as evidenced by different capsule size ranges occurring in *C. nekrassovi* and *C. cf. jugensis*. More such exceptionally preserved fossils, ideally associated with gastropod shells, are needed to decipher their true affinity.

Preservation

The egg capsules investigated here were originally laid down by gastropods within empty body chambers of *Craspedites* ammonites. Similar egg capsule deposition was previously noted in Early Jurassic (Pliensbachian) gastropods by Kaiser and Voigt (1983). This should not be surprising as empty ammonite shells provided a suitable cryptic space, both for spawning as well as sheltering (e.g., Fraaije 2003; Vullo et al. 2009; Klompaker and Fraaije 2012; Wilson and Taylor 2012). Deposition of the egg capsules in such places also certainly promoted their survival as they were well protected from other animals and extrinsic physical factors.

As the egg capsules are well preserved without signs of degradation and destruction by biological and physical agents, it is likely that after their deposition they were relatively quickly buried in sediment filling the ammonite body chamber. Such circumstances provided additional positive factors for their preservation. First, they were sufficiently separated from potential scavengers. Second, they thrived in a specific diagenetic microenvironment allowing for rapid mineralization. The excellent preservation of the gastropod egg capsules studied was due to phosphatization processes. Although the egg capsules may have originally been tough, they were certainly soft and flexible, as shown by the partial collapse of the hemisphere in some specimens (Fig. 3C–E). As with the egg capsules of recent caenogastropods, most were probably composed of organic compounds such as proteins, carbohydrates, and mucopolysaccharides (e.g., Tamarin and Carriker 1967; Soliman 1987; Hawkins and Hutchinson 1988; Rawlings 1999), and also contained protein-gel fluid in which embryos developed (Hawkins and Hutchinson 1988; Rawlings 1999). Therefore, their phosphatization may have proceeded in a similar way as phosphatization of other eggs and animal soft tissues known from the literature (e.g., Briggs and Kear 1994; Sagemann et al. 1999; Martin et al. 2005).

It is currently well known that phosphatization is controlled by microbial activity during the decay of soft tissues, and that it proceeds in anaerobic conditions at lowered (~ 6.3) pH (e.g., Briggs and Kear 1994; Briggs and Wilby 1996; Wilby et al. 1996; Sagemann et al. 1999). The empty ammonite shell where the egg capsules were deposited was an ideal site for phosphatization to occur, because, as in the case of *C. nekrassovi*, it was filled by various organic debris (other mollusks, sponges, pellets, Fig. 2C). Such accumulation of organic matter could have provided the resources for microbial activity. Moreover, the phosphorus ions must have been abundant in the environment, as indicated by the phosphatic sandstone host deposits.

The microbial activity within the ammonite shells is evidenced by the presence of characteristic microstructures. On the inner part of the thin layer forming the base and covering of the exterior part of the capsules, phosphatized, dense aggregations of rodlike, filamentous, curled, and branching structures up to 2 μm in width occur (Figs. 4A, B, 5C). They are best visible on the imprints of the upper hemisphere preserved within the apatite mold of *C. nekrassovi* (Fig. 3E). The structures are similar to microbial consortia developing in microbial mats (e.g., Chafetz and Buczynski 1992) and to biofilms formed on decaying eggs and embryos (e.g., Martin et al. 2005; Raff et al. 2008; Cunningham et al. 2012). Within the egg capsules of *C. cf. jugensis*, some larger (up to 5 μm in width), bifurcating filaments covered by tiny globular apatite microcrystals, which also densely cover the interior of the capsules, occur as well (Fig. 4C). Without encrustation by these globular apatites, the filaments would certainly be thinner. Similar filaments, tentatively

interpreted as invading bacterial microbes covered by micron-sized apatite spherules, were previously noted in the Ediacaran Doushantuo embryos (e.g., Xiao and Knoll 1999). Similar micron-sized calcite and apatite spherules have also been noted in both recent microbial mats (Chafetz and Buczynski 1992) and fossil material like coprolites (e.g., Lamboy et al. 1994; Cosmidis et al. 2013; Zatoń and Rakociński 2014), or fossilized soft tissues (e.g., Briggs and Kear 1994; Briggs et al. 2005). Thus, the microcrystals reported here may be the products of bacterially driven, extracellular phosphatization (e.g., Lamboy et al. 1994). Additionally, the egg capsule interiors are also filled with characteristic cauliflowerlike, apatite hemispheres, up to ~ 70 μm , covering both the base and inner side of the capsules preserved on *C. nekrassovi* and *C. cf. jugensis* (Figs. 3E, F, 4C, D). In cross section they have spherulitic fabric and thus are similar to bacterially mediated crystals formed in decaying soft tissues (e.g., Briggs and Kear 1994). According to the latter authors, such crystals are characteristic of mineralization processes taking place in anaerobic, closed diagenetic systems. It is possible that in the present case they have formed by bacterially mediated mineralization of the protein-gel matrix. Thus, the phosphatization of the excellently preserved egg capsules studied here must have been a fast process (weeks?) controlled by microbial activity in a closed microenvironment. As there is no evidence of replication of the egg capsules by microbes (see Raff et al. 2008), their phosphatization was a direct process. However, no signs of preserved embryos were noted within the egg capsules investigated. It is highly probable that before phosphatization the egg capsules had already hatched.

CONCLUSIONS

Exceptionally preserved gastropod egg capsules occur within the body chambers of two Late Jurassic ammonites from Central Russia and are described in detail for the first time. Due to phosphatization, the egg capsules are exceptionally well preserved, which facilitates their comparison to both recent and known fossil gastropod egg capsules. These egg capsules clearly differ from those produced by both recent and fossil neritimorph gastropods by a number of features, such as the presence of a circular opening at the top of the capsule and the presence of a common capsule wall for both its base and upper hemisphere. The comparisons with the egg capsules of modern caenogastropods show that they are most similar to those produced by some rissoids and muricid neogastropods. Although the true affinity of the Jurassic egg capsules is uncertain, it is evident that they were produced by caenogastropods. This is the first certain evidence of fossil caenogastropod egg capsules. The presence of distinct microbial consortia in the form of various rodlike and filamentous structures, as well as micron-sized apatite globules, preserved within the egg capsules indicates that their phosphatization was mediated by bacterial activity under closed, anaerobic conditions.

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