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A new look at the bivalve *Anomia ephippium* Linnæus, 1758 from the Miocene of the Central Paratethys: an example from the Nowy Sącz Basin in Poland

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ABSTRACT:

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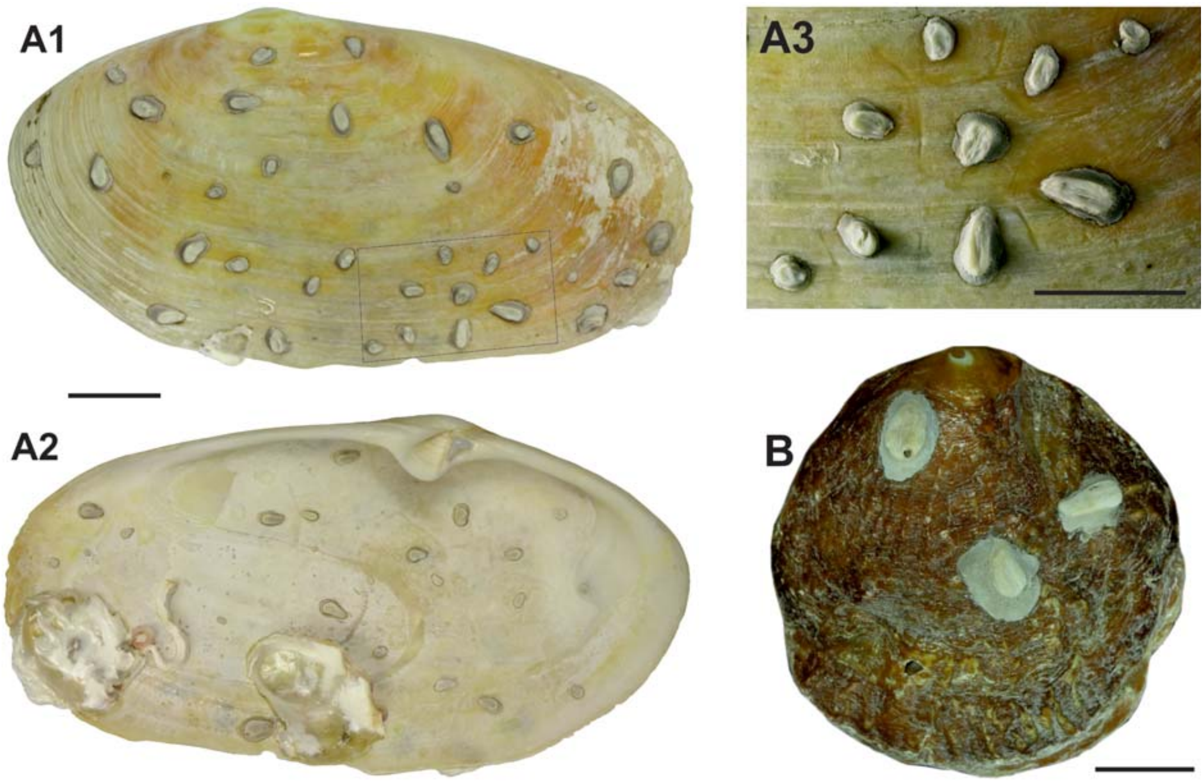
For the first time, articulated shells of *Anomia ephippium* Linnæus, 1758, the bivalve species widely distributed in the Egerian–Late Badenian (latest early Oligocene to late middle Miocene) in the Central Paratethys, are described and illustrated. The most astonishing fact is the presence of a heavily calcified byssus that anchored the animal to hard substrates, which is still preserved inside the byssal notch. The investigated material derives from the Badenian (middle Miocene) Niskowa Formation in the Nowy Sącz Basin, a small intramontane basin situated in the Polish Outer Carpathians. Apart from articulated shells and left valves, the collected material contains some dozen of calcified byssi fixed to rigid substrate, SEM images of which are presented. Examination of the *A. ephippium* specimens stored in the Polish Academy of Sciences, Museum of the Earth in Warsaw revealed other Paratethyan records of anomiid calcified byssi attached to other specimens of *A. ephippium.* Finally, the paper provides an overview of the previous studies on the representatives of the genus *Anomia* Linnæus, 1758 from the Central Paratethys and its specific assignment.

Key words: Bivalvia; Anomiidae; calcified byssus; Kamienica Nawojowska, Nowy Sącz Basin; Badenian (middle Miocene); Central Paratethys.

INTRODUCTION

Among the bivalve families that live permanently attached to a rigid substrate – either by cementing one valve to a hard surface or by using special anchoring byssal threads – the family Anomiidae Rafinesque, 1815 is unique in its mode of attachment. Representatives of this family live closely adhering to the substrate by means of a strong byssus passing from the inside of the left (upper) valve through an irregularly pear-shaped byssal notch in the right (lower) valve. As demonstrated by Yonge (1977), the juveniles of all living anomiid genera can attach themselves temporarily to the substrate by proteinaceous byssal threads that are secreted by the byssal gland in the foot. With the only known exception of the highly specialised genus *Enigmonia* Iredale, 1918, highly adapted to live in mangrove swamps, the organic byssus is gradually modified during ontogeny to become a highly complex hierarchical structure, where both aragonite and calcite are present (Yamaguchi 1998; Leemreize *et al*. 2013). The calcareous content accounts for 90% of the weight of the byssus, with some magnesium present in the calcitic part of the byssus (Leemreize *et al*. 2013). A detailed and highly imaginative description of the development of the byssal structure in *Anomia chinensis* Philippi, 1848 has been provided by Yamaguchi (1998).



Text-fig. 1. A1-A3. An unusually high number of anomiid calcified byssi observed on both external (A1) and internal surfaces (A2) of the left valve of *Lutraria angustior* Philippi, 1844 (MZ VIII Ml-3988); A3 – Magnified area marked in A1; conspicuous multiangular imprints are observed around each byssal plug corresponding to the trace fossil *Centrichnus eccentricus* Bromley and Martinell, 1991. The outlines of these etched traces of (unpreserved) shell margins suggest a contemporaneous phase of colonisation by several specimens. B – Calcified byssi of three specimens attached to the external surface of the left valve of *Anomia ephippium* Linnæus, 1758 (MZ VIII Ml-3986/1). Recent specimens from Atlantic coast of Portugal (Costa da Caparica). Scale bars = 10 mm. Photographs by D. Nast

As the anomiid shell is thin and delicate, the calcified base of the byssus which is still attached to other shells (Text-fig. 1) is the only reference of the once living animal. In some cases, however, the only records of anomiids are the etching traces produced by the byssus, named by Bromley and Martinell (1991) as *Centrichnus eccentricus*. Recently, this ichnotaxon, which is known from the Upper Cretaceous, has been revised and re-described by Neuman *et al*. (2015). Their detailed work, including a revision of the original material of Bromley and Martinell (1991) has shown that etching traces could be produced not only by the byssus but also by the mantle edge. *Centrichnus eccentricus* corresponds now to the conspicuous imprint of the byssus and a shallow groove around the margins of the right valve.

The earliest certain record of a typical anomiid shell is *Juranomia calcibyssata* Fürsich and Werner, 1989 from the Upper Jurassic of the Lusitanian Basin, Portugal (Fürsich and Werner 1989). It should be emphasised that, with a few exceptions, only left valves of the anomiid body fossil are reported in almost all records, whereas right valves are documented very sporadically. As pointed out by Fürsich and Werner (1989) in their Portuguese collection containing altogether more than 300 left valves (usually 10 to 15 mm in height), tens of calcitic byssal remains and several articulated shells fixed to the large bivalve shell of *Myophorella lusitanica* (Sharpe, 1850), the right valve could be observed only after removing the left valve of articulated specimens.

One of the conspicuous discoveries concerning right valves is that described recently by Zarubá *et al*. (2002) from the Upper Cretaceous of the Bohemian Cretaceous Basin, Czech Republic. About one hundred right valves of *Anomia subtruncata* d'Orbigny, 1850 were found fixed to lydite clasts, seven of them with fragments of the left valve. Irregularities in the surfaces of each lydite clast have been perfectly mirrored in the shape of both valves. However, only the interior of the right valves could be observed, as also in *Juranomia calcibyssata*.

As in the case of other fossil representatives of the family Anomiidae, reports of the presence of right valves and articulated shells of *Anomia ephippium* Linnæus, 1758 are extremely scarce, despite the fact that this species occurs in the earliest Oligocene in the North Sea Basin (Anderson 1959) and during the Neogene was widespread in all European provinces. There are, however, numerous reports of the occurrence of left valves. The most complete references are those of Janssen (1979) and Schultz (2001).

To my knowledge the occurrence of right valves and articulated shells is known only from a few localities, all confined to the Pliocene and Pleistocene of the Mediterranean area. Several right valves were found in the Pliocene of Malaga, Spain (Lozano-Francisco 1997), Roussillon, France (Bucquoy *et al.* 1888, as var. *radiata* Brocchi, 1814), the Piacenza province, Italy (Sacco 1897, as var. *plicata* Brocchi, 1814) and in the Pleistocene of Monte Mario, Italy (Cerulli-Irelli 1907, as var. *aspera* Philippi, 1844). The only records of articulated shells are those of Bucquoy *et al.* (1888), who figured two shells from the Pliocene of Roussillon (referred to the *patellaris* Lamarck, 1819 and *electrica* Linnæus, 1758 varieties) and Bromley (1999), who described *A. ephippium* shells from the Pleistocene of Rhodes, Greece attached to the valves of *Pecten jacobeus* (Linnæus, 1758) and *Aequipecten opercularis* (Linnæus, 1758). In this case, after removing the left valve from an articulated specimen not only interior of the right valve was observed but also the etching traces produced by the calcitic byssus referred to as *Centrichnus eccentricus* Bromley and Martinell, 1991.

Thus, the articulated shells of *A. ephippium* from the middle Miocene of the Central Paratethys presented in this paper, preserved with a strong byssal plug that emerges through a byssal notch, are unique among the hitherto described and illustrated specimens. The interpretation of the byssi presented herein gained significantly from discussions with the late Professor Andrzej Radwański, to whom this volume is dedicated.

PREVIOUS STUDIES ON *ANOMIA EPHIPPIUM* FROM THE MIOCENE OF THE PARATETHYS

Although *Anomia ephippium* is known to occur in the Central Paratethys since the latest early Oligocene (Egerian of Hungary; Báldi 1973), the species has been hitherto represented exclusively by isolated left (upper) valves. As can be seen from the description and illustrations, this is a highly variable species, and it is not surprising that many palaeontological approaches have been taken to impose some order to this variability but the results of these efforts has led to quite different, sometimes contradictory, opinions. The review below is far from being exhaustive.

Specimens of *Anomia ephippium* from the lower Miocene of the Eastern Alpine Foreland Basin and the middle Miocene of the Vienna Basin were primarily referred to *Anomia costata* Brocchi, 1814 by Reuss (in Hörnes 1870, pp. 462–464, pl. 85, figs 1–7). In addition, Reuss synonymised *Anomia radiata* Brocchi, 1814, *Anomia sinistrorsa* de Serres, 1829, *Anomia porrecta* Partsch in Hauer and Bronn, 1837, *Anomia burdigalensis* Grateloup, 1838 and *Anomia polymorpha* Forbes, 1844 with *A. costata*, and regarded *A. ephippium* as a different extant species. Consequently, the specimens from the Pliocene Coralline Crag Formation of England assigned to *A. ephippium* by Wood (1851, pp. 8, 9, pl. 1, fig. 3a–d) were included by Reuss (in Hörnes 1870) in the synonymy of *A. costata*.

In the opinion of Foresti (1893, pp. 395–396), the specimens ascribed by Reuss (in Hörnes 1870) to *A. costata* were incorrectly referred to this species and represent a new variety of *A. ephippium* named by him *Hörnesi*, which was subsequently recorded in the Turin Hills, Italy by Sacco (1897). Furthermore, Sacco (1897, p. 37, pl. 10, figs 40–44) treated Brocchi's species of *A. costata* as a variety of *A. ephippium*. The latter concept was adopted by Schaffer (1910, pp. 22, 23), who undertook studies on the material from the lower Miocene (Eggenburgian) of the Eastern Alpine Foreland Basin and recognised amongst the anomiid specimens (referred to *A. costata* by Reuss in Hörnes 1870) the following varieties of *A. ephippium*: *Hörnesi* Foresti, 1893, *rugulosostriata* Brocchi in Bronn, 1831, *pergibbosa* Sacco, 1897, *aspera* Philippi, 1844, *costata* Brocchi, 1814 and *ornata* Schaffer, 1910. He also distinguished a new species *Anomia rugosa* within the material.

On the other hand, Dollfus and Dautzenberg (1920, pp. 460–462, pl. 47, figs 11–19) thought that the well-illustrated specimens assigned by Reuss (in Hörnes 1870) to *A. costata* had been confused with *A. ephippium* var. *rugulosostriata*, therefore the varietal name *Hörnesi* proposed by Foresti (1893) should be considered as a synonym of *rugulosostriata*. In the opinion of these authors, fossil representatives of the latter variety reported from the early Miocene to the Pleistocene were thought to be ancestors of the extant *A. ephippium*, differing from the latter primarily by the presence of numerous thin ribs bearing short thorns. Based on Dollfus and Dautzenberg's (1920) authority many authors (e.g., Friedberg 1936; Moisescu 1955; Kojumdgieva 1960) classified the Paratethyan specimens as *A. ephippium* var. *rugulosostriata*.

Contrary to the statement of Dollfus and Dautzenberg (1920), Sieber (1955, p. 176), who revised the Austrian material, claimed that only specimens ascribed to *A. costata* by Reuss (in Hörnes 1870, pl. 85, figs 5–7) belong to *A. ephippium* var. *rugulosostriata*, whereas those presented on his pl. 85, figs 1–4 were certainly incorrectly assigned either to *A. costata* (Reuss in Hörnes 1870) or to *A. ephippium* var. *hörnesi* by Schaffer (1910) and represent another species, *viz. A. burdigalensis* Defrance, 1816. This concept of *A. burdigalensis* was accepted by Studencka *et al.* (1998).

Tejkal (1956, pp. 278–279), who studied the anomiid shells from the Lower Badenian (correlated with the Langhian) near Mikulov (former Nikolsberg) in Moravia, northern part of the Vienna Basin, presented an opinion that the sculptural characters did not provide adequate ground for separating *A. ephippium rugulosostriata* from *A. ephippium costata*. Based on about 150 left valves, he argued that that it is difficult to find meaningful criteria to distinguish particular subspecies (Tejkal 1956). The largest specimen of *A. ephippium* from this locality attains a diameter of 76 mm. So far no specimens of this size have been reported from the uppermost lower Oligocene to the middle Miocene strata of the Central Paratethys.

More recently, taxonomic studies of the Austrian material were performed by Schultz (2001, pp. 282–295, pl. 45, figs 1–5, pl. 46, figs 1–5), who provided also an extensive synonymy list. In his opinion, however, Sieber (1955) was astray in regarding the specimens referred to *A. costata* and figured by Reuss (in Hörnes 1870, pl. 85, figs 1–4) as *A. burdigalensis*. According to Schultz, they represent a different taxon *A. ephippium hoernesi*, whereas the illustrations of *A. costata* by Reuss (in Hörnes 1870, pl. 85, figs 5–7) agree well with *A. ephippium rugulosostriata*, as noticed also by Sieber (1955). Moreover, Schultz (2001) maintained Schaffer's (1910) attributions and identified two species: *A.* (*A.*) *rugosa* Schaffer, 1910 and *A.* (*A.*) *ephippium* within the material gathered from the lower Miocene of the Eastern Alpine Foreland Basin and the middle Miocene of the Vienna Basin. Moreover, following the work of Schaffer (1910), Schultz (2001) reported six subspecies of the latter species: *aspera*, *costata*, *hoernesi*, *ornata*, *pergibbosa* and *rugulosostriata*.

GEOLOGICAL SETTING AND THE BIVALVE MATERIAL

The Nowy Sącz Basin is a small intramontane basin situated in the Polish Outer Carpathians (c. 50 km to the south of the Carpathian overthrust upon the Miocene strata of the Carpathian Foredeep Basin), with sedimentary successions providing good records of palaeoenvironmental changes that affected this area of the Central Paratethys in the Miocene. Its middle Miocene succession consists of both freshwater and marine deposits. The freshwater deposits distinguished by Oszczypko *et al.* (1991) as the Biegonice Formation unconformably overlie the folded and eroded flysch deposits of the Magura Nappe and are overlain by marine deposits. Sedimentary facies and the micropalaeontological content allow these marine deposits to be subdivided into the Iwkowa and Niskowa formations (Oszczypko *et al.* 1992). On the basis of calcareous nannofossils and foraminifera detected in the Iwkowa Formation (represented by lagoonal deposits with reduced salinity), a Late Badenian (early Serravallian) age was assigned. In turn, both calcareous nannofossils and foraminifera recorded in the Niskowa Formation (sandy-silty marine deposits) define its age as the Late Badenian and/or Sarmatian (early and/or middle Serravallian).

The Niskowa Formation, approximately 60 m thick, covered by Pleistocene and Holocene alluvial deposits up to 12 m thick (Oszczypko-Clowes *et al.* 2009), shows a patchy appearance and only two localities have yielded a diverse mollusc fauna: Niskowa near Nowy Sącz town and the Kamienica Nawojowska site situated along the river at the southeast outskirts of Nowy Sącz. The first fossil-bearing site has attracted the attention of researchers for almost 150 years (see Bałuk 1970), whereas the second was exposed during flooding in 2001 (Gonera and Styczyński 2002). Detailed stratigraphy and facies description of both freshwater and marine deposits discovered here has been provided by Oszczypko-Clowes *et al.* (2009). Based on calcareous nannofossils, the age of the Niskowa Formation has been regarded as Late Badenian and/or Sarmatian (early and/or middle Serravallian; Oszczypko-Clowes *et al.* 2009). However, a biostratigraphic study performed by Gonera (2012) has allowed for the definition of its stratigraphic position within the *Orbulina suturalis* Zone which roughly corresponds to the latest Early Badenian (late Langhian). Consequently, the precise stratigraphic position within the Badenian remains unresolved (see also Szczechura 2006).

Text-fig. 2. Palaeogeography of Central Paratethys in the late Badenian. Modified after Kováč *et al.* (2007) and Bartol *et al.* (2014). Asterisks mark fossiliferous sites yielding bivalve material discussed and illustrated in this paper: 1 – Kamienica Nawojowska and Niskowa, Nowy Sącz Basin, Poland; 2 – Borský Mikuláš and Rohožník, Vienna Basin, Slovak Republic

This new outcrop is very rich in a mollusc fauna that occurs mainly in homogenous, poorly consolidated silty mudstones, greenish and dark grey in colour cropping out along the left bank of the river (Bitner and Kaim 2004; Gonera 2012). It has yielded a moderately diverse bivalve fauna dominated by the well-preserved *Anadara diluvii* (Lamarck, 1805), *Anadara turonica* (Dujardin, 1837) and *Linga columbella* (Lamarck, 1818). The bivalve collection which is the topic of this study was gathered from this new site and donated by Professor Wacław Bałuk to the Polish Academy of Sciences, Museum of the Earth in Warsaw. The bivalves are represented either by disarticulated and fragmented valves or by articulated shells with well-preserved ornamentation. The studied material reveals articulated shells of *Anadara diluvii* (Lamarck, 1805), *Anadara turonica* (Dujardin, 1837), *Glycymeris deshayesi* (Mayer, 1868), *Gibbomodiola adriatica* (Lamarck, 1819), *Oppenheimopecten revolutus* (Michelotti, 1847), *Flabelipecten besseri* (Andrzejowski, 1830), *Talochlamys multistriata* (Poli, 1795), *Pelecyora* (*Cordiopsis*) *islandicoides* Lamarck, 1818, *Venus nux* Gmelin, 1791 and *Circomphalus subplicatus* (d'Orbigny, 1852).

The unique feature of the studied bivalves, however, is the occurrence of large (with a length up to 72 mm and a height up to 70 mm), still articulated shells of *A. ephippium*. Among these shells, two possess a greatly enlarged and calcified byssal plug (aragonite and calcite) retained inside an embayment in the right valve. In addition, newly collected material contains several calcified byssi, which had attached the animal securely to a rigid substrate.

The investigated material comes from the Nowy Sącz Basin and includes both new material and that derived from Niskowa by Bałuk (1970). Other specimens studied herein, from the Upper Badenian (lower Serravallian), were obtained from Borský Mikuláš and Rohožník fossiliferous sites in the eastern part of the Vienna Basin in the Slovak Republic (Text-fig. 2). The discussed material is deposited in the Polish Academy of Sciences, Museum of the Earth in Warsaw, Poland (abbr. MZ) under the catalogue numbers MZ VIII Ml-2821 and MZ VIII Ml-3988 to MZ VIII Ml-3992.

SYSTEMATIC DESCRIPTION

Class Bivalvia Linnæus, 1758
Subclass Autobranchia Grobben, 1894
Superorder Pteriomorphia Beurlen, 1944
Order Pectinoida Gray, 1854
Superfamily Anomioidea Rafinesque, 1815
Family Anomiidae Rafinesque, 1815
Genus *Anomia* Linnæus, 1758

TYPE SPECIES: *Anomia ephippium* Linnæus, 1758, by subsequent designation of Schmidt, 1818.

Anomia ephippium Linnæus, 1758
(Text-figs 3–7)

1870. *A.* [*nomia*] *costata* Brocchi; A. Reuss in M. Hörnes, pp. 462–464, pl. 85, figs 1–7.
1956. *Anomia* (*Anomia*) *ephippium* Linnæus, 1767; J. Tejkal, pp. 278, 279, pl. 5, figs 4–6.
1970. *Anomia* (*Anomia*) *ephippium rugulosostriata* Bronn; W. Bałuk, pl. 3, figs 1a, b.
1981. *Anomia* (*Anomia*) *ephippium rugulosostriata* (Bronn, 1831); J. Švagrovský, p. 404, pl. 2, fig. 5.
1998. *Anomia* (*Anomia*) *ephippium rugulosostriata* Brocchi in Bronn; B. Studencka *et al*., pp. 296, 297.
1998. *Anomia* (*A.*) *burdigalensis* (Defrance); B. Studencka *et al*., pp. 296, 297.

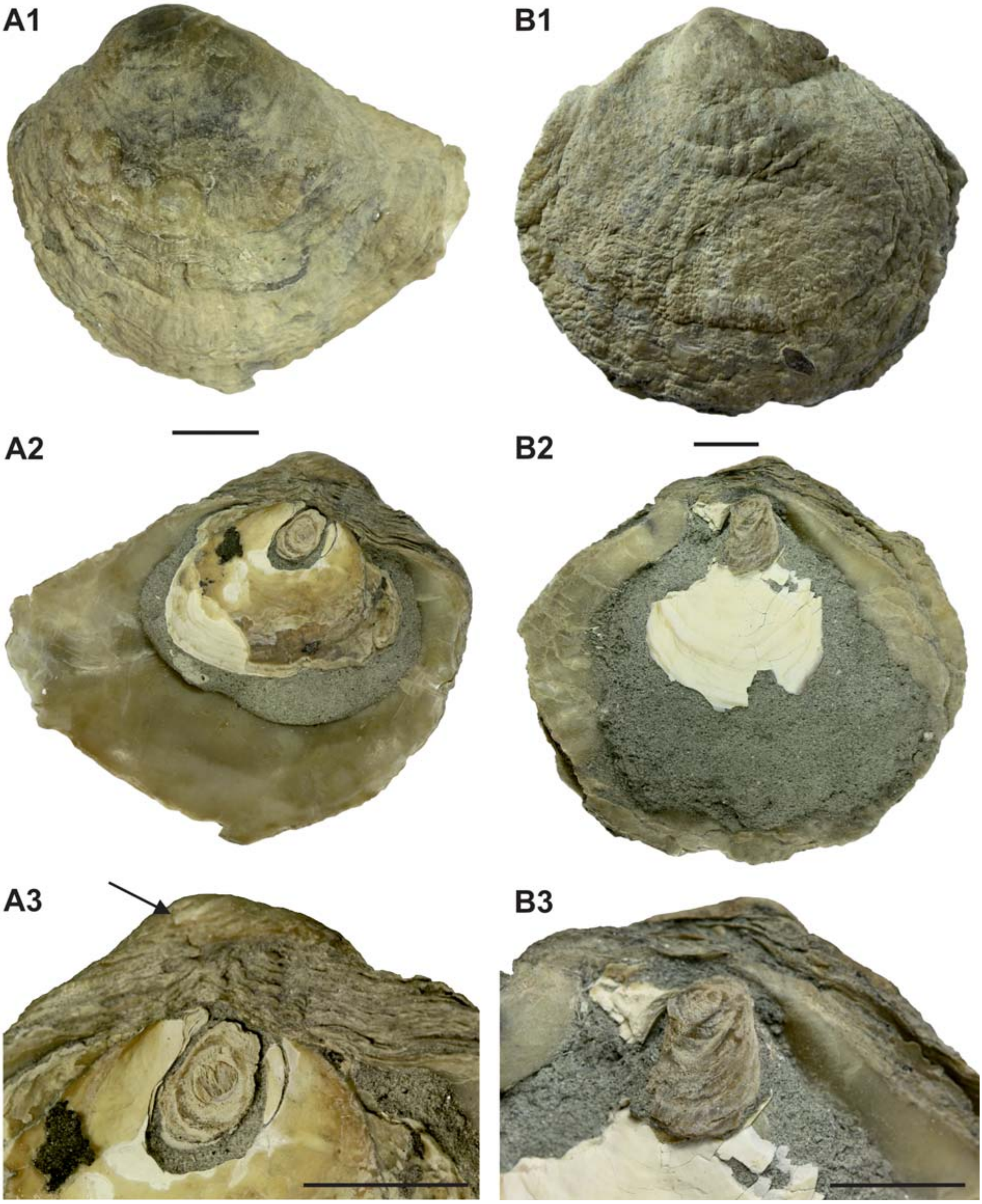
MATERIAL EXAMINED: Kamienica Nawojowska site, Nowy Sącz Basin, Poland (MZ VIII Ml-3990): 7 articulated shells (28 mm to 72 mm long), one partly preserved right (lower) valve attached to the left valve of *Oppenheimopecten revolutus* (Michelotti, 1847) and 90 left valves (9 mm to 72 mm long), as well as 13 heavily mineralised byssi still fixed to a rigid substrate; Niskowa, Nowy Sącz Basin, Poland (MZ VIII Ml-2821): 23 poorly preserved left valves (8 mm to 14 mm long) and two large left valves incompletely preserved that are about 45 mm long and 40 mm high; Borský Mikuláš, Vienna Basin, Slovakia (MZ VIII Ml-3989): 93 left valves (4 mm to 60 mm long) and one valve with a byssal plug attached to its external surface; Rohožník, Vienna Basin, Slovakia (MZ VIII Ml-3391): 5 left valves (25 mm to 40 mm long) and one byssal plug attached to the external surface of one valve.

DESCRIPTION: Shell markedly inequivalve, highly variable and often irregular in shape, depending upon the hard substrate to which it is attached by means of a calcified byssus, commonly called a byssal plug. Moderately large; length up to 72 mm, height up to 70 mm. It is unusual that among seven articulated shells of *A. ephippium* from the Kamienica Nawojowska site, two shells show a strong byssal plug still inside the byssal notch (Text-fig. 3). This feature, mostly unexpected in fossil record, allows observing the basal part of the byssal plug that anchored the animal to hard substrates.

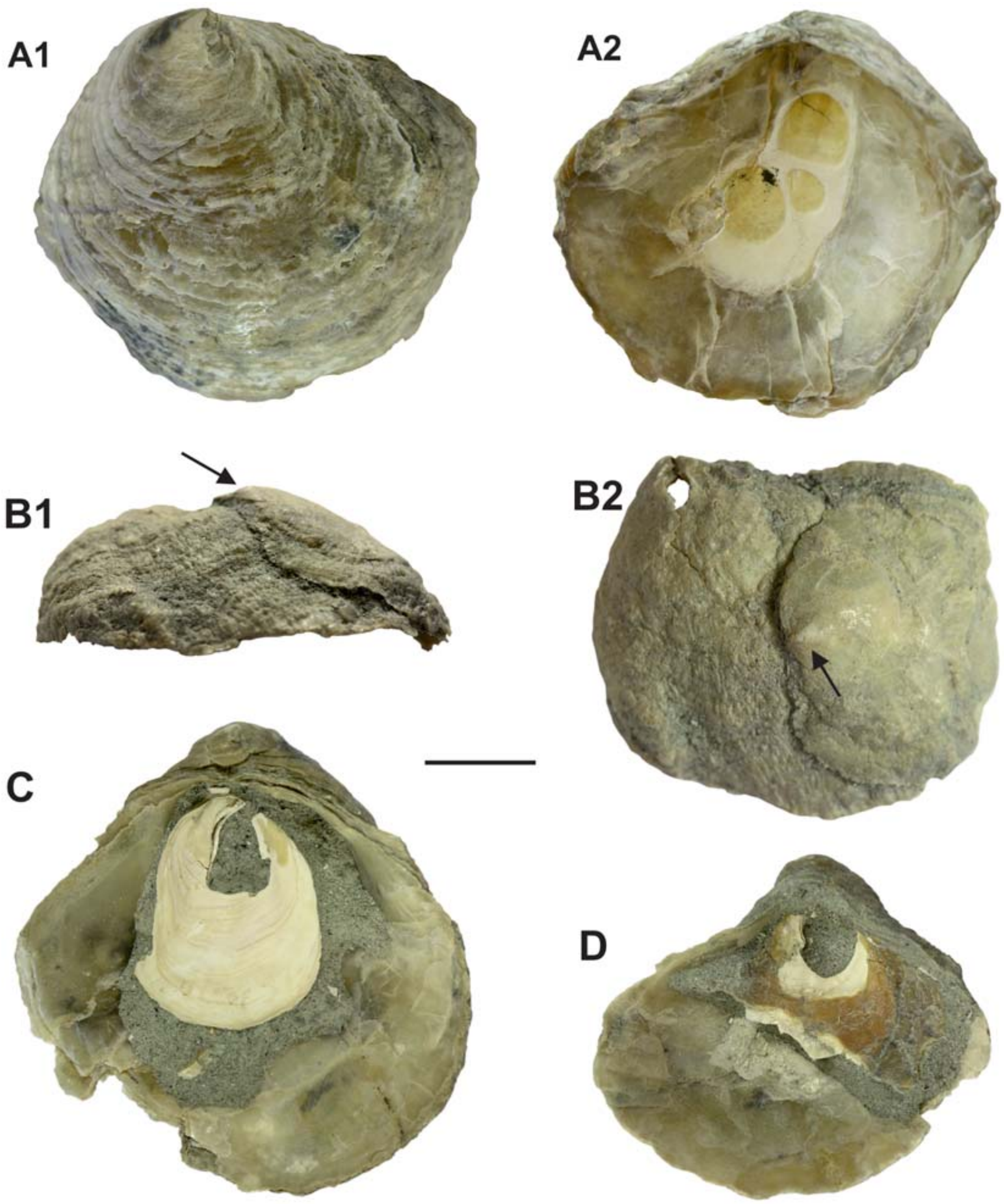
Right valve thin and fragile, flat or concave, with oval byssal notch near umbo, through which the calcified byssal plug projected. External surface ornamented with delicate concentric lines. Growth stages not clear. Internal surface of right valve not observed. However, where the outer shell layer has been totally or partly removed, inner layer is observed, restricted to central region surrounding the byssal notch (Text-figs 3A2, 3B2, 4C, 4D). Aragonitic, porcelaneous microstructure is characteristic for this oval white area, whereas calcitic simple prismatic structure constitutes the outer layer of right valve. Calcitic simple prisms retained only in the adult right valve, whereas foliated struc-

Locality	Specimen no.	Length	Height	Illustration
Kamienica Nawojowska	MZ VIII Ml-3990/1	72	64	Text-fig. 3B1–B3
	MZ VIII Ml-3990/2	67	>60	Text-fig. 5D1–D3
	MZ VIII Ml-3990/3	57	44	Text-fig. 3A1–A3
	MZ VIII Ml-3990/4	40	44	Text-fig. 4C
	MZ VIII Ml-3990/5	40	37	Text-fig. 4A1–A2
	MZ VIII Ml-3990/6	35	32	Text-fig. 4D
	MZ VIII Ml-3990/7	32	32	Text-fig. 4B1–B2
	MZ VIII Ml-3990/8	20	31	Text-fig. 5B
	MZ VIII Ml-3990/9	19	23	Text-fig. 5C
Borský Mikuláš	MZ VIII Ml-3989/1	59	55	Text-fig. 5E1–E2
Rohožník	MZ VIII Ml-3991/1	29	36	Text-fig. 5A

Table 1. Lengths and heights (in mm) of illustrated left valves of *Anomia ephippium* Linnæus, 1758 with repository numbers and localities



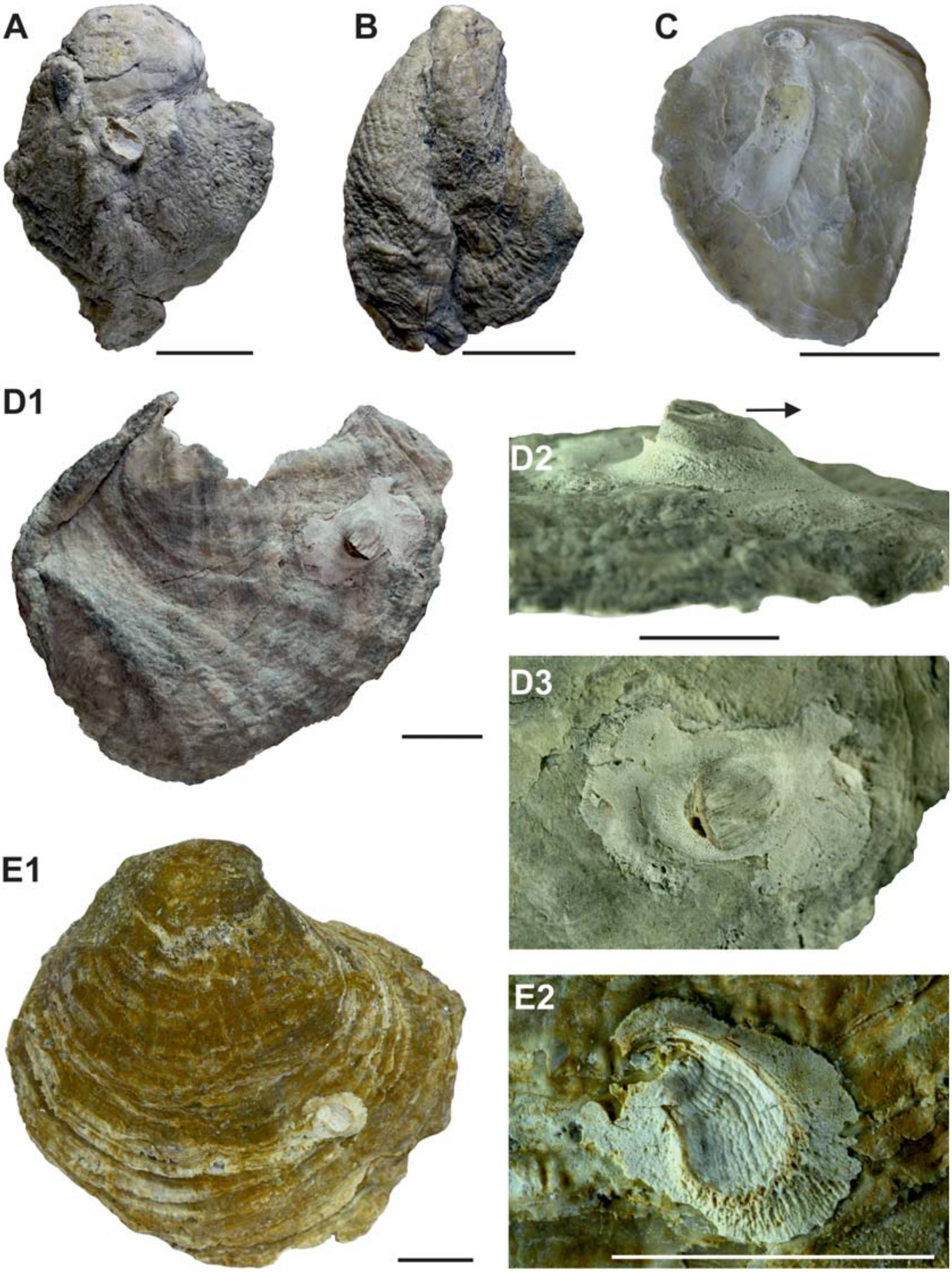
Text-fig. 3. Articulated shells of *Anomia ephippium* Linnæus, 1758 from Kamienica Nawojowska. A1-A3 – Specimen (MZ VIII Ml-3990/3). A1 – View from the markedly inequilateral, convex left (upper) valve; A2 – The same specimen viewed from the partly preserved right (lower) valve, with well-developed calcified byssal plug projecting through the oval byssal hole; A3 – Enlarged view of the area around byssal notch presented on A2. Arrow shows the very small beak of the left valve; B1-B3 – Specimen MZ VIII Ml-3990/1. B1 – View from almost circular, slightly convex left valve; note replicated ornament of its substratum, most probably of the left valve of *Oppenheimopecten revolutus* (Michelotti, 1847); B2 – The same specimen with partial remnants of the right valve (only the prismatic aragonite inner shell layer) and large calcified byssus; B3 – Enlarged view of the byssal region presented on B2. Scale bars = 10 mm. Photographs by D. Nast



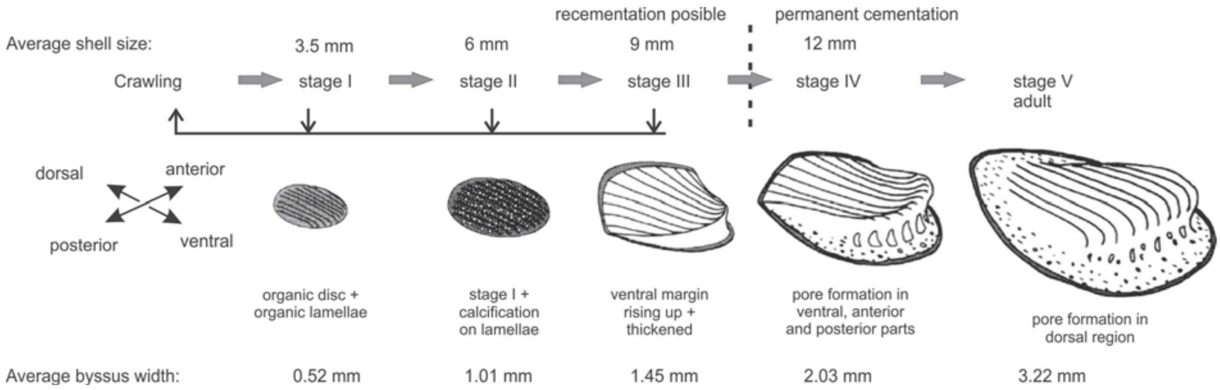
Text-fig. 4. *Anomia ephippium* Linnæus, 1758 from Kamienica Nawojowska. A1-A2 – Specimen MZ VIII Ml-3990/5. A1 – External view of the left valve with small beak clearly seen; A2 – Internal view of the same specimen with single adductor muscle scar clearly seen and two byssal retractor muscle scars above it. B1-B2 – Specimen MZ VIII Ml-3990/7 in life position, preserved on its original substratum, fixed to the left valve of another specimen of the same species. Arrows show the very small beak of the left, attached valve; B1 – Ventral view of the left, larger valve; B2 – Exterior view of two specimens. C – Specimen MZ VIII Ml-3990/4. Articulated shell viewed from the fragmentarily preserved right valve. Only white inner aragonitic shell layer retained. D – Specimen MZ VIII Ml-3990/6. Articulated shell viewed from the fragmentarily preserved right valve with oval byssus notch. Close to the byssal hole the white inner aragonitic shell layer is visible below the very thin prismatic outer shell layer. Scale bar = 10 mm. Photographs by D. Nast

ture constitutes the outer layer of the adult left valve (see also Carter 1990).

Left valve bigger and more solid than right valve, entirely overlapping right valve and quite markedly convex. Most specimens irregular in outline, with tendency to be somewhat trigonal, with the posterior end longer and pointed. Very small, orthogyrate beak not prominent, tending to be central in juveniles,



Text-fig. 5. *Anomia ephippium* Linnæus, 1758 from Rohožník (A), Kamienica Nawojowska (B-D) and Borský Mikuláš (E). A – Specimen MZ VIII Ml-3991/1. External view of the left valve with the calcified byssus of another individual of the same species firmly attached. B – Specimen MZ VIII Ml-3990/8. External view of tumid left valve with highly irregular sculpture. C – Specimen MZ VIII Ml-3990/9. Internal view of small, flat left valve with, clearly visible, the well developed half-moon-shaped pit for the internal ligament. D1-D3 – Specimen MZ VIII Ml-3990/2. D1 – External view of left valve, damaged in its umbonal region, with xenomorphic (scallop) ornament developed; D2 – Lateral view of calcified byssal plug along ventral-dorsal line; arrow oriented towards dorsal margin of attached shell; D3 – Plan view of byssal plug showing its aragonitic lamellar part surrounded by extensive calcite porous structure. E1-E2 – Specimen MZ VIII Ml-3989/1. E1 – External view of the left valve; E2 – Twisted byssus aragonitic lamellae indicating that attached specimen moved its shell by gradually changing its byssal growth direction. Scale bars =10 mm. Photographs by D. Nast



Text-fig. 6. Five stages in the development of the juvenile byssus of *Anomia chinensis* Philippi, 1848. Not to scale. Adopted from Yamaguchi (1998)

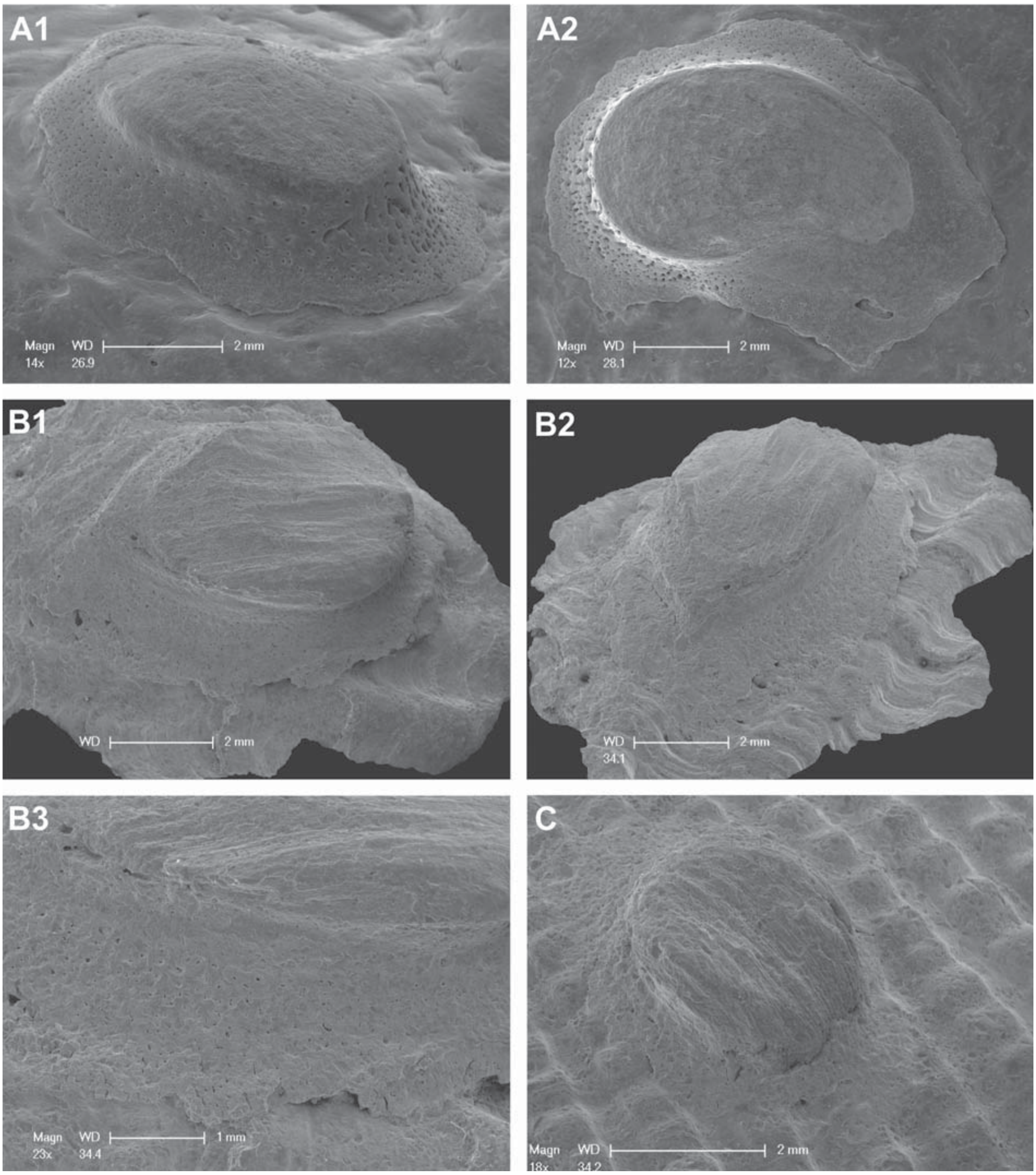
reinforced in the same specimens by an occasionally preserved white, smooth pseudoprodissoconch (Text-fig. 4A1, B2). Specimens regularly oval to circular in outline and those tumid and drop-like in outline less common in the material from Kamienica Nawojowska. Sculpture of left valve extremely variable, ranging from fine, densely spaced concentric lines or with delicate, undulated radial lines to moderately coarse imbricated, concentric lamellae. In the largest specimen studied, irregular, coarse, somewhat foliaceous concentric sculpture also observed. External surface dark grey (Kamienica Nawojowska and Rohožník) to yellowish-brown (Borský Mikuláš) in colour (Text-fig. 5E1), sometimes with white concentric belts variable in width. Growth stages usually clear except in largest specimens. Many specimens showing additional xenomorphic sculpture: irregularities of the substrate may be perfectly mirrored in the left valve. Such markings may be oblique to the normal direction of the valve sculpture, depending upon the position in which it became attached (Text-figs 3B1, 5D1). On a flat substrate such as scallop shell, left valve is only gently convex; the shell was extremely flattened (Text-fig. 5D1).

Hinge line without teeth. Ligament internal located in deep, well developed half-moon-shaped pit, just below the umbo (Text-fig. 5C). Interior of left valve, glossy light brown in colour, very characteristic with three scars arranged in a triangle within its central white area made of aragonite (Text-figs 4A2, 5C). Large adductor muscle scar placed beneath divided byssal retractor muscle scars: the uppermost is the largest, the other, central small in size. Furthermore, an additional small, almost circular muscle scar situated just ventrally to the anterior end of the resilifer clearly seen on several specimens. Byssal retractor muscle scars best seen opposite byssal notch. Pallium line impression not visible. Ventral margin smooth.

REMARKS ON THE BYSSUS DEVELOPMENT: Several tough calcified byssi still fixed to other specimens of *A. ephippium* occur in the material from Borský Mikuláš, Kamienica Nawojowska and Rohožník. In the material from Kamienica Nawojowska occur also calcified byssi that had been attached to heavily fragmented valves of *Anadara diluvii* (Lamarck, 1805) and/or *Anadara turonica* (Dujardin, 1837), and scallops, most probably attached to *Flabellipecten besseri* (Andrzejowski, 1830) or *Oppenheimopecten revolutus* (Michelotti, 1847).

As demonstrated by Yamaguchi (1998) and Leemreize *et al*. (2013) the byssus of both present-day *A. chinensis* Philippi, 1848 and *A. simplex* d'Orbigny, 1853 has a highly complex hierarchical structure, where both aragonite and calcite are present. It consists of a lamellar part (made of aragonite) that forms the interface with the musculature of the animal, and a porous part (made of calcite) closer to the substrate. The two structures are best recognised in the fossil material of *A. ephippium* from Kamienica Nawojowska and Rohožník. According to Yamaguchi (1998) byssus development takes place in five distinct stages (Text-fig. 6). All studied fossil byssi represent the fifth, adult stage of the byssus with the porous calcitic layer surrounding the entire base of the lamellar aragonitic part. Since the main function of the pores is to supply an adhesive to the bottom of the byssus, the difference in size of the porous calcitic part may be related to the size of the adult shell (see Text-figs 3A3, 5A, D1–D3, 7B1–B3, C).

The study of Yamaguchi (1998) shows that, con-



Text-fig. 7. SEM microphotographs of calcified byssal plugs attached to a Recent specimen of *Anomia ephippium* Linnæus, 1758 from the Portuguese coast of the Atlantic (A) and to the Badenian specimens of *Anadara diluvii* (Lamarck, 1805) and *Anadara turonica* (Dujardin, 1837) from the Kamienica Nawojowska site (B-C). A1-A2 – Specimen MZ VIII Ml-3986/1. A1 – Lateral view; A2 – Plan view. B1-B3 – Specimen MZ VIII Ml-3990/10. B1 – Lateral view; B2 – Dorsal view; B3 – Higher magnification of B1, showing aragonitic lamellae structure and a calcitic porous region in lateral view. C – Specimen MZ VIII Ml-3990/11 in plan view. Photographs by A.M. Bitner

trary to earlier assumptions (e.g., Yonge 1977), even adult individuals of *A. chinensis* byssally attached to the substrate can rotate their shells by gradually changing the byssal growth direction. In this case, instead of being almost straight and parallel to the long axis of the byssal notch, twisted byssi with curved lamellae may form. Such byssal shapes also occur in the material studied (Text-fig. 5E1, E2). Thus, following the work of Yamaguchi (1998), it is likely that also *A. ephippium* might have applied the same type of mobility as *A. chinensis*.

It should be added that no etched traces of the valve margins, corresponding to the ichnospecies *Centrichnus eccentricus*, have been observed on the surface of specimens with attached calcified byssi.

REMARKS ON THE TAXONOMY: The Kamienica Nawojowska material includes specimens that can be matched closely with the subspecies *costata*, *hoernesi*, *rugulosostriata* and *pergibbosa* as indicated by Schultz (2001). The studied material allows for the proposition that the shells of *A. ephippium*, which lived permanently attached to the rigid substrate or to other shells, show a xenomorphic sculpture strongly reflecting that of its host. Thus, both ornamentation characters and shape may perfectly imitate irregularities of the substrate, and in fact, are obviously insufficient to warrant subspecies separation. According to the World Register of Marine Species, as many as 24 specific names were created for the modern species *A. ephippium* having considerable variation in shape, sculpture and colour. Among them there are also Philippi's *aspera* and Brocchi's *costata* species, regarded by Schultz (2001) as the subspecies of Linnæus' species *ephippium*.

In spite of the fact that *A. ephippium* was widely dispersed in the Central Paratethys (see Schultz, 2001) during the middle Miocene, its occurrence in Poland has been nearly exclusively limited to the Niskowa Formation in the Nowy Sącz Basin. Outside this area only one left valve (specimen MZ VIII Ml-3992; 21 mm in height) was found in the Lower Badenian (correlated with the upper Langhian) Korytnica Clays in the Polish part of the Carpathian Foredeep Basin. As pointed out by Studencka (1986), the juvenile specimens from Korytnica and those from the Upper Badenian (lower Serravallian) of Roztocze Hills (Monastyrz and Długi Goraj), unfortunately assigned by Jakubowski (1972, 1977, respectively) to *A. ephippium rugulosostriata* Brocchi in Bronn, 1831, have been confused with *Heteranomia squamula* (Linnæus, 1758).

STRATIGRAPHIC AND GEOGRAPHIC RANGE: Early Oligocene (Anderson 1959) to Recent (Tebble 1966). The species, which originated in the North Sea Basin during the Early Oligocene (early Rupelian of Germany; Anderson 1959) later dispersed into other parts of the North Sea Basin and the Central Paratethys. It has been documented in the Chattian of Germany, where it was reported in older literature under the name *Anomia goldfussi* Deshayes, 1861 (records and synonyms in Janssen 1979), and in the Egerian (latest early Oligocene–earliest Miocene) of Hungary (Báldi 1973).

The presence of *A. ephippium* in both the Atlantic and Mediterranean provinces is confirmed at least since the early Miocene. It has been documented in the Aquitanian of the Loire Basin, France (Dollfus and Dautzenberg 1920) and in the Burdigalian of the Lower Tagus Basin, Portugal (Zbyszewski 1957). In the Mediterranean province, *A. ephippium* has been reported (as the *rugulosostriata* and *pergibbosa* varieties) from the Aquitanian of the Turin Hills, Italy (Sacco 1897). It is also known from the early Miocene of Paratethys. Its presence was documented in the Eggenburgian (correlated with uppermost Aquitanian–lower Burdigalian) of the Eastern Alpine Foreland Basin, Austria (Schaffer 1910; Schultz 2001).

In the middle Miocene, the species was definitely rare in the Fore-Carpathian basins in Poland (Jakubowski's collection housed in the Polish Academy of Sciences, Museum of the Earth in Warsaw), Ukraine (Friedberg 1936) and Bulgaria (Kojumdgieva 1960). In contrast, it seems to have been widely spread in the intra-Carpathian basins of the Central Paratethys, yet formed a relatively rare component of the faunas (e.g., in Romania: Moisescu 1955; in the Czech Republic: Tejkal 1956; in Austria: Schultz 2001). The only exception is Borský Mikuláš in Slovakia, where thousands of left valves have been found (Švagrovský 1981; Švagrovský's collection stored at the Department of Geology and Paleontology, Comenius University in Bratislava). In the Eastern Paratethys it has been reliably reported from as far as east Turkmenistan and Kazakhstan (Merklin and Nevesskaja 1955).

Furthermore, *A. ephippium* has been reported from the Pliocene of both the Mediterranean (Spain: Lozano-Francisco 1997; Italy: Brambilla 1976; Morocco: Ben Moussa 1994) and the Atlantic provinces (France: Lauriat-Rage 1981), and from the Pleistocene of the Mediterranean (Italy: Cerulli-Irelli 1907 as the *aspera* and *Hörnesi* varieties; Rhodes, Greece: Bromley 1999).

Presently, *A. ephippium* is a widespread species, ranging from Iceland in the north to the Mediterranean region in the south and along the Atlantic coast of Morocco to Ghana. It is common in the Mediterranean Sea and the Black Sea. Its occurrence is also reported from the South Atlantic off to Falkland, Nightingale and Gough isles (Tristan da Cunha group of isles) (Tebble 1966).

CONCLUSIONS

Articulated shells and calcified byssi of *Anomia ephippium* have been found in bivalve assemblages from the Badenian Niskowa Formation at the Kamienica Nawojowska site in the Nowy Sącz Basin (Polish Outer Carpathians). This discovery is of great interest because it proves to be the oldest finding of complete shells of this species.

The study of the fossil *A. ephippium* has revealed that the structure of its calcified byssus is similar to those of *A. chinensis* and *A. simplex* (Yamaguchi 1998; Leemreize *et al.* 2013). All studied fossil byssi represent the fifth stage of Yamaguchi (1998). Furthermore, the presence of the byssus with twisted aragonitic lamellae implies also that adult individuals of *A. ephippium* might have applied the same type of mobility as *A. chinensis*.

The shells of *A. ephippium* show a xenomorphic sculpture strongly reflecting that of its host. Thus, both ornamentation characters and shape may perfectly imitate irregularities of the substrate, and are obviously insufficient to warrant subspecific separation.

The presence of the large articulate shells of *A. ephippium* together with the delicate shells of byssally attached *Gibbomodiola adriatica* and *Talochlamys multistriata*, as well as with large shells of free moving bottom dwelling *Oppenheimopecten revolutus* and *Flabelipecten besseri*, which show no evidence of post-mortem transport, such as disarticulation, fragmentation or physical erosion of the shell surface, suggests that they have been buried without significant transport.

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