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GASTROPOD EGG CAPSULES PRESERVED ON BIVALVE SHELLS FROM THE LOWER JURASSIC (HETTANGIAN) OF POLAND

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ABSTRACT

Fossil gastropod egg capsules have rarely been reported from the fossil record. This paper describes gastropod egg capsules preserved exclusively on cardiniid bivalves from Lower Jurassic (Hettangian) deltaic deposits of the Holy Cross Mountains area, central Poland. In most instances, only the bases of the egg capsules are preserved as dark outer rings with hollow cavities inside. Some specimens, however, are preserved as dark circular spots or even shallow depressions on the bivalve molds. The general occurrence, morphology, size and composition of the egg capsules as revealed by Energy Dispersive Spectroscopy (EDS) analyses and elemental mapping point to neritimorphs as the most probable producers. The egg capsules are composed primarily of organic matter with some calcium. Recent neritid gastropods possess aragonitic spherules within the egg capsule walls composed of conchiolin or chitin, which strengthen them and increase their chance of fossilization compared to egg capsules of other gastropods. Recent neritids lay their egg capsules on mollusk shells as well. The occurrence of Early Jurassic egg capsules only on redeposited cardiniid bivalve shells may suggest that the shells were the best medium for egg-capsule deposition. The occurrence of egg capsule bases together with dark circular spots, interpreted as compressed unhatched capsules, suggests that these egg capsules either hatched or were deposited at different times in the same place. The Early Jurassic egg capsules were preserved due to the strengthening role of the carbonate phase within the wall and rapid burial coupled with limited bioturbation in deltaic settings. The prodelta-delta front depositional environment, with high rates of sedimentation by rivers and sediment redistribution by wave and current action, was favorable for preserving these fossils.

INTRODUCTION

In this paper we describe egg capsules preserved on several bivalve shells from the Lower Jurassic (Hettangian) deltaic to nearshore deposits of Poland. The occurrence, morphology, and composition of these egg capsules point to gastropods as the most probable producers. These egg capsules are the earliest reported for gastropods. Data presented here provide new information about the fossil occurrence, morphology, composition, and preservation of such labile biological structures as gastropod egg capsules.

Invertebrate eggs are not common in the fossil record due to their tiny size and composition. In some unusual taphonomic circumstances, however, invertebrate eggs may be exceptionally preserved and numerous in deposits of different ages. Some selected examples of invertebrate fossil eggs, preserved as isolated bodies and *in situ* associated with their putative producers are shown in Table 1. In general, the striking feature of the fossil record of invertebrate eggs is that they mostly belong to arthropods; those of molluscan affinity are rare. The eggs of gastropods have an especially poor paleontological record (see Table 1). Apart from Paleogene and Neogene eggs of land snails (e.g., Cox, 1960; Tompa, 1976; Pierce, 1993), which have calcareous capsules (eggshells) and thus a better fossilization potential, the only known aquatic gastropod egg capsules were reported from the Lower Jurassic (Pliensbachian) marine deposits of Germany, preserved on fragmentary bivalve shells and ammonite body chambers (Kaiser and Voigt, 1977, 1983). Riegraf and Schubert (1991) and Schubert et al. (2008) reported pyritized hemispheric structures preserved on fossil wood from the Pliensbachian of Germany (Bielefeld), which were also interpreted as possible eggs spawned by gastropods. Possible gastropod egg capsules preserved on bivalve shells are also known from the Miocene of the Czech Republic (Mikuláš and Dvořák, 2001).

GEOLOGICAL SETTING: SEDIMENTARY AND PALEOENVIRONMENTAL BACKGROUND

The egg capsule material was collected in two Lower Jurassic (Lower to Middle Hettangian) sites at Gromadzice (upper outcrop) and Podole in the Holy Cross Mountains (HCM), central Poland. These deposits belong to the Skłoby Formation and formed in the eastern part of the Early Jurassic HCM basin in the southeastern part of the Polish Basin, constituting the eastern arm of the Early Jurassic European epicontinental basin (Pieńkowski, 2004) (Fig. 1). The Skłoby Formation ranges from 40 m thick in Gromadzice to 23 m thick in Podole. The Skłoby Formation is underlain by the siliciclastics of the Lower Hettangian Zagaje Formation and is overlain by the Upper Hettangian Przysucha Ore-bearing Formation. Overlying the Przysucha Formation are Sinemurian to Toarcian clastic deposits (Fig. 2A; for details see Pieńkowski, 2004). Deltaic successions exposed in Gromadzice and Podole (see Figs. 2B–C) are nearly contemporaneous, although the Podole outcrop is slightly younger, according to the detailed sequence stratigraphic correlation (Pieńkowski 2004). Both outcrops were located in a marginal part of the basin (Fig. 1), where fluvial input dominated depositional processes and the wave activity was diminished. This is most prominent in the Podole outcrop where an interdistributary bay was located on the delta plain (Pieńkowski 2004). Deltaic successions produced the majority of the Skłoby Formation in this part of the basin (from ~60% in Gromadzice to 90% in Podole); reoccupation-abandonment autocyclic processes produced the deltaic cycles. In Hettangian times, the tidal activity was negligible in the HCM basin. Wave action was relatively more prominent in the upper Gromadzice outcrop, where both fluvial sediment input and wave-energy flux controlled the lithofacies and depositional subsystems (cf. Coleman, 1981; Postma, 1995).

Environmental succession at Gromadzice (Fig. 2B) was responsible for a composite vertical column of stacked, aggradational or progradational cycles instead of simple coarsening-upward cycles. This type of deltaic sequence is rather poorly known from previous work, particularly in vertical sequences from the geological record (Horne et al., 1978; Emery and Myers, 1996; Pieńkowski, 2004). The Podole outcrop (Fig. 2C), on the other hand, shows a typical autocyclic

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TABLE 1—Examples of fossil invertebrate eggs, egg capsules, and embryos; * = eggs reported *in situ* associated with their putative producers.

Age	Type of structures	Putative producers	Preservation	Locality	References
Ediacaran	eggs, embryos	generally metazoans	phosphatized	China	e.g., Xiao et al. (1998), Xiao and Knoll (1999, 2000), Dornbos et al. (2005)
Cambrian	eggs, embryos	probably stem-group arthropods and priapulid-like organisms	phosphatized	China, Siberia, Australia	e.g., Bengtson and Yue (1997), Steiner et al. (2004), Donoghue et al. (2006)
	eggs	generally metazoans	silicified	China	Lin et al. (2006)
	eggs*	bradoriid arthropods	probably organic	China	Shu et al. (1999)
Ordovician	eggs, embryos	probably priapulid-like organisms	phosphatized	North America	Donoghue et al. (2006)
Silurian	eggs*	ostracodes	calcitized	England	Siveter et al. (2007)
Carboniferous	eggs*	tealliocaridid malacostracans	phosphatized	Scotland	Briggs and Clarkson (1985)
	eggs*	branchiopod crustaceans	silicified (at least the outer layers)	France	Vannier et al. (2003)
	eggs*	syncarid crustaceans	phosphatized	France	Perrier et al. (2006)
Triassic	eggs	insects	organic and impressions	Austria	Pott et al. (2008)
	eggs*	branchiopod crustaceans	no data	China	Shen and Huang (2008)
Jurassic	egg capsules*	ammonoids	phosphatized (at least some)	England	Etches et al. (2009)
	eggs	insects	impressions	Germany	van Konijnenburg-van Cittert and Schmeißner (1999)
	eggs*	branchiopod crustaceans	casts and molds, ?organic	Mongolia	Shen and Huang (2008)
	egg cases	hirudinean annelid	organic	Australia	Jansson et al. (2008)
	eggs*	mantophasmatodean insects	no data	Mongolia	Huang et al. (2008)
	egg capsules	gastropods	?organic, casts and molds	Germany	Kaiser and Voigt (1977, 1983)
	egg capsules	putative gastropods	pyritized	Germany	Riegraf and Schubert (1991), Schubert et al. (2008)
Cretaceous	eggs	probably ostracodes	phosphatized	Brazil	Smith (1999)
Neogene	egg capsules	putative gastropods	probably organic	Czech Republic	Mikuláš and Dvořák (2001)

sedimentation by a fluvial-dominated (bird-foot delta) depositional system (Pieńkowski, 1985; 2004). The wave processes in the basin were not strong enough to completely remove the mud fraction in the sandstones; the lack of hummocky cross stratification in the Podole outcrop is noteworthy. The depth of the receiving basin (interdistributary bay) in the case of Podole delta system was ~5–6 m, based on the rule that the regular progradational sequence of sediments approximates the local water depth—assuming a low rate of reworking and compaction (Pieńkowski, 2004). Plant fragments are common, particularly throughout the Podole succession. Plant roots (preserved as rhizoliths) indicate that plants colonized the topsets of deltaic cycles and formed bounding Histosol paleosols (Arndorff, 1993) (Figs. 2B–C). Bivalve resting burrows (*Lockeia* isp.) are more frequent in the Gromadzice outcrop in the wave-dominated parts of the profile, and a single bivalve burrow, *Lockeia czarnockii* (Karaszewski, 1975), was reported from the delta-front deposits of Podole (Pieńkowski, 1985; Niedźwiedzki and Pieńkowski, 2004). Occurrences of dinosaur footprints in both outcrops (see Gierliński et al., 2001; Niedźwiedzki and Pieńkowski, 2004; Gierliński and Niedźwiedzki, 2005) are found in the delta plain–distributary (inner delta) zone (Figs. 1–2B–C).

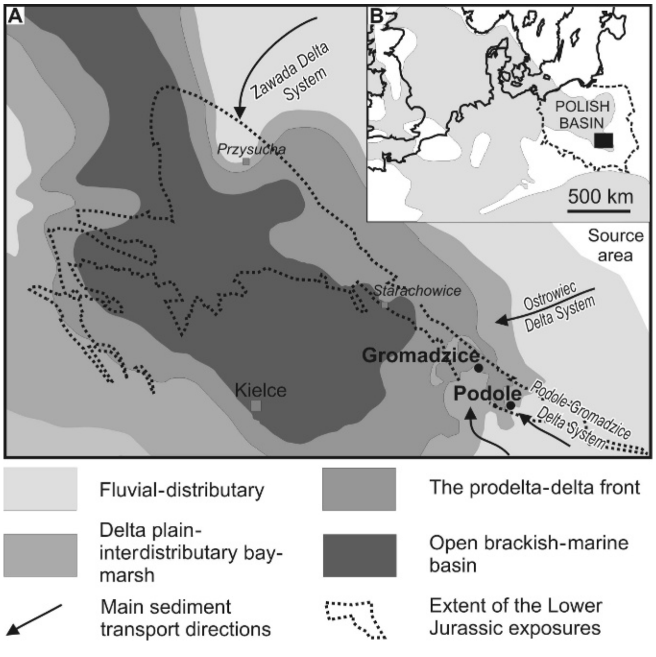

FIGURE 1—Paleogeography and location of study area. A) Outcrops at Gromadzice and Podole superimposed on the general paleogeography of the Lower Jurassic deposits in the Holy Cross Mountains Basin. B) Paleogeographic map of the Early Jurassic Basin in Europe and Poland with the Holy Cross Mountains Basin (after Pieńkowski, 2004).

Bivalve associations in both outcrops show a characteristic mixed character—both Cardiniidae and Unionoidea are present—indicating oligohaline faunas (Hudson et al., 1995). All the bivalve shells described herein were subject to postmortem redeposition and subsequently accumulated along the bedding planes. Rare occurrences of articulated shells (i.e., butterfly preservation) imply redeposition over a short distance and quick burial.

MATERIAL AND METHODS

The material for the present study was collected from two mudstone–sandstone units in the upper Gromadzice outcrop and one mudstone layer at the Podole outcrop (Figs. 2 B–C). All the samples come from the prodelta–delta front and nearshore heteroliths. In total, 16 bivalves with attached putative egg capsules of 137 bivalve specimens of the family Cardiniidae were collected. Apart from them, five specimens of *Taeniodon* and three specimens of *Modiolus* were also found; however, they lacked putative egg capsules. The material was gently cleaned, and the best specimens were photographed using a digital camera.

The following characteristics were noted: bivalve shell sizes, arrangement and state of preservation of the egg capsules, total number of the egg

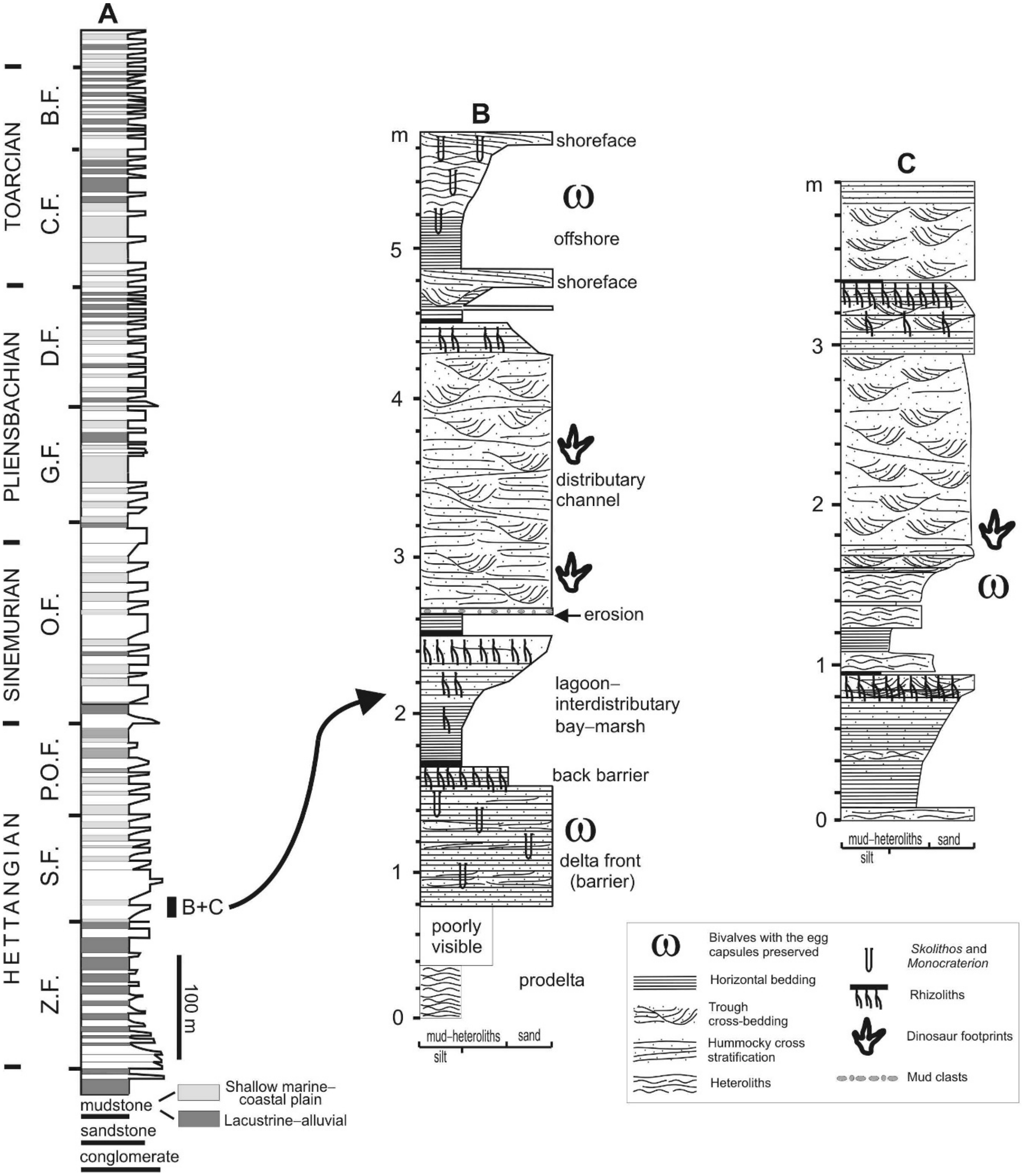

FIGURE 2—Lithologic sections of the Lower–Middle Hettangian deltaic deposits in the eastern part of the Holy Cross Mountains Basin. A) Schematic lithostratigraphic section of the Lower Jurassic of the Holy Cross Mountains, showing position of the Skłoby Formation and study sections. B) Upper Gromadzice outcrop. C) Podole outcrop. Lithoformations: Z.F.= Zagaje Formation, S.F.= Skłoby Formation, P.O.F.= Przysucha Ore-bearing Formation, O.F.= Ostrowiec Formation, G.F.= Gielniów Formation, D.F.=Drzewica Formation, C.F.=Ciechocinek Formation, B.F.=Borucice Formation. Egg capsule–bearing bivalve horizons are marked within sedimentological background (for all details, see Pieńkowski, 2004).

capsules, egg capsule sizes, and the egg capsule outer rim width (Table 2). Eleven bivalve specimens, covering both localities and both horizons (in the case of Gromadzice outcrop), with variously yet well-preserved egg capsules, were selected for detailed measurements. Uncoated specimens were investigated using a Philips XL30 Environmental Scanning Electron Microscope (ESEM) in back-scattered electron mode. The measurements of the egg capsules were conducted directly, using the ESEM internal measuring device, as well as on several microphotographs taken on the ESEM. Additionally, the preserved egg capsules and surrounding sediment were analyzed using Energy Dispersive Spectroscopy (EDS) performed on a Philips XL30 ESEM coupled with an EDS detector for elemental mapping in high vacuum conditions.

TABLE 2—Bivalve, locality, and egg capsule data; LH = lower horizon, UH = upper horizon, r = size range, m = mean value, sd = standard deviation, n = number of measurements.

Specimen # Host bivalve *Cardinia* sp.	Locality	Shell length (mm)	Encrusted valve	Total number of egg capsules	Egg capsule diameter (μm)			Outer rim width (μm)		
					r	m	sd	r	m	sd
MWG 009696	Gromadzice (LH)	~36	left	>100	400–570 (n = 15)	499	56.2	110–170 (n = 10)	136	17.1
MWG 009697	Gromadzice (LH)	~36	right	>100	380–550 (n = 12)	459	44.8	80–150 (n = 10)	113	5.59
MWG 009706	Gromadzice (UH)	67	left	~50 visible	900–1200 (n = 15)	1053	112.5	–	–	–
MWG 009698	Podole	35	left	~33 visible	640–810 (n = 10)	719	51.9	–	–	–
MWG 009699	Podole	33.5	right	~104 visible	610–880 (n = 15)	765	60.9	83–166 (n = 13)	108	28.7
MWG 009700	Podole	40	right	~42 visible	524–850 (n = 11)	626	89.8	112–121 (n = 2)	116.5	6.4
MWG 009701	Podole	31	right	only 2 visible	736–710 (n = 2)	723	18.4	130	130	0
MWG 009702	Podole	28	left	~15 visible	660–1000 (n = 7)	738	120.9	80–160 (n = 6)	117	26.6
MWG 009703	Podole	37	left	>126	415–550 (n = 15)	472	37.6	55–125 (n = 12)	96	16.9
MWG 009704	Podole	18	right	23 visible	870–1129 (n = 12)	1024	64.6	181–214 (n = 8)	199	16.1
MWG 009705	Podole	29	right	~55 visible	735–1092 (n = 16)	988	81.3	102–235 (n = 9)	160	42.4

The material collected is housed at the Geological Museum of the Faculty of Geology, University of Warsaw (under the prefix MWG) and the Polish Geological Institute, Warsaw (prefix MUZ PIG).

THE EARLY JURASSIC EGG CAPSULES AND THEIR MEDIA

Characteristics of the Substrate

All egg capsules collected in the Hettangian deposits were found exclusively on bivalve shells (Fig. 3). At both study sites, a similar faunal assemblage of four or five bivalve species was found. This assemblage is dominated by representatives of the Family Cardiniidae, but a few specimens of *Modiolus* and *Taeniodon*, as well as unionoid bivalves, were also identified (Pieńkowski, 2004). All the egg capsules, however, are preserved only on shell surfaces of *Cardinia*.

The Family Cardiniidae is well represented in the Skłoby Formation, but the original shells, being for the most part replaced by sandstone or mudstone, rarely show good generic characters. As a rule, the exterior sculpture of growth lines and riblike structures is rather well developed. Sometimes, however, the shell material is completely dissolved and, thus, both external and internal molds are left.

Using Troedsson's (1951) description and revision of the Lower Jurassic fauna from southern Sweden, we identified three *Cardinia* species in the Skłoby Formation that served as media for egg capsule deposition (*Cardinia follini* Lundgren, 1878; *C. inglensis* Troedsson, 1951; *C.* cf. *kullensis* Troedsson, 1951). *Cardinia* species can likely be restricted to two species, but the present available material does not allow us to make such intepretations. The shell length of the egg capsule-bearing bivalves ranges from 18 to 67 mm.

Preservation, Composition, Size, and Arrangement of the Egg Capsules

The egg capsules under discussion are preserved mainly as carbonaceous films (Figs. 3–4), although they are preserved as concave depressions on two bivalve valves as well (Fig. 3F). The preserved egg capsules are circular to semicircular in outline and consist of an outer black rim surrounding the hollow cavity filled with host sediment (see Fig. 4). Some, however, are preserved as entirely black films without the hollow cavity (Fig. 4A). Those preserved as concave depressions do not possess any remnants of the carbonaceous film. In many, the outer rims are only partially preserved and appear as a crescent shape (Figs. 4A, F); they may be lighter in color than the neighboring egg remnants.

Elemental analyses of the egg capsules from the Podole section reveal that the carbonaceous films are significantly enriched in carbon (C) and contain some amount of calcium (Ca) (Fig. 5). These two elements, on the other hand, are lacking or occur in very small amounts both within the sediment-filled cavities and surrounding sediment. This sediment is mainly composed of aluminosilicates of the illite-smectite group (Fig. 5). The total organic carbon (TOC) of the host mudstone is very low: 0.7%. Elemental mapping (Fig. 6) also revealed that C is the dominant element, albeit irregularly distributed, mainly in the egg capsules. Calcium, as well as magnesium (Mg), on the other hand, is scattered in very low amounts in the egg capsule films and host sediment. The concentration of Ca in the host mudstone, however, is lower than in the egg capsules (Figs. 5–6). If the amount of C and other elements in the spectra of the egg capsules are compared with those of the calcite standard (Fig. 5), it is evident that the egg capsule remains are predominantly composed of organic carbon and do not constitute a pure carbonate phase.

The egg capsules range from 380 to 1200 μm in diameter (mean = 459–1053 μm), and the egg capsules on particular bivalve specimens may be of different diameters (Table 2). The outer rim width (see Table 2), on the other hand, ranges from 55 to 235 μm (mean = 96–199 μm). In a single capsule, however, the rim width may differ.

The egg capsules are attached mainly on the posterior part of the bivalve valves, in more or less densely packed aggregations (Fig. 3). The capsules may contact each other or may be isolated (Fig. 4). Some of them, however, may occur in more central positions on the valve, but still closer to its posterior part (Figs. 4F, H). The number of putative egg capsules per valve ranges from as few as 2 to more than 100. As some bivalve specimens are incomplete, however, the precise number of egg capsules attached to them is difficult to ascertain. The striking feature is that the egg capsules do not occur beyond the boundary marked by the shell outline, so they have certainly been laid only on the bivalve shells and not on the surrounding sediment.

DISCUSSION

The organic structures reported in the present paper are interpreted as gastropod egg capsules, although they could belong to different organisms, such as algae or foraminifers. We do not know any examples, however, of algae that leave traces in the form of rims with hollow cavities inside, crescentlike structures, or even whole black spots, all of which are often found in close proximity on the same bivalve specimens. A foraminiferan origin is also rejected. The only described foraminiferan of similar size and morphology to the structures described here (especially black spots) is represented by the genus *Hemisphaerammina* (see Adegoke et al., 1969). This taxon, however, is agglutinated and thrives in a deeper marine environment. Moreover, the black spots reported here do not show any signs of being agglutinated (cf. Adegoke et al., 1969).

Several lines of evidence presented below point to the gastropod affinity of the structures described here. The first is their appearance and arrangement. The majority of recent gastropods lay their eggs in spawn masses that range from shapeless and gelatinous to those with regular forms, arranged in soft membranous capsules incubated in a

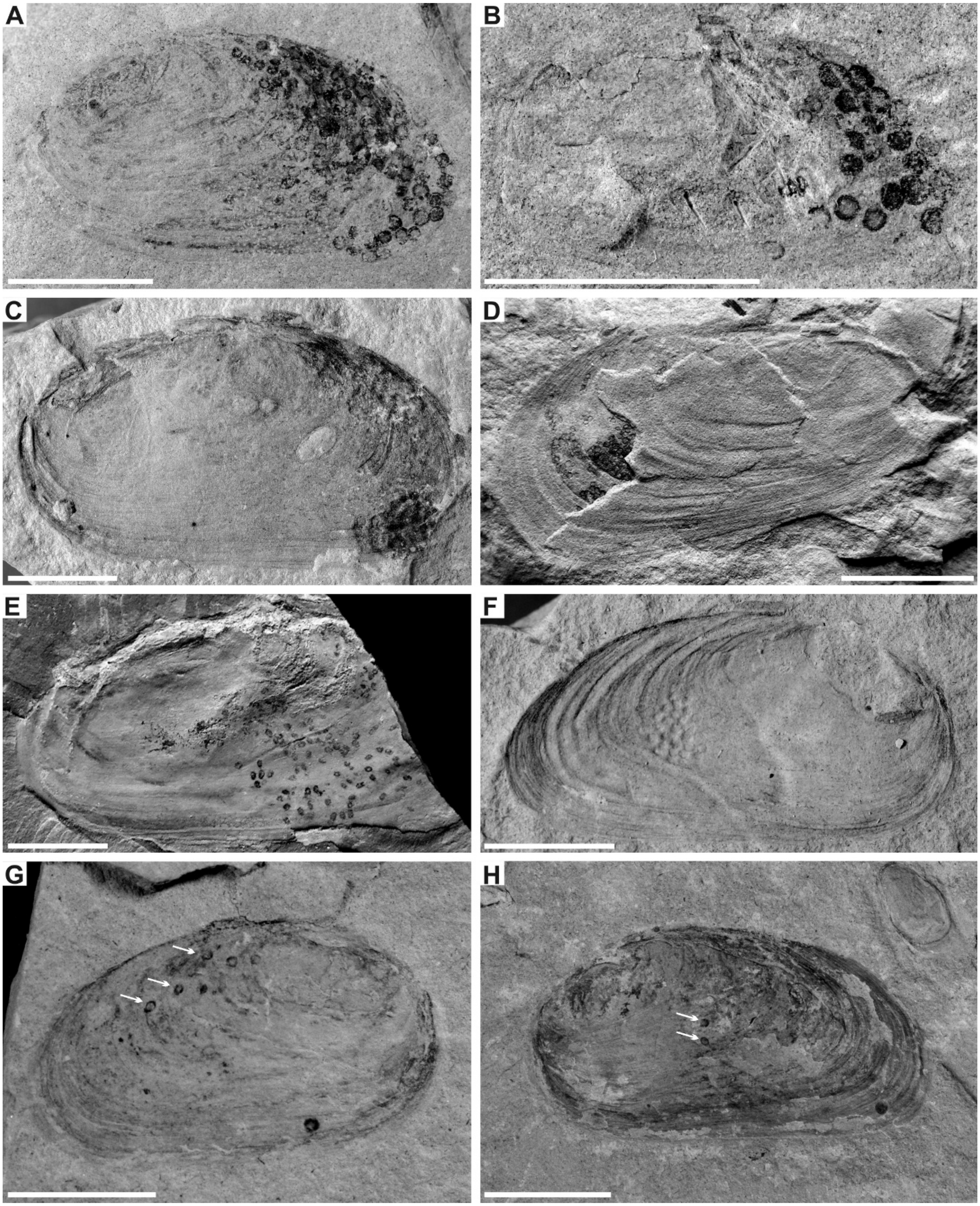

FIGURE 3—Early Jurassic (Hettangian) cardiniid bivalves with egg capsules. A–D, F–H. Cardiniids from Podole; arrows in G and H indicate the position of the egg capsules. E) Cardiniid bivalve from Gromadzice. Scale bars equal 1 cm.

pallial cavity of the mother; in conchiolin-flattened capsules; or in solid-walled capsules attached to the media as single individuals or aggregated in groups (e.g., Soliman, 1987; Rawlincs, 1999; Przeslawski, 2004). Egg capsules with resistant walls are most likely to be preserved in the fossil record, whereas the gelatinous masses are unlikely to be preserved and are not represented in the fossil record.

Media for egg deposition may be varied and includes mollusk shells (e.g., Adegoke et al., 1969; Soliman, 1987; Beeby and Richmond, 1998).

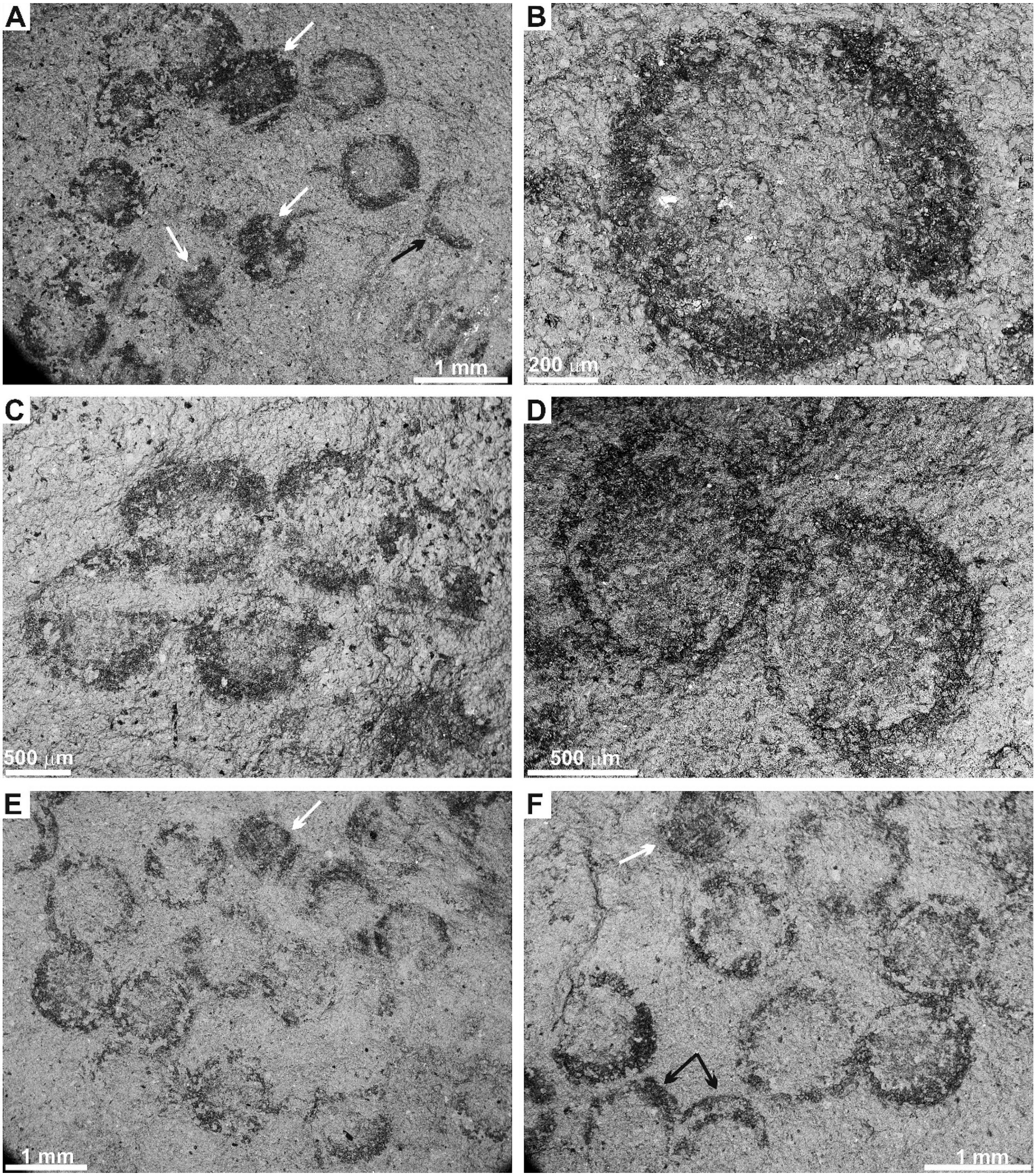

FIGURE 4—ESEM photomicrographs of the egg capsules. A–C) Egg capsules preserved on the cardiniid bivalve shown in Fig. 3B. A) More or less aggregated cluster; white arrows point to possible unhatched egg capsules; black arrow points to partially preserved, crescentic basal ring. B) Single base of egg capsule showing distinct ringlike structure with hollow cavity inside. C) Cluster of variously preserved egg capsules, preserved mainly as their bases. D–F) Egg capsules preserved on the cardiniid bivalve shown in Fig. 3A. D) Two egg capsule bases lying close to each other, showing rings of different width. E) Large cluster of variously preserved egg capsules, the majority of which are preserved as basal parts; white arrow points to possible unhatched egg capsule. F) Cluster of egg capsule bases; white arrow points to possible unhatched capsule; black arrows point to crescentic, partially preserved bases.

Indeed, all the egg capsules in this study were preserved on cardiniid bivalve shells, where they form distinct, more or less aggregated clusters consisting of similar-sized, single specimens. Although less numerous, they are similar in the appearance to the circular structures described and interpreted as gastropod egg capsules by Kaiser and Voigt (1977, 1983) from the fragmentary shell of the bivalve *Pseudopecten* and ammonite body chambers (*Pleuroceras* and lytoceratids) from Lower Jurassic deposits (Pliensbachian) of Germany. Apart from the circular

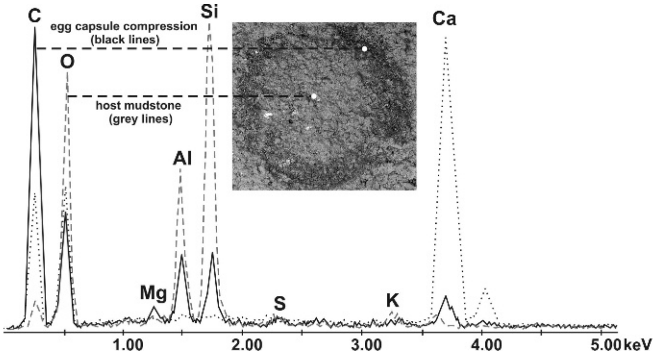

FIGURE 5—EDS spectra of the egg capsule ring (black lines) and host mudstone within the hollow cavity (grey lines); dotted lines represent the calcite standard for comparison. Note the significantly higher amount of C and Ca in the egg capsule ring as compared to the host sediment. The egg capsule's organic composition is clearly marked (C and Ca concentration) as compared to the calcite standard. The original EDS spectra were redrawn for better visibility.

egg capsules, Kaiser and Voigt (1977, 1983) also described net- and honeycomb-like aggregations, certainly produced by different gastropod species. The latter features do not occur on the bivalves from Poland. It must be noted that similar structures as described here have previously been illustrated, but not discussed, by Lundgren (1878) from Early Jurassic bivalves similar in age and composition from southern Sweden (see also Troedsson, 1951). The circular to discoid casts preserved on the external molds of bivalve shells (*Pseudoanodonta* sp.) were also reported from the Miocene limnic to swamp facies of the Czech Republic by Mikuláš and Dvořák (2001). On the same bivalves, Mikuláš and Dvořák (2001) also reported different branching, string-like structures. Both the circular bodies and strings were ambiguously interpreted by them as gastropod or fish eggs. The circular structures (biogenic structures Type 2 of Mikuláš and Dvořák, 2001; see especially those illustrated on their pl. II, fig. 3), however, are more reminiscent of the structures presented by Kaiser and Voigt (1977, 1983) and those reported in this study.

Tough-walled egg capsules are produced today by various gastropods (Soliman, 1987, and references therein) represented by neritimorphs and caenogastropods (e.g., Bouchet and Rocroi, 2005; Frýda, 2005). Kaiser and Voigt (1983) claimed that their egg capsules were laid down by neritaceans (i.e., neritimorphs, in the current classification; Bouchet and Rocroi, 2005), because they resembled such structures produced by recent neritids. Egg capsules of recent neritids are tough and sturdy, flattened, oval, sometimes spherical in shape, made of conchiolin as well as chitin, and composed of convex upper parts (caps or lids) and cup-shaped bases (Adegoke et al., 1969; Bandel, 1982; Kaiser and Voigt, 1983; Soliman,

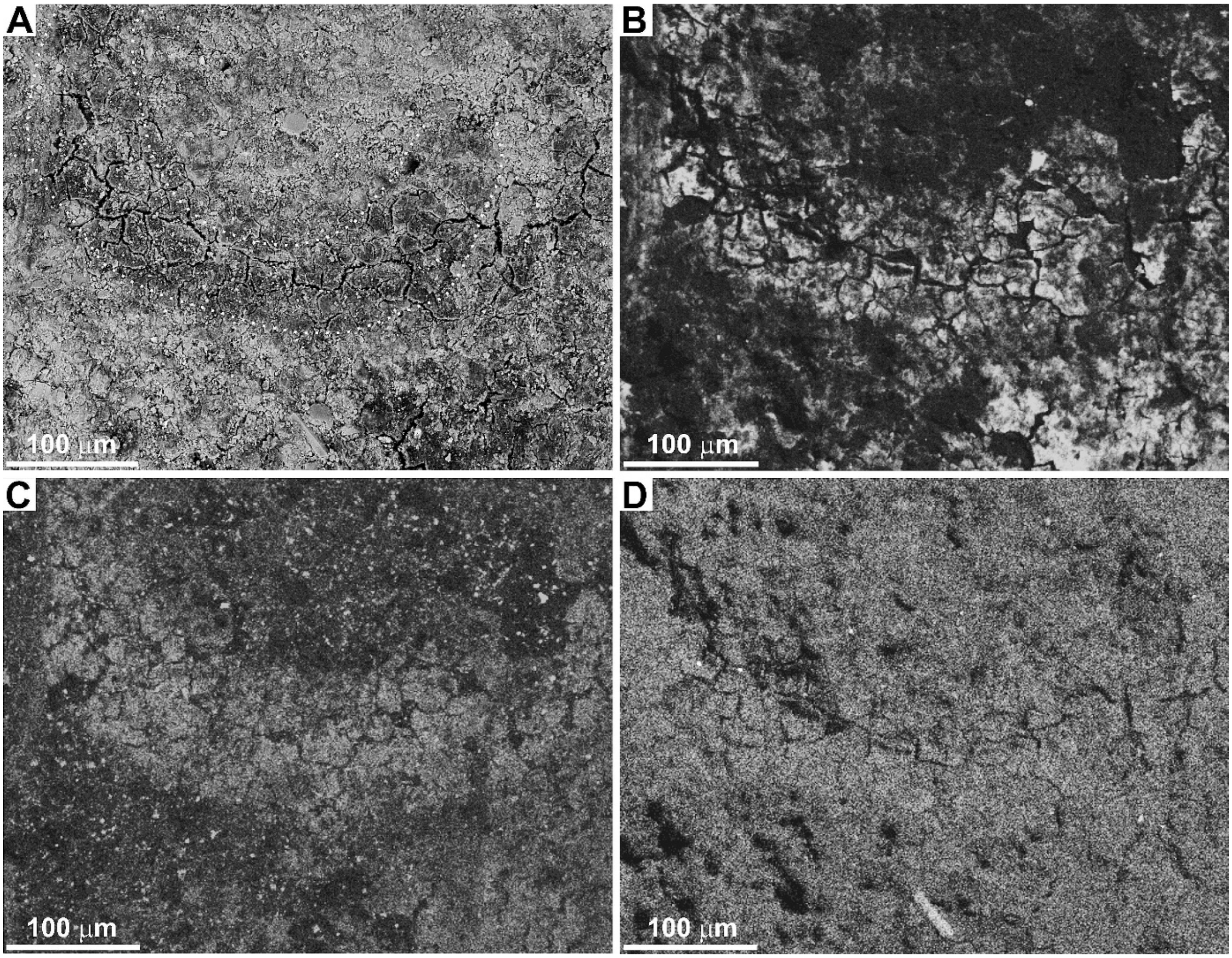

FIGURE 6—Results of elemental mapping of micro-area of the egg capsule ring and surrounding sediment. A) Back-scattered electron (BSE) image with dotted lines outlining egg capsule ring. B–D) Images showing distribution and abundance of C (B), Ca (C), and Mg (D), with, brighter tone indicating greater abundance of elements. The concentration of C in the egg capsule ring (B) produces the brightest tone; Ca concentration is expressed by brighter tone in the egg capsule ring than in the surrounding mudstone (C). Mg concentration is somewhat greater in the egg capsule than in the sediment, expressed by slightly brighter coloration (D).

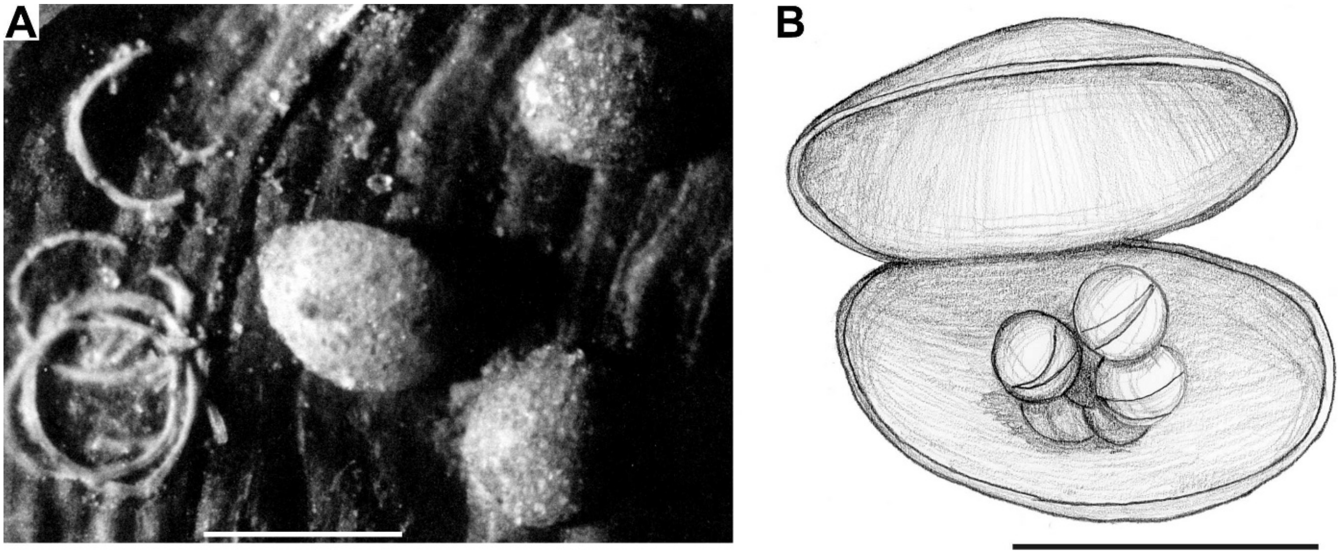

FIGURE 7—Egg capsules of a recent *Neritina* gastropods. A) Unhatched egg capsules covered by a lid (right) and the egg capsule bases preserved both as complete rings and crescentic fragments deposited on the mollusk shell (from Adegoke et al., 1969, with permission of the Micropaleontology Press). B) Restoration of the neritid egg capsule, consisting of the upper lid and lower base, with the juveniles inside (modified from Adegoke et al., 1969). Scale bars equal 0.5 mm.

1987; Warén and Bouchet, 2001). When the juveniles are hatched, the entire cap detaches and only the attached base remains (Kaiser and Voigt, 1983; Soliman, 1987) (see Fig. 7B). The thickened margin is characteristic of the capsule bases and is well illustrated by Adegoke et al. (1969) and based on recent *Neritina* egg capsules from Nigeria (see also Figs. 7A–B). Moreover, in the neritids, the walls of conchiolin egg capsules may contain aragonitic spherules that strengthen them and, thus, they may be more likely fossilized (Bandel, 1982; Klaus Bandel, personal communication in Kaiser and Voigt, 1983). Although the egg capsules reported by Kaiser and Voigt (1977, 1983) and those reported here may seem to be insufficiently preserved to be unequivocally assigned to a certain gastropod group, their appearance and composition supports a neritimorph affinity.

The interesting feature of the egg capsules described here, and those presented by Kaiser and Voigt (1977, 1983), is that they are mainly preserved as hollow cavities surrounded by circular dark rims, which may represent the thickened margin of the egg capsule bases. Indeed, the capsule bases of recent neritids have only thickened rims with hollow cavities composed primarily of dense chitin, which produce ringlike structures (Fig. 7A). Inside them, on the other hand, the media to which they are fixed is visible (see Adegoke et al., 1969, pl. 1; Fig. 7A). It must be noted that the width of the rings also varies in the same *Neritina* egg capsule. The different ring widths in the preserved Jurassic capsules investigated here, therefore, must have been their natural feature, even with the later compaction.

The thick and dark outer margins of the egg capsules investigated here are composed of significantly higher amount of organic C and Ca than the host mudstone (Figs. 5–6). In effect, the C and Ca must be an integral part of the egg capsules. Their elemental composition, therefore, reflects the presence of organic matter, possibly together with some amount of residual carbonate phase. It is evident that the morphology and composition resemble the egg capsules of recent neritids. Moreover, the diameters of majority of the egg capsules from the Jurassic of Poland (see Table 2) fall within the size-range of recent neritimorph egg capsules. For example, Adegoke et al. (1969) noted that recent *Neritina* egg capsules measure 500–1200 µm in diameter, and Warén and Bouchet (2001) reported 700–900 µm for Phenacolepadidae and 900–1200 µm for Neritidae egg capsules. The egg capsules from the Jurassic of Germany have a similar size-range, but some may be larger: 1000–3000 µm (see Kaiser and Voigt, 1977, 1983). The circular structures from the Miocene of Czech Republic are slightly smaller: 500–650 µm (see Mikuláš and Dvořák, 2001). The size of egg capsules, however, may be of little importance, as it may vary according to the salinity levels. For example, on the basis of observation of a single species *Neritina fluviatilis*, Bondesen (1941) found that the egg capsule size increases from brackish water (from 670 to slightly more than 900 µm) to freshwater (over 900 µm) environments. Indeed, some of the egg capsules reported here, especially those from the lower horizon of Gromadzice (specimens MWG 009696-7) and Podole (specimen MWG 009703), are smaller (380–570 µm in diameter, see Table 2). It is difficult to ascertain, however, whether they were deposited in different salinity conditions or by different gastropod species. The most plausible explanation is that they might have been deposited by different gastropod species, based on the co-occurrence of the Podole specimen (MWG 009703) with smaller egg capsules together with other bivalves hosting larger egg capsules in the same horizon.

Recent neritoids lay their eggs on hard media of many kinds, including stones, leaves, mollusk shells, and echinoderm skeletons (e.g., Bondesen, 1941; Adegoke et al., 1969; Fischer, 1980; Soliman, 1987; Kano et al., 2001). Fossil examples have been found attached to such mollusk shells as bivalves (Kaiser and Voigt, 1977; Mikuláš and Dvořák, 2001) and ammonites (Kaiser and Voigt, 1983), and, as noted previously, all egg capsules reported here were preserved exclusively on bivalve shells. As the sample of bivalves with preserved egg capsules is small in comparison to the overall number of bivalves found in the localities investigated, it is difficult to conclude there was a particular selectivity with respect to media. Apart from bivalves, organic structures of plant origin also occur in the levels studied. No egg capsules have been found attached to them, however. Moreover, a few other bivalve specimens such as *Taeniodon* and *Modiolus* do not possess any traces of the egg capsules. Cardiniids are considered to be active, shallow-burrowing suspension-feeders (Palmer, 1975)—a mode of life of that may have resembled the recent unionoids based on their similar shell morphology. Recent unionoids are semiburrowers with the posterior part of the shell standing above the medium (Bauer, 2000). The shells of cardiniid bivalves might, therefore, have been exposed on the bottom first before the egg capsules were laid down, which is consistent with the state of preservation (disarticulated valves, with only two specimens from Podole were found in the butterfly position). Exhumation and redeposition may have created a bottom covered with empty cardiniid shells that served as the most common and best substrate for the egg capsule deposition.

Most of the egg capsules were laid down on the surface of the cardiniid bivalve shells. In some cases, however, the egg capsules are presumably preserved within the closed bivalve shells (see Fig. 3D). This may suggest that some eggs were laid down by gastropods within empty bivalve shells that were still articulated, but before the valves were closed, most probably by sediment loading. Such slightly opened, empty shells must have provided suitable environments for gastropod egg deposition. The eggs were laid either in shaded or hidden (cryptic) places where they would be protected against potential predators. It is known that recent *Neritina* lay their egg capsules on the undersides of stones (Bondesen, 1941). Ammonite body chambers (see Kaiser and Voigt 1983) could have been similarly protected environments for eggs.

In addition to the egg capsule bases preserved in the form of rings with hollow cavities, there are also entirely organic egg capsules on the bivalves in the form of black circular spots (Figs. 4A–B). These may be interpreted as unhatched egg capsules still covered by a lid and preserved as flat compressions, due to later burial and compaction. This may indicate that not all the egg capsules hatched at the same time, or that some of them were laid down by gastropods at different times. Additionally, among the egg capsules discussed here, there are distinct concave depressions, which are devoid of any remnants of organic matter, preserved on the internal surface of one of the bivalve shells (see Fig. 3F). Similar depressions were reported by Fischer (1980) from limestones and carbonate sandstones just beneath recently deposited *Nerita* egg capsules. According to Fischer (1980), these structures were chemically etched by the egg capsules themselves and potentially caused by: (1) the dissolution of carbonate media by diffusion of CO_2, produced during respiration through the capsule wall; (2) the dissolution of the carbonate media by the egg capsule's mucus; or (3) the drawing out of Ca ions from the media for the shell formation of hatchlings. Some such gastropods as *Lymnaea* preferentially lay their eggs on shells when the concentration of Ca in the water is low, thus supplying the Ca from the shell for this purpose (Beeby and Richmond, 1998). In the case of the egg capsules investigated here, however, it is not clear whether the concave depressions resulted from etching or are simply molds of the deposited egg capsules on the opposite valve.

The preservation of the egg capsules certainly must also have been enhanced by rapid burial, isolating them enough from destructive processes (especially oxidation) occurring above the water-sediment interface, as well as by limited bioturbation that might have exhumed them or destroyed them directly. Although the egg capsules reported here are the evidence of a probable gastropod breeding in the Hettangian deltaic environment of the Podole and Gromadzice area, the gastropod themselves are nearly absent. One inner mold of a small gastropod (with shell height of ~75 mm) from the upper horizon of Gromadzice was recently found by one of the authors (GN); though the shell shape may indicate a neritimorph, the state of preservation is too poor to allow determination (Andrzej Kaim, personal information, 2009). Poorly preserved gastropods were also collected from the Hettangian deposits elsewhere in the northern slopes of the HCM by Karaszewski and Kopik (1970); however, their state of preservation prevents assignment to certain taxonomic groups.

The nearly complete lack of gastropods in the egg capsule– bearing horizons, despite their having similar shell mineralogy (aragonite) with co-occurring cardiniids, may be either because small gastropods possessed much thinner aragonitic shells and were prone to faster dissolution, or because cardiniid bivalves were probably much more numerous than gastropods in the area studied and thus bivalve shells had a greater chance of preservation.

CONCLUSIONS

Relatively abundant ringlike structures with hollow cavities and black organic films, preserved on Hettangian bivalve shells found within two sections in the area of the Holy Cross Mountains in Poland, are here interpreted as the remnants of gastropod egg capsules. Their appearance, size, and arrangement on the media, as well as their composition, suggest that they were probably produced by neritimorph gastropods. All the features observed in these fossils correspond well with recent neritid egg capsules and similar fossil structures interpreted as eggs. Their occurrence on cardiniid bivalve shells also supports their gastropod affinity as similar behavior is observed in gastropods today. EDS analyses and elemental mapping show that the amount of Ca within the egg capsules is higher than in the surrounding sediment and, thus, this element must have been an integral component of the capsules themselves. The presence of a carbonate phase within the egg capsule wall, together with rapid burial in fine-grained sediment and limited activity of bioturbators during the final burial, must have been responsible for the preservation of such labile biological structures. A prodelta-delta front environment, with significant delivery of sediment by adjacent rivers, and sediment redistribution by wave and current action was a favorable setting for preservation of these fossils.

Additionally, the gastropod egg capsules reported here indicate that the reproductive strategy of neritimorphs has not changed since at least the Hettangian. The preservation of such labile structures as gastropod egg capsules, albeit rarely reported from the fossil record, should be taken into consideration when exploring older, mainly Paleozoic, organic media in order to find similar objects. This type of information would provide important paleobiological information concerning the evolution of gastropod reproductive strategies and behavior.

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