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Fossil pearls and blisters in molluscan shells from the Neogene of Austria

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(With 1 figure and 5 plates)

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Abstract

Pearls, blister pearls and related structures in various species of bivalves are described from the Middle- and Late Miocene of Austria. The pearls were found in marine and lacustrine deposits. The focus of this publication is the description of various formed blister pearls and the exploration of the different causes of formation. These fossils were found in the genera *Arca*, *Barbatia*, *Glycymeris*, *Perna*, *Pinna*, *Isognomon*, *Gigantopecten*, *Spondylus*, *Hyotissa*, *Crassostrea*, *Ostrea*, *Codakia*, *Megaxinus*, *Saxolucina*, *Chama*, *Mactra* and *Congeria* from were recorded in marin and lacustrine deposits in Austria. Herein are figured the largest blister of the Middle Miocene (Badenian) and the largest blister pearl of the Late Miocene (Pannonian). This paper adds information concerning pearl and blister occurrences and discusses the mechanisms, that might have played a role in their formation and exhibits several figures of fossil blisters caused by parasitic infestation of polychaetes and trematodes.

Keywords: Pearls, blister pearls, blisters, parasites, polychaeta, trematoda, bivalvia, Neogene.

Zusammenfassung

Der Schwerpunkt der Veröffentlichung ist die Beschreibung verschieden geformter Blisterperlen und die Klärung der Ursachen ihrer Bildung. Diese Fossilen fanden sich in Exemplaren der Genera: *Arca*, *Barbatia*, *Glycymeris*, *Perna*, *Pinna*, *Isognomon*, *Gigantopecten*, *Spondylus*, *Hyotissa*, *Crassostrea*, *Ostrea*, *Codakia*, *Megaxinus*, *Saxolucina*, *Chama*, *Mactra* und *Congeria* stammen aus marinen und lakustrinen Ablagerungen in Österreich. Darunter sind die größte Blisterbildungn aus dem Mittelmiozän (Badenium) und die größte Blister Perle aus dem Ober-Miozän (Pannonium) abgebildet. Diese Arbeit erweitert die Kenntnis über die Mechanismen der Perlen- und Blisterbildungen und zeigt auch mehrere Abbildungen von fossilen Blisterbildungen, entstanden durch parasitären Befall durch Polychaeten und Trematoden.

Schlüsselwörter: Perlen, Blisterperlen, Blister, Parasiten, Polychaeta, Trematoda, Bivalvia, Neogen.

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Introduction

Modern pearls – some famous for their beauty or their remarkable dimensions – attract the public but also scientists. LANDMAN *et al*. (2001) provided an extensive overview of modern pearls. Pearls and blisters are caused by the extraordinary production of nacre or lime of the hypostracum. Free pearls are mostly globoid, consisting of several concentric layers and are separated from the shell.

Blister pearls were original free pearls, which are grown with the shell together and are obligatorily attached to the inner surface of the shell. In both cases- free pearls and blister pearls, the internal structure of prismatic or nacreous layers is identical. Some specimens of blister pearls exhibit a thin seam, where the pearl is attached to the shell (see STRACK 2001: p. 124, fig. 84). Baroque pearls are dominated by a conspicuous macro-sculpture with convex elevations, irregular bladders and sometimes nodes or ridges. Blisters in contrast, are irregular elevations or bulges on the inner surface. Mud blisters lack the concentric structure and contain mud, which is covered by prismatic or nacreous material (BLAKE & EVANS 1973). Pearl warts (pearly protuberances) are small outgrowths on the inner surface of the shell (*e.g.*, SZÓNOKY 1980).

Formation of pearls and blisters

Several hypotheses have been advanced to account for pearl- formation. Various presumed causes have been discussed: 1) Mechanical or predation-related shell damage, which subsequently is repaired by the formation of calcite layers (LOMOVASKY *et al.* 2005). 2) Foreign bodies *e.g.*, organic or in organic objects enveloped by nacreous material (*e.g.*, pearlfishes, MARKL & OLNEY 1990). 3) Infestation by macroscopic organisms boring into the shell threatening the soft body. Consequently, the bivalve tries to wall off the intruder. Well-known triggers are boring polychaetes of the genus *Polydora* (compare SAVAZZI 1995) and the bivalve *Rocellaria*. Traces of polychaetes are present in bivalves and they produced blisters (BLAKE & EVANS 1973).

4) Stimulation by commensal organisms living in the mantle cavity, *e.g.*, copepods and annelids (*e.g.*, CÁCERES-MARTINEZ & VÁSQUES-YEOMANS 1999, OLIVAS-VALDEZ & CÁCERES-MARTINEZ 2002, CÁCERES-MARTINEZ *et al*. 2005, SUAREZ-MORALES *et al*. 2010).

5) Stimulation by parasites like trematodes in the tissues is possible. Larvae of trematodes are abundant in extant Lucinidae. These cause lesions in the mantle, which induce the formation of nacreous material. CHENG (1967) had coined the term nacrezation for the process of walling off foreign bodies by layers of nacre. The author of this paper prefers the term calcification, because several groups of bivalves had reduced the nacreous layers. GÖTTING (1979) had described and figured pearl-formation and supposed encystation of dead trematodes. Also LAUCKNER (1983) had suggested the hypothesis that only dead larvae of trematodes are encapsulated. CÁCERES-MARTINEZ & VÁSQUES-YEOMANS (1997, 1999) discussed pearl-formation in bivalves, which were infected by trematodes.

In the same way small pearls were mentioned by ITUARTE *et. al.* (2001), and CREMONTE & ITUARTE (2003). Hence in a subsequent process the mantle is able to secrete shell material and a globoid pearl with concentric layers is formed.

Fossil pearls

Some fossil blisters and pearls have been found and published (*e.g.*, DARTEVELLE 1934; KÜMEL 1935; ZILCH 1936). THORNE (1973) provided an overview, focusing on conspicuous fossil pearls. Large nodes from Cretaceous layers of Canada were interpreted by KAUFFMAN (1990) as the largest fossil pearls of the Mesozoic time. The largest blister pearl from the Cenozoic Era found so far derives from a specimen of *Perna haidingeri* (HÖRNES, 1865) from the Neogene (Early Miocene, Karpatian) was found and published (BACHMAYER & BINDER 1967, BINDER 2002a). Additional numerous pearls are documented herein mainly from the marine Miocene (Karpatian), Middle Miocene (Badenian) of the Paratethys Sea, and the lacustrine Late Miocene (Pannonian) of Lake Pannon. Isolated true fossil pearls found in the sediment, but in these cases, the species, produced the pearls, remain enigmatic (*e.g.*, ČTYROKY 1972; MÜLLER 1989).

Blisters can be caused by the infestation of various parasites. Fossil blister pearls are often found still attached to the pearl-forming specimen and were formed usually by walling off the intrusion of parasite. Such blisters pearls as the result of infestation of polydorids were described (BINDER 2002a). The coincidence of parasitism by trematodes with the formation of fossil and extant pearls was published in an overview by LITTLEWOOD & DONOVAN (2003). Remarkable is the occurrence of pearls in ammonoids with tubes interpreted as traces of trematodes (DE BAETS *et al*. 2011). This paper adds information concerning pearl and blister occurrences from the Neogene of Austria and discusses the mechanisms that might have played a role in their formation.

The locations of bivalves with pearls and blisters

Fossil bivalve specimens are exceptional finds, among the thousands of shells preserved in Austrian palaeontological collections only few bear pearl formations. The studied specimens derive from the following localities:

Grund: northern range of Lower Austria (Fig. 1: 1).

Stratum and age: Grund Formation, early Badenian (= Langhian), early Middle Miocene, see ZUSCHIN *et al*. (2001: p. 225, 2004b) and MANDIC (2004) for geological and stratigraphic details.

Hauskirchen: northern range of Lower Austria (Fig. 1: 2).

Stratum and age: Sarmatian deposits with reworked specimens from Badenian strata, (Middle Miocene), see GRILL (1968: p. 90).

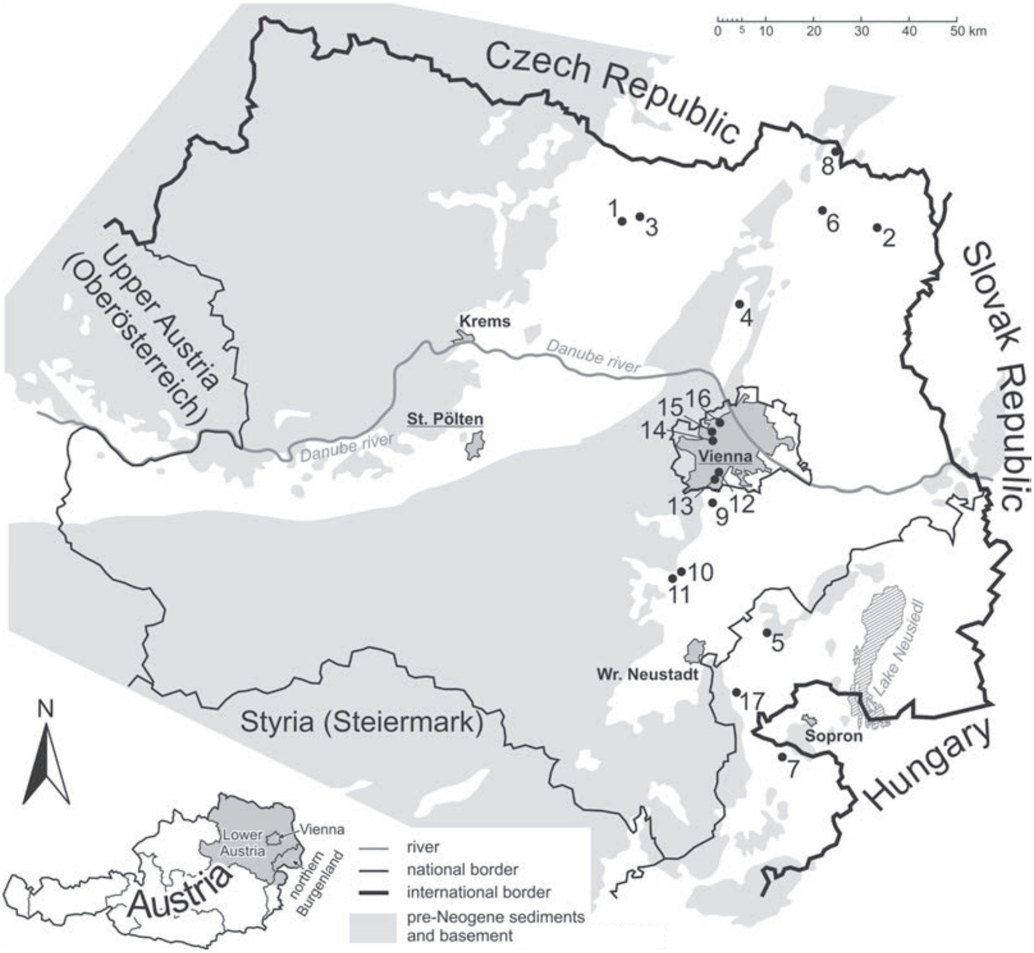

Fig. 1: Localities from which the pearl-bearing mollusc shells derive (modified from KROH 2005: fig. 3).

Immendorf: northern range of Lower Austria (Fig. 1: 3).

Stratum and age: Grund Formation, Badenian, early Middle Miocene. (HARZHAUSER *et al.* 2003: p. 331).

Kleinebersdorf: Lower Austria, in the basin of Korneuburg (Fig. 1: 4).

Stratum and age: Korneuburg Formation, Karpatian, late Early Miocene, see ZUSCHIN *et al.* (2004a) for geological and stratigraphic details.

Müllendorf: northern range of the Burgenland, Austria (Fig. 1: 5).

A chalk-quarry at the road near to Eisenstadt.

Stratum and age: Leitha limestone, Badenian, Middle Miocene, HARZHAUSER *et al.* (2003) for geological and stratigraphic details.

Poysdorf: northern range of Lower Austria (Fig. 1: 6).

Stratum and age: Lower Badenian, GRILL (1968: p. 77).

Ritzing: Burgenland, Austria (Fig. 1: 7).

Stratum and age: Badenian, Middle Miocene, (see JANOSCHEK 1931).

Steinebrunn (= former Steinabrunn): northern range of Lower Austria (Fig. 1: 8).

Stratum and age: Badenian, Middle Miocene (GRILL 1968: 76).

Vösendorf: in the S of Vienna in Lower Austria (Fig. 1: 9).

Stratum and age: Bzenec Formation, Pannonian E, Late Miocene, see PAPP (1985: p. 187); see HARZHAUSER & MANDIC (2004) and HARZHAUSER *et al*. (2004) for geological details.

Vöslau: the former pit of BREYER in the southern part of the basin of Vienna in Lower Austria (Fig. 1: 10).

Stratum and age: Badenian, Middle Miocene, see HARZHAUSER *et al*. (2003), ZUSCHIN *et al*. (2007: p. 286) for geological and stratigraphic details.

Vöslau-Gainfarn: southern part of the basin of Vienna; in Lower Austria (Fig. 1: 11).

Stratum and age: Badenian, Middle Miocene, see ZUSCHIN *et al*. 2007: p. 286 for geological and stratigraphic details.

Wien-Matzleinsdorf: 5th district of Vienna; Austria (Fig. 1: 12).

Stratum and age: Pannonian D, Late Miocene, see PAPP 1953.

Wien-Wienerberg: 10th district of Vienna, Austria (Fig. 1: 13).

This location was in former times a clay-pit.

Stratum and age: Bzenec Formation, Pannonian E, Late Miocene.

Wien-Ottakring: 16th district of Vienna, Austria (Fig. 1: 14).

Stratum and age: Sarmatian, Skalica Formation, Late Middle Miocene, HARZHAUSER & PILLER (2004).

Wien-Pötzleinsdorf: 18th district of Vienna, Austria (Fig. 1: 15).

Stratum and age: Badenian, Middle Miocene.

Wien-Grinzing: 19th district of Vienna, Austria (Fig. 1: 16).

Stratum and age: Badenian, Middle Miocene.

Wiesen: Austria, northern part of Burgenland (Fig. 1: 17).

A sandpit on the road to Mattersburg.

Stratum: and age: Skalica Formation, Sarmatian, late Middle Miocene (HARZHAUSER & PILLER 2004).

Methods, material & abbreviations

Essential were investigations in extant bivalves and, especially of material from subtropical and tropical sea, because comparisons with extant organisms are important in finding an explanation of the formation of pearls (overviews are in LANDMAN *et al.* 2001, STRACK 2001, *etc*.).

The taxonomic arrangement of the bivalves follows the Catalogus fossilium Austriae of SCHULTZ (2001–2005).

The investigated specimens are stored in the collections of the following institutions:

GBA – Geological Survey of Austria, Vienna, Austria

NHMW-G – Natural History Museum Vienna, Geological-Paleontological Department

NHMW-M – Natural History Museum Vienna, 3. Zoological Department

UVPI – University of Vienna, Institute of Paleontology

Descriptions of the fossil pearls and comparison with modern examples

Family Arcidae LAMARCK, 1809

***Arca* (*Arca*) *grundensis* (MAYER, 1868)**
(Pl. 1, Fig. 1)

Material: UVPI 7002 (Grund).

Description: In the inner side of left valve below the hinge a broad blister is attached. The outer surface of the shell is partly destroyed by boring organisms.

Dimensions of the figured blister: *c*. 10 mm × 5.5 mm.

***Arca* sp.**
(Pl. 1, Fig. 2)

Material: NHMW-G 1851/0002/0125 (Grund).

Description: In a left valve near the hinge a rising blister is visible.

Dimensions of the figured blister: 23 mm × 11 mm.

***Barbatia* (*Barbatia*) *barbata* (LINNAEUS, 1758)**
(Pl. 1, Fig. 3)

Material: NHMW-G 2012/0232/0001 (Grund).

Description: One specimen (Pl. 1, Fig. 3) shows the characteristic blister triggered by *Polydora* infestation. It is initially thin and curling and increases in thickness and width thereafter. Another specimen in the same lot exhibits borings on the outside of the shell. Inside are blister-like elevations partly broken off, showing the characteristic "double grooved" traces of polychaetes (see BINDER 2002b).

Interpretation: The presence of these borings and the shape of the blisters strongly suggest that the polychaete *Polydora* had triggered the formation of the blisters. This parasite is commonly found in fossil molluscan shells (BINDER 2002b).

Dimensions of the figured blister: *c*. 21 mm × 5 mm.

Family Glycymerididae DALL, 1908

***Glycymeris* (*Glycymeris*) *pilosa deshayesi* (MAYER, 1868)**

Specimen A (Pl. 1, Fig. 8)

Material: NHMW-G 2010/0278/0001 (Vöslau-Gainfarn).

Description: A blister is attached on the inner surface of a right valve near the hinge. It is an elongate, thickened structure, which terminates in a tapering top.

Interpretation: The shape of this blister, especially the rising point, indicates an endobiont as the potential trigger: It could have been a commensal copepod living in the mantle (see BOXHALL & HALSEY 2004: vol. 2: p. 591).

Dimension of the valve: 58 mm; dimensions of the figured blister: 5.5 mm × 15.6 mm.

Remarks: An extant pearl of *Glycymeris* (*Glycymeris*) *pilosa* (L., 1758) was described and figured by FRAUSSEN & FRAUSSEN (2000).

Specimen B (Pl. 1, Figs 6, 7)

Material: NHMW-G 2002z0181/0186 (Hauskirchen).

Description: A thick calcification on a right valve on the scar of the anterior adductor covers nearly the entire muscle-scar. The posterior adductor-scar is only partly covered by a thin coating. The outer surface of the shell displays numerous traces of boring organisms, suggesting the cause of blister formation.

Dimensions of the valve: 10.1 mm × 9.8 mm; dimensions of the figured calcification on the scar of the anterior adductor: 14.6 mm × 10 mm, thickness 4 mm.

Interpretation: The adductor muscles are well-nourished by the pelecypods and therefore parasites prefer this tissue. The thickened lime-layer is likely secreted in defence.

***Glycymeris glycymeris* (LINNAEUS, 1758)**
(Pl. 4, Fig. 3)

Material: two extant specimens, NHMW-M 1700 (from Dalmatia, Croatia), 52009 (Island Pag, Dalmatia, Croatia).

Description: The first specimen (1700) shows several large blister pearls arranged in rows in each valve.

Description: Both valves show rose of tiny blisters on the inner surface

Dimensions: valve: 79 mm × 80 mm; blister pearls: 12.8 mm in diameter to 3.3 mm in diameter.

***Glycymeris* (*Glycymeris*) *obtusata* (Partsch in Hörnes, 1865)**

Material: UVPI 7003 (Vöslau-Gainfarn).

Description: In a right valve a tiny blister is attached to the inner surface.

Dimension of the blister: 0.5 mm in diameter.

Family Mytilidae Rafinisque, 1815

***Perna* (*Perna*) *haidingeri* (Hörnes, 1867)**

Material: NHMW-G 1816/0035/0085 (Grund).

Description: Two flat blisters are attached to the inner surface in the upper region of a valve. On the outside of the shell the characteristic traces of boring by polydorids are visible.

Dimensions of the blisters: *c.* 5 mm and *c.* 12 mm in diameter.

Family Pinnidae Leach, 1819

***Pinna* (*Pinna*) *tetragona* Brocchi, 1814**

(Pl. 2, Figs 4, 5)

Material: NHMW-G 2012/0230/0001 (Wien-Grinzing).

Description: A single, flat, irregular blister clings like a bladder to a fragment of a pen shell. The main part is built up by the prismatic layer, which is visible at a broken point; the nacreous layer is preserved at the edges. These are bright, whereas the part formed by the prismatic layers is dark. On the outer shell, the surface exhibits characteristic growth lines. A fracture is visible on the outer surface of the pen shell. Traces of bioerosion on the surface of the blister and along that fracture were obviously caused by post mortem borings of *Polydora.* The margin of the blister partly covers the fracture (Pl. 2, Fig. 5).

Dimensions of the figured blister: 24 mm × 36 mm.

Interpretation: The covering of the fracture indicates that the formation of the blister occurred after shelltrauma and therefore, the building of the blister was an attempt by the bivalve to close the gap.

Remarks: The growth lines of the musclescar are similarly visible in another fossil specimen found in Kalksburg (NHMW-G 1958/0002/0011), figured by SCHULTZ (2001: pl. 10, fig. 4). Other fossil pearls of the genus *Pinna* were mentioned by ZILCH (1936: 248). LANDMAN *et al.* (2001: 26) presented a coloured photo of a *Pinna* from the Eocene with pearls that had retained their exquisite nacre.

Pinna nobilis (LINNAEUS, 1758)
(Pl. 2, Fig. 2)

Material: NHMW-G 1971/1432/0007 (extant, Poreč, Croatia, Adriatic Sea).

Description: A fragment shows several red blisters on the inner side and on the outer side the characteristic tubes built by the bivalve *Rocellaria*. Some blisters contain the valves of this bivalve. Dimensions of these blisters range from 20 mm × 10 mm to 24 mm × 12 mm.

Family Isognomidae WOODRING, 1925

Isognomon (_Hippochaeta_) _maxillata soldanii_ (DESHAYES, 1836)
(Pl. 1, Fig. 4–5)

Material: NHMW-G 1855/0045/0724, 1884/0002/1930 (both from Immendorf).

This specimen has been well-figured by SCHULTZ (2001: pl. 13).

Description (1855/0045/0724): The left valve contains an irregular bladder with a curved structure below the hinge; where it is broken, a small, rounded blister is visible inside the curved blister. The outer surface of the shell exhibits the borings of polychaetes.

Description (1884/0002/1930): In a right valve, a round mud blister, partly broken, is attached to the upper part of the valve.

Dimensions of the figured blister: 13 mm × 11 mm (1855/0045/0724), 5.6 mm × 5 mm (1884/0002/1930).

Interpretation: The screw-shaped traces of boring in specimen 1855/0045/0724 presumably were caused by polychaetes.

Remarks: Other fossil *Isognomon* shells with pearls were published by ZILCH (1936). SAVAZZI (1995) documented traces of borings by the polychaete *Polydora.*

Family Pectinidae RAFINISQUE, 1815

Gigantopecten nodosiformis (PUSCH, 1837)
(Pl. 2, Fig. 1)

Material: NHMW-G 1987/0042/0008 (Müllendorf).

Description: A well-formed convex blister pearl is attached near the umbo of the shell. On the outer surface of the valve appear several traces of bioerosion.

Dimensions of the figured blister: 3.8 mm × 3.5 mm.

Remarks: See the reports of McGladdery *et al.* (2006) concerning infestation in extant scallops.

Family Spondylidae Gray, 1826

Spondylus (_Spondylus_) _crassicostatus_ Lamarck, 1819

Material: NHMW-G 1845/0032/0001 and 1846/0037/0858 (both from Wien-Grinzing).

This fossil was well-figured by Hörnes (1867) and by Schultz (2001: pl. 43, fig. 3, pl. 44, figs. 1a, b, 7).

Description: In a right valve is a blister near the scar of the adductor visible. At the margin of the scar the blister begins with a thick node, continuing as a wormlike outgrowth and tapering to a small node (see Hörnes 1867: pl. 76, fig. 7).

Dimensions of the valve: 88 mm × 91 mm; dimension of the large node of the blister: 9 mm in diameter.

Remarks: An example of a pearl in a valve of an extant *Spondylus* is published by Mienis (2001).

Family Gryphaeidae Vialov, 1936

Hyotissa squarrosa (de Serres, 1843)
(Pl. 3, Fig. 3)

Material: NHMW-G 2014/0456/0001 (Vöslau).

Description: In the left valve is a node-like blister near to scar of the adductor muscle.

Dimension of the figured blister: 6.2 mm in diameter

Remarks: Similar specimens from the Karpatium of the basin of Korneuburg were described in Binder (2002a: pl. 3, figs 1a, 1b).

Family Ostreidae Rafinisque, 1815

Crassostrea gryphoides (Schlotheim, 1813)
(Pl. 2, Fig. 3)

Material: NHMW-G 2002z0084/0001 (Kleinebersdorf).

Description: On the right valve, a blister pearl is attached to the scar of the adductor muscle. On the outline of the pearl, a blunt angle is visible and the growth ridges are distinct.

Dimensions of figured blister: 5 mm width × 7.5 mm length.

Remarks: Several blister pearls were found in fossil oysters (*e.g.*, KÜMEL 1935; BINDER 2002a). In oysters are infestations by polydorids abundant (BINDER 2002b).

Crassostraea gryphoides sarmatica (FUCHS, 1873)

Material: NHMW-G 2010/0278/0004, (Wien-Ottakring).

Description: In the adductor muscle scar of the left valve, a wormlike blister is embedded, the result of a polychaete parasite

Dimensions of the valve: 97 mm × 77 mm; dimension of the blister pearl: *c.* 3.5 mm.

Ostrea (_Ostrea_) _fimbriata_ RAULIN & DELBOS, 1855
(Pl. 2, Figs 6–7)

Material: NHMW-G 2012/0226/0001, 2012/0226/0003 (both from Ritzing).

Description (2012/0226/0001): The left valve has a large, flattened blister covering the adductor muscle scar. The attachment to the scar shows that growth of the blister began distally.

Description (2012/0226/0003): In the adductor muscle scar of a left valve, a well-formed convex blister with nodes is visible. The outer layer of the blister is partly broken and the structure of thick-walled layers is visible.

Dimensions of the valves: 2012/0226/0001: 91.6 mm × 64.9 mm; dimensions of the figured blister: 39.1 mm × 17.9 mm; 2012/0226/0003: 59.6 mm × 39.6 mm; dimensions of the figured blister: 19.2 mm × 12.8 mm.

Remarks: Several additional specimens with blisters are stored at the NHMW.

Family Lucinidae FLEMING, 1828

Codakia (_Epilucina_) _haidingeri_ (HÖRNES, 1865)
(Pl. 3, Fig. 8)

Material: NHMW-G 2013/0444/0005 (Grund).

Description: A conspicuous blister is visible on the margin on the valve. On the margin of the valve is a conspicuous blister visible.

Dimensions of the figured blister: 2.5 mm × 2 mm.

Remarks: A similar pearl of the extant *Codakia tigerina* (LINNAEUS, 1758) was figured by POPPE (2011).

Megaximus (*Megaximus*) *incrassatus* (DUBOIS DE MONTPÉREUX, 1831)

Specimen A (Pl. 3, Fig. 4)

Material: NHMW-G 2010/0278/0003 (Vöslau).

Description: This specimen bears 14 small, flattened blisters, arranged as rows of little plates, in a left valve. One platelet is broken off and a pit in the shell is visible below.

Dimensions of the figured blisters: 1–1.5 mm in diameter.

Interpretation: The small pits were caused by larvae of trematodes . The formation of the platelets was an attempt of healing the lesions with an occlusion with platelets.

Specimen B (Pl. 3, Fig. 7)

Material: NHMW-G 2010/0278/0002 (Vöslau).

Description: In the upper part of the inner side of a right valve near the groove of the pallial vessel, a spherical blister pearl is developed, which exhibits growth layers.

Dimensions of the valve: 48 mm × 49 mm; dimension of the figured pearl: 2.5 mm in diameter.

Remarks: Pearls in Austrian fossils of *Megaximus* are rare, but a specimen from Lapugiu (former Lapugy) in Romania with many blisters is stored in NHMW-G 2014/0102/0001.

Specimen C (Pl. 3, Fig. 6)

Material: NHMW-G 2014/ 0100/0002 (Vöslau).

Description: Only a fragment of a valve is present. The inner surface is covered by many nodes, arranged from the hinge distally to the edge of the impression of the mantle. These nodes have distal short cords (see Pl. 3, Fig. 6).

Dimensions of the blister: *c.* 2 mm

Specimen D (Pl. 3, Fig. 1)

Material: NHMW-G 2013/0444/0006 (Vöslau).

Description: A valve shows on the left side a curved trail of lesions and small pearls. On the right side are small platelets visible.

Dimensions of the figured platelets: *c.* 1 mm.

Interpretation: The metacercariae larvae were migrationg through the tissue of the mantle. Later the caused lesions were regenerated by the building of platelets and tiny pearls.

Specimen E

Material: GBA 2008/187/0088/01 (Poysdorf).

Description: Two valves with small blister pearls.

Dimensions of the blister pearls: 2.5 mm × 2.5 mm and 2.2 mm × 2.8 mm

***Megaximus* (*Megaximus*) *incrassatus subscopulorum* (D'ORBIGNY, 1852):**

Material: NHMW-G 1846/0737/0587 (Wien-Pötzleinsdorf).

Description: A left valve with two small, round blister pearls. The right valve contains tiny platelets

Dimensions of the pearls: 2 mm and 2.8 mm× 1.8 mm in diameter.

Remarks: The fossil was figured by SCHULTZ (2003: pl. 58, fig. 10a).

***Saxolucina* (*Plastomiltha*) *suessi* (CSEPREGHY-MEZNERICS, 1954)**

Material: NHMW-G 2003z0015/0003a (Vöslau).

Description: On the right valve, a smooth blister pearl is attached near the hinge and a node appears near the impression of the adductor muscle. On the distal margin of the impression from the mantle edge are several tiny platelets.

Dimensions of the valve: 58 mm × 58 mm; dimension of the blister: *c.* 1.5 mm.

Family Chamidae LAMARCK, 1809

***Chama* (*Psilopus*) *gryphoides gryphoides* LINNAEUS, 1758**
(Pl. 4, Fig. 1)

Material: NHMW-G A1164 (Steinebrunn).

Description: In a left valve near the hinge and the adductor muscle scar are five flat blisters.

Dimensions of the figured blisters: 6.2 mm × 4.7 mm.

Family Mactridae LAMARCK, 1809

***Mactra* (*Sarmatimactra*) *vitaliana* (D'ORBIGNY, 1844)**
(Pl. 4, Fig. 2)

Material: NHMW-G 2010/0278/0006 (Wiesen).

Description: One valve exhibits a blister with irregular nodes and partially formed wormlike tube.

Dimensions of the figured blisters: large blister: 7.6 mm × 7.3 mm; small blister: 3 mm in diameter.

Remarks: Holes in the shell especially near the blisters indicate that formation might have been caused by parasites such as boring worms, which irritate the mollusc by drilling near the shell-building tissue.

Family Dreissenidae GRAY in TURTON, 1840

***Congeria subglobosa subglobosa* PARTSCH, 1836**

Specimen A (Pl. 4, Fig. 4, Pl. 5, Fig. 9)

Material: UVPI 7005 (Vösendorf).

Description: A blister pearl is attached to the inner surface of the left valve. Additionally, there are small elevations or pearl-like knobs, which are in part arranged in lines.

Dimension of the figured blister: *c.* 6 mm in diameter.

Specimen B (Pl. 4, Fig. 5)

Material: NHMW-G 2010/0278/0005 (Vösendorf).

Description: A small dreissenid on the inner surface of a right valve is covered by a roof-like shell-layer. Obviously, the dreissenid bivalve triggered the formation of this envelope.

Dimension of the foreign valve: 5 mm × 4.9 mm.

Remarks: This fossil should demonstrate the mechanism in defending foreign organisms.

Specimen C (Pl. 4, Fig. 6)

Material: UVPI 7006 (Vösendorf).

Description: This right valve exhibits tiny pearl-like warts arranged in rows.

Dimensions: 2.6 mm – 0.3 mm in diameter.

Specimen D (Pl. 5, Figs 1, 2)

Material: UVPI 7004 (Vösendorf).

Description: A large blister pearl is attached near the umbo of the right valve. It is a remarkably globular and regularly formed.

Dimension of the figured blister: 27 mm in diameter.

Specimen E (Pl. 5, Figs 3, 4)

Material: NHMW-M 62233, (Wien-Wienerberg).

Description: A left valve exhibits a well-formed, ovoid blister pearl.

Dimensions of the figured blister: 6.4 mm × 4.4 mm.

Specimen F (Pl. 5, Fig. 5)

Material: NHMW-G 2010/0278/0007 (Wien-Wienerberg).

Description: In a fragment of a left valve is attached to the inner surface a compound baroque pearl consisting of several blisters of different sizes. Further cover several small blisters are visible.

Dimensions of the blister: 15 mm × 10 mm.

Specimen G (Pl. 5, Figs 6, 7)

Material: UVPI 1019 (Vösendorf).

Description: A huge, spherical blister pearl is attached to the right valve near the umbo and distinct nodes cover the surface.

Dimension of the figured blister: 29.6 mm in diameter; dimensions of the nodes: 7-9 mm in diameter.

Specimen H (Pl. 5, Fig. 8)

Material: NHMW-G 2013/0444/0004 (Vösendorf).

Description: The valve shows a small blister- pearl with a cordlike elongation.

Dimension of the figured blister pearl: *c.* 3 mm in diameter.

Interpretation: The elongation might indicate an endosymbiont as the cause.

Congeria partschi globosatesta PAPP, 1953

Material: NHMW-G 1946/0037/0770 (Wien-Matzleinsdorf).

Description: In both valves, small conspicuous warts are visible.

Dimensions of the valve: 61 mm length, 41 mm width; dimension of the warts: 1.5 mm.

Remarks: In Hungary blister pearls also have been found in other species of *Congeria* (see SZÓNOKY 1980, and LENNERT *et al.* 1999). It was figured by HÖRNES (1867: pl. 49, fig. 1) and by SCHULTZ (2005: pl. 111, fig. 6b).

Conclusions

The various existing fossil pearls and blisters from Austrian locations exhibit evidence concerning the causes of pearl formation.

Blisters caused by lesions of the shell: (see Pl. 2, Figs 4, 5).

Blisters caused by the presence of foreign bodies or organisms living in lamellibranchs: *e.g.* a small bivalve that settled in a *Congeria subglobosa* is partly covered (see Pl. 4, Fig. 5).

Boring organisms: bivalves such as *Rocellaria* (*e.g.*, in *Pinna*, see Pl. 2, Fig. 2).

Boring polychaetes in bivalves: *Arca*, *Barbatia* (see Pl. 1, Figs 1–3) and in *Spondylus.*

There are two ways of infection possible:

Boring into the outer surface of the shell, in which a borehole is visible (see Binder 2002b*)*.

Living between the mantle and shell: *e.g. Ostrea fimbriata* (see Pl. 2, Figs 6, 7).

Parasites in tissues (see introduction): The pits, caused by the metacercariae-larvae in fossil Lucinidae, are very distinct (see Pl. 3, Figs 1, 2). The specimens of Lucinidae exhibit the development of the following stadiums:

Lesions in tissue and shell → platelets → pearls or pearls warts.

Discussion

Hypothetical interpretation concerning the species *Congeria*:

Pearl warts (see introduction) are a very conspicuous and frequent occurrence in specimens of the dreissenid genus *Congeria.* The genus *Congeria* – although only distantly related to lucinids and thysarids – probably lived under similar dysaerobic conditions and might have developed a similar adaptation (see Harzhauser & Mandic 2004, 2010).

The arrangement of small warts on the interior surface of the shells exhibits a remarkable pattern. Several specimens have such elevations, but others are lacking them. The presence or absence of parasites and the formations of warts might have been also a reaction against this infestation. Lauckner (1983) had observed chalky concretions in rows in the adductors of bivalves and had coined for this the term “comet trails”. He had claimed that they are formed by migrating trematode larvae penetrating the muscle tissue. Remarkable is the above-described trail of lesions presumably caused by a migrating metacercaria in a specimen of *Megaxinus incrassatus* from Vöslau. Some other fossil bivalves exhibit similar arrangements on the inner surface of the shell (*e.g.*, *Glycymeris glycymeris*, Pl. 4, Fig. 3, *Chama gryphoides*, Pl. 4, Fig. 1 and *Congeria subglobosa*, Pl. 4, Fig. 4). These traces have led this author to a hypothesis: Larvae of trematodes lived in the mantle and produced tiny pits that were later filled with organic and chalky material. During growth of the bivalve, the parasites were continually forced to migrate to the outer edge of the mantle, and arrangements of the warts in rows are established (see Pl. 4, Fig. 6).

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Plate 1

Fig. 1: *Arca* (*A.*) *grundensis* (Mayer); UVPI : 7002, Grund; a left valve shows in the hind part several nodes.

Fig. 2: *Arca* sp.; NHMW-G 1851/0002/0125, Grund; a left valve shows on the inner surface several blisters.

Fig. 3: *Barbatia* (*B.*) *barbata* (L.); NHMW-G 2012/0232/0001, Grund; a left valve exhibits on the inner surface a wormlike blister.

Fig. 4: *Isognomon* (*Hippochaeta*) *maxillata soldanii* (Deshayes); NHMW-G 1855/0045/0724, Immendorf; a left valve shows on the inner surface a helical trace of boring.

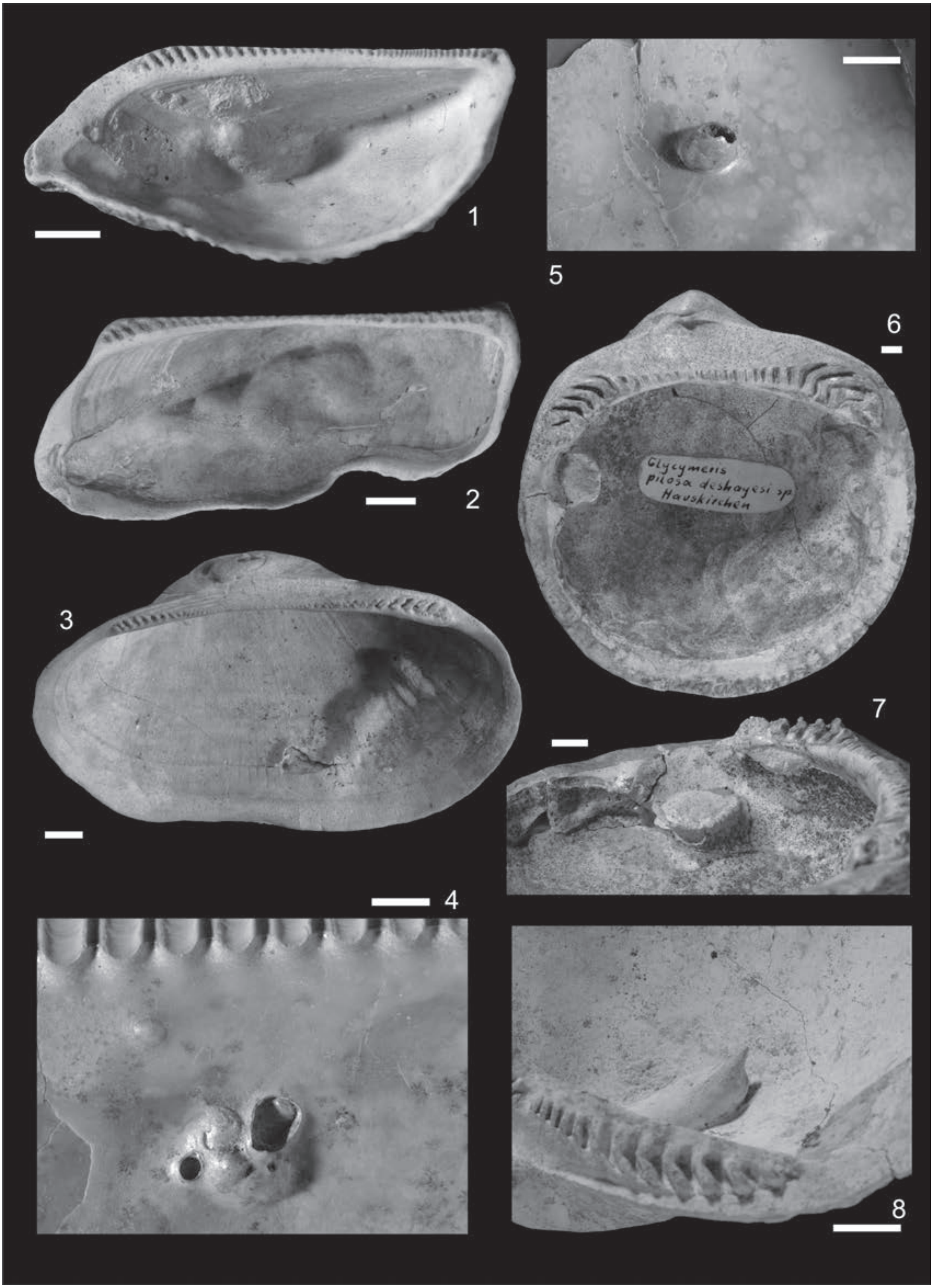
Fig. 5: *Isognomon* (*Hippochaeta*) *maxillata soldanii* (Deshayes); NHMW-G 1884/0002/1930, Immendorf; a round mud blister shows the outer envelope and the innermost hole.

Fig. 6: *Glycymeris* (*G.*) *pilosa deshayesi* (Mayer); NHMW-G 2002z0181/0186, Hauskirchen; a right valve exhibits a thickened adductor muscle-scar.

Fig. 7: *Glycymeris* (*G.*) *pilosa deshayesi* (Mayer); NHMW-G 2002z0181/0186, Hauskirchen; a detail figure shows a thick calcification in the adductor muscle-scar.

Fig. 8*: Glycymeris* (*G.*) *pilosa deshayesi* (Mayer); NHMW-G 2010/0278/0001, Vöslau-Gainfarn; a right valve shows near the hinge a distal elevated blister.

Scale bars equal 5 mm.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Glycymeris
pilosa deshayesi sp.
Hauskirchen

Plate 2

Fig. 1: *Gigantopecten nodosiformis* (Pusch); NHMW-G 1987/0042/0008, Müllendorf; a right valve exhibits near the hinge a small blister pearl.

Figs. 2: *Pinna nobilis* (Linnaeus); NHMW-G 1971/1433/0007, extant, Mediterranean Sea, Porec; a fragment shows blisters, induced by small bivalves (*Rocellaria*).

Fig. 3: *Crassostrea gryphoides* (Schlotheim); NHMW-G 2002/0084/0004, Kleinebersdorf; a right valve exhibits in the right part of the muscle scar a blister.

Fig. 4: *Pinna tetragona* Brocchi; NHMW-G 2012/0230/0001, Wien-Grinzing; a fragment of a valve (light) with a blister (dark) in top view.

Fig. 5: *Pinna tetragona* Brocchi; NHMW-G 2012/0230/0001, Wien-Grinzing; a fragment of a valve shows in side-view the layers of the shell with a blister. In the right part of the layers is a fracture visible, which is partly covered by the blister.

Fig. 6: *Ostrea fimbriata* Raulin & Delbos; NHMW-G 2012/0226/0001, Ritzing; a left valve bears a flattened blister, which covers nearly completely the adductor muscle scar.

Fig. 7: *Ostrea fimbriata* Raulin & Delbos; NHMW-G 2012/0226/0003, Ritzing; a left valve with a blister, which is attached to the distal margin of the muscle scar.

Scale bars equal 5 mm.

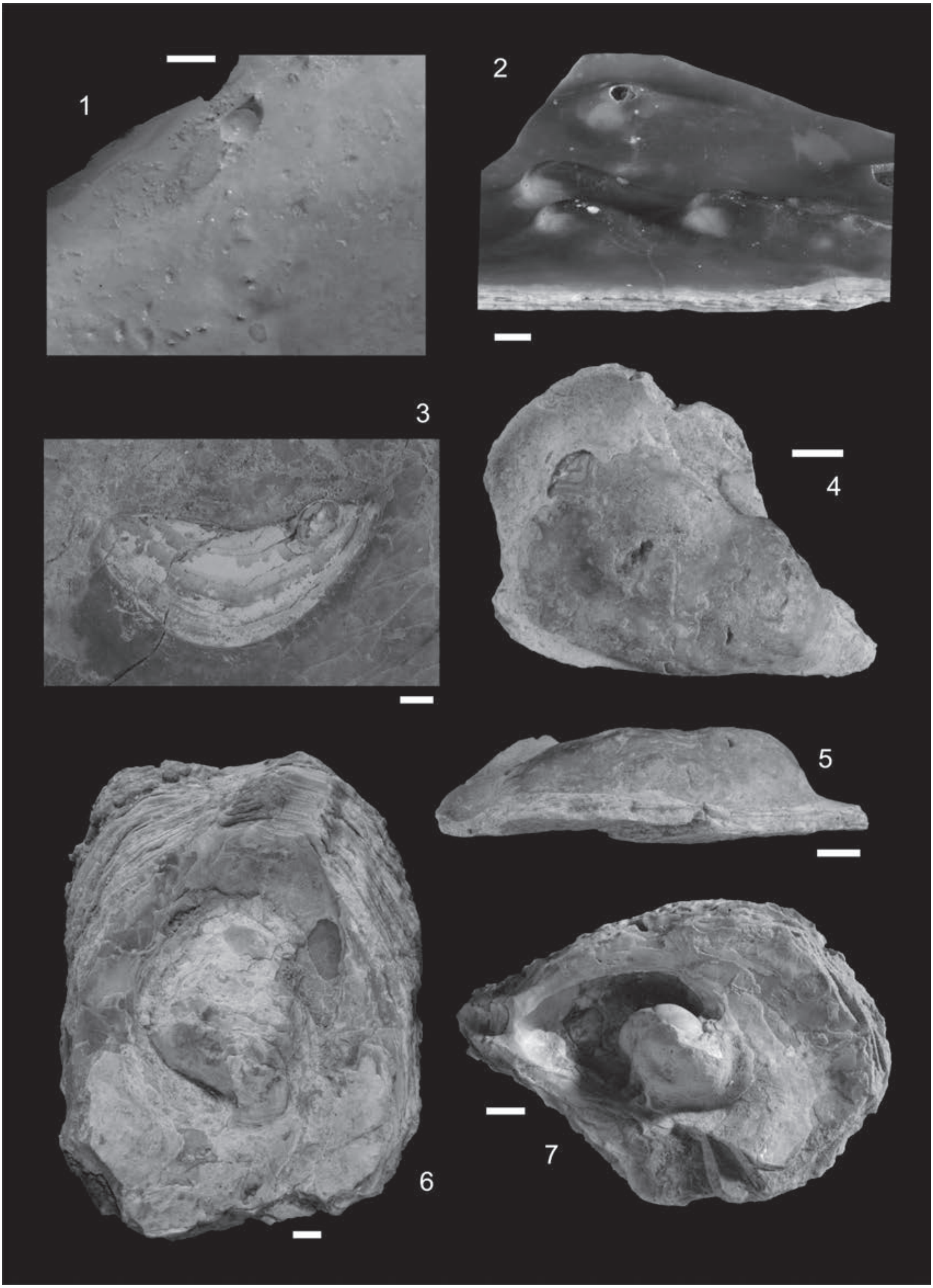
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Plate 3

Fig. 1: *Megaximus* (*M.*) *incrassatus* (Dubois de Montpéreux); NHMW-G 2013/0444/0006, Vöslau; a left valve shows on the left part of the inner surface lesions, caused by larvae of trematodes. On the right part of a valve are small platelets.

Fig. 2: *Codakia* (*C.*) *leonina* (Basterot); NHMW-G 2013/0444/0001, Vöslau; a left valve shows many pits, caused by larvae of trematodes.

Fig. 3: *Hyotissa squarrosa* (de Serres); NHMW-G 2014/0456/0001, Vöslau; a left valve with a wormlike blister, caused by polychaetes.

Fig. 4: *Megaximus* (*M.*) *incrassatus* (Dubois de Montpéreux); NHMW-G 2010/0278/0003, Vöslau; a left valve shows platelets, covering the leisons, caused by larvae of trematodes.

Fig. 5: *Saxolucina* (*Plastomiltha*) *suessi* (Csepreghy-Meznerics); NHMW-G 2003z0015/0003a, Vöslau; a right valve with a blister pearl and a calcification in the muscle-scar.

Fig. 6: *Megaximus* (*M.*) *incrassatus* (Dubois de Montpéreux); NHMW-G 2014/0100/0002, Vöslau; a left valve shows blisters, arranged in bands and leading from proximal to distal part.

Fig. 7: *Megaximus* (*M.*) *incrassatus* (Dubois de Montpéreux); NHMW-G 2010/0278/0002, Vöslau; a right valve with a round blister near the hinge.

Fig. 8: *Codakia* (*Epilucina*) *haidingeri* (Hörnes); NHMW 2013/0444/0005, Grund; a left valve exhibits a blister attached on the inner surface near the margin.

Scale bars equal 5 mm.

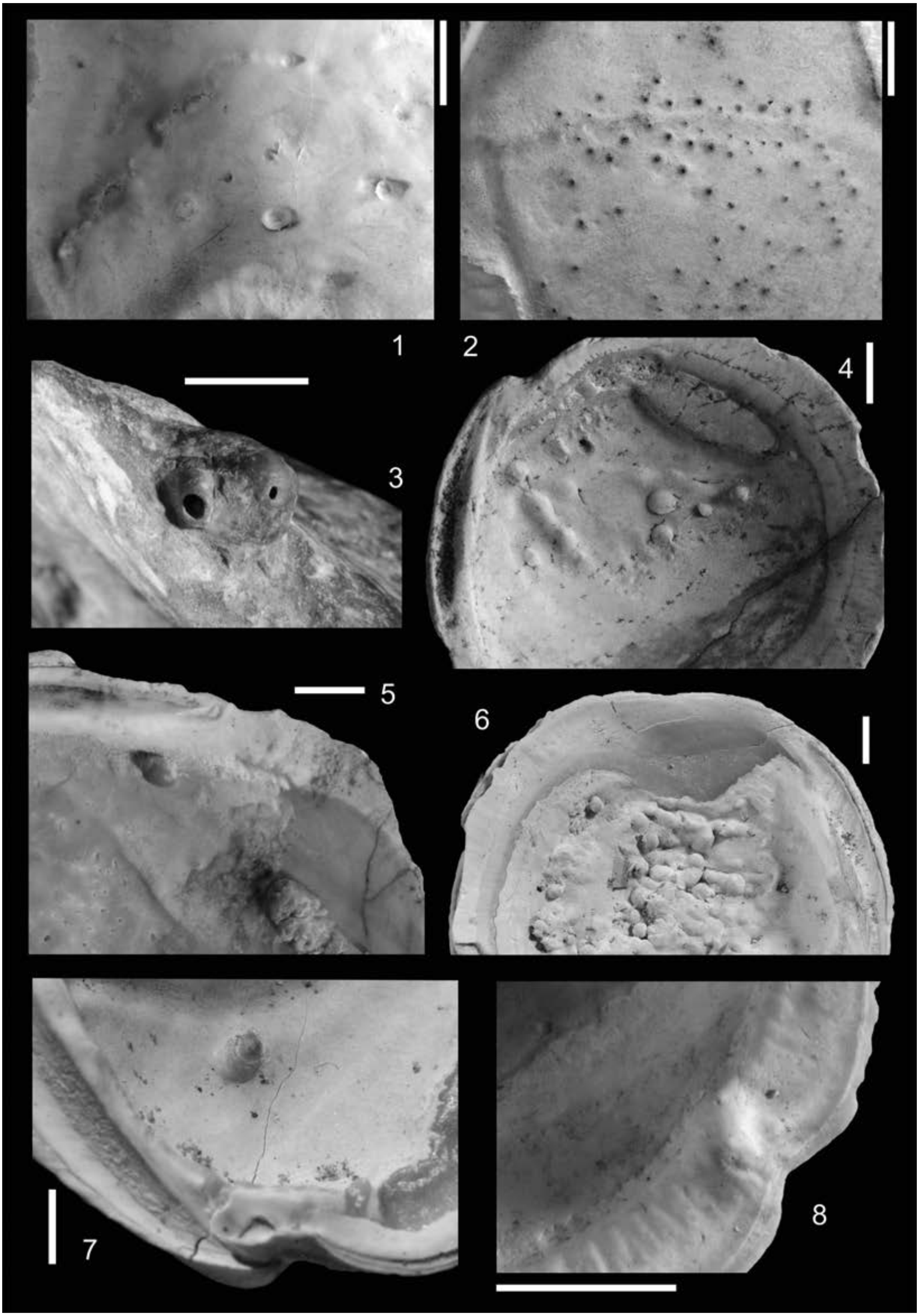
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Plate 4

Fig. 1: *Chama* (*Psilopus*) *gryphoides gryphoides* Linnaeus; NHMW-G A1164, Steinebrunn; a valve shows on the left side an adductor scar and on right side flat blisters.

Fig. 2: *Mactra* (*Sarmatimactra*) *vitaliana* (d'Orbigny); NHMW-G 2010/02787/0006, Wiesen; a left valve with a blister, beginning with a narrow tube, and following with nodes.

Fig. 3: *Glycymeris* (*Glyycymeris*) *glycymeris* (Linnaeus); NHMW-M 1700 Dalmatia (Croatia), extant; a right valve shows conspicuous blister pearls arranged in rows.

Fig. 4: *Congeria* (*Congeria*) *subglobosa* Partsch; UWPI 7004, Vösendorf; a right valve shows on the inner surface tiny blisters, which are arranged in a "comet tail".

Fig. 5: *Congeria* (*Congeria*) *subglobosa* Partsch; NHMW-G 2010/0278/0005, Vösendorf; a left valve shows on the inner surface a little bivalve as commensal. The *Congeria* had tried to defense this commensal with secretion of shell-material in a rooflike formation.

Fig. 6: *Congeria* (*Congeria*) *subglobosa* Partsch; UVPI 7005, Vösendorf; a right valve exhibits many tiny pearl-warts arranged in rows.

Scale bars equal 5 mm.

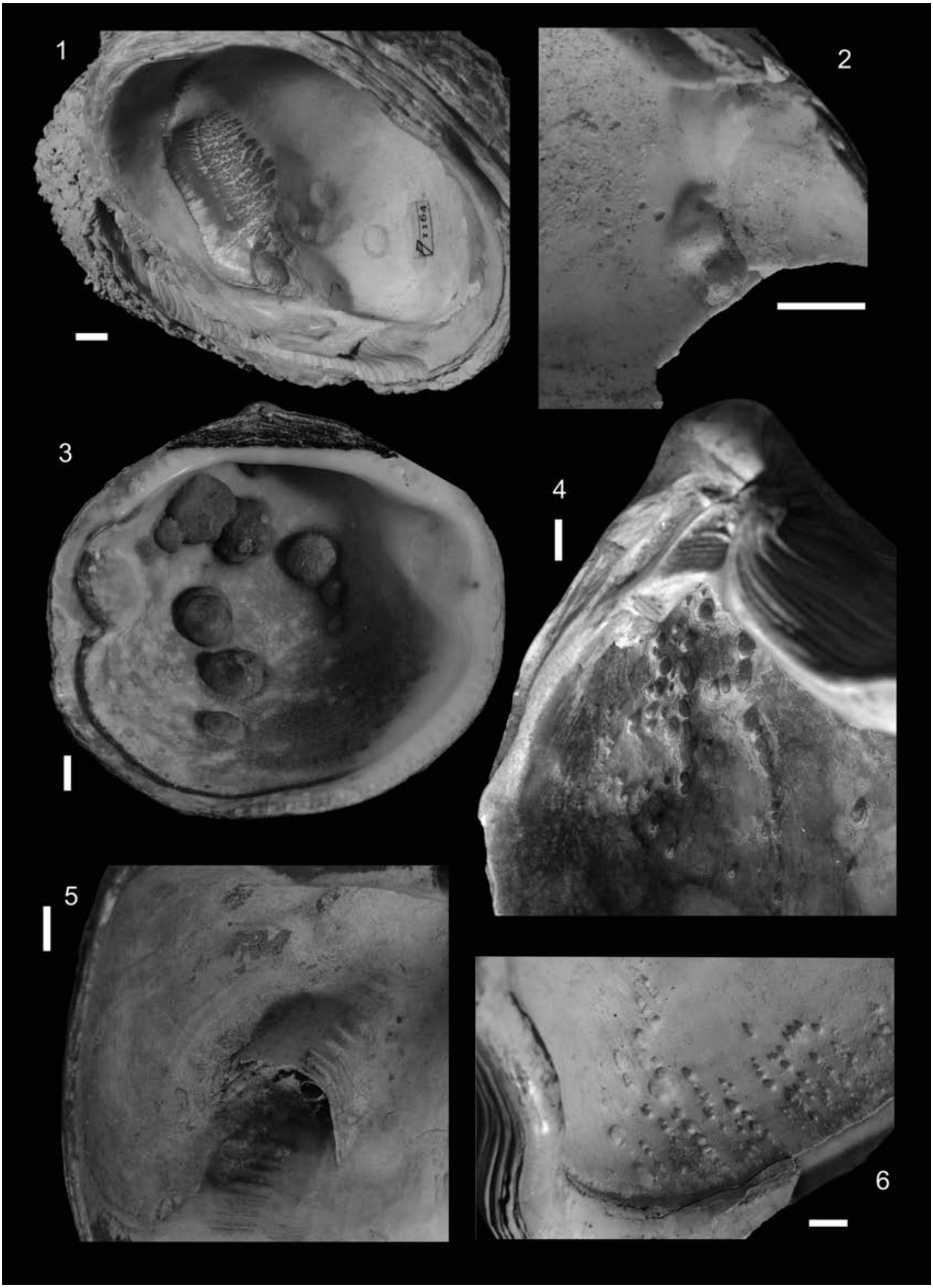
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Plate 5

Congeria (*Congeria*) *subglobosa* Partsch

Fig. 1: UVPI 7005, Vösendorf; a right valve in top view with a large blister pearl, attached near the umbo.

Fig. 2: UVPI 7005, Vösendorf; a large blister pearl in side view.

Fig. 3: NHMW-M 62233, Wien-Wienerberg; a blister pearl in top view.

Fig. 4: NHMW-M 62233, Wien-Wienerberg; a blister pearl in side view.

Fig. 5: NHMW-G. 2010/0278/0007, Wien-Wienerberg; a fragment with a baroque blister pearl and several blisters.

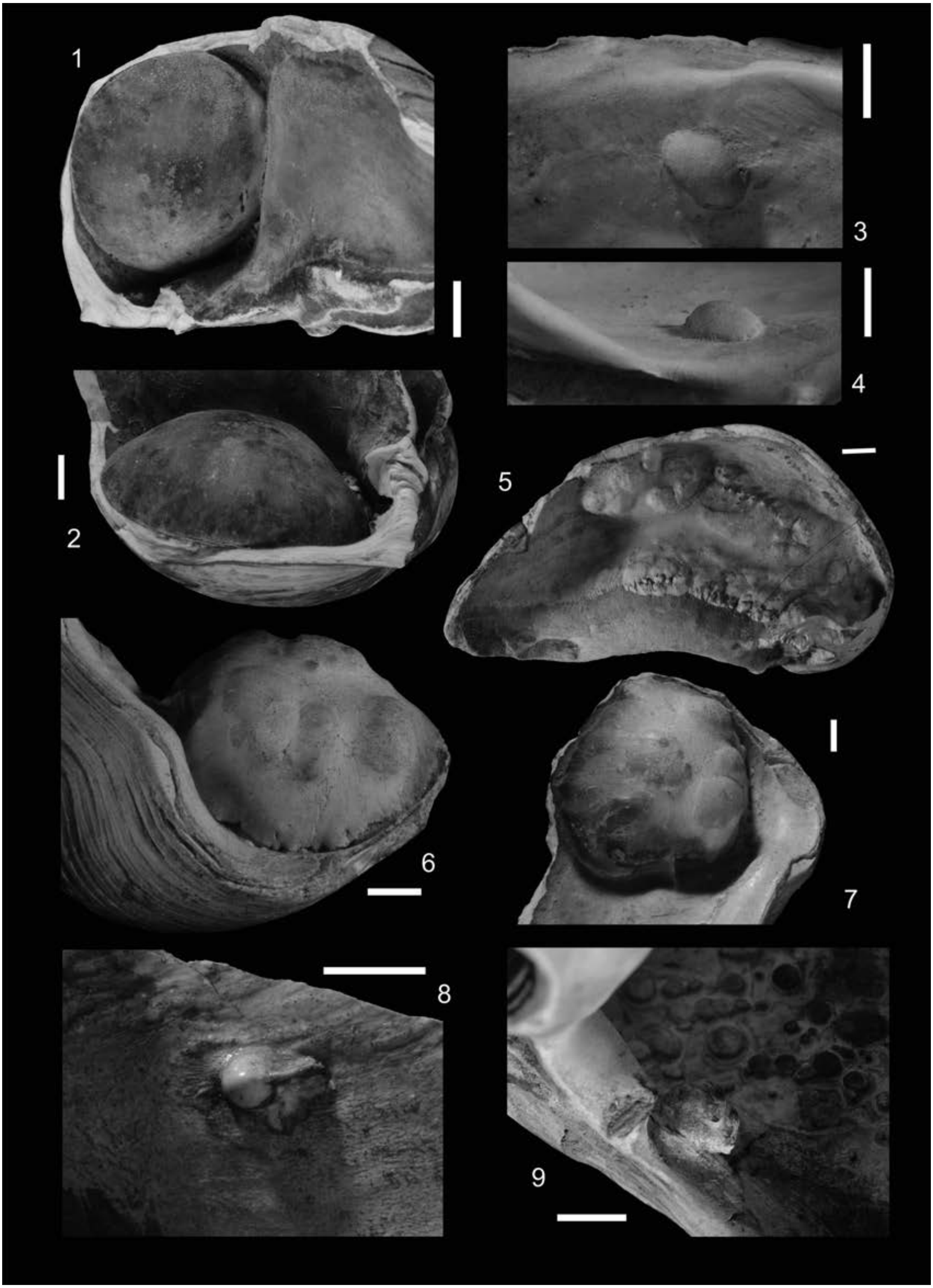
Fig. 6: UVPI 1019, Vösendorf; a right valve in side view with a large blister pearl attached to the distal part.

Fig. 7: UVPI 1019, Vösendorf; a right valve in top view with a large blister pearl, bearing some nodes

Fig. 8: NHMW 2013/0444/0004, Vösendorf; a blister beginning with a cord like tube and succeeded from a round blister.

Fig. 9: UWPI 7004, Vösendorf; a right valve with a blister pearl, attached to the shell. Visible is the seam between blister pearl and shell. In the background are small pearl-warts.

Scale bars equal 5 mm.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