

A possible terrestrial egg cluster in driftwood from the Lower Jurassic (Late Pliensbachian) of Buttenheim (Franconia, Germany)

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Abstract

Our paper shows several clusters of circular fossil egg capsules from the Franconian Amaltheenton Facies (Lower Jurassic, Upper Pliensbachian), mostly found in the clay pit south of Buttenheim. The egg capsules are scatteredly and irregularly arranged on various substrates like calcareous nodules, mollusk shells, or sunken driftwoods. Marine gastropods have been presumed as their producers spawning their eggs autochthonous. Only one specimen exhibits a regular honeycomb-like pattern of small pyritized eggs deposited seemingly within driftwood but originally lead in a small deadwood break. We interpret it as representing a possible allochthonous insect spawn drifted off from the about 70 km removed coastal region.

Keywords

Liassic, egg capsules, gastropods, insects

Introduction

In the fossil record, non-vertebrate eggs have been described in all ages (for review, see Zatoń et al. 2009; Boucot and Poinar 2010). For instance, authors interpreted Ediacaran fossils as “resting zygotes within egg cases” (Xiao et al. 1998, p. 557) or “animal-like eggs” (Willman et al. 2020, p. 1) and Cambrian fossils as “eggs containing identifiable embryos of metazoans” (Bengtson and Zhao 1997, p. 1645). For example, the phosphatized (Orsten type preservation) Cambrian egg like *Markuelia* has been interpreted as an embryo of stem-priapulid worms (Dong et al. 2010). In rare cases, fossils show eggs in combination with putative producers as shown for the eggs of the bradoriid arthropod *Kunmingella* from the Lower Cambrian (Shu et al. 1999). Some fossilized egg producers indicate parental brood care, for example, Silurian ostracods

(Siveter et al. 2007) or Carboniferous both spinicaudatans (Vannier et al. 2003) and syncarid crustaceans (Perrier et al. 2006). Late Carboniferous fossils also revealed the first gastropod egg capsules, attached to bivalve shells (Emrich et al. 2017), and the first insect egg clusters, oviposited on or in plants (Béthoux et al. 2004; Laaß and Hauschke 2019). Mesozoic ages added annelid egg cases (Late Triassic, Manum et al. 1991) and ammonite egg sacs (Late Jurassic, Etches et al. 2009) to the known fossil record. With the increasing occurrences of Mesozoic and particularly Cenozoic amber Lagerstätten, many ovipositions of insects became available (e.g., Xing et al. 2021), preserved often jointly with their producers (e.g., Keupp 2021d). However, “most of these cases could reflect false oviposition due to death stress” (Hörnig et al. 2019, p. 123).

Beside the below mentioned findings in the clay pit south of Buttenheim, fossil record of gastropod egg capsules is

“extremely poor due to their low fossilization potential” (Zatoń and Mironenko 2015b, p. 1). The known findings include imprints on bivalve shells, on gastropod shells or on ammonite body chambers from the Lower Jurassic (Kaiser and Voigt 1977; Kaiser and Voigt 1983), the Upper Jurassic (Zatoń and Mironenko 2015b) or the Cretaceous (Zatoń et al. 2013; Zatoń et al. 2017) as well as one three-dimensional record in mid-Cretaceous amber (Xing et al. 2021). To our knowledge, there are only two examples of pyritized gastropod eggs on driftwood (Riegraf and Schubert 1991; Schubert et al. 2008).

Analysis of fossil evidence for insect oviposition has shown that “almost all fossil structures on plants, which have been identified as oviposition, are of the endophytic mode” (Laaß and Hauschke 2019, p. 1). That is, there are scars as ovipositional records on plant fossils, very most of which are on leaves (e.g., Moisan et al. 2012; Gnaedinger et al. 2014; Laaß and Hauschke 2019). In contrast to the scars on leaves, to our knowledge, fossil record shows only one endophytic ovipositional scar on a fruit (Middle Jurassic, China; Meng et al. 2019) and very few scars on stems (e.g., Béthoux et al. 2004). Exophytic oviposition is a large minority on plant fossils, for instance, on a *Cordaites* leaf (Upper Carboniferous, Germany, Laaß and Hauschke 2019). Additionally, there are three ichnogenera of fossil insect egg clusters that are not attached to specific plant fossils and interpreted as eggs of aquatic insects, for instance, *Monilipartus* (Upper Buntsandstein, France; Gall and Grauvogel 1966).

In our paper, we summarize previous findings of autochthonous non-vertebrate eggs in the clay pit south of Buttenheim (Lower Jurassic, Germany), describe new egg findings, and discuss their relevance for the fossil record of non-vertebrate eggs.

The clay pit south of Buttenheim

Lower Jurassic strata occur in northern Bavaria along the mountainside of the Franconian Alb. The clay pit of the LIAPOR Company Altendorf south of Buttenheim (49°47'34"N, 11°02'30"E) lies about 8 km south-eastwards of Bamberg and crop out both, the Lower Jurassic Amaltheenton Formation (Upper Pliensbachian) and the Posidonia Shale (Lower and Middle Toarcian) (Fig. 1). The about 35 m thick section of the Amaltheenton Formation is characterized by homogenous dark clay intercalated with irregularly distributed calcareous concretions. The profile can be subdivided by four thin horizons that represent short phases of reworking by high water energy settings due to sea level low stands, resulting in the winnowing of smaller grain sizes and enrichment of the reworked concretions (Keupp and Schobert 2015; Keupp et al. 2016a, 2016b). The stratigraphic boundary between the top of the Margaritatus ammonite zone (Gibbosus subzone) and the basal Spinatum ammonite zone (Apyrenum subzone) is marked by the ‘pyrite-bed’ containing up to 600 mm large ammonites of *Amaltheus margaritatus* and the first *Amaltheus salebrosus* and *Pleuroceras solare*. It is further characterized by an enrichment of small calcareous nodules of 10–40 mm in diameter exhibiting bioerosion scratch marks on its surface. The second reworking horizon, the ‘Quellhorizont’ (spring horizon), marks the stratigraphic boundary between the Apyrenum subzone and the Hawskerense subzone, bearing the first *Pleuroceras spinatum*. The third reworking horizon, the so-called echinid-pectinid-bed (EPH), is characterized by pebbly coquina and by largely reworked calcareous nodules

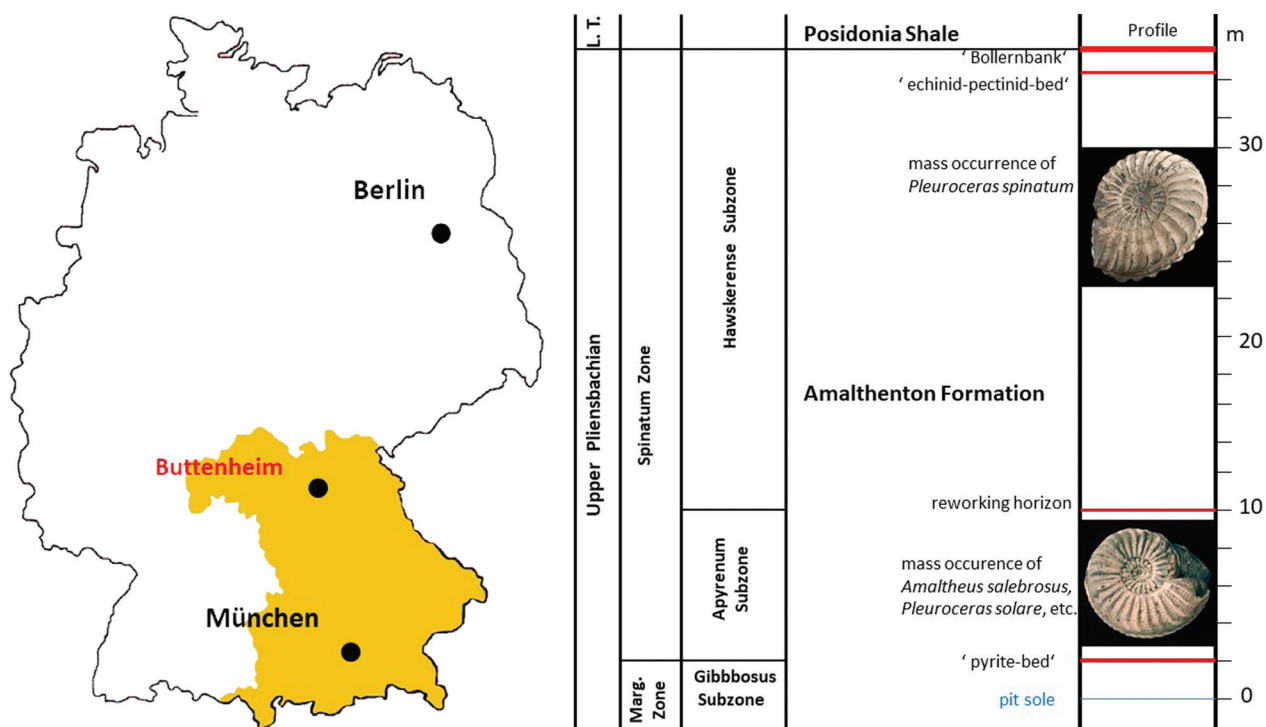


Figure 1. Map of Germany (Bavaria coloured) with the position of the clay pit south of Buttenheim (left) and its schematized profile (right): The red lines mark the four reworking horizons.

which are syndementarily settled by a diverse association of hardground settlers (Keupp 2021c). The fourth reworking horizon, the so-called ‘Bollernbank’ marks the Pliensbachian top and represents a sedimentary gap of about 150 ky (Keupp 2021a). The more or less condensed sections between the first three reworking horizons are fossil rich comprising mass occurrences of ammonites and other fossils. They represent sea level highs with reduced sedimentation rates and faunal immigration from the Tethyan Ocean in the south (Keupp and Schweigert 2017). The section above the ‘pyrite-bed’ of about 6 m thickness corresponds with the Apyrenum subzone and contains aragonitic shells of a diverse ammonite association, often preserved with color patterns. Above the ‘Quellhorizont’ the increasing fossil enrichment culminates in a mass occurrence of *Pleuroceras spinatum* about 6 m below the ‘Bollernbank’.

Autochthonous non-vertebrate eggs from the Amaltheenton Facies of Buttenheim

Keupp et al. (2016b) described for the first time pyritized remnants of a presumed molluscan spawn (pyritized fixation bases and flattened egg capsules) from the Late Pliensbachian sediments of the Buttenheim clay pit. They

discussed *Hayamia reticulata*, a gastropod found in the same outcrop, as the originator, owing to comparisons with similar findings of the Lower Jurassic of Poland and the Early Cretaceous of Daghestan (Zatoń et al. 2009; Zatoń and Mironenko 2015a) as well as modern spawns of neritimorph gastropods. The loosely arranged cluster of about 40 egg capsules is attached to the surface of a calcareous nodule (75 × 32 mm) of EPH and occupies an area of about 300 mm² (Fig. 2A, B). Calcareous nodules of this horizon were syndementarily washed out from the muddy sediment. Afterward, mostly all sides were settled by hard ground colonizers and at least enriched with coarse shell chills.

The second report is given by Keupp and Doppelstein (2018). The authors figured a presumed gastropod spawn, which was fixed at the navel of a large ammonite shell (*Pseudamalteus engelhardti*) found in the EPH. More than 100 irregularly arranged circular egg capsules of about 1 mm in diameter cover an area of about 900 mm² (Fig. 2D).

The third report presented two additional findings (Keupp 2021b): First, a couple of nine scatteredly arranged and three-dimensionally preserved pyritized egg capsules are fixed on the surface of a *Pleuroceras spinatum*, which are included in the private collection of Bernd Doppelstein, Berlin. The diameter range is also about 1 mm. Their slightly wrinkled surface indicates a taphonomic shrinkage process (Fig. 2C). Size and preservation correspond with the

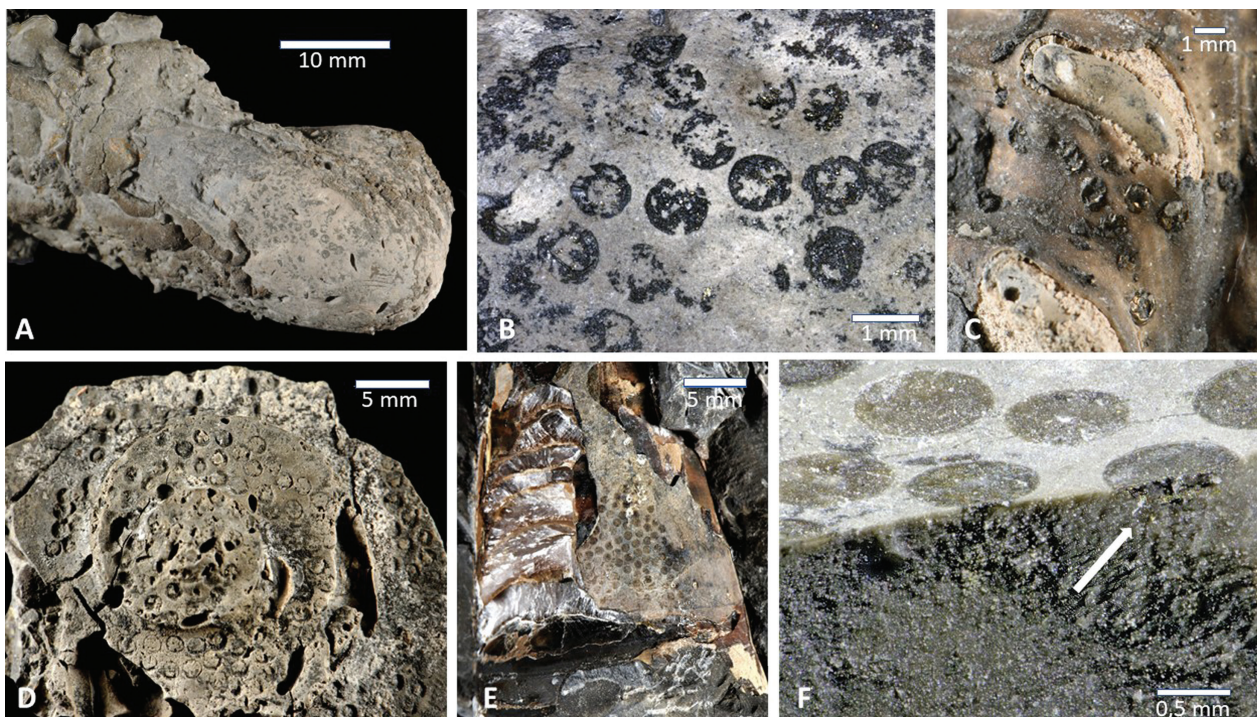


Figure 2. Autochthonous clusters of probable gastropod spawns with pyritized egg capsules, each of about 1 mm in diameter, found in the Late Pliensbachian claystones (Amaltheenton Facies) of Buttenheim. **A, B:** Attached on the surface of a carbonatic concretion of the EPH (from Keupp et al. 2016b, SNSB-BSPG 2014 XXV 332). **C:** Three-dimensional preserved egg capsules on the shell of *Pleuroceras spinatum*, image width 11 mm (from Keupp 2021b). **D:** Covering the navel of *Pseudamalteus engelhardti* from the EPH (from Keupp and Doppelstein 2018). **E, F:** On the belemnite rostrum of *Passaloteuthis* sp., at the transverse fracture of the surrounding concretionary limestone, the lens-shaped configuration of the egg capsules is visible (arrow) (from Keupp 2021b, SNSB-BSPG 2011 XI 1333).

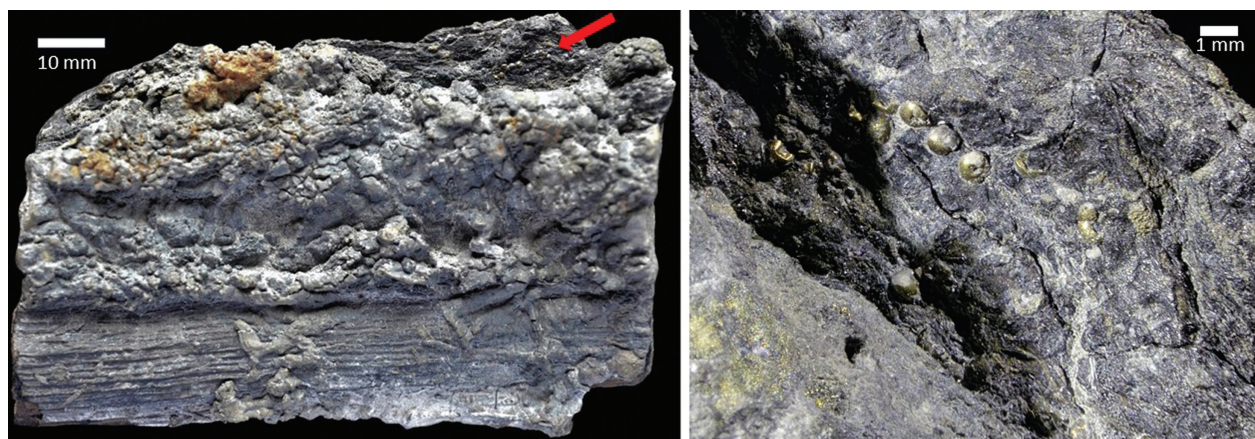


Figure 3. Hitherto unpublished presumed gastropod spawn (red arrow) from the Late Pliensbachian of the clay pit south of Buttenheim (leg. J. Schobert, SNSB-BSPG 2011 XI 1334) fixed on the surface of 88 mm long driftwood piece (left). Right: Irregular cluster of pyritized, circular, and scatteredly arranged egg capsules of about 0.9 mm diameter.

probable gastropod spawn described by Schubert et al. (2008) which was attached to the surface of a driftwood from the Late Pliensbachian of northern Germany. Second, an about 70 mm long belemnite phragmocone (*Pasaloteuthis*), collected by one of us (J. S.), is partly covered by thin relicts of the rostrum. On its surface, one can see imprints of a cluster of circular and irregularly arranged egg capsules of 1 mm diameter, along a 35 mm long and 10 mm broad stripe (Fig. 2E). Within the transverse fracture of the concretion surrounding the belemnite rest, the lens-shaped outlines of the slightly compressed pyritized egg capsules are visible (arrow in Fig. 2F).

Hitherto unpublished egg findings

First, a pyritized 88 mm long piece of driftwood shows a spawn of about 16 scatteredly arranged circular egg capsules of about 0.9 mm diameter. The three-dimensional preserved pyritized eggs are partly shrunk, partly

hemispherical with smooth surfaces (Fig. 3). The center of each egg bears a small, about 0.25 mm broad pore. Arrangement, settlement on a pyritized driftwood, habitus and dimensions of the eggs correspond with the presumed gastropod spawn described by Riegraf and Schubert (1991) and also the example described by Schubert et al. (2008), besides of the egg diameters (0.9 mm vs. 0.35 mm). Both stem from the contemporaneous sediments of northern Germany.

Second, one of us (J. S.) found an additional hitherto unpublished specimen from the Amaltheenton facies from Buttenheim. A cluster of pyritized egg capsules attached to the inside of a small, 3 mm long pectinid bivalve fragment has been identified among the sieve residues of micropaleontological samples of the EPH (Fig. 4). With irregularly and scatteredly arranged egg capsules, the pattern corresponds with the examples from the same locality described above, but their diameters of 0.5 mm reach only half the size. Also, the egg capsules described by Kaiser and Voigt (1977) inside of a pectinid bivalve from the

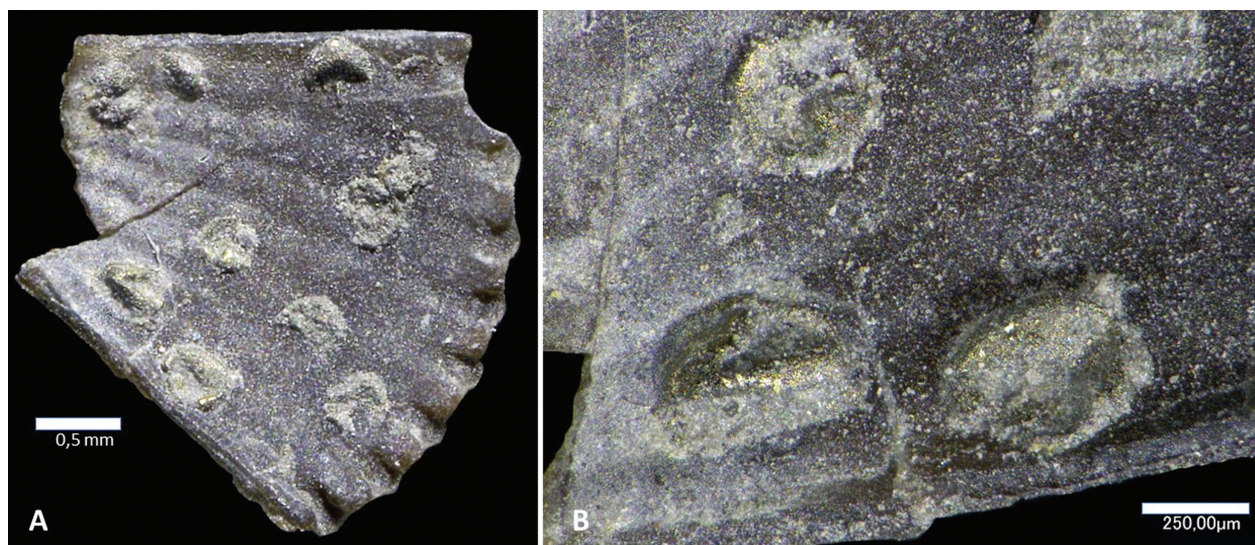


Figure 4. A: Fragment of a pectinid bivalve (3 mm) showing inside attached pyritized egg capsules of about 0.5 mm in diameter (**B**). Late Pliensbachian (EPH) of the clay pit south of Buttenheim (collected by J. Schobert, SNSB-BSPG 2011 XI 1332).

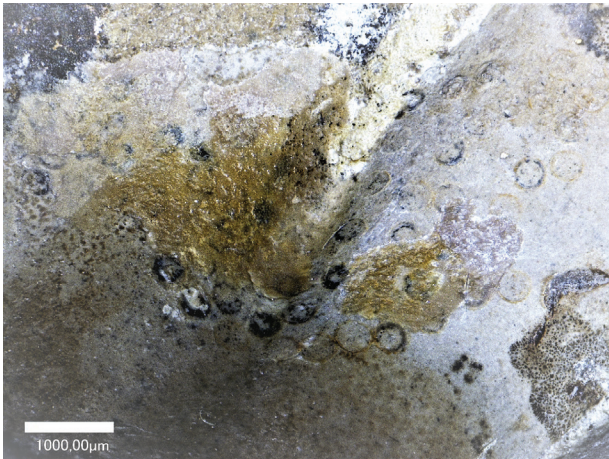


Figure 5. Adhesive rings of presumed gastropod egg capsules of about 0.36 mm in diameter inside a *Pleuroceras* body chamber, Late Pliensbachian of Hummeltal-Creez SW of Bayreuth (leg. F.-J. Scharfenberg, SNSB-BSPG 2022 | 2).

Late Pliensbachian of northern Germany are significantly larger, reaching diameters of 1.3–1.5 mm.

Third, one of us (F.-J. S.) identified adhesive rings of scatteredly arranged egg capsules inside a *Pleuroceras* body chamber from the Late Pliensbachian Amaltheenton facies (Fig. 5), found in a small creek (“Mistel”) near Creez-Hummeltal southwestern of Bayreuth (49°52'34"N, 11°30'4"E). Their diameter only reaches 0.36 mm.

We conclude that the dimensions of presumed gastropod egg capsules found in Late Pliensbachian marine sediments differ between 0.35 and 1.5 mm. Their shape is primarily hemispherical with or without a visible central pore. They are always arranged scatteredly, touch each other only occasionally, and do not exhibit any regular geometrical patterns.

Egg capsules with honeycomb-like arrangement

In 2008, one of us (F.-J.S.) found a non-bed-by-bed collected piece of a fossil driftwood in the Amaltheenton facies of the LIAPOR Company’s claypit south of Buttenheim. The about 80 × 30 mm large wood fragment is preserved partly as black glittering jet coal, partly pyritized exhibiting excellent cellular structures (Fig. 6). Enclosed into the wood is a crescent-shaped area of 8 × 2.5 mm showing a crescent-sized cluster of densely, nearly seamless packed pyritized egg capsules of 0.4–0.5 mm in diameter (Fig. 7A). The reniform to polygonal egg capsules exhibit their basal side upwards tracing the fibrous wood structure (Fig. 7B). At the one end of the spawn area, 13 egg capsules are broken out. Their molds reveal the smooth convex upper side of the egg capsules, each bearing a circular central opening of 90 μm width (Fig. 7C). The position of the egg cluster seemingly enclosed within the wood is difficult to explain. The imprints of wood fibers on the base of the egg capsules prove that the eggs have been laid on a flat wood level probably of a torn deadwood break casting its structure similar to bioimmuration process (Voigt 1979). This basic wood layer changed during fossilization into jet coal. The wood surface and the attached egg cluster are covered by a thin massive pyrite layer bridging the distance of 1 to 1.5 mm to the next layer of woody matter. During egg-laying, the break was probably wider and was afterward reduced due to taphonomic processes. Therefore, the upper side of the spawn did not originally have direct contact with wood material, as shown by its smooth surfaces without any signs of casted wood structure. Zatoń and Mironenko (2015b) figured similar egg capsules,



Figure 6. Fragment of driftwood from the Upper Pliensbachian of Buttenheim. The red arrow marks the enclosed spawn with pyritized egg capsules on the 80 × 30 mm large find (SNSB-BSPG 2022 | 1).

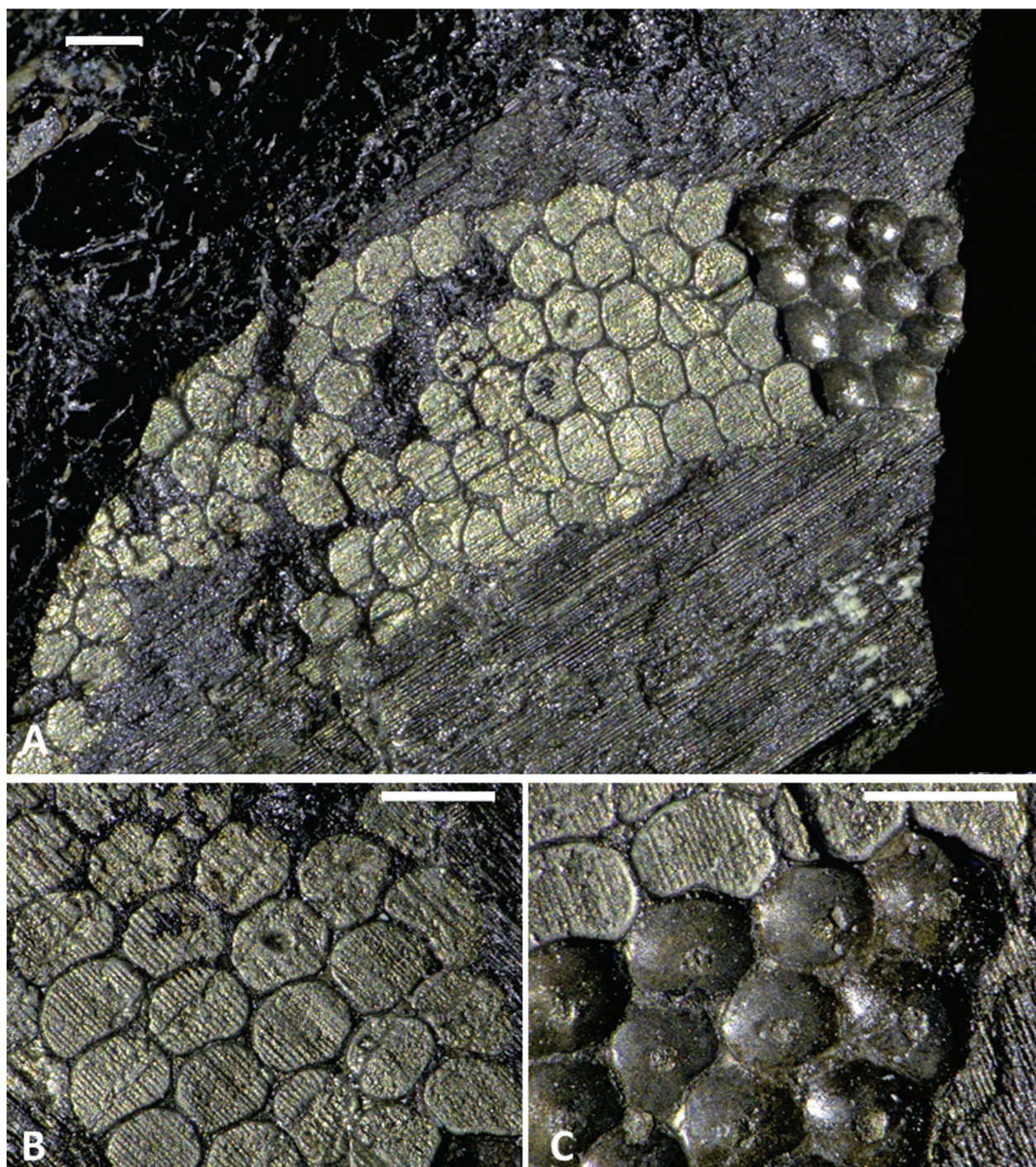


Figure 7. Basal surface of the honeycomb-like arranged pyritized egg capsules cluster enclosed in driftwood from Late Pliensbachian of Buttenheim (SNSB-BSPG 2022 I 1). **A:** Complete crescent-sized cluster. The original wood basis changed due to fossilization processes into jet coal (on the picture above left). **B:** On the egg bases, the fine wood fibers of the original basement are preserved by bioimmuration and, therefore, visible. **C:** The molds of broken-out egg capsules exhibit their smooth surfaces with a small central pore. Scale bars 500 μm .

but they were irregularly attached inside of ammonite body chambers from Russian Late Jurassic sediments.

The new finding differs from the hitherto described presumed gastropod spawns from Late Pliensbachian strata of Buttenheim and other localities for three reasons (Kaiser and Voigt 1977, 1983; Riegraf and Schubert 1991; Schubert et al. 2008):

- 1) It is positioned in a small slit of the woody matter.
- 2) Its regular pattern forms a honeycomb-like arrangement.
- 3) The dimensions of the individual egg capsules are in the lower range of most of the clusters of scatteredly arranged presumed gastropod egg capsules.

Discussion

Deposition of egg capsules on the driftwood could have happened on land, during marine drifting or after they sank on the ground. Besides of gastropod eggs, only few reports exist about fossile egg clusters of other marine non-vertebrate animals. Etches et al. (2009) described presumed cephalopod (ammonites) egg-sacs from the Upper Jurassic Kimmeridge Clay. They represent three-dimensional accumulations of irregularly arranged 1–2 mm sized subspherical eggs with a pimpled surface texture. Authors still speculate about the egg-laying behavior of ammonites, discussing three possible options (De Baets et al. 2015): (1) the laying of eggs at the bottom of the sea (Tanabe et al. 1993), (2) the gelatinous pseudoplanktonic formation of eggs, and (3) the floating of egg sacs (Westermann 1996). Mesozoic ammonitic eggs had dimensions of at least 1 mm generally due to the corresponding diameter of ammonitella. The differences in terms of position in a deadwood break of a driftwood, small size and regular arrangement of eggs suggest that other organisms as marine molluscs and/or another environment originated the new finding of an egg cluster. That is, our fossil contrasts to the presumed gastropod spawns attached on the surfaces of mollusk shells and driftwoods hitherto known from contemporaneous marine sediments. Therefore, we discuss marine gastropods vs. possible terrestrial organisms like pulmonate gastropods and insects as producers.

The oviposition within a small deadwood break by marine gastropods would be very unusual because all hitherto known egg clusters have been laid on open surfaces (e.g., mollusk shells) and larger cavities respectively (e.g., ammonite body chambers). Kaiser and Voigt (1983) described a unique partly net-like arrangement of 1.2 to 1.5 mm large circular egg capsules inside a body chamber of a representative of *Pleuroceras* from Haverlahwiese near Salzgitter (marine facies, northern Germany). These circular egg capsules were located among several gastropod egg clusters of the same locality, which show a similar irregularly arranged pattern like most of the findings from Franconia do. However, the eggs of the partly net-like arranged cluster are three times larger than the eggs of our new finding from Buttheim are. Thus, we presume that the eggs were probably laid in the wood on land before they drifted into the marine environment. We know some recent pulmonate freshwater gastropods laying their eggs outside the water (e.g., Burks et al. 2010) as well as various landsnails laying their eggs in deadwood (Strätz 2006), for instance the tropical Camenidae *Amphidromus* (e.g., Schilthuizen 2013) – But the egg depositions of pulmonate gastropods always form irregular bunches and do not show geometrically arranged clusters (see Figure, Schilthuizen 2013).

On the other hand, regular patterns of epiphytic oviposition are well known and widely distributed among fossil and modern insects, particularly roaches and many butterflies. Roaches (Blattodea) are one of the oldest insect

orders known since the Carboniferous, while the radiation of Lepidoptera started during the Late Triassic (Van Eldijk et al. 2018). Laaß and Hauschke (2019) described the oldest exophytic oviposition of insect eggs on Carboniferous *Cordaites* leaves. The individual circular eggs show diameters of nearly half a millimeter (388–482 µm) forming curved arcs of net-like densely packed clusters. The authors presume insects with short abdomens and ovipositors like roaches as producers. Some extant Lepidopterans produce mono-layered and crescent-sized egg clusters which are similar in size of their egg capsules and in shape of the cluster to our fossil, for example, *Spodoptera frugiperda* (see fig. 02(f), Kasige et al. 2022).

Conclusion

The producer of the regular honeycomb-like pattern of egg capsules found within a Pliensbachian piece of driftwood from Buttenheim (Figs 6, 7) still remains enigmatic. We cannot completely exclude marine or terrestrial gastropods as possible producers of this fossil. However, owing to the corresponding dimension and similar patterns of their arrangement with Carboniferous blattoidean eggs (Laaß and Hauschke 2019), as well as their deposition within a small deadwood break, we presume rather a terrestrial origin by unknown insects than a marine deposition by gastropods. Fossil driftwoods are often responsible for allochthonous depositions of organisms that settle on their surface and therefore they causes taphocoenoses of heterogenous environments (Keupp et al. 2018).

The specimens figured on Fig. 2A, B, E, F and Figs 3–6 are housed at the Bavarian State Collection, Munich (SNSB-BSPG), specimens figured on Fig. 2C, D at the private collection of Bernd Doppelstein, Berlin.

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