

Changes in bivalve assemblages at the onset of the OAE2 event in the Peri-Tethyan area (Bohemian Cretaceous Basin)



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ABSTRACT

The Ocean Anoxic Event (OAE2) at the Cenomanian-Turonian boundary presents a unique record of gradual global warming and its effects on benthic organisms. The present research considers a palaeoecological, systematical and statistical evaluation of bivalve assemblages from the Pecínov Member in the Bohemian Cretaceous Basin. The well-exposed succession of Cenomanian through lower Turonian strata contains one of the most complex records of the OAE2 in central Europe. In total, 392 specimens have been studied and assigned to 24 genera within 21 families and 9 orders. The bivalve association prior to the positive shift of the $\delta^{13}\text{C}_{\text{org}}$ (peak “a” *sensu* global carbon curve; lower part of the *Metoicoceras geslinianum* Zone) is strongly dominated by infaunal suspension feeders, followed by semi-infaunal suspension feeders. The near-absence of free-living epifaunal bivalves may be linked to a very fine, muddy substrate and water turbidity, a limiting factor for many epifaunal species. Infaunal deposit feeders are also present but comparatively rare, indicating a nutrient-rich environment with energy levels sufficiently high to keep organic matter in suspension. The *Cucullaea glabra* – *Pseudoptera anomala* assemblage of this level is considered to have formed during normal, shallow (15–20 m, supported by abundant material of *Pinna*) marine conditions. The association inhabiting the area above this level (upper part of the *M. geslinianum* Zone, *S. gracile*/*E. septemseriatum* Subzone) is characterized by the *Panopea gurgitis* – *Rhynchostreon suborbiculatum* assemblage suggesting considerably shallower depths and higher energy. Clusters of *Modiolus* and small oysters characterize the upper parts directly prior to the prominent positive $\delta^{13}\text{C}_{\text{org}}$ peak “b” (the major peak of OAE2 CIE; ? base/lower part of the *N. juddii* Zone). No benthic fauna occurs above this level.

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1. Introduction

The Bohemian Cretaceous Basin (BCB) is a large sedimentary basin located in the Czech Republic and Germany (Bohemian-Saxonian Basin in wider context). The basin was situated in a unique palaeobiogeographical location, positioned between the Peri-Tethyan shelf and the northern Boreal basins (Wiese et al., 2004; Košťák et al., 2020). This location allowed for the exchange of marine fauna between the Tethyan and Boreal Realms, resulting in a diverse and distinct biota.

Of high interest there are the upper Cenomanian strata, especially the second Ocean Anoxic Event (OAE2). One of the most suitable localities of these strata is the Pecínov working quarry (N

50°7.76', E 13°55.03' coordinates, Fig. 1) in central Bohemia. The OAE2 interval at the Pecínov quarry corresponds to ca 7 m thick Pecínov Member of local lithostratigraphic terminology (Uličný et al., 1997a). Excellent exposure of these strata at the quarry has been investigated in great detail by several authors in the past (Uličný et al., 1993, 1997a, 1997b, 2009, 2014; Košťák et al., 2018). Stratigraphically well-constrained framework represented by high-resolution $\delta^{13}\text{C}_{\text{org}}$ data, ammonite, and inoceramid biostratigraphy is, therefore, a very good basement for further studies, including bivalve assemblages presented in this paper. However, the faunal response to the OAE2 event is still poorly studied and understood. Except for ammonites, inoceramids (Čech et al., 2005; Košťák et al., 2018) and partly rudists (El-Shazly et al., 2011; Krížová et al., 2022), almost no other studies of macro-fauna have been published from this area (BCB) yet.

The studied interval also represents the highest sea-level rise during the geological time, significantly affecting micro- and macrofaunal record changes. The impact of the OAE2 on

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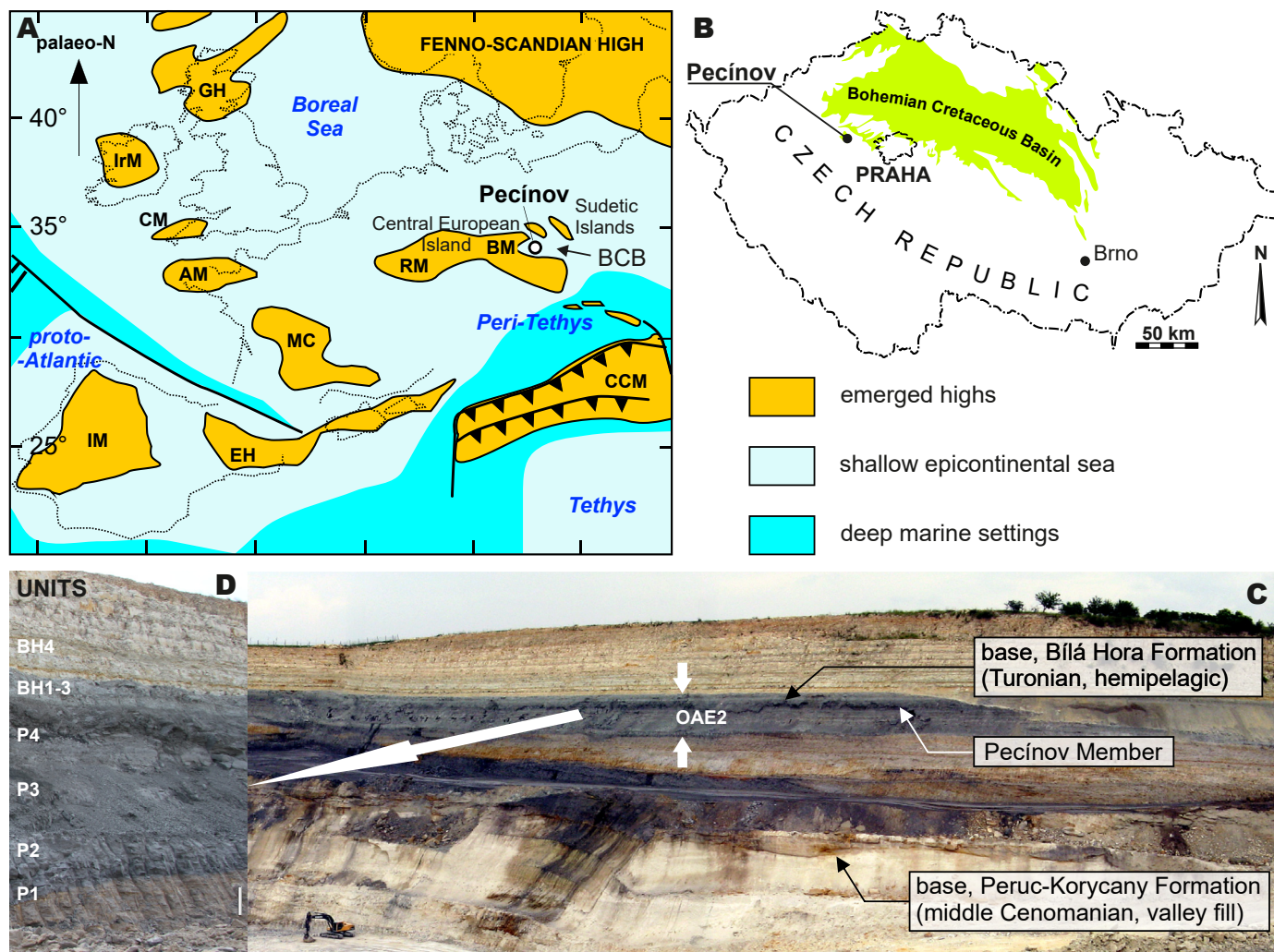


Fig. 1. A. The palaeogeographic map of NW and central Europe showing position of the BCB at the northernmost Peri-Tethyan margin. Emerged landmasses abbreviations: AM – Armorican Massif, BM – Bohemian Massif, CM – Cornubian Massif, CCM – Central Carpathian Massif, EH – Ebro High, GH – Grampian High, IM – Iberian Massif, IrM – Irish Massif, MC – Massif Central, RM – Rhenish Massif. B. Position of the BCB within the Czech Republic with marked Pecínov quarry location. C. Photo of the Pecínov working quarry. D. Detailed photo of units within the Pecínov Member (Peruc-Korycany Formation, Cenomanian) and lower part of the Bílá Hora Formation (Lower Turonian): for details see the text and Fig. 2 (Modified after Uličný et al., 2014; Košťák et al., 2018).

macrofauna (significant extinction/faunal turnover) is discussed in numerous papers (Jefferies, 1963; Elder, 1987; Harries, 1993; Gale et al., 2000, and others), however, relatively few complex studies are focusing the shallow-water sequences (Nagm, 2015 and references therein). In this point, the Pecínov quarry provides a unique possibility for the investigation of shallower-water faunal assemblages in relation to both regional and global oceanographic changes. Notably, the shallower-water character of sedimentation persisted up to the major peak of the anoxia in this area and was not influenced by a rapid sea-level rise.

Fossil bivalve assemblages are generally recognized as reliable palaeoecological indicators of the sea bottom environment due to their abundance in the fossil record, para-autochthonous preservation and the valuable information that can be gleaned from their presence. As filter feeders, bivalves play a significant role in ecosystem dynamics and are highly sensitive to environmental changes. Therefore, variations in bivalve species composition, diversity, and abundance can provide essential clues about past environmental conditions such as temperature, salinity, nutrient availability, and substrate type (e.g. Fürsich, 1993; Brenchley and Harper, 1998). Additionally, the functional morphology of bivalves

can reveal specific adaptations to environmental conditions, providing further insight into the ecological context in which they lived (e.g. Stanley, 1970; Vermeij, 1978). The use of bivalves as palaeoecological indicators is significant in marine environments, where they are often one of the most abundant and diverse groups of organisms in the fossil record (Brenchley and Harper, 1998).

The major aim of this study was to investigate bivalve assemblages at the marginal Peri-Tethyan location during the OAE2 event. The research objectives were focused on the diversity and disparity of bivalve complexes and their relation to lithological content and the $\delta^{13}\text{C}_{\text{org}}$ variations. The priority questions were: Have they seen some diversity/trophic changes prior to, during and post- OAE2 event? If yes, did the diversity/disparity change significantly, and how did they correspond to the upcoming peak of anoxia? Another point was to try to reconstruct bathymetric conditions (in the light of the late Cenomanian sea-level rise) and palaeoenvironment within the OAE2 at the locality Pecínov which represents a key section in the BCB (and central Europe as well) in this interval.

Geological and palaeogeographical settings are provided in great detail by Uličný and Špičáková (1996), Uličný et al. (1997a, 1997b; 2009), Čech (2011) and Košťák et al. (2018).

2. Stratigraphy

2.1. Biostratigraphy

The majority of sampled specimens come from Unit P1(b-f) *sensu* Košťák et al. (2018, Fig. 2). This interval is characterized by a relatively rich ammonite assemblage, including index taxon *Metoicoceras geslinianum*, other important taxa are represented by *Lotzeites aberrans*, *Calycoceras naviculare* and others – suggesting the lower part of the *M. geslinianum* Zone. New sampling (2020–2021) specified the stratigraphic position of *C. naviculare*, which has been recorded just at the P1 and P2 boundary (base of the glauconitic horizon). Compared to the reference sections (e.g. Pueblo GSSP and Eastbourne, England; Gale et al., 2005; Jarvis et al., 2006), the FO of this taxon is newly shifted upwards – i.e. closer to the beginning of $\delta^{13}\text{C}_{\text{org}}$ peak “a” and simultaneously to the beginning of the Plenus Cold event (PCE – after belemnite *Praeaetionocamax plenus* (de Blainville, 1827); see discussion below, 5.6. PCE in the Pecínov section). Inside the new material, we have recorded one additional ammonite taxon, *Puzosia dibleyi* (not figured herein), increasing ammonite diversity within the P1 unit. Inoceramids are represented by *Inoceramus pictus* (Sowerby, 1829) and *Inoceramus* sp. aff. *M. praeturonicus* (Košťák et al., 2018) clearly indicating *I. pictus* Zone.

The overlain glauconitic horizon (unit P2a) yields *Euomphaloceras septemseriatum* (FO), *Allocrioceras annulatum* (FO), *Sciponoceras gracile* (FO) and others. The co-occurrence of *E. septemseriatum* with abundant *S. gracile* (P2a-P2e) represents *E. septemseriatum*/*S. gracile* subzone, within the upper part of the *M. geslinianum* and *I. pictus* Zones. It is worth mentioning that the overlying *Neocadioceras juddii* Zone (base of the P3 unit) is not yet supported by an ammonite record but is clearly indicated by the excursion of the $\delta^{13}\text{C}_{\text{org}}$ curve (see below).

2.2. Isotopic record – chemostratigraphy

The isotopic record $\delta^{13}\text{C}_{\text{org}}$ is well supported by data of Uličný et al. (1997a, 1997b, 2009) and slightly supplemented by Košťák et al. (2018). While the lower part of the section – e.g. unit P1 shows consistent values reaching -25.8‰ to -25.2‰ and -25.2‰ (V-PDB) at the glauconitic base of the P2 unit. At the top of the P2a, a first visible positive excursion of the carbon-isotope curve (-24.3‰) is linked to the $\delta^{13}\text{C}_{\text{org}}$ peak “a” OAE2 (Jarvis et al., 2006).

The prominent carbon-isotope excursion (-21.8‰ – peak “b” OAE2 *sensu* Jarvis et al., 2006) is recorded at the base of the P3 unit (P3b), where the macro-faunal record has already disappeared (with the exception of aptychii referred to *Sciponoceras*, Košťák et al., 2018). According to calibrations of $\delta^{13}\text{C}_{\text{org}}$ curves (Pueblo, Eastbourne), this excursion may represent the base/lower part of the *N. juddii* Zone. However, the last macro-faunal assemblages have been recorded at the base of the P2f unit (i.e. slightly below the base of the P3 unit).

Units P3c through the P4 represent the “plateau” with a continuous decrease of $\delta^{13}\text{C}_{\text{org}}$ values, and they do not yield any benthic faunal assemblages.

3. Material and methods, abbreviations

The specimens described in the systematic part of this paper were all collected from the Pecínov quarry during the last few years. More than 170 bivalve specimens have been newly collected and determined; the new material is deposited in the Chlupáč Museum of Earth History, Faculty of Science, Charles University, Prague (ChMHZ). Additionally, the collection of the National

Museum in Prague (NM) was revised. In total, around 400 specimens from the Pecínov member were studied, of which 386 were relevantly assessed and determined to the genus or species level. All measurements and a list of specimens are given in the [Supplementary File](#).

Regular visits to the locality were documented in detail, including photo reports and marking the positions of newly founded specimens. Close attention was also dedicated to the manner of preservation, the orientation of shells in the deposits, their spacing and their position in relationship to each other on the bedding plane.

Specimens from the Pecínov section are preserved only as internal moulds, the shell, whether originally calcitic or aragonitic, is not present (with the exception of *Pycnodonte* shells from the Bílá Hora Fm.). This type of preservation is not ideal as it is not just prone to deformation and even destruction, but it also complicates the determination due to the poor preservation of crucial parts of the shell (e.g. hinge, adductor scars, pallial line, ornamentation).

Individual specimens were gently exposed from the soft sediment by mechanical instruments, predominantly by hand preparation needles. Measurements were taken by digital calliper Vorel TO-15240 in millimetres with official accuracy of ± 0.02 mm. However, due to the manner of preservation, measurements can be only approximate and this accuracy is only theoretical – all measurements were subsequently rounded to the closest integer. For the typical bivalve shells, measurement abbreviations are as follows: A – height, L – length, C – depth. Parameter C is measurable for only a few specimens, as all these individuals show signs of compaction and deformation, these measurements are only approximate. Measurements of Pinnidae follow Bengtson et al. (2017), abbreviations used for this family are: L – height, H – length and W – depth. Parameter W is not measurable for any specimen from the Pecínov section (Fig. 3).

Material is very prone to degradation. The silty sandstones and siltstones are sensitive to changes in humidity and air temperature. When freshly exposed, the material is moist and malleable and, therefore, prone to manual damage and deformation – it needs to be dried in a controlled environment. The material is also susceptible to sulfide decomposition (volume changes and crystallisation of pyrite degradation products) and gypsum crystallization. Following the methodology of the NM (Sklennár et al., 2015), a solution of Acrylic resin Paraloid B72 was applied for the consolidation of the most endangered specimens.

Other abbreviations: FO (first occurrence), LO (last occurrence), BCB (Bohemian Cretaceous Basin), OAE2 (second Ocean Anoxic Event), PCE (Plenus Cold Event), RV (right valve), LV (left valve).

4. Systematic part

Systematics follow Carter et al. (2011) and Bouchet et al. (2010). As those are currently the best multi-disciplinary papers regarding the topics, we do not repeat their systematics up to the family level. Unless updated revision was published lately for the taxa, a combination of online databases, *The Paleobiology Database (PBDB)*, *World Register of Marine Species (WoRMS)* and *MolluscaBase*, was used for the more detailed and updated systematics to the species level. All data adopted were valid up to 12/05/2023. The bivalve shell form terminology, as well as the general morphological features terminology, follows Jain (2017). Genera diagnoses primarily follow Cox et al. (1969) with the exception of newly revised taxa (e.g. *Stegoconcha*) which respect the modern re-assessment. The assemblage comprises only already known taxa – no new species are described in this paper. Only basic synonymy lists are used, containing the most important works with extensive synonymies and more recent papers in relation to the region.

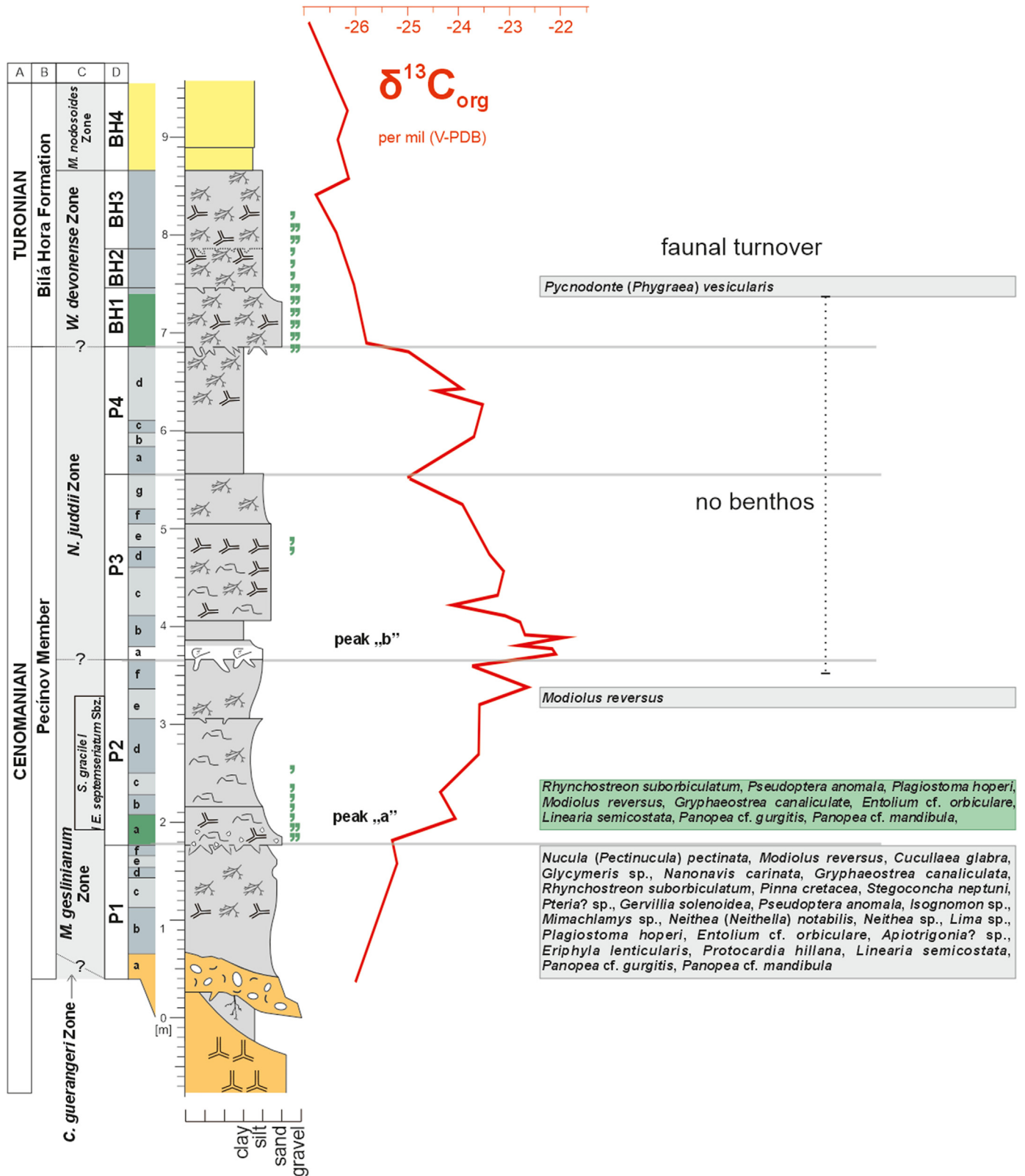


Fig. 2. Ammonite bio-zonation, lithology, lithostratigraphy and the $\delta^{13}C_{org}$ carbon isotope curve (from Košťák et al., 2018; for units description see therein) in relation to bivalve assemblage occurrences. The most diversified bivalve fauna occurs in the Unit P1 (lower part of the M. geslinianum Zone). The decrease in diversity is seen in the lower part of the Unit P2a-c (base of the S. gracile/E. septemseriatum Subzone) resulting to a monospecific assemblage of M. reversus (P2e) just prior the prominent positive peak in the $\delta^{13}C_{org}$ curve. The faunal turnover after OAE2 starts within the BH1–BH3 Units with P.(P). vesicularis. Peaks “a” and “b” of OAE2 CIE (Košťák et al., 2018). Green marks – glauconite.

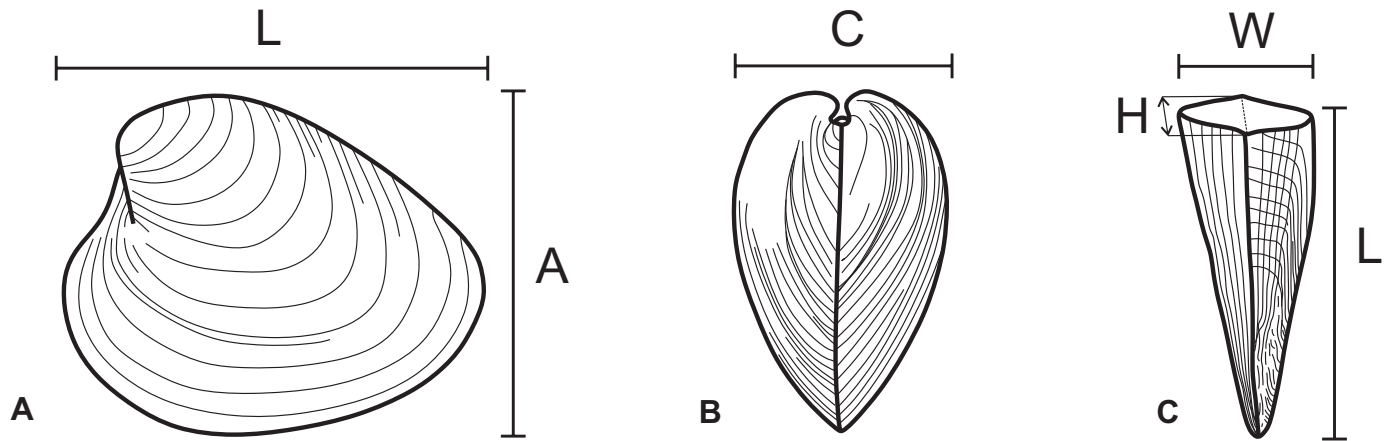


Fig. 3. Orientation and measurements of common shell bivalves: (A) lateral view of the valve (B) dorsal view (modified after Jain, 2017) and (C) orientation and measurements of Pinnidae (modified after Bengtson et al., 2017).

Family Nuculidae J. Gray, 1824

Subfamily Nuculinae J. Gray, 1824

Genus *Nucula* Lamarck, 1799

Type species: *Arca nucleus* Linnaeus, 1758

Nucula (*Pectinucula*) *pectinata* (J. Sowerby, 1812)

Fig. 4A

1879 *Nucula pectinata* Sowerby: Frič, p. 111, fig. 79.

1903 *Nucula pectinata* Sowerby: Woods, p. 16, pl. 2, figs. 22–27; pl. 3, fig. 13 (with extensive synonymy).

1909 *Nucula pectinata* Sowerby: Wanderer, p. 39, pl. 7, fig. 5.

2010 *Pectinucula pectinata* J. Sowerby: Young et al., p. 63, pl. 8, figs. 3–7.

Material. 12 specimens: one closed shell, one articulated, in the butterfly position, ten individual valves (five RVs, five LVs), all from the P1 unit, Peruc-Korycany Fm., Pecínov Member, *M. geslinianum* Zone.

Description. Small (A 8–16 mm, L 11–21 mm; average A 12 mm, average L 15 mm), rounded triangular to trigonal, slightly elongated shell, convex, inequilateral. Rounded, opisthogyrous beak projecting slightly above the hinge line. Anterodorsal and posterodorsal margins long, straight to slightly convex; in symmetrical arc converting into the considerably curved ventral margin. Resilifer present; ligament internal. Fine concentric sculpture with two distinctive radial ribs in approximately two-thirds of the shell. Primary sculpture of very fine, closely-spaced radial riblets recognizable near the ventral margin of a few of the better-preserved specimens. Inner ventral margin crenate. Taxodont hinge preserved and visible on one single specimen (ChMHZ-LK-0006).

Discussion. The *Nucula* genus is very ancient, fossils are known from the Lower Ordovician, and Recent species occur almost worldwide (Keen, 1969). However, the preferred habitat of different species significantly varies; they occur on almost all types of substrata ranging from sand and/or mud to gravel, with the only exception being the rock bottom (Allen, 1954). In modern times, members of the *Nucula* genus are considered ubiquitous infaunal components of silt-clay sublittoral and deep-sea benthic communities (Scheltema and Williams, 2009); in some localities of the New England coast, *Nucula* species account for more than a half of all infaunal organisms in silt-clay sediments (Sanders, 1960). Fossils from the Pecínov quarry are preserved as internal moulds and are more or less laterally or dorsoventrally compressed, however, specimens of *N. pectinata* are manifestly more deformed when in comparison with other species, probably due to having a very

thin and fragile shell easily deformed during the diagenesis. Moreover, according to Allen (1954), the *Nucula* genus shell thickness can be correlated to its habitat – the mud-dwelling species are expected to have the lightest shells.

Dhondt (1987) considered it possible for the specimens of *N. pectinata* from the Saxonian and Bohemian Upper Cretaceous, as well as *N. tenera* Müller, 1847 from the lower Campanian near Aachen, to belong to *N. stachei* Zittel, 1865. However, the preservation of most of these specimens makes definite conclusions impossible. Woods (1903) distinguished them primarily based on ornamentation, which is a simple matter of preservation and not a good distinguishing feature. However, he described the *N. pectinata* from England as different from the ones from central Europe – the latter having the posterior part rounded and relatively long. This description agrees more with *N. semilunaris* (e.g. sensu Frič, 1879) than with the specimens commonly described as *N. pectinata*.

Occurrence. Worldwide during the Cretaceous (Schenck, 1939).

Family Mytilidae Rafinesque, 1815

Genus *Modiolus* Lamarck, 1801

Type species: *Mytilus modiolus* Linnaeus, 1758.

Modiolus reversus (Sowerby, 1836)

Fig. 4B, E

1875 *Mytilus reversa* Sowerby: Geinitz, p. 216, pl. 48, fig. 9.

1903 *Modiola reversa*, Sowerby: Woods, p. 94, pl. 15., figs. 15–18; pl. 16, figs. 1–3 (with extensive synonymy).

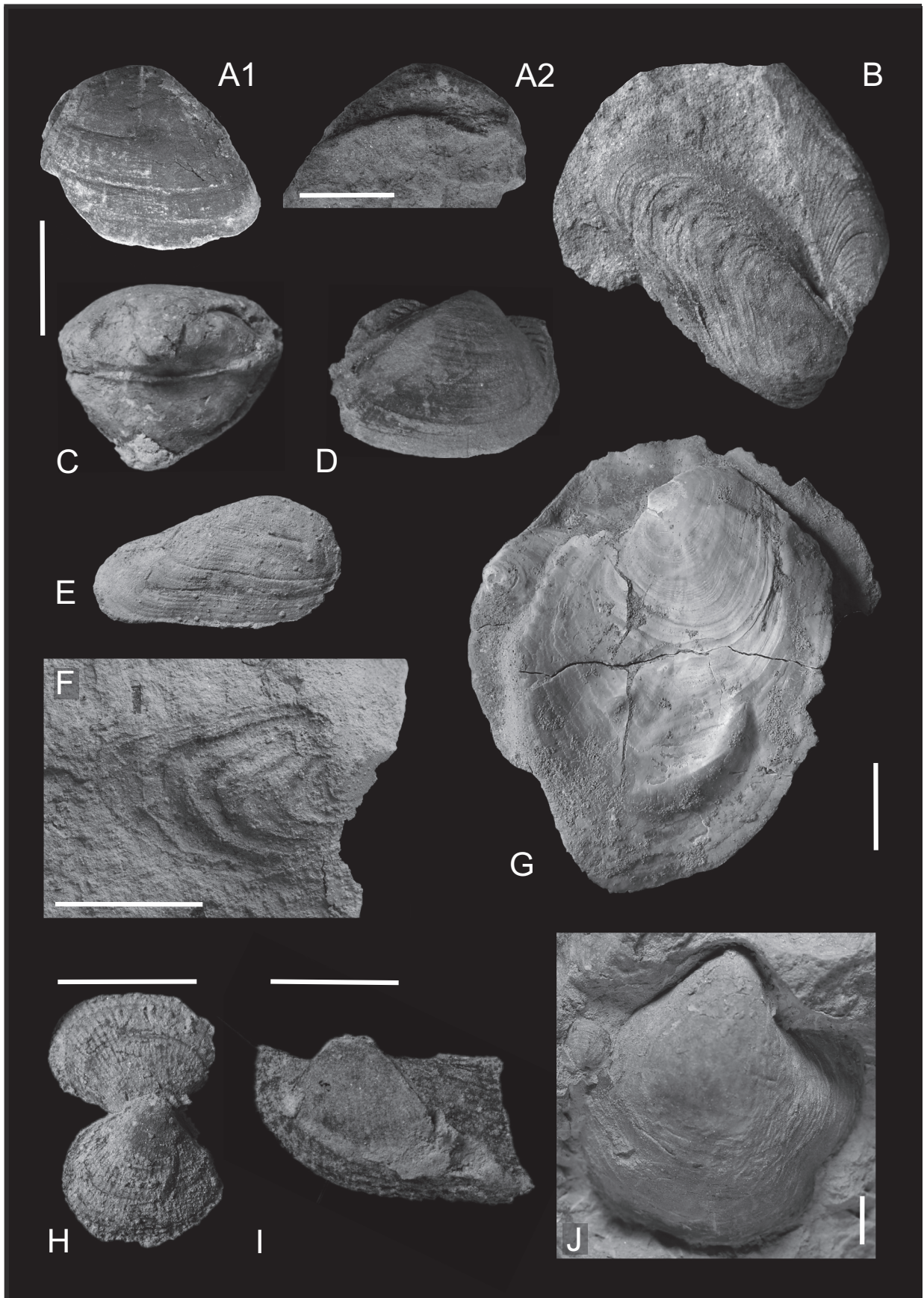
2013 *Modiolus reversus* J. de C. Sowerby: Schneider et al., p. 568, fig. 9D.

2014 *Modiolus reversus* (Sowerby in Fitton, 1836): Niebuhr et al., p. 90, fig. 1e.

Material. 46 specimens; most of them from the P1 unit, only one from the P2a sub-unit and two from the P2d sub-unit, Peruc-Korycany Fm., Pecínov Member, *M. geslinianum* Zone.

Most of the specimens were collected as closed shells on densely packed monospecies surfaces. Only the specimens which were complete enough to identify the main morphological features were taken into the evidence; however, the actual number of individuals is probably considerably higher.

Description. Small (A 5–11 mm, L 5–22 mm; average A 9 mm, average L 15 mm), inflated, oblong internal moulds, distinctively modioform; equivalve, strongly inequilateral. Shape transversely arcuately gibbous, anteriorly rounded, posteriorly broadly expanded due to allometric growth, ventral margin nearly straight.



Prosogyrous beak slightly behind anterior end, only slightly exposed, well-rounded and inflated; hinge margin smooth; umbones obtuse, distinctly behind the anterior end. The surface concentrically striated, probably representing fine growth lines.

Discussion. Described specimens fully correspond to *M. reversus* described by Woods (1903), with the exception of fine radial ribs, which are supposed to extend from the umbo to the ventral. However, their absence was also recorded by Dhondt (1987) as well as Schneider et al. (2013) and is considered to be a matter of preservation. Niebuhr et al. (2014) described *M. reversus* from considerably similar strata (e.g. upper Cenomanian) from Saxony (Dölzsch Fm.)

Occurrence. Albian to Cenomanian of UK (Woods, 1903), Cenomanian to Turonian of Germany (Schneider et al., 2013; Niebuhr et al., 2014) and the BCB (Geinitz, 1875).

Family Cucullaeidae R. Stewart, 1930

Genus *Cucullaea* Lamarck, 1801.

Type species: *Cucullaea auriculifera* Lamarck, 1801

Cucullaea glabra (Parkinson, 1811)

Fig. 4C, D

1875 *Arca glabra* Parkinson: Geinitz, p. 221, pl. 49, figs. 1–3 (with extensive synonymy).

1903 *Cucullaea glabra* Parkinson: Woods, p. 57, pl. 11, figs. 8–12; pl. 12, figs. 1–5 (with extensive synonymy).

1909 *Cucullaea glabra* Parkinson: Wanderer, p. 39, pl. 7, fig. 6.

1911 *Cucullaea* (*Arca*) *subglabra*, D'Orbigny: Frič, p. 35, figs. 155a,b.

2019 *Cucullaea* (*Idonearca*) *glabra* (Parkinson): Young et al., p. 69, pl. 10, figs. 3–4.

Material. 100 specimens; all of them from the P1 unit, Peruc-Korycany Fm., Pecínov Member, *M. geslinianum* Zone.

Description. Small to moderate-sized (A 8–22 mm, L 11–27 mm; average A 15 mm, average L 21 mm), considerably inflated, outline subquadrate to subtrapezoidal. The anterior margin curved, passing gradually into the ventral margin, the posterior margin straight. Rounded posterior umbonal ridge leads to an obliquely truncated ventroposterior margin. Strongly inequilateral valves, LV projecting slightly beyond RV along rear and ventral margins. Projecting orthogyrate beak situated at about one-third of the total valve length, closer to the anterior end. Hinge line long and straight with three or four lateral teeth, nearly parallel to the hinge line, symmetrically located both on the anterior and posterior. Surface smooth with hardly discernible concentric growth lines, occasionally with traces of radial ornamentation preserved only as several mm long, thin, regular lines near the ventral margin.

Discussion. In modern times, members of the *Cucullaea* genus prefer fine sand or mud bottoms and most commonly inhabit depths ranging from 15 to 150 m. Studies done on living specimens of the *Cucullaea* genus shows great variability in the shell morphology, often connected to the specific environmental setting. Individuals collected in cooler waters have flatter ribs, darker colours and a more subquadrate outline. Ornamentation varies on the two valves of the same shell. Valve outline, ornamentation, and hinge teeth vary from one locality to another (Nicol, 1950). The implication of this issue in the palaeontological record was thoroughly discussed by many authors (e.g. Woods, 1903; Dhondt and Dieni, 1988; Radulović et al., 2019).

Occurrence. Albian of the UK (Woods, 1903) and Serbia (Radulović et al., 2019), Albian to Cenomanian of Belgium, France, Switzerland, Italy, Germany, Poland, Ukraine (incl. Crimea), Moldova, Caucasus and Russia (for more detail see Dhondt and Dieni, 1988), Cenomanian to Turonian of the BCB (Frič, 1879; Wanderer, 1909; Frič, 1911).

Family Glycymerididae Dall, 1908

Subfamily Glycymeridinae Dall, 1908

Genus *Glycymeris* Mendes da Costa, 1778

Type species: *Arca glycymeris* Linnaeus, 1758

Glycymeris sp.

Fig. 4H

Material. 14 specimens; two articulated, in the butterfly position, others either as individual valves or just a negative imprint, all of them from the P1 unit, Peruc-Korycany Fm., Pecínov Member, *M. geslinianum* Zone.

Description. Small-shelled (A 4–12 mm, L 5–14 mm; average A 8 mm, average L 9 mm), inflated, subcircular to suboval, slightly elongated in posteroanterior direction, equilateral. Outline rounded. Central beak, slightly projecting. Hinge line not visible on any of the specimens. Surface covered by ca 30 closely spaced, slightly divergent radial ribs, crossed by several concentric ridges. In several specimens, ornamentation consists of many very fine radial and concentric lines.

Discussion. Most of the specimens seem to agree well with Frič (1911) depiction of *Pectunculus subpulvinatus* and with Woods (1903) *P. sublaevis*. However, the preservation does not allow a more detailed determination. There also seems to be a correspondence of general shape and ornamentation – the specimens with just a few distinct concentric ridges are more rounded, while specimens with softer, decussate patterns are more oval. It is unclear if the variation in shape and ornamentation represents numerous species or is just a matter of preservation. The considerable interspecies variety of Glycymeridid bivalves is also a possible explanation, as it was described even at a single locality (Tschudin, 2001).

Family Paralleodontidae Dall, 1898

Subfamily Paralleodontinae Dall, 1898

Genus *Nanonavis* Stewart, 1930

Type species: *Arca carinata* Sowerby, 1813

Nanonavis carinata (Sowerby, 1813)

Fig. 4I

1875 *Arca carinata* Sowerby: Geinitz, p. 223, pl. 49, figs. 5,6.

1889 *Arca Geinitzii*, Reuss: Frič, p. 74, fig. 63.

1903 *Grammatodon Carinatus* (Sowerby), 1813: Woods, p. 45, pl. 8, figs. 3–8 (with extensive synonymy).

1937 *Parallelodon* (*Nanonavis*) *carinatum* (Sowerby): Reinhart, pl. 27, fig. 6a–c.

1969 *Grammatodon* (*Nanonavis*) *Carinata* (Sowerby): Cox et al., p. N258, figs. C6 – 6a,b

1997 *Nanonavis carinata* (Sowerby, 1813): Smettan, p. 103, pl. 1, figs. 4a,b.

2010 *Nanonavis carinatus* (J. Sowerby): Young et al., p. 68, pl. 9, figs. 9–11.

Material. 12 specimens; half of them articulated, all of them from the P1 unit, Peruc-Korycany Fm., Pecínov Member, *M. geslinianum* Zone.

Fig. 4. **A1,2** – *Nucula* (*Pectinucula*) *pectinata*, ChMHZ-LK-0006, RV with preserved and visible hinge line. **B** – *Modiolus reversus*, ChMHZ-LK-0054c, articulated valves in a butterfly position. **C, D** – *Cucullaea glabra*, C – ChMHZ-LK-0001a, preserved mould of a closed shell, from a nodule D – ChMHZ-LK-0029b, RV. **E** – *Modiolus reversus*, NM O8288, RV. **F** – *Gryphaeostrea canaliculata*, NM O9340, RV. **G** – *Pycnodonte* (*Phygraea*) *vesicularis*, NM O7611, RV. **H** – *Glycymeris* sp., NM O9398, disarticulated valves. **I** – *Nanonavis carinata*, NM O9403, LV. **J** – *Rhynchostreon suborbiculatum*, ChMHZ-LK-0080a, LV. Scale bar = 10 mm.

Description. Small-sized (A 8–16 mm, L 16–31 mm; average A 15 mm, average L 26 mm), trapezoidal; elongated – height about one-half of the length (average A/L = 0.53). Inequilateral, moderately inflated. Hinge line long and straight, its length almost the same as the length of the shell; the anterior margin passes into the ventral margin in a curve. The posterior margin truncated. Proso-gyrate, slightly protruding, but rather incurved beaks situated about one-third of shell length, closer to the anterior margin. Prominent umbonal carina connecting the umbones and poster-oventral corner, separating the flank from the posterior area. The surface is covered by 12–20 closely spaced, slightly divergent threads (on the external mould, smaller second-order lines can be recognised in the interspaces); ornamentation in the posterodorsal area is almost parallel to the hinge line.

Discussion. A number of species of taxodont bivalves have in the past been described in a simplified way or evidently incorrectly under the cumulative “Arca” genus. As other authors later tried to divide or synonymise these into separate taxons, the systematics grew complicated. *Grammatodon* and *Parallelodon* genera were often used for the species, sometimes even considered one and the same. Stewart (1930) determined a new subgenus *Parallelodon* (*Nanonavis*) while using the *Grammatodon carinatus* as a type species – he reasoned that while both genera are probably related, they are not identical; however, the *Grammatodon* genus is not very well described, so the usage of *Parallelodon* is “more reasonable”. Reinhart (1937) followed these systematics with substantiation based on the differences in the hinge line – while the anterior teeth of *Nanonavis* are almost parallel to the hinge line, in *Grammatodon* and *Parallelodon*, the anterior teeth are typically oblique to the hinge. He considered both *Nanonavis* and *Grammatodon* as subgenus of *Parallelodon*. Naturally, this led other authors to wonder if the difference is enough for *Nanonavis* to be regarded as a separate genus – it is viewed as such by, for example, Smettan (1997) and is listed as a genus by Sepkoski (2002).

Although the designation of the correct genera stays complex, the determination of the species is without a doubt. It seems the preservation of *N. carinata* is much less facially dependent than that of the other species. All the species from the locality are absolutely in agreement with the portrayal made by Geinitz (1875), Woods (1903), Reinhart (1937) and even Cox et al. (1969). There is no other fossil bivalve of similar age that could be mistaken for *N. carinata* or the other way around. The characteristic trapezoidal shape, sharp umbonal carina and prominent divergent sculpture are undeniable features of this species.

Occurrence. Albion of the UK (Casey, 1961; Woods, 1903; Young et al., 2010), France (Delamette et al., 1997), Cenomanian to Turonian of Germany (Geinitz, 1875; Smettan, 1997), Cenomanian (herein) and Turonian (Frič, 1889) of the BCB.

Family Gryphaeidae Vialov, 1936

Subfamily Gryphaeinae Vialov, 1936

Genus *Gryphaeostrea* Conrad, 1865

Type species: *Gryphaea eversa* Melleville, 1843

***Gryphaeostrea canaliculata* (Sowerby, 1813)**

Fig. 4F

1875 *Ostrea* (*Exogyra*) *lateralis* Nilsson: Geinitz, p. 179, pl. 41, figs. 28–35.

1911 *Exogyra lateralis* Reuss: Frič, p. 46, fig. 210.

1913 *Ostrea canaliculata* (Sowerby), 1813: Woods p. 375, pl. 56, figs. 2–16.

1933 *Exogyra canaliculata* (Sowerby): Häntzschel, p. 139, pl. 4, figs. 24,25.

1994 *Gryphaeostrea canaliculata* (Sowerby, 1813): Malchus et al., p. 124, pl. 5, figs. 1–3, 5–11 (with extensive synonymy).

2002 *Gryphaeostrea canaliculata* (J. Sowerby): Smith and Batten, p. 145, pl. 24, figs. 5,7.

2014 *Gryphaeostrea canaliculata* (Sowerby, 1813): Niebuhr et al., p. 104, fig. 5d.

Material. Four specimens; all of them RVs, two from the P1 unit, one from the P2a sub-unit, one from the P2c sub-unit, Peruc-Korycany Fm., Pecínov Member, *M. geslinianum* Zone.

Description. Small, rounded rhomboidal to suboval shape with rounded posterior, anterior and ventral margins, inequivalve. The convexity of valves is no longer recognisable. Beaks broken off. Characteristic shell ornamentation consists of widely spaced growth lamellae separated by wide interspaces.

Discussion. In the past, the species has been referred to as belonging to the subfamily Exogyrinae, genus *Gryphaea* or subgenus *Amphidonte* (e.g. Woods, 1913; Záruba, 1996). Some authors (e.g. Woods, 1913; Radulović et al., 2019) discussed the distinction between *G. canaliculata* and *Gryphaeostrea lateralis* (Nilsson, 1827); however, Malchus et al. (1994) presented sufficient arguments to consider *G. lateralis* as a junior synonym of *G. canaliculata*.

The genus predominantly never forms true oyster reefs in which conspecific individuals grow mainly on one another (Stenzel, 1971); however, Kirkland (1996) describes the *Gryphaeostrea* genus as including both free-living species as well as fully cemented one. In the case of the Pecínov locality, only free-living specimens have been recorded. Frič (1879) described its appearance in the BCB as clusters of specimens, many of which are almost unrecognizably deformed.

Occurrence. Aptian to Maastrichtian; widely distributed over Europe, northern Africa and central Asia (Malchus et al., 1994). It is widely spread but more frequently inhabits shallow seas (Dhondt, 1985).

Subfamily Exogyrinae Vialov, 1936

Genus *Rhynchostreon* Bayle, 1878

Type species: *Rhynchostreon chaperi* Bayle, 1878

***Rhynchostreon suborbiculatum* (Lamarck, 1801)**

Fig. 4J

1875 *Ostrea* (*Exogyra*) *Columba* Lamarck: Geinitz, p. 181, pl. 40, fig. 4–7.

1911 *Exogyra columba*, Goldfuss: Frič, p. 47, fig. 212.

1913 *Exogyra columba* (Lamarck), 1819: Woods p. 413, fig. 243–248.

2013 *Rhynchostreon suborbiculatum* (Lamarck, 1801): Schneider et al., p. 574, fig. 11C,D.

2014 *Rhynchostreon* (*Rhynchostreon*) *suborbiculatum* (Lamarck, 1801): Niebuhr et al., p. 101, fig. 5j,k.

2014 *Rhynchostreon suborbiculatum* (Lamarck, 1801): Ayoub-Hannaa et al., p. 86, pl. 5, figs. 7–10 (with extensive synonymy).

Material. Nine specimens; one RV and 3 LVs from the P1 unit, 5 LVs from the P2a sub-unit, Peruc-Korycany Fm., Pecínov Member, *M. geslinianum* Zone.

Description. Small to medium-sized (A 13–53 mm, L 13–47 mm), elongated-oval to exoryform, inequilateral, highly inequivalve. LV inflated, highly convex; RV flat to slightly convex. Beak orthogyrate, highly incoiled, round (average A/L = 1.03). Surface smooth, RV with circular growth lines.

Discussion. Some authors (e.g. Ayoub-Hannaa et al., 2014; Ahmad et al., 2015) discussed the possibility of synonymisation of the names *Rhynchostreon mermeti* (Coquand, 1862) and *Rhynchostreon columbum* with *R. suborbiculatum* based on the lack of distinguishing features which are not a result of either abrasion or preservation of the specimens. Others (e.g. Malchus, 1990) regard them as separate taxons separated either by their palaeogeographic

placement (North America or Europe province) or related to the nature of substrate or other environmental factors. *R. suborbiculatum* is a common taxon in the Cenomanian and Turonian sandstones of the BCB, in some parts of the basin appearing as almost monospecies beds (e.g. [Vodrážka, 2006](#)), generally considered synonymised with *Exogyra columba*, *Gryphaea columba* and *R. columbum*. The ornamented, wrinkled form (*R. mermeti*) has never been described from the BCB.

R. suborbiculatum is relatively common in the Cenomanian deposits of the Tethys region; its abundance, however, rapidly decreases towards the Cenomanian-Turonian boundary, remaining scarce throughout the Turonian. Most authors (e.g. [Dhondt et al., 1999](#); [Ayoub-Hannaa and Fürsich, 2011](#)) attribute this to the sea level change – the oysters generally prefer shallow waters (25–50 m), and the global sea-level rise at the Cenomanian-Turonian boundary is assumed to have drowned previous oyster habitats below their optimum water depth.

Rhynchostreon is generally considered to be an epifaunal, free-living genus. However, some specimens were reported to be fully cemented through life. As noted by [Kirkland \(1996\)](#), the majority of specimens of *R. suborbiculatum* from Black Mesa, Arizona, appear to have been firmly cemented throughout life. Most specimens from the Pecínov section are not preserved well enough to determine if they were cemented or not; however, specimens from the sample ChMHZ-LK- 0039 could be cemented to each other. Cementation would also explain their presence in the deposits otherwise very destitute of epifauna. Nevertheless, no direct case of *Rhynchostreon* cementation was observed in any part of the BCB.

Occurrence: Cenomanian to Turonian, near worldwide ([Dacqué, 1939](#)); e.g. North America, Europe, North Africa and Asia ([Stenzel, 1971](#)), Coniacian of Northern Ireland ([Dhondt et al., 1999](#)).

Family Pycnodonteinae [Stenzel, 1959](#)

Genus *Pycnodonte* [Fischer Von Waldheim, 1835](#)

Type species: *Pycnodonte radiata* [Fischer Von Waldheim, 1835](#)

***Pycnodonte (Phygraea) vesicularis* ([Lamarck, 1806](#))**

Fig. 4G

1875 *Ostrea Hippopodium* Nilsson: Geinitz, p. 177, pl. 39, fig. 12–27; pl. 40, figs. 1–3.

1913 *Ostrea Vesicularis*, [Lamarck, 1806](#): Woods, p. 360, pl. 55, figs. 4–14, pl. 56, fig. 1 (with extensive synonymy).

1933 *Ostrea vesicularis* ([Lamarck](#)): Häntzschel, p. 138, pl. 4, figs. 22,23.

1994 *Pycnodonte (Phygraea) vesicularis* ([Lamarck, 1806](#)): Malchus et al., p. 125, pl. 3, figs. 1,3,5 (with extensive synonymy).

2002 *Pycnodonte (Phygraea) vesicularis* ([Lamarck](#)): Smith and Batten, p. 147, pl. 24, figs. 8–10.

2014 *Pycnodonte (Phygraea) vesicularis* ([Lamarck, 1806](#)): Niebuhr et al., p. 105, fig. 5e,h.

Material. One RV and one LV, and a fair amount of shell fragments from the BH1/BH2 boundary, the Bíla Hora Fm., lowermost Turonian, *W. devonense* Zone.

Description. Extremely variable, small (1 cm) to moderately large (ca 10 cm); obliquely ovate to rhomboidal outline. The RV flat to slightly concave; dorsal and ventral margins form acute angles, anterior and posterior margins form obtuse angles. The residue of the posterior auricle present, demarcated by a radiating elevation followed by a slight depression. Surface smooth or with very fine growth lines. Shell preserved and unusually thick. The LV rounded, considerably convex, including the incurved umbo.

Discussion. The BH1/BH2 boundary of the Bíla Hora Fm. is characterised by abundant fragments of the shells. This marks the only

bed of the Pecínov section with shell preservation. This phenomenon is linked to changes in sedimentation resulting in the preservation of calcitic shells.

Pycnodonte is a sessile genus, adults are free-living recliners on firm substrates. The firmness of the substrate seems to be the primary limiting factor of their appearance in the lower parts of the Pecínov section. As noted by [Kirkland \(1996\)](#), depth is also an important factor in their distribution, as they are not found in the shallowest, open marine settings.

Occurrence. Aptian to Maastrichtian of the UK ([Woods, 1913](#); [Smith and Batten, 2002](#)), worldwide distributed from the Cenomanian (rare, deposits of temperate seas), through Turonian (more common, regular especially in the chalk deposits) to the latest Maastrichtian ([Dhondt, 1985](#)).

Family Pinnidae [Leach, 1819](#)

Genus *Pinna* [Linnaeus, 1758](#)

Type species: *Pinna rudis* [Linnaeus, 1758](#)

***Pinna cretacea* ([Schlotheim, 1813](#))**

Fig. 5A

1846 *Pinna decussata* Goldfuss: Reuss, p. 14, pl. 37, figs. 1,2.

1875 *Pinna decussata* Goldfuss: Geinitz, p. 213, pl. 47, figs. 4,5.

1911 *Pinna quadrangularis*, Goldfuss: Frič, p. 40, fig. 179.

1911 *Pinna decussata*, Goldfuss: Frič, p. 40, fig. 180.

2002 *Pinna decussata* Goldfuss: Smith and Batten, p. 101, pl. 17, fig. 3.

2003 *Pinna cretacea* ([Schlotheim, 1813](#)): Seeling and Bengtson, p. 477, fig. 4A–C.

2014 *Pinna cretacea* ([Schlotheim, 1813](#)): Niebuhr et al., p. 92, fig. 2a,b (with extensive synonymy).

2017 *Pinna cretacea* ([Schlotheim](#)): Wilmsen, p. 38, fig. 4C.

Material. 20 specimens; all of them from the P1 unit, Peruc-Korycany Fm., Pecínov Member, *M. geslinianum* Zone. The material consists of moderately well-preserved internal moulds of articulated shells, predominantly horizontally deposited on the bedding plane and laterally compressed by the diagenetic processes. Occasionally, only an imprint of a shell fragment can be found on the complex shell bed surfaces. All specimens lack the posterior end. Some specimens are preserved *in situ*: either the central part of the shell or just the anterior part of the shell.

Description. Medium-sized to large (maximum length of preserved, anterior part: 197 mm), narrow, very elongate, wedge-shaped, mytiliform to cuneiform. Equivalve with a well-defined median ridge. Posterior margin straight, ventral margin straight to concave with a long narrow gape near the anterior end for protrusion of a bunch of long silky byssal threads. Pointed umbones at extreme anterior end; hinge margin long, edentulous. Apex angle 20–36°. Characteristic sculpture of symmetrical radial ribs separated by broad interspaces.

Discussion. Members of the family are all thin-shelled and, therefore, susceptible to fast fragmentation after the specimen's death. Any transport leads to imminent destruction. Considering the relatively good preservation of the specimens and only the singular occurrence of shell fragments, we can assume para-autochthonous origin even for the horizontally deposited specimens. Vertically deposited specimens are considered to be preserved *in situ* in their original living position. Discussion on bathymetry in relation to living conditions is provided below (5.2.2. *Pinna cretacea* in comparison with its recent-living relatives).

Two very similar species from the Cenomanian of the BCB (as well as from the Cretaceous deposits from around Europe) are *P. cretacea* and *Pinna decussata* ([Goldfuss, 1837](#)). *P. decussata* is supposed to be wider with strong ribs, especially from the Cenomanian and the early to middle Turonian, while *P. cretacea* should be the leaner

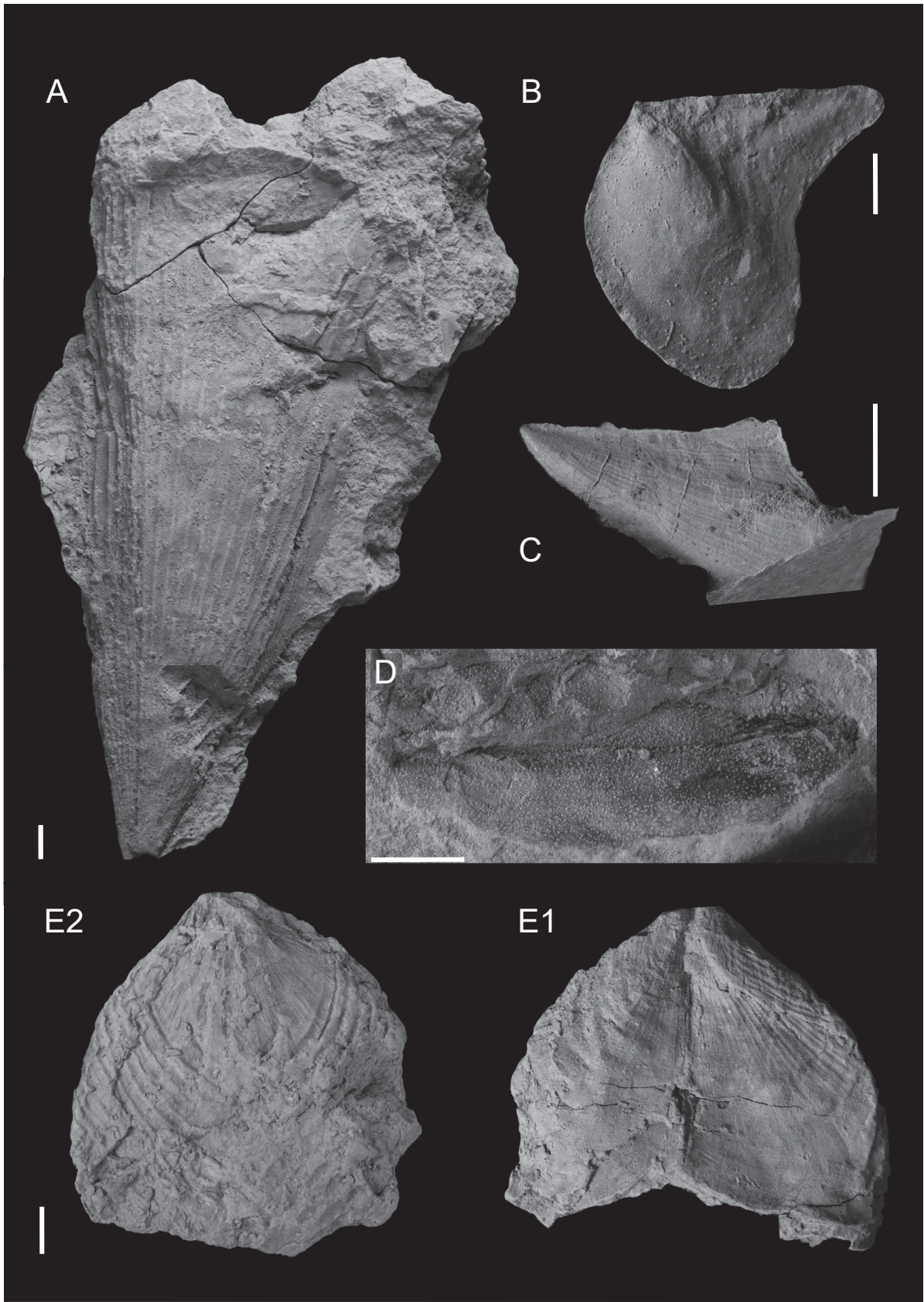


Fig. 5. **A** – *Pinna cretacea*, ChMHZ-LK-0055. **B** – *Pteria?* sp., NM O8297, RV. **C** – *Pseudoptera anomala*, ChMHZ-LK-0082. **D** – *Gervillia solenoidea*, ChMHZ-LK-0061a. **E1,2** – *Stegoncha neptuni*, ChMHZ-LK-0052a. Scale bar = 10 mm.

form from the Turonian and “Senonian” deposits combined. As their main morphological differences are minor and are probably caused by post-diagenetic deformation, most modern authors consider these synonymised (e.g. Dhondt, 1987; Seeling and Bengtson, 2003; Schneider et al., 2013). *P. quadrangularis*, as pictured by Frič (1911), seems to be only a result of deformation and is most likely also *P. cretacea*.

Occurrence. Stratigraphically and geographically widely distributed species. European Cenomanian to upper Maastrichtian deposits (Kříž and Soukup, 1975; Dhondt, 1987; Seeling and Bengtson, 2003), Albian to late Campanian of the UK (Woods, 1913; Smith and Batten, 2002), but also reported from the eastern Mediterranean and the Near East, Africa, southern India, Brazil and possibly North America (for more detail see Seeling and Bengtson, 2003).

Genus *Stegoconcha* Böhm, 1907

Type species: *Pinna granulata* Sowerby, 1822

***Stegoconcha neptuni* (Goldfuss, 1837)**

Fig. 5E

1837 *Cardium neptuni* Goldfuss: Goldfuss, p. 221, pl. 144, fig. 9a.

1875 *Mytilus (Modiola) Neptuni* Goldfuss: Geinitz, p. 213, pl. 47, figs. 1,2.

1879 *Mytilus Neptuni* Goldfuss: Frič, p. 114, fig. 87.

1909 *Stegoconcha neptuni* Goldfuss: Wanderer, p. 25, pl. 4, fig. 3.

1933 *Stegoconcha neptuni* (Goldfuss): Häntzschel, p. 118.

1987 *Gervillaria neptuni* (Goldfuss, 1837): Dhont, p. 61, pl. 2, figs. 5,6 (with extensive synonymy).

2002 *Stegoconcha* sp.: Smith and Batten, p. 102, pl. 17, fig. 1.

2013 *Gervillaria neptuni* (Goldfuss, 1837): Schneider et al., p. 576, fig. 9G.

2014 *Gervillaria neptuni* (Goldfuss, 1837): Niebuhr et al., p. 107, fig. 6e.

2017 *Gervillaria neptuni* Goldfuss: Wilmsen, p. 38, figs. 411,2.

Material. One incomplete specimen from the P1 unit, Peruc-Korycany Fm., Pečínov Member, *M. geslinianum* Zone. It was collected from the same bedding plane as the well-preserved *P. cretacea* (ChMHZ-LK-0055). The same surface contained another poorly preserved specimen of *S. neptuni*, which was not possible to collect, however, it was photographed and catalogued.

Description. A poorly preserved, deformed mould of the anterior part of the shell. Posterior and ventral margins are poorly preserved but most likely straight. Broad pointy beak, apex angle approximately 90°. Outer shell ornamentation distinct, first few cm with dense but thin radial lines, from 4.5 cm further nine strong concentric ribs (in some places broken up into granules) with broad interspaces (ca 2–3 mm). Inner structure preserved heart-shaped lobe with radial lines, more prominent around the edges and thin growth lines; noticeable groove in the middle and well-defined rounded posterior margin. The lobe is probably the residue of the original nacre.

Discussion. Cox et al. (1969) considered the genus restricted to the Jurassic; currently, the known range goes to Paleocene. Koppka (2018) attributes the stratigraphic range errors to the systematic inconsistencies – just the species *S. neptuni* used to be assigned to genera such as *Mytilus*, *Gervillaria*, *Trichites* or *Cardium*. Due to the variability in the record, *S. neptuni* was often overlooked or considered rare (e.g. Dhondt, 1987) – however, Niebuhr et al. (2014) report *Gervillaria neptuni* as a relatively common fossil of the Cretaceous deposits of the Elbe Valley. When considering the complex record, *Stegoconcha* seems to be a long-ranging, cosmopolitan genus with a preference for shallow-marine environments, usually found in biodetritic horizons of carbonate and siliciclastic shelves. *In situ* findings and the taphonomy indicate a semi-

infaunal lifestyle in a subtidal area; in a protected position close to a high-energy zone Koppka (2018).

Occurrence. Late Cenomanian to Campanian in central Europe, Germany and France (Dhondt, 1987; Smettan, 1997; Niebuhr et al., 2014).

Family Pteriidae J. Gray, 1847

Genus *Pteria* Scopoli, 1777.

Type species: *Mytilus hirundo* Linnaeus, 1758.

***Pteria?* sp.**

Fig. 5B

Material. One specimen from the P1 unit, Peruc-Korycany Fm., Pečínov Member, *M. geslinianum* Zone.

Description. A poorly preserved external mould of an LV. Moderately sized, obliquely ovate, slightly inflated umbo defining the anterior end. No anterior auricle but a relatively large, elongated posterior wing. The surface is smooth, without any traces of a sculpture. No other characteristic feature can be recognised on the specimen (hinge, muscle scar, etc.).

Discussion. *Pteria* does not belong to common fossils found in the European deposits of this age. Some findings from the related areas are assigned to the genera due to the characteristics form; however, determination on the species level is mostly non-existent. Moreover, specimens recognised as *Pteria* (e.g. Smettan, 1997; Schneider et al., 2013) differ significantly in size as well as in general shape. Woods (1913) recognised several specimens of different species that could (in general shape) correspond to our specimen. However, all of these are mainly defined by their surface sculpture, either not preserved or entirely missing on our specimen. Both of these species are also described as considerably smaller (1–3 cm) and are generally depicted as very variable.

Family Bakevelliidae W. King, 1850

Genus *Gervillia* Defrance, 1820

Type species: *Gervillia solenoides* J. A. Eudes-Deslongchamps, 1824

***Gervillia solenoidea* (Defrance, 1820)**

Fig. 5D

1846 *Gervillia solenoides* Defrance: Reuss, p. 22, pl. 32, figs. 13,14.

1875 *Gervillea solenoides* Defrance: Geinitz, p. 209, pl. 48, fig. 19.

1911 *Gervillia solenoides*, Defrance: Frič, p. 41, fig. 186.

1987 *Gervillia solenoidea*, Defrance, 1820: Dhondt, p. 59, pl. 3, figs. 6,7 (with extensive synonymy).

Material. 15 specimens; 14 of them from the P1 unit, one from the P2b/c sub-unit, Peruc-Korycany Fm., Pečínov Member, *M. geslinianum* Zone.

Description. Medium-sized (A 26–161 mm, L 5–28 mm), longitudinally elongated, narrow, ensiform, slightly curved. Pointed, terminal beak. Short, obtuse, triangular, keel-like posterior wing, finely crenulated. Surface smooth with delicate, symmetrical growth lines. All specimens with traces of the original dark colouration.

Discussion. The preservation of *Gervillia* genera in European deposits is generally poor, and almost no typical characteristics can be recognised (e.g. Dhondt, 1987) – and therefore were almost never fully described. Strongly elongated specimens were generally described as *G. solenoides*. Several authors attempted to subdivide them into several species e.g. *Gervillia Holzapfeli* (Frič, 1898), which is probably a synonymous species (Dhondt, 1987). *Gervillia* is locally relatively common in some strata within the BCB, especially in Cenomanian sandstone/siltstone deposits (Frič, 1898) and in the upper Turonian marly limestones to limestones (MK observation). Therefore, it inhabited different types of substrate.

Some authors (Kirkland, 1996; Rodrigues et al., 2022) described the genera as epifaunal, byssally attached (pending from objects above the substrate) due to its shell form. Other studies, however, expect a mode of life for *Bakevelliidae* to be ranging from epibyssate to endobyssate (e.g. Savazzi, 1984; Lazo, 2003), living near the sediment-water interface. Stanley (1972) proposed that elongate forms (like *Gervillia* and *Girvillella*) lived semi-infaunally, similar to the Pinnidae. This observation is consistent with the ChMHZ-LK-0078 sample, which comprises nine *G. solenoides* specimens that resemble either the shell pavement (typical for the Pinnidae preservation) or possibly even the original life position (Fig. 6).

Occurrence. Aptian to Maastrichtian; very widely distributed from Coniacian to Maastrichtian in warm temperate and Tethys deposits (Dhondt, 1987; Smettan, 1997), Cenomanian to Turonian of the BCB (Reuss, 1846; Frič, 1911).

Genus *Pseudoptera* Meek, 1873

Type species: *Avicula anomala* J. de C. Sowerby, 1836

Pseudoptera anomala (J. de C. Sowerby, 1836)

Fig. 5C

1843 *Gervillia (Avicula) anomala* Sowerby: Geinitz, p. 15, pl. 3, fig. 8.

1846 *Avicula anomala* Sowerby: Reuss, p. 22, pl. 32, figs. 1–3.

1875 *Avicula anomala* Sowerby: Geinitz, p. 207, pl. 46, figs. 5,6.

1911 *Avicula anomala*, Sowerby: Frič, p. 41, fig. 184.

1913 *Pteria (Pseudoptera) anomala* (Sowerby), 1936: Woods, p. 64, pl. 9, figs. 2–4 (with extensive synonymy).

Material. 48 specimens; 44 from the P1 unit, four from the P2a sub-unit, Peruc-Korycany Fm., Pecínov Member, *M. geslinianum* Zone.

Description. Small to medium-sized (A 9–42 mm, L 6–24 mm), inequilateral, inequivalve. On a bedding plane, the shape appears flat, trigonal, with a sharply protruding umbo – however, the whole shell is more rounded, suboval, elongated, and bent. Terminal beaks rarely preserved, with an apex angle of 45–50°. Distinctive auricles – smaller, round anterior ear; larger, triangular posterior wing connected in the whole length. The anterior margin convex, forming a rounded angle with the sinuous posteroventral margin. Surface smooth or (in most cases) with fine radial lines. On external moulds or on well-preserved specimens, also apparent thin concentric lines – altogether forming a decussate sculpture.

Discussion. The various species of the genus *Pseudoptera* are characterised mainly by their ornamentation. However, as discussed before, differences in the sculpture are (in most cases) considered to be a matter of preservation. Two very similar species are described from similar localities of this age – *P. anomala* and *Pseudoptera glabra* (Reuss, 1846). Geinitz (1875) describes *P. glabra* as being shorter in length, having a lower posterior wing and more pronounced radial lines. Frič (1879) described *A. glabra* as the “smooth-shelled species” and first proposed the idea of there being only one species with different preservation due to the sediment type. Woods (1913) describe the better-preserved specimen of *P. anomala* as having radial ribs crossed at regular intervals by concentric ridges which form squares or oblongs – that description corresponds with our specimens. Smettan (1997) described *P.*



Fig. 6. Nine specimens of *G. solenoides* on one sample (ChMHZ-LK-0078), the preservation resembles either the shell pavements or a possible life position. Scale bar = 10 mm.

glabra as smooth, opposite to the radially sculptured *P. anomala*. Niebuhr et al. (2014) discussed this and mentioned the eventual possibility of only one type of *Pseudoptera* present in the chalk of Saxony.

Savazzi (1984) investigated the functional morphology of an undescribed species from the *Pseudoptera* genus (but according with close affinities to *P. anomala*) and came to the conclusion that the species perfectly adapted to life on muddy substrates (e.g. the weight of the posterior of the shell is distributed on a wider surface, which reduces the risk of sinking into a soft substrate).

Occurrence. Albian of the UK (Woods, 1913), Cenomanian to Turonian of Germany (Niebuhr et al., 2014) and the BCB (Frič, 1879, 1911).

Family Malleidae Lamarck, 1818

Subfamily Isognomoninae Woodring, 1925

Genus *Isognomon* Lightfoot, 1786

Type species: *Ostrea perna* Linnaeus, 1767

***Isognomon* sp.**

Fig. 7A

Material. Five specimens, most of them incomplete but with visible hinge line, all of them from the P1 unit, Peruc-Korycany Fm., Pecínov Member, *M. geslinianum* Zone.

Description. Medium-sized, obliquely ovate to oval moulds with concentric lines, more visible closer to the ventral margin. Characteristic ligamental grooves present (at least four).

Discussion. As both specimens are incomplete, it is not possible to make correct identification up to a species level. However, the presence of several angular ligamental grooves indicates the genus *Isognomon* (in the past described as *Perna* sp.).

Our specimens exactly agree with the portrayal of *Perna Cretacea* by Frič (1879, 1911). Reuss (1846) describes three species of *Perna* from similar (or even the same) localities – *Perna cretacea* (Reuss, 1844), *Perna subspatulata* (Reuss, 1844) and *Perna lanceolata* (Geinitz, 1842). As he also mentions the common variability in their shape, and he states the size and the number of ligamental grooves as the main difference, these names probably belong to only one species and represent a different growth stage. In this respect, all the above-mentioned taxa could probably be synonymized in the future.

Family Pectinoidae Rafinesque, 1815

Subfamily Pedinae Bronn, 1862

Genus *Mimachlamys* Iredale, 1929

Type species: *Pecten asperrimus* Lamarck, 1819

***Mimachlamys* sp.**

Fig. 7K

Material. One specimen, RV (NM O8291), from the P1 unit, Peruc-Korycany Fm., Pecínov Member, *M. geslinianum* Zone.

Description. Small, rounded, ovate, flat. Auricles on both sides of the straight hinge line; unequal in size, wave-like anterior larger than the triangular posterior. Number (40+) of delicate radial lines.

***Mimachlamys?* sp.**

Material. Three specimens, all from the P1 unit, Peruc-Korycany Fm., Pecínov Member, *M. geslinianum* Zone.

Description. Very similar to the specimen NM O8291, however, the preservation is not as good, and the auricles are not visible.

Family Neitheidae Sobetski, 1960

Genus *Neithea* Drouët, 1825

Type species: *Pecten quinquecostata* Sowerby, 1814

***Neithea (Neithella) notabilis* (Münster, 1834 in Goldfuss, 1833) Fig. 7J**

1875 *Vola notabilis* Münster: Geinitz, p. 202, pl. 45, figs. 10–12.

1879 *Vola (Janira) longicauda*, d'Orbigny: Frič, p. 129, fig. 131.

1909 *Vola (Neithea) notabilis* Münster: Wanderer, p. 33, pl. 5, fig. 16.

1933 *Neithea notabilis* Münster: Häntzschel, p. 132, pl. 4, figs. 17, 18.

1973 *Neithea (Neithella) notabilis* (G. von Münster in Goldfuss, 1833): Dhondt, p. 66, pl. 4, fig. 2 (with extensive synonymy).

2014 *Neithella notabilis* (Münster in Goldfuss, 1834): Niebuhr et al., p. 132, fig. 10d–f (with extensive synonymy).

Material. A single specimen (NM O9404) from the P1 unit, Peruc-Korycany Fm., Pecínov Member, *M. geslinianum* Zone.

Description. Small (ca 9 mm), rounded, subtrigonal, convex, narrow. Inequivalve, inequilateral; beak curved inward. Well-developed, elongated, wing-like anterior auricle, triangular but with a rounded angle; posterior auricle not visible. At least four prominently raised radial folds of first-order. Ventral margin crenate with small radial lines.

Discussion. *Neithella* is currently considered to be a subgenus within the genus *Neithea* (Dhondt, 1973). *Neithea* s. s. has been established as a subgenus including all the “symmetrical” species (ribs, auricles), while subgenus *Neithella* has been created for taxa with 4–6 asymmetrical ribs and unequal auricles. *N. notabilis* possesses all morphological features typical for the *Neithella* subgenus, and, therefore, it corresponds only to species typical for the “middle” Cretaceous European deposits (Dhondt, 1973). While the variability of the species seems to be significant (Niebuhr et al., 2014), it is easy to determine and differ from other *Neithea* species due to unequal, wing-like auricles and asymmetrical shape.

Occurrence. Aptian to Cenomanian of Great Britain, Cenomanian of Belgium, France, Germany (Dacqué, 1939) and the Czech Republic (for more detail, see Dhondt, 1973). Typical for the Plenus Zone of Germany and the Czech Republic (Häntzschel, 1933).

***Neithea* sp.**

Material. Two specimens; one RV, one LV, both from the P1 unit, Peruc-Korycany Fm., Pecínov Member, *M. geslinianum* Zone.

Description. Small (ca 6–7 mm), inequivalve, equilateral (or sub-equilateral). Hinge line straight. RV convex, rounded to subtrigonal; beak curved inward; four visible, prominently raised radial folds; signs of smaller radial lines. LV orbicular to oval, typically drop-shaped, symmetrical, flat or only slightly convex/concave.

Family Limidae Rafinesque, 1815

Subfamily Liminae Rafinesque, 1815

Genus *Lima* Bruguière, 1797

Type species: *Lima alba* Cuvier, 1797

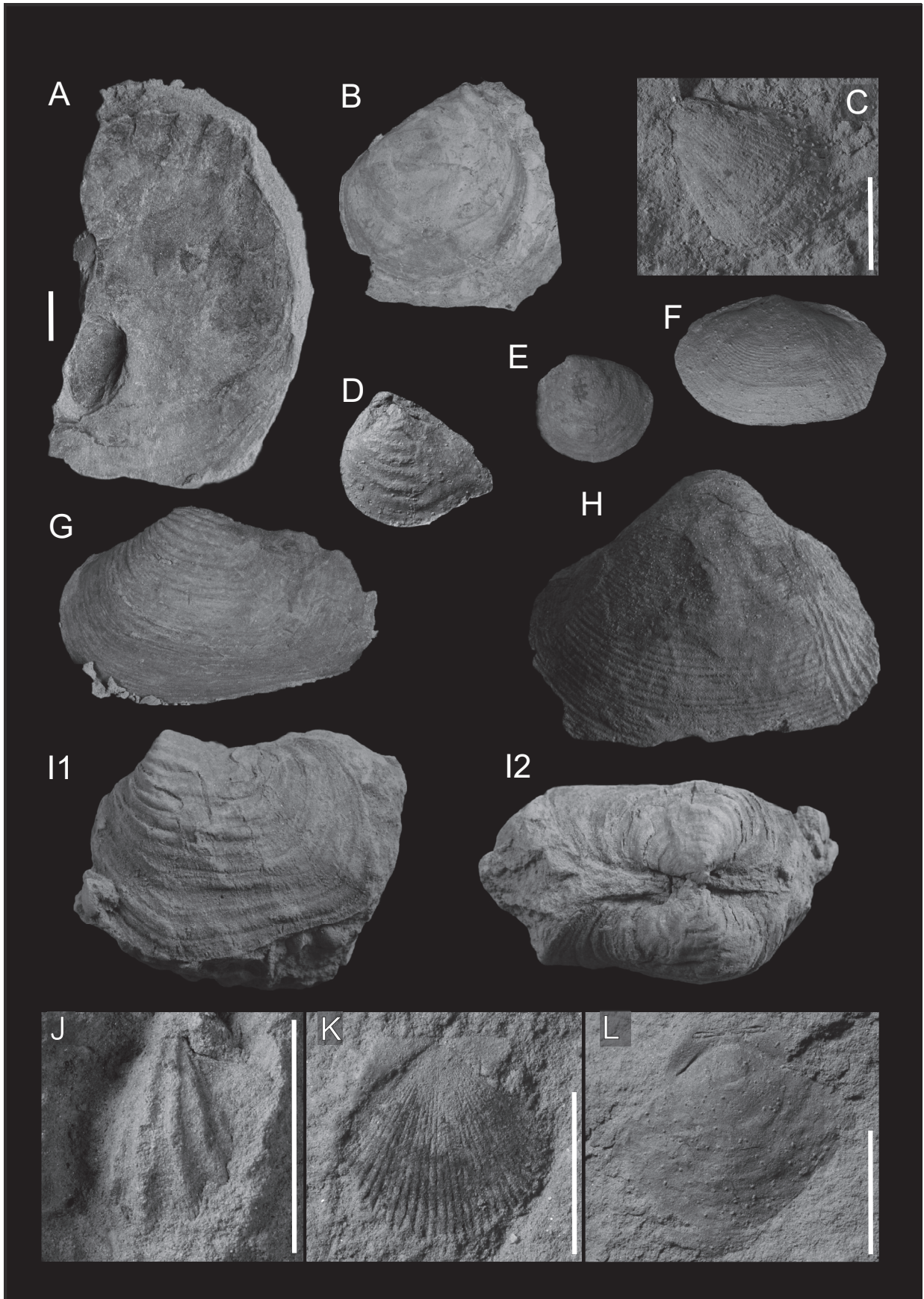
***Lima* sp.**

Fig. 7C

Material. Two LVs, both from the P1 unit, Peruc-Korycany Fm., Pecínov Member, *M. geslinianum* Zone.

Description. Small to medium-sized shell (A 11–19 mm, L 8–17 mm), ovate, higher than wide, slightly inflated. Inequilateral, notably elongated in the anteroventral direction. Terminal beak rounded, apex angle 90°. The anterior auricle is absent or not visible, the posterior auricle small, obtuse, connected in the whole length, almost not distinguished from the rest of the shell. Anterodorsal and posterodorsal margins are long and straight, the ventral margin convex, round, and connected to the anterodorsal margin with an obtuse, rounded angle. Surface with fine radial ribs (20+).

Subfamily Plagiostominae Kasum-Zade, 2003



Genus *Plagiostoma* Sowerby, 1814Type species: *Plagiostoma gigantea* Sowerby, 1814***Plagiostoma hoperi*** (Mantell, 1822)

Fig. 7B

1822 *Plagiostoma Hoperi*: Mantell, p. 204, pl.26, fig. 2.1846 *Lima Hoperi*, Deshayes: Reuss, p. 34, pl. 38, figs. 11,12.1879 *Lima Sowerbyi*, Geinitz: Frič, p. 126, fig. 120.1909 *Lima (Plagiostoma) Hoperi*, Mantell: Wanderer, p. 3, pl. 5, fig. 6.1913 *Lima (Plagiostoma) Meyeri*, Woods: Woods, p. 15, pl. 6, figs. 2,3.1913 *Lima (Plagiostoma) Hoperi*, Mantell: Woods, p. 17, pl. 6, figs. 7–12 (with extensive synonymy).1913 *Lima (Plagiostoma) Cretacea*: Woods, p. 22, pl. 4, figs. 13–15, pl. 5, figs. 1–4.1933 *Lima (Plagiostoma) Hoperi*, Mantell: Häntzschel, pl. 4, fig. 8.2014 *Plagiostoma hoperi* Mantell: Niebuhr et al., p. 119, fig. 7h,n.

Material. Two specimens; one LV from the P1 unit, one LV from the P2a sub-unit, Peruc-Korycany Fm., Pecínov Member, *M. geslinianum* Zone.

Description. Medium-sized (A 34–43 mm, L 31–3 mm), obliquely ovate, length slightly exceeding height. Inequilateral, extended obliquely in the anteroventral direction. The anterodorsal margin long and straight; the posterodorsal margin also straight but about half the length. The rest of the shell margin rounded. Beak rather sharp, apex angle 90°. The anterior auricle is absent or cannot be seen, the posterior auricle small, obtuse, with growth lines. The surface smooth with concentric grooves, especially closer to the ventral margin. Remains of weak radial ribs near the posterior-ventral margin (only on the negative imprint).

Discussion. Our specimens perfectly correspond with the original depiction by Mantell (1822), including the timeframe of the occurrence of the species (Cenomanian to Campanian).

Geinitz (1875) described *Lima simplex* (d'Orbigny, 1847) as an “almost smooth *Lima*, which has some resemblance to *L. Hoperi*”, which differs from the latter in being more elongated and having a more pointed beak. The specimen he pictured seems to bear a resemblance to ours; however, the main difference is that anterodorsal and posterodorsal margins are not straight but rather concave.

d'Orbigny (1850) described *Lima Calypso* as very similar to *L. hoperi* but with numerous punctated grooves. Jukes-Browne and Hill (1896) mentioned *L. Calypso* from the French Cenomanian in the same paragraph as *P. hoperi* and stopped just short of considering them synonymised.

Woods (1913) described the *P. hoperi* as having an apex angle of 115°–117° and appearing in the Turonian. However, he newly defines *Lima (Plagiostoma) cretacea* (Woods, 1913) by a smaller apex angle and rib-like ornamentation – he also cited an unspecified specimen described by d'Orbigny with a smaller apex angle, which he considers a variety of *P. hoperi*. Several authors (Dhondt, 1985; Niebuhr et al., 2014) since then questioned the existence of *P. cretacea* as an independent species. *Lima (Plagiostoma) Meyeri* (Woods, 1913), described as having a smaller apex angle and being more subtrigonal, seems to also be just a variety of the same species (or a matter of preservation). However, Wood's separation to several species led many authors since then to consider *P. hoperi* as strictly Turonian (Dhondt, 1985; Niebuhr et al., 2014).

Häntzschel (1933) describes both *P. hoperi* and *P. cretacea* as typical species from the Plenus-zone in Germany.

Occurrence. Cenomanian to Campanian of the UK (Mantell, 1822), Cenomanian of Germany (Häntzschel, 1933), France (d'Orbigny, 1850), Turonian to Maastrichtian found in non-Tethyan European seas (Dhondt, 1985), first description from the late Cenomanian of the BCB herein.

Family Entoliidae Teppener, 1922

Subfamily Entoliinae Teppener, 1922

Genus: *Entolium* Meek, 1864Type species: *Pecten demissus* Phillips, 1829***Entolium* cf. *orbiculare***

Fig. 7L

Material. Two poorly preserved specimens; one from the P1 unit, one valve fragment from the P2a sub-unit, Peruc-Korycany Fm., Pecínov Member, *M. geslinianum* Zone.

Description. Small, suborbicular to oval, flat, equilateral, pectenoid form. Well-developed symmetrical auricles of triangular shape, on one specimen auricles dorsally protruding from the umbo, forming a depression in the middle with an acute angle between the auricular margins. On the other, connected in a straight dorsal margin. Surface smooth.

Discussion. The systematics of Pectinid-like bivalves is complex, and its determination in the Cretaceous deposits is inconsistent at least. Poor specimens' preservation prevents better description, and identifiable features often point to several possible genera. Many genera were occasionally synonymised and divided again; it is clear the whole systematics require comprehensive revision based on better-preserved specimens. One of these instances is the differentiation of “smooth” Cenomanian pectinids *Entolium orbiculare* and *Syncyclonema nilsoni*, which were often described interchangeably or even simply as *Pecten* genera. Several authors made efforts to solve this problem, most notably Dhondt (1971), according to whom even though both genera share a smooth shell appearance, the outside of the *Entolium* shell can bear concentric ornamentation of various nature but never a diverging radial one, while all *Syncyclonema* species have a more or less developed very fine radial ornamentation.

Similar questions arise when comparing *E. orbiculare* and *Entolium membranaceum* (Nilsson, 1827). *E. orbiculare* may differ from *E. membranaceum* in having macroscopical concentric ridges on its left valve. Niebuhr et al. (2014) consider this to be the main difference; however, as was discussed before (see *M. reversus*, *P. anomala*), the absence of sculpture is often simply a matter of preservation, moreover when comparing internal moulds. The apex angle is slightly narrower in *E. orbiculare* (84°–118°; *E. membranaceum*: 94°–122°); however, some measurements can fall within the variability of both. The most notable difference seems to be *E. membranaceum* auricles and the usually straight hinge margin; even when the auricles are projecting dorsally, they are less elevated, and their angle seems to be more obtuse. These are, however, very hard to distinguish in the incomplete specimens. Dhondt (1971) simply considered them closely related but chronologically following each other – *E. orbiculare* disappeared in the late Cenomanian and was replaced by *E. membranaceum* in the early Turonian.

Family Trigoniidae Lamarck, 1819

Fig. 7. A – *Isognomon* sp., ChMHZ-LK-0040. B – *Plagiostoma hoperi*, ChMHZ-LK-0088, LV. C – *Lima* sp., NM 09403, LV. D – *Apiotrigonia?* sp., NM 08300; LV. E – *Eriphylla lenticularis*, ChMHZ-LK-57e, RV. F – *Linearia semicostata*, NM P0098; LV. G – *Panopea* cf. *gurgitis*, ChMHZ-LK-0080f, RV. H – *Protocardia hillana*, ChMHZ-LK-0032b, LV. I, J – *Panopea* cf. *mandibula*, ChMHZ-LK-22. J – *Neithea (Neithella) notabilis*, NM 09404, RV. K – *Mimachlamys* sp., NM 08291, RV. L – *Entolium* cf. *orbiculare*, NM 08290. Scale bar = 10 mm.

Subfamily Trigoniinae [Lamarck, 1819](#)

Genus *Apiotrigonia* L. R. Cox, 1952

Type species: *Trigonia sulcataria* [Lamarck, 1819](#)

***Apiotrigonia?* sp.**

Fig. 7D

Material. Four specimens, all of them from the P1 unit, one valve fragment from the P2a sub-unit, Peruc-Korycany Fm., Pecínov Member, *M. geslinianum* Zone.

Description. Small-sized (A 13–23 mm, L 14–28 mm), trigonal to trigonally ovate. The anterior margin rounded, posteriorly elongated and truncated in a typical trigonia shape. Length bigger than the width (average A/L = 0.83). Beaks mildly protruding appear pointed but very poorly preserved. Marginal carina not prominent; flank slightly bulging. Surface smooth or with 4–6 wave-like concentric ribs, distinguishable on the flank and continuously fading in the posterior direction (area).

Discussion. Typical member of the Trigoniidae family from the BCB is *Trigonia sulcataria* ([Lamarck, 1819](#)), which is now mostly (e.g. [Niebuhr et al., 2014](#)) considered *Apiotrigonia sulcataria* ([Lamarck, 1819](#)). As all the characteristic features are missing or unrecognisable (hinge line, adductor scars, pallial line) on our specimens, the only prevailing characteristic being the typical shape, the specimens remain undetermined.

Family Astartidae [d'Orbigny, 1844](#)

Subfamily Eriphyliinae [Chavan, 1952](#)

Genus *Eriphyla* [Gabb, 1864](#)

Type species: *Eriphyla umbonata*, [Gabb, 1864](#)

***Eriphyla lenticularis* ([Goldfuss, 1841](#))**

Fig. 7E

1846 *Lucina lenticularis* [Goldfuss: Reuss, p. 4, pl. 33, figs. 20–24.](#)

1909 *Eriphyla lenticularis* [Goldfuss: Wanderer, p. 40, pl. 7, fig. 10.](#)

1911 *Eriphyla (Lucina) lenticularis*, [Goldfuss: Frič, p. 35, fig. 156.](#)

1930 “*Venus*” *lenticularis*, [Gabb: Steward, p. 212, pl. 1, fig. 12.](#)

1938 *Astarte (Eriphyla) lenticularis* [Goldfuss: Dacque, p. 143, pl. 8, fig. 1.](#)

1994 *Eriphyla cf. lenticularis* ([Goldfuss, 1841](#)): [Malchus et al., pl. 3, figs. 1,3,5; pl. 6, figs. 1–12.](#)

Material. 22 specimens, all of them from the P1 unit, one valve fragment from the P2a sub-unit, Peruc-Korycany Fm., Pecínov Member, *M. geslinianum* Zone.

Description. Small to medium-sized (A 13–24 mm, L 15–26 mm), equivalve, inequilateral. Lenticular, rounded, moderately inflated to convex. Protruding beak pointed, prosogyrous. The posteroventral margin straight and oblique, passing into the rounded margin of the rest of the shell. The surface smooth with traces of fine growth lines.

Discussion. The general form of the shell can be mistaken for the *Lucina* genus. Both genera were interchanged by some authors in the past (see synonymy). The significant differences are the shapes of anterior adductors (prolonged, protruding from the pallial line towards the centre), pallial line (symmetrical, rounded, comarginal for the *Lucina* genus) and hinge line. Considering the preservation of the presented specimens, all of these features are virtually undetectable. Therefore, when determining the specimens, the general shape and traditional literature were the primary sources – while *Eriphyla lenticularis* is a common fossil for the Bohemian Cenomanian, the *Lucina* genus occurred first in the Turonian.

Occurrence. Cenomanian to Campanian of central and western Europe ([Malchus et al., 1994](#)), Cenomanian to Turonian of Germany ([Wanderer, 1909](#); [Dacque, 1939](#)) and the BCB ([Frič, 1879, 1911](#)).

Family Cardiidae [Lamarck, 1809](#)

Subfamily Protocardiinae [Reuss, 1846](#)

Genus *Protocardia* von [Beyrich, 1845](#)

Type species: *Cardium hillanum* [Sowerby, 1813](#)

***Protocardia hillana* ([J. Sowerby, 1813](#))**

Fig. 7H

1875 *Protocardium hillanum* [Sowerby: Geinitz, p. 230, pl. 50, figs. 11,12.](#)

1909 *Protocardia hillana* ([Sowerby](#)): [Wanderer, p. 42, pl. 7, fig. 16.](#)

1911 *Protocardium hillanum*, [Sowerby: Frič, p. 32, fig. 140.](#)

1913 *Protocardia Hillana* ([Sowerby](#)), 1813: [Woods, p. 197, pl. 31, fig. 6; pl. 32, figs. 1–6 \(with extensive synonymy\).](#)

2014 *Protocardia hillana* ([J. Sowerby, 1813](#)): [Ayoub-Hannaa et al., p. 115, pl. 10, figs. 8,9 \(with extensive synonymy\).](#)

2019 *Protocardia (Protocardia) hillana* ([J. Sowerby, 1813](#)): [Ayoub-Hannaa et al., p. 176, pl. 4, figs. K–N \(with extensive synonymy\).](#)

Material. 29 specimens; all of them from the P1 unit, Peruc-Korycany Fm., Pecínov Member, *M. geslinianum* Zone. Commonly found as articulated specimens on the bedding surface in the butterfly position (5), occasionally closed-shelled (3). Of 21 disarticulated valves, 9 were RVs and 12 LVs.

Description. Small to medium-sized (A 19–58 mm, L 24–85 mm), subtrigonal to broadly subovate, moderately inflated. Subcentral, orthogyrate beak, slightly protruding. Hinge line long, slightly arched, passing through an obtuse angle onto the straight, crenulated posterior margin. Ventral and anterior margins rounded and connected in a continuous arc. Characteristic sculpture of well-developed concentric ribs on a majority of the shell, posterior slope with 9–14 radial ribs.

Discussion. Genus *Protocardia* is generally considered to be one of the most common Mesozoic bivalve fossils. Besides the normal marine settings, which it complements, it also dominates the assemblages from the brackish settings ([Fürsich, 1993](#)), and it was also described from the disoxic deposits ([Hradecká et al., 2005](#)).

The affiliation to the *P. hillana* is indisputable. The characteristic posterior ornamentation of the genus is present in all specimens. While there are several species of *Protocardia* in the deposits of this age, they differ considerably in their general shape (e.g. [Woods, 1913](#)). *Protocardia hillana* is a common fossil described from different parts of the BCB.

Occurrence. Cosmopolitan, wide-ranging species, e.g. Albian to Cenomanian of the UK ([Woods, 1913](#)), Aptian to Cenomanian of Egypt ([Ayoub-Hannaa et al., 2014](#)), Cenomanian of Algeria ([Ghenim et al., 2019](#)), Cenomanian to Turonian of Brazil ([Ayoub-Hannaa et al., 2019](#)), Cenomanian to Coniacian of Germany ([Dacque, 1939](#); [Smettan, 1997](#); [Niebuhr et al., 2014](#)), Cenomanian to Turonian the BCB ([Wanderer, 1909](#); [Frič, 1879, 1911](#) and numerous later authors).

Family Tellinidae [Blainville, 1814](#)

Genus: *Linearia* [Conrad, 1860](#)

Type species: *Linearia metastrata* [Conrad, 1860](#)

***Linearia semicostata* ([Roemer, 1841](#))**

Fig. 7F

1875 *Tellina (Arcopagia) semicostata* A. Römer: [Geinitz, p. 231, pl. 51, figs. 7,8.](#)

- 1879 *Tellina semicostata* Reuss: Frič, p. 120, fig. 102.
 1911 *Tellina semicostata*, Reuss: Frič, p. 35, fig. 157; fig. 174.
 1939 *Tellina (Linearia) semicostata* Roemer: Dacque, p. 160, pl.7, fig. 28.
 2011 *Linearia subdecussata* (Roemer, 1841): Schneider et al., p. 802, figs. 10A, B.

Material. Seven specimens, six from the P1 unit, only one valve from the P2a sub-unit, Peruc-Korycany Fm., Pecínov Member, *M. geslinianum* Zone.

Description. Small- to moderate-sized (A 8–24 mm, L 12–38 mm), suboval, elongated, rounded. Beak subcentral, orthogyrous. The anterior, posterior and ventral margins are well-rounded; the anterior and posterior upper margins are straight and form an obtuse angle. Adductor muscle scars connected by a pallial line with a distinct sinus. Surface with fine, concentric lines; sometimes residue of radial lines on the posterior end.

Discussion. The general systematics of tellinids is problematic with modern-time specimens, much more in the fossil record. Cox et al. (1969) discussed the attempts to divide tellinids into several genera and subgenera and the related problems. As a result of these attempts, many members of the group have changed their names and affiliation throughout history. *Tellina semicostata* is the name predominantly appearing in classical literature; however, its actual position in the systems is variable. Modern papers (e.g. Schneider et al., 2011; Niebuhr et al., 2014) consider the species and its close relatives as belonging to the genus *Linearia*, which, however, is described as having a sculpture of beaded radials (Cox et al., 1969) – which is not a feature generally appearing on the specimens of this species. Nevertheless, this can be simply a matter of preservation, and, especially when working with inner moulds, other characteristic features (e.g. hinge) would be needed for a throughout revision.

Two very similar species are described from the Czech and German Cretaceous deposits: *L. semicostata* and *L. subdecussata* (Roemer, 1841). While *L. semicostata* is characterized by having a central (or subcentral) beak, the beak of *L. subdecussata* is supposedly positioned at about one-third of the shell length. The affiliation of the species to *L. semicostata* is therefore beyond doubt; nevertheless, some authors questioned the difference only as a morphological intra-species variability (Schneider et al., 2011) – in that case, the name *L. subdecussata* would have a taxonomic priority. Occurrence. Cenomanian to Coniacian of Germany (Schneider et al., 2011; Niebuhr et al., 2014) and the BCB (Geinitz, 1875; Frič, 1911).

Family Hiatellidae J. Gray, 1824
 Subfamily Panopeinae Bronn, 1862

Genus *Panopea* Ménard de la Groye, 1807
 Type species: *Panopea aldrovandi* Ménard de la Groye, 1807

Panopea cf. gurgitis Fig. 7G

Material. Six specimens: one articulated mould from the P1 unit in the butterfly position, four from the P2a sub-unit, and one from the P2b sub-unit, Peruc-Korycany Fm., Pecínov Member, *M. geslinianum* Zone.

Description. Medium-sized to large (A 24–48 mm, L 60–85 mm), elongated, oblong, rounded. Inequilateral, equivalved with valves widely gaping. The dorsal margin straight, slightly protruding beak situated about one-third of the shell length from the anterior margin. The anterior margin convex, passing onto the ventral margin in a broad, rounded arc. The posterior margin slightly compressed but still round. Surface structure smooth with irregular co-marginal wrinkles, more distinct in the centre of the shell. Hinge structures, adductor scars or pallial lines not visible.

Discussion. Several species of *Panopea* are described from the uppermost Lower to Upper Cretaceous deposits and are often mistaken for each other. Probably the biggest question is about the individual differences between *P. gurgitis* (Brongniart, 1822) and *Panopea mandibula* (Sowerby, 1813). As even the original depiction seems to be a bit unclear, and many authors seem to project their own opinion into their distinguishing.

Sowerby (1813) describes *P. mandibula* as having “anterior side square, posterior straight”. He does not characterize the specimen much further, and, unfortunately, the illustration is from an unfavourable angle. However, the beaks seem to be approximately central, and the posterior part is notably truncated. The original depiction of *P. gurgitis* (Brongniart, 1822) shows an oblong specimen with a projecting beak situated in about one-third of the total valve length and co-marginal undulations following a convex shape of the posterior ventral. No additional information is present except the justification the species is different from the one described from the Jurassic. Most later authors seem to adopt the general shape and beak location as the main differences between the species – however, as both descriptions are incomplete and the species seem to be very variable, errors often occur. For example, the illustration of *P. gurgitis* by Frič (1879) shows a typical angular specimen from the BCB with its posterior distinctively truncated.

What seems to present an issue with this distinguishing is the aspect of preservation. All the *P. gurgitis* from the locality are preserved *in situ*, with their shell buried in the sediment under a considerable angle – while all of the *P. mandibula* are preserved as lying on the bedding surface, either in the butterfly position or as individual valves. Their differences, therefore, seem to be a result of vertical pressure during the diagenesis, not a reliable mould of the original shell form. However, this seems to be the case in the Pecínov section – if these two described species could actually be one, a complex study of the original material would be needed.

Panopea cf. mandibula Fig. 7I

Material. 15 specimens: twelve articulated internal moulds of closed shells *in situ* from the unit P1 and three from the sub-unit P2a, the Peruc-Korycany Fm., Pecínov Member, *M. geslinianum* Zone.

Description. Medium-sized to large (A 27–52 mm, L 37–64 mm), elongated, oblong to subquadrate, shells robust, inflated. Inequilateral, equivalved with valves widely gaping. Dorsal margin straight with slightly protruding beaks situated about one-third of shell length from the anterior margin, slightly incurved anteriorly. Anterior margin convex, passing onto the ventral margin in a broad, rounded arc. Posterior margin substantially truncated, usually straight or just slightly convex. The surface structure of well-developed but irregular co-marginal undulations, wrinkles and/or folds, separated by wide interspaces. Hinge structures, adductor scars or pallial lines not seen.

Discussion. See previous species.

4.1. *Ostreoidea*

Oysters represent a minor sub-group in the bivalve association from the locality. Only three genera are described: *Pycnodonte*, *Rhynchostreon* and *Gryphaeostrea* and their occurrences are not mutually linked. Their occurrence is not very common; they do not define singular layers (with the exception of *Pycnodonte* in the Bílá Hora Fm.).

Small-shelled moulds of *G. canaliculata* and *R. suborbiculatum* are rarely present in the P1 unit. Unit P2a contains larger and more common *R. suborbiculatum*. Elder (1987) also reports “common to

abundant *Exogyra*” in the basal *S. gracile* Zone from the Western Interior Seaway. A similar situation is also seen in the BCB, where the P2 unit marks approximately the level of the *S. gracile*/*E. septemseriatum* Sbz. Elder (1987) attributed the occurrence of *Exogyra* to the time of rapid transgression and low sedimentary rate – this is also in agreement with the *Panopea* burrows at the same level in the Pecínov section (see 5.1. Taphonomy or 5.2.1 Taphonomy and function morphology as palaeobathymetry indicators). Abnormally small (2 mm), unidentified oyster shells (only RV) emerge at the base of sub-unit P2d. Elder (1987) described the appearance of small *Pycnodonte* as characteristic of the *N. juddii* Zone in Black Mesa, Arizona and suggested it is due to increased sedimentary rates, turbidity, and decreased sediment firmness. The occurrence of these oysters slightly precedes the base of *N. juddii* in the BCB. Unfortunately, the exact base of the zone is unknown in the Pecínov section (Košťák et al., 2018). However, the sub-unit P2d is still in the *M. geslinianum* Zone (middle to upper part of the *S. gracile*/*E. septemseriatum* Sbz.), and therefore the appearance of rare, small oysters in the deposits of slightly different strata age seems to be rather an ecologic phenomenon than an isochronous biostratigraphical marker.

When working with the material from the Pecínov quarry, it is rare to stumble upon unidentifiable oyster-like moulds. Cenomanian oyster genera have significant variability in shell morphology. Most of the variability (e.g. shell outline, thickness and umbo coiling) is most likely related to environmental parameters, such as substrate consistency, water energy and sedimentation rate (Ayoub-Hannaa and Fürsich, 2011) – however, the exact morphological adaptations to these specific conditions have not yet been thoroughly studied and are not beneficial to the palaeoecological interpretation. It also presents an obstacle for many authors when trying to determine the correct taxon, as many of these variations were described as separate species. This makes their determination complicated even when the shell is preserved. Out of all the specimens seen while doing this study (the ones seen while working on this study as well as the ones deposited in the National Museum), the amount of indeterminable oyster-like mould would be less than 10. Being extremely rare, they do not seem to be essential for any palaeoecological interpretation.

4.2. Inoceramidae

This paper does not include inoceramids in the systematic part as well as in the statistical evaluation because the assemblage from the locality has been thoroughly described by Čech in Košťák et al. (2018). The inoceramid bivalves are considered to be rare in the entire section; however, several recorded specimens of *Inoceramus pictus* define the *I. pictus* Zone in units P1 and P2. As their numbers are meagre, their significance in the palaeoecology analysis is negligible. Nevertheless, their near absence in the Pecínov member is still palaeoecologically peculiar. As Elder (1987) quotes Kauffman (pers. comm. in their paper): “Inoceramids are found in virtually every marine and slightly brackish facies and over a great range of inferred palaeodepth, from near intertidal to abyssal”. However, their rarity at Pecínov locality is not still well explained.

5. Palaeoecological analysis and discussion

Bivalves are the dominant element of the late Cenomanian benthic assemblage from the Pecínov member. The relatively rich molluscan fauna (especially ammonites) from the locality has been thoroughly studied, however, the bivalve association and its potential for palaeoenvironmental reconstructions has received very little attention until now. In total, 392 specimens have been

studied, most of them (358) from the P1 unit of the Pecínov Member, others from the P2 unit (32) and some from the overlaying Turonian BH2 unit (2 nonfragmented valves, numerous fragments). Specimens which were successfully determined to (at least) the genera level (386) have been catalogued and assigned to 24 genera within 21 families and 9 orders. Nineteen taxa have been identified at the species level; another seven taxa were left in an open nomenclature at the genus level.

All bivalve taxa have been divided into palaeoecology guilds (Figs. 8,9). Guilds are clusters of species that are not necessarily systematically related, but all taxa within a guild have similar feeding habits and/or ecospace utilization. Therefore, due to their ecological resource requirements, they occupy similar niches. The guild assignments of fossil taxa can be made either by comparison with their extant relatives and/or by the interpretation of their functional morphologies. In the evolutionary history of the bivalves, even distantly related bivalves adopted similar shell structures or forms in response to the same environmental controls. The shell commonly reflects the preferred habitat and mode of life of the animal. Environmentally adaptive morphology may be used for the comparison and interpretation of many extinct groups, as well as their responses to changing environments or habitats (e.g. Kauffman, 1973; Aberhan, 1994; Lazo, 2007; Sørensen et al., 2012; Wilmsen, 2017), regardless of their age and phylogenetic classification.

Four guilds were recognised in the bivalve assemblage from the Pecínov section:

- (1) *infaunal suspension feeders*: most of the bivalves of the Pecínov member belongs to this group; they strongly dominate the association. This guild can be further divided into shallow (*Protocardia*) or deep burrowing (*Panopea*) bivalves.
- (2) *semi-infaunal suspension feeders*: second most abundant group, with the most notable members of the Pinnidae and Bakevelliidae.
- (3) *epifaunal suspension feeders*: the most copious group in most bivalve assemblages but rare in the entire Pecínov section. The assemblage from the locality can be divided into two sub-groups based on their function morphology: (a) byssate, closely attached, exposed forms (*Pteria*, *Mimachlamys*), (b) free-living epifauna (*Rhynchostreon*, *Gryphaeostrea*, *Neithea*, *Entolium*). However, in order not to split the bivalve fauna into too many guilds with just a few specimens, the epifaunal suspension feeders are described as one guild in this paper.
- (4) *infaunal deposit feeders*: members of this guild are very rare, represented by just a single genus.

It is frequently suggested that species diversity reflects the stability of the physical world, the ecosystem, and the availability of resources. Considering the presence of all main bivalve ecospace guilds and the moderately rich assemblage (Fig. 8), the **P1 unit** is considered to be deposited at the onset of the OAE2, during normal marine conditions. The association include relatively large specimens, e.g. *Pinna cretacea* (5.6%), *Stegoconcha neptuni* (0.56%) and *Panopea* sp. (3.63%); however, it is strongly dominated by small to medium-sized specimens, especially *Cucullaea glabra* (27.93%), *Pseudoptera anomala* (12.29%) and *Modiolus reversus* (12.01%). The association can be termed the *Cucullaea glabra* – *Pseudoptera anomala* assemblage.

The main parameters controlling the bivalve's distribution are the substrate, environment energy, salinity, temperature, nutrient input and oxygen sufficiency. The strong dominance of suspension feeders (ca 95%) in the P1 unit indicates a sufficiently high energy

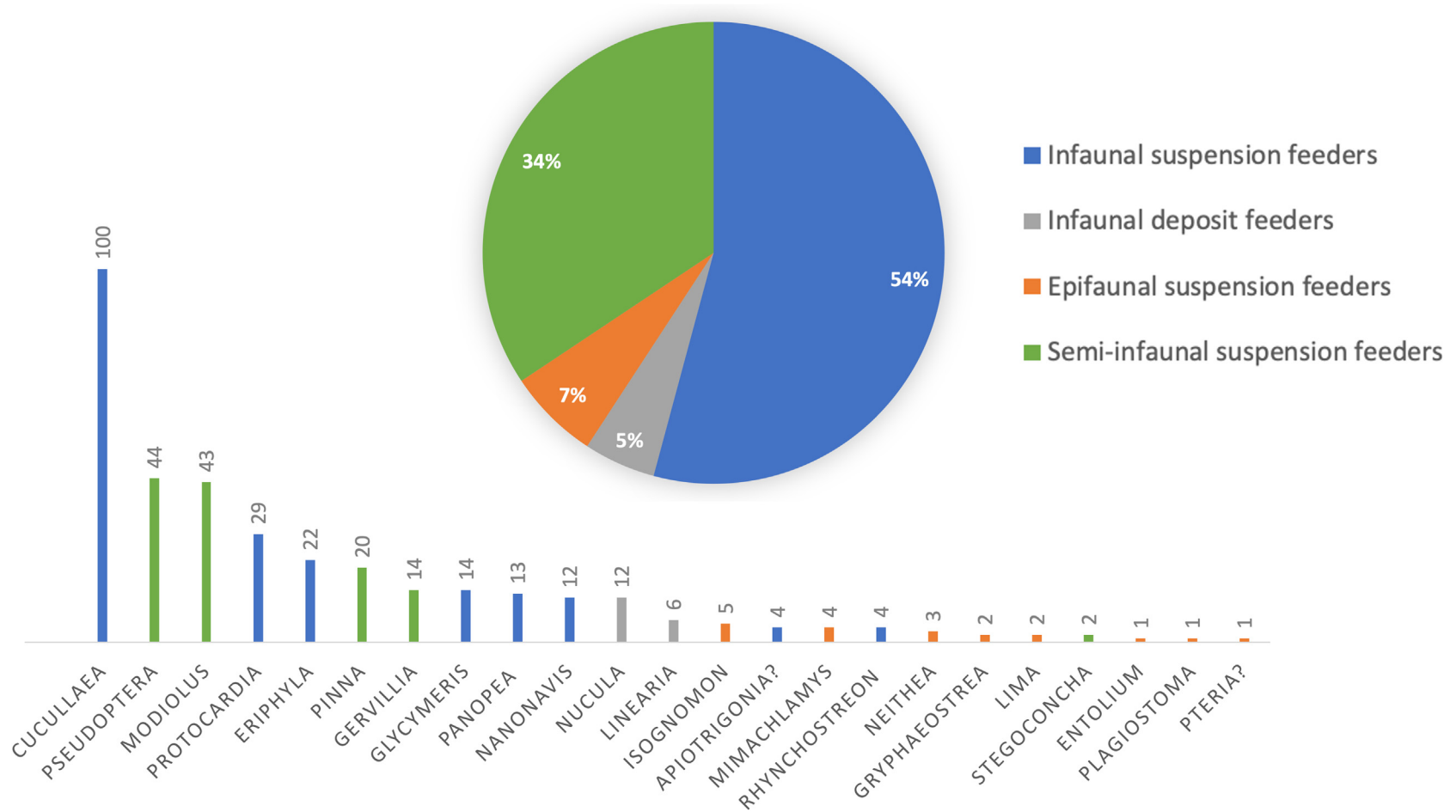


Fig. 8. Guild composition of the bivalve assemblage from the P1 unit, the Peruc-Korycany Fm., Pecínov Member (*M. gestinianum* Zone).

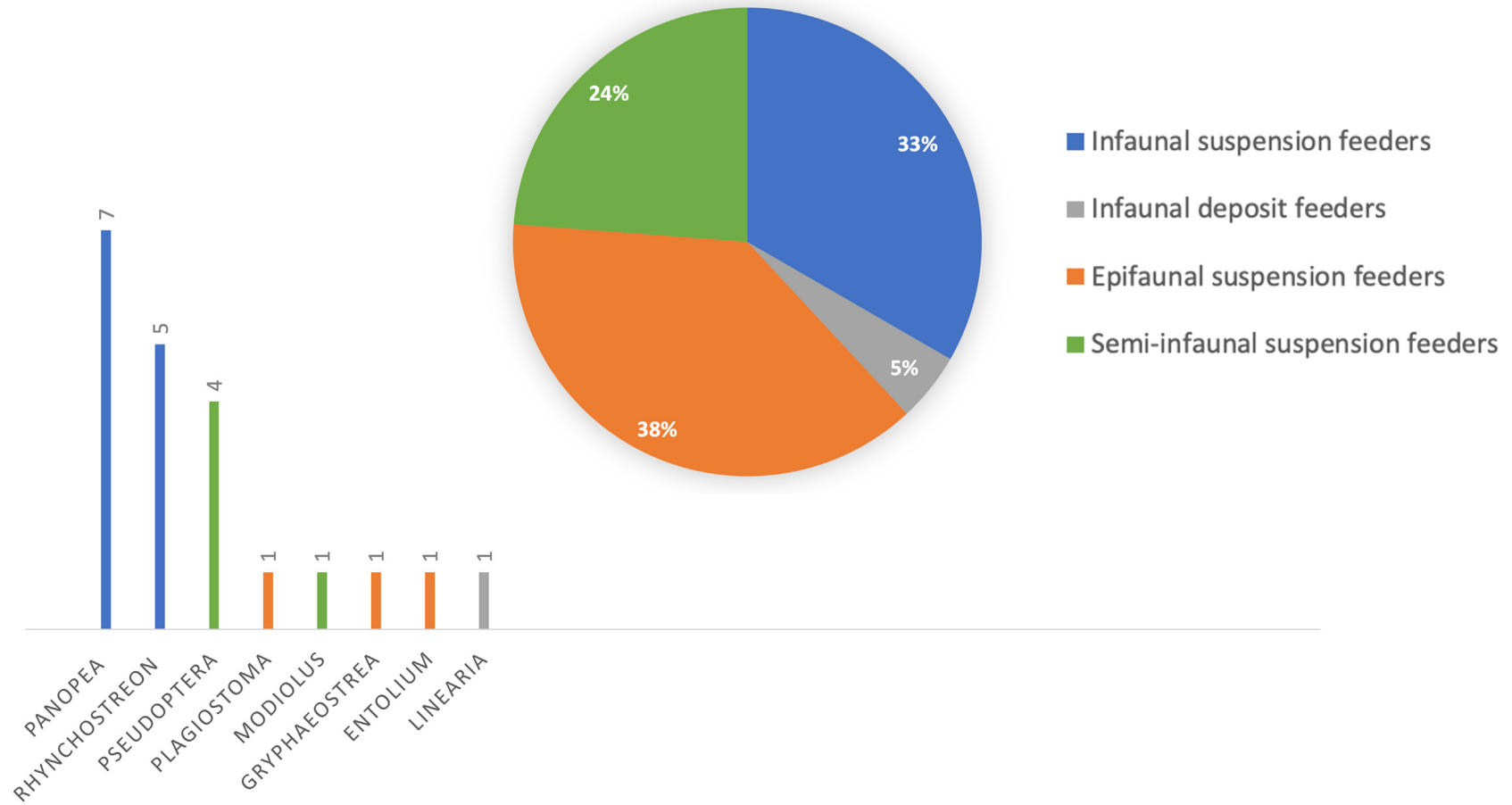


Fig. 9. Guild composition of the bivalve assemblage from the P2a sub-unit, the Peruc-Korycany Fm., Pečínov Member (upper part of the *M. geslinianum* Zone, base of the *S. gracile*/*E. septemseriatum* Subzone).

level to keep organic matter in the suspension. In such an environment, we can expect an abundance of nutrients and oxygen in the whole water column (Moussavou, 2017). On the other hand, the near absence of deposit feeders suggests a minimal amount of organic matter in the sediment – the area could be interpreted as an environment significantly influenced by waves and/or currents (Ayoub-Hannaa and Fürsich, 2012).

The dominance of infaunal (59%) and semi-infaunal specimens (34%) is remarkable. Most of the analogous localities of similar age (e.g. Smettan, 1997; Ayoub-Hannaa and Fürsich, 2012; Schneider et al., 2013; Ayoub-Hannaa et al., 2014; Wilmsen, 2017) are dominated by epifaunal bivalves; its presence in the Pecínov section is, however, sporadic (6.4%). This seems to be due to the particular substrate. The abundance and diversity of epifauna generally tend to positively correlate with the grain size (Fürsich, 1976), as the soft, muddy, moving substrate and water turbidity can be a significant limiting factor for many epifaunal species, especially in shallow, near-shore conditions (Brenchley and Harper, 1998). The dominating infauna from the locality can react to the sediment movement by rapid excavation or burrowing in the case of their uncovering. This explanation is also supported by the fact that all the present members of epifauna have a functional adaptation to the moving substrate – they are either attached by byssus or cemented to the fixed spots, alternatively are able to “swim” on the substrate using the “iceberg” (*Gryphaeostrea*, *Neithea*) or “snowshoe” (*Plagiostoma*) strategy (e.g. Thayer, 1975; LaBarbera, 1981; Aberhan, 1994).

The bivalve assemblage from the **P2a sub-unit** shows a significant decrease in diversity and abundance, however, the trophic structure does not seem to change drastically (Fig. 9). Fossils are rarer, preservation is generally poorer, and the whole unit is much less homogeneous; for the correct result, every sub-unit should be considered separately. The *Panopea gurgitis* – *Rhynchostreon suborbiculatum* assemblage characterises the P2a sub-unit; however, the prevalence of larger shells is probably due to better preservation and may not necessarily indicate environmental conditions. The P2a sub-unit was probably deposited in a similar environment as the P1 unit but in a considerably shallower depth with higher energy (see 5.2. Palaeobathymetry). The palaeontological ((more abundant *Rhynchostreon* (Elder, 1987)), sedimentological (glauconite-rich layer) and taphonomical ((higher number of separate shells as well as the presence of endobionts on the shells (bryozoans)) records indicate a considerably slower sedimentary rate.

Clusters of *Modiolus* (Fig. 10) and very small oysters (RVs) characterise **higher parts of the P2 unit**, the terminating bivalve assemblages prior (interpreted as an onset herein) to the major peak of the OAE2. Some remarks on the palaeoecology of the P2 unit are mentioned in relevant parts of the subsequent sections; unfortunately, there is not enough data for the separate interpretations of each individual sub-unit.

No benthic fauna occurs above the sub-unit P2f, coinciding with the beginning of the most prominent positive peak ($\delta^{13}\text{C}$ peak “b” *sensu* global carbon curve) of the OAE2 at the base of unit P3 (Košťák et al., 2018), which has recently repeatedly been confirmed by numerous field works. The overlain “plateau” (*sensu* $\delta^{13}\text{C}$ carbon curve terminology within OAE2) corresponds to units P3 and P4 and is also characterized by the complete absence of any benthic fauna.

The pioneer benthic fauna occurs in the overlaying **BH1** (topmost parts) and BH2 units of the Bílá Hora Fm. (*Watinoceras devonense* Zone) and is presented by inoceramids (*M. puebloensis*) and frequent *P. vesicularis*. This association indicates biotic recovery in this area and also faunal turnover seen, especially in ammonites.

A resembling appearance of “larger and more abundant *Pycnodonte*” is also marked in the *W. devonense* Zone of the Western Interior Seaway. Elder (1987) interprets this as a return to a firmer substrate and less turbid water. However, the shell fragments in the

Pecínov section of the same age suggest strong turbidity, if not a direct reworking of sediment. Their presence probably represents the quick colonization of the area by explosive opportunistic species (Levinton, 1970).

5.1. Taphonomy

Specimens from the Pecínov quarry section are preserved only as internal or external moulds; all shells have been entirely dissolved during the diagenesis (with a notable exception of the oyster genus *Pycnodonte*). The moulds of the specimens do not differ due to their original composition – no selective preservation of either calcite or aragonite shells seems to have taken place at the locality. This phenomenon is explained by the total secondary decalcification (both calcite and aragonite) of these strata, including all groups with carbonate shells – from Ca-nannofossils, forams to ammonites (Košťák et al., 2018 and discussion therein).

The total absence of the shell has its positive as well as negative consequences – due to the sediment fineness, many details, which would normally not be preserved, are possible to recognise, e.g. on some exceptionally preserved specimens, the whole palial line or adductor muscles can be identified. On the other hand, the samples are susceptible to deformation, either during the process of diagenesis or during the early stage of the research, when the wet material is malleable. This primarily affects the vertically (across the bedding surface) deposited specimens, but recognizable deformation can also be seen with the horizontally deposited fossils, sometimes only partially, e.g. sample ChMHZ-LK-0032b (Fig. 11) consisting of an articulated shell in the butterfly position deposited horizontally, the RV is longitudinally deformed.

The prevalent fossils are the *in situ* infaunal specimens (*Panopea*, *Cucullea*), but accumulations of shells are relatively common. These shell pavements can be monospecies or mixed, including other groups (e.g. ammonites, gastropods, echinoids, scaphopods, etc.). The shells can still be closed, but mainly in the butterfly position (*Protocardia*) or as separated valves. Shells in these accumulations do not have a congruent orientation.

The preservation of bivalve individuals (including the relative number of articulated and disarticulated specimens, stage of abrasion and destruction) presents a good indicator of the transport intensity and duration (Boucot et al., 1958). After the death of the bivalve, the shell opens, but the valves tend to hold together. The shell disarticulates into separate valves only after the complete decomposition of the soft parts, including the ligament. The significant number of articulated shells preserved in the “butterfly” position indicates relatively short transport and only for a limited distance – the burial took place before the soft tissue decomposition. The association from the P1 unit of the Pecínov member is therefore considered para-autochthonous. The rate of disarticulation varies significantly between different species. The thin and fragile valves of the *Pinna* genus are unsuitable for even a short transport as it leads to immediate damage, fragmentation or destruction. Specimens from the Pecínov member are mostly intact, with only an insignificant quantity of fragments. All of them are found with their shell still closed, in a horizontal position or, sporadically, only the anterior part of the shell preserved vertically *in situ*.

5.1.1. Predation marks

Two specimens bear signs of possible predation. The trace fossil on the *Panopea* (ChMHZ-LK-0081, Fig. 12) shell fragment is a hole punched through the shell. It has dimensions of approx. 4.2×4.8 mm. Its shape can be defined as an irregular half of an ellipse, with the ellipse bisected along its shorter axis. The margins are not a geometrically regular ellipse at high magnification, which excludes their belonging to the ichnogenus *Oichnus* Bromley, 1981;

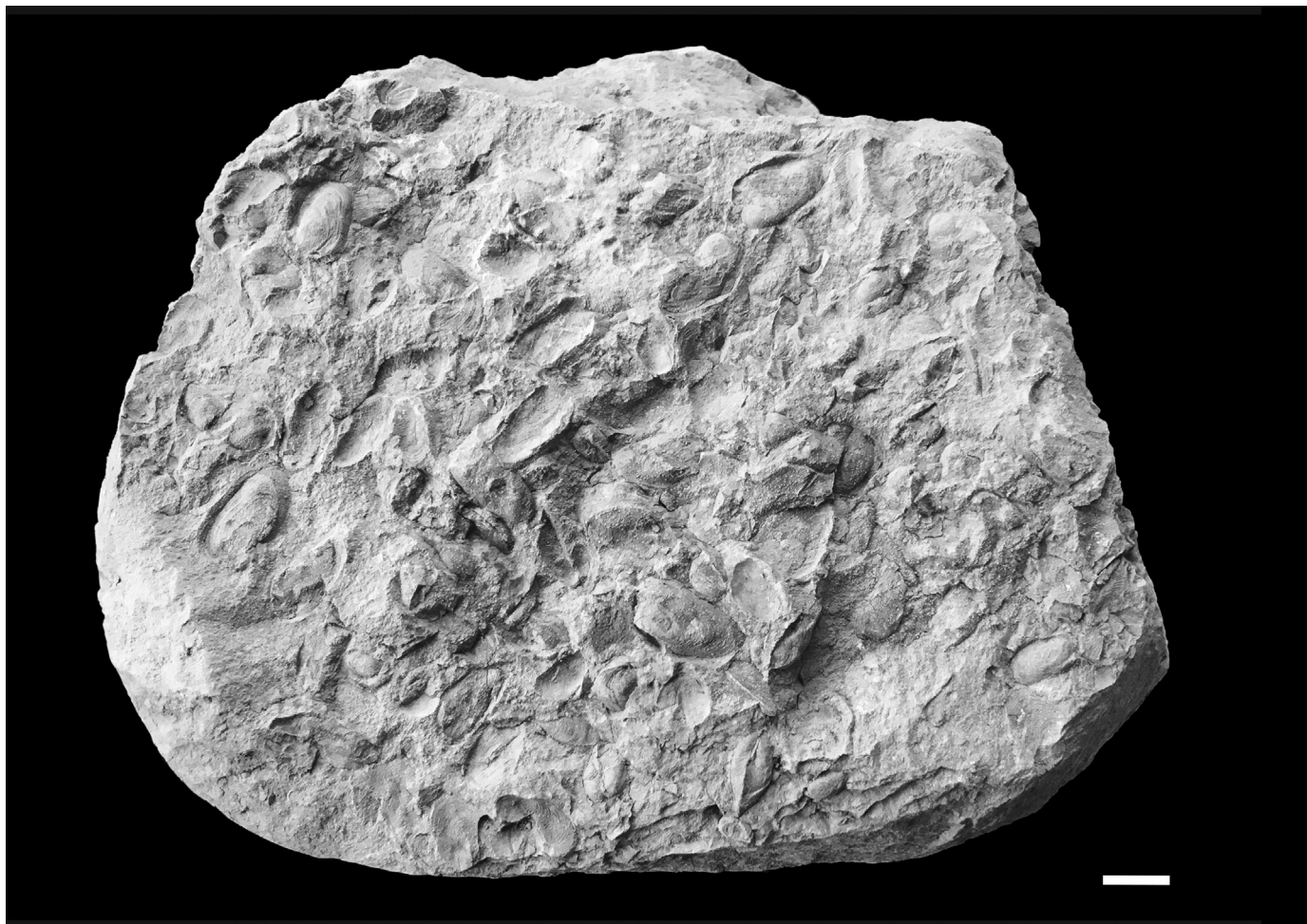


Fig. 10. Example of the densely packed monospecies shell pavement consisting of *M. reversus* (P2e Unit). Scale bar = 10 mm.

Wisshak et al., 2015). In contrast, the irregular, broken edges of the perforation of the bone or shell are the main distinguishing feature of the ichnogenus *Nihilichnus* Mikuláš et al., 2006. It is very difficult to directly place this trace in the same ichnotaxon as a similar trace recorded on the sculptural (? rather internal) core of *Protocardia hillana* (ChMHZ-LK-0033a, Fig. 13). This shell is characterized by the presence of zigzag grooves, which probably represent the early ontogenetic stage of the ichnogenus *Arachnostega* Bertling, 1992. An elliptical cut of dimensions 0.7×0.7 mm is geometrically more accurate than the previously described find, but it is characterized by obvious healing. This is almost impossible in the ichnogenus *Oichnus*, or at least it is not described in any of the very numerous works on *Oichnus*.

Literature published in recent years has noted the possible importance of the ichnogenus *Nihilichnus*, because well-defined ichnospecies can directly indicate food relations in the community. Most finds, and also literary interpretations, come from the Cenozoic of North America (e.g. Hunt and Lucas, 2021). In our conditions (Mesozoic shallow marine invertebrates), the stage of research is such that “broken” shells were mostly neglected already during collection, and therefore even basic non-selective material is missing. In the future, however, it might be possible to obtain more finds of identical morphology and assign them probable trace makers.

5.2. Palaeobathymetry

The upper Cenomanian is characterised by the prominent sea-level rise in Earth's history. Therefore, we expected significant facial changes within the OAE2 interval linked to changes in bivalve assemblages. However, the local geological development in this part (and time interval) of the BCB seems to be relatively independent of the global trend, showing only minor sedimentological changes which shows some signs of an inverse character (e.g. slight shallowing episode prior to the major peak of the anoxia – i.e. the P2 unit; see below) at Pecínov section. In this point of view, the regional character of sedimentation triggered only smaller bathymetric fluctuations.

Although the bivalve association from the Pecínov quarry is relatively rich, most specimens are not convenient for an accurate palaeobathymetry interpretation. The assemblage is predominantly composed of cosmopolitan genera living in the sublittoral zone of a shallow shelf. This, however, does not specify the depth on a satisfying scale.

A good depth indicator, in this case, can be a degree of preservation, association deposited on a bedding plane and general shell orientation. A convenient method of depth analysis can also be a statistical evaluation of functional morphology. In a limited way (and with caution) can be an effective comparison with recent-

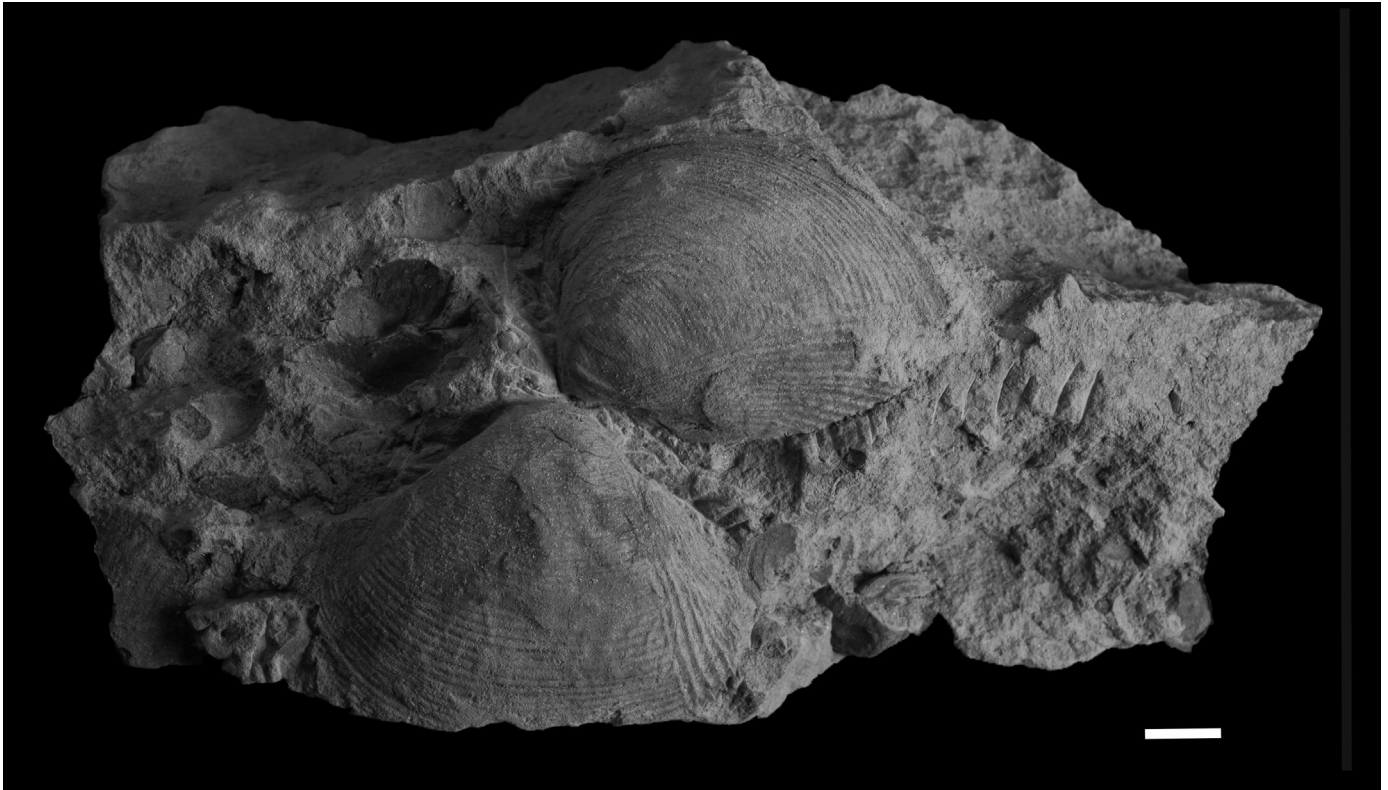


Fig. 11. An articulated valves of *P. hillana* (ChMHZ-LK-0032b) deposited horizontally in a butterfly position; the RV is longitudinally deformed. Scale bar = 10 mm.

living relatives, in this case, especially *Pinna* taxa. The living conditions of modern members of Pinnidae, particularly *Pinna nobilis*, are well studied and present a unique literature archive for the comparison of extinct and extant species.

5.2.1. Taphonomy and function morphology as palaeobathymetry indicators

Pickerill and Brenchley (1991) recognise six different environments in the shelf area, distinguished by depth and distance from

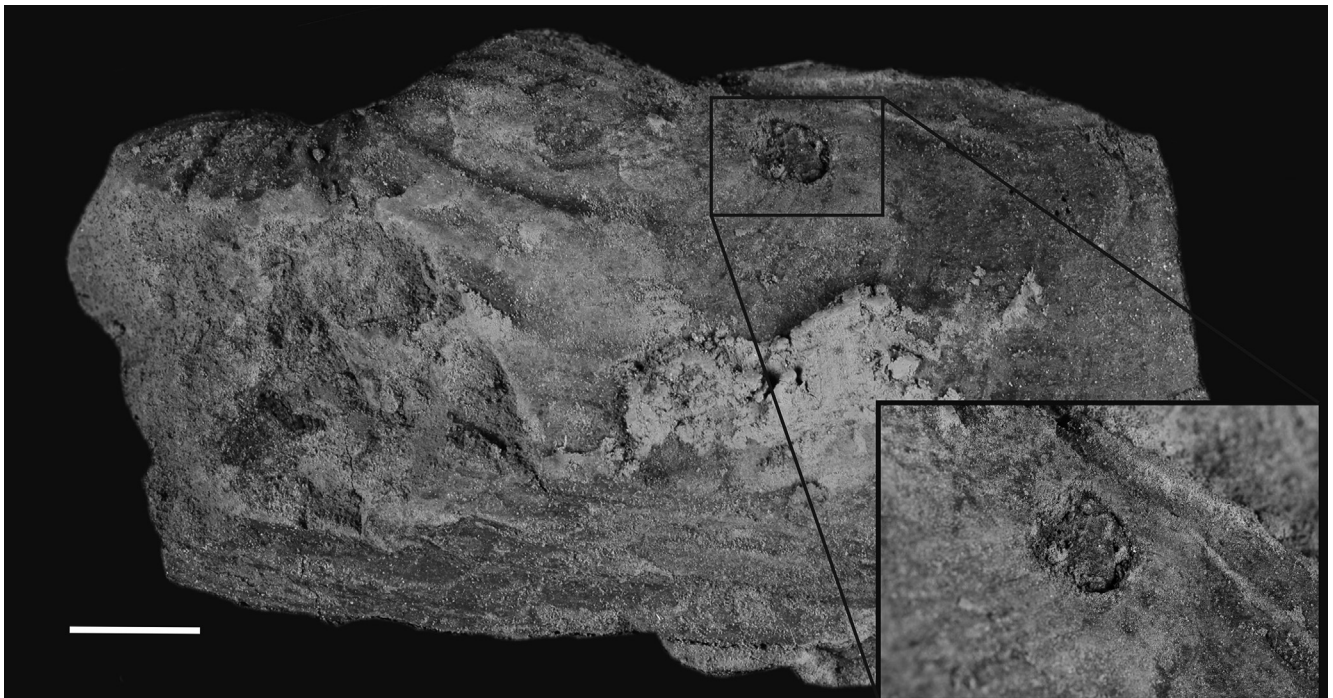


Fig. 12. A possible trace fossil (predation mark) on the *P. gurgitis* specimen (ChMHZ-LK-0081). Scale bar = 10 mm.



Fig. 13. A possible trace fossil (predation marks) on the *P. hillana* specimen (ChMHZ-LK-0033a). Scale bar = 10 mm.

the shore – the main criterion being the distance from the fair-weather wave base (10–15 m) and storm wave base (ca 50–60 m). An absence of cross and/or graded bedding and an occurrence of closed *in situ* shells in the **P1 unit** exclude an extremely shallow environment above the fair-weather wave base. On the contrary, an equal ratio of articulated and disarticulated shells indicates a higher energy level and at least partially reworked sediment. *Pinna* specimens from the locality typically lack their posterior ends, which is standard preservation of the genera commonly attributed to heavy storms (e.g. Wilmsen, 2017; Koppka, 2018). That is supported by the existence of complex shell beds in repeated, not singular, appearances. These densely packed shell pavements can be interpreted as tempestites leading to the shell enrichment within distinct coquina beds. These patterns assign the unit to the A3 environment *sensu* Pickerill and Brenchley (1991), representing the middle shelf environment and the depth of 15–30 m (below the fair-weather wave base but above the average storm wave base). Apart from the previously mentioned patterns, the A3 environment is characterised by muddy, strongly bioturbated sediment, clusters of *in situ* or locally reworked disturbed neighbourhood assemblages, and the typical association of bivalves and gastropods, echinoderms, bryozoa and sometimes brachiopods – this description perfectly represent the deposits of the P1 unit of the Pecínov member.

An additional method for depth reconstruction is the analysis of the functional morphology. By dividing bivalves into functional morphology guilds based on Kauffman (1969), the general affiliation of the bivalves suggests the middle shelf environment. As was explained earlier, the near lack of epifauna is attributed to the combination of the soft, moving substrate and water turbidity, which can be expected in shallow, near-shore conditions (Brenchley and Harper, 1998). Semi-infaunal specimens are abundant (34%), and their style of life is generally considered to be a specialisation to a gently sloping sand to silt bottom of the offshore area just below the wave base (e.g. Kauffman, 1969; Smettan, 1997).

Shallow to moderately deep infaunal suspension feeding bivalves formed by far the most important guild of both coarse- and fine-grained shallow-shelf environments during the Late Cretaceous (Aberhan, 1994). Last but not least, a good bathymetry indicator is the presence and ratio of the infaunal species. The deeply burrowing species are prevalent in the intertidal and shallow subtidal zones (up to 60 m depth) and are more notably found among the groups living in unstable nearshore environments. Meanwhile, species capable of horizontal movement and shallow burrowing are more characteristic of the deeper waters of the outer shelf (McAlester and Rhoads, 1967; Pickerill and Brenchley, 1991). The presence of both groups in the P1 unit probably represents the shallow, mid-shelf environment with higher energy.

The **P2a sub-unit** deposition environment seems to differ from the P1 unit. Many genera otherwise common in the previous beds are missing (*Cucullaea*, *Protocardia*, *Pinna*), others are generally bigger (*Pseudoptera*, *Panopea*), *in situ* faunas rare (with the exception of the *Panopea* burrows), and most of the fossil material seems to be para-autochthonous faunas, typically dispersed and disarticulated. The majority of the fossils are deposited right at the base of the bed. In contradiction with the P1 unit, the P2a sub-unit also contains dispersed shells of *Panopea* deposited on the bedding plane – either in butterfly position or as disarticulated valves (nevertheless, deposited only a few cm apart). Specimens of the genus *Panopea* live deeply burrowed in the sediment (up to one meter deep, as can be seen in the section by the contrast of the green glauconitic burrows with the previous bed, Fig. 14) – their unearthing indicates an energy level high enough to dislodge even as deeply burrowed specimens as *Panopea*. The record seems to agree with the A2 environment *sensu* Pickerill and Brenchley (1991), representing the absolute depth of 5–15 m, the shallow shelf affected by storms with little addition of sediment and commonly reworked.

The more considerable presence of *Panopea* genus in the P2a sub-unit could also be interpreted as indirect evidence of a shallowing –

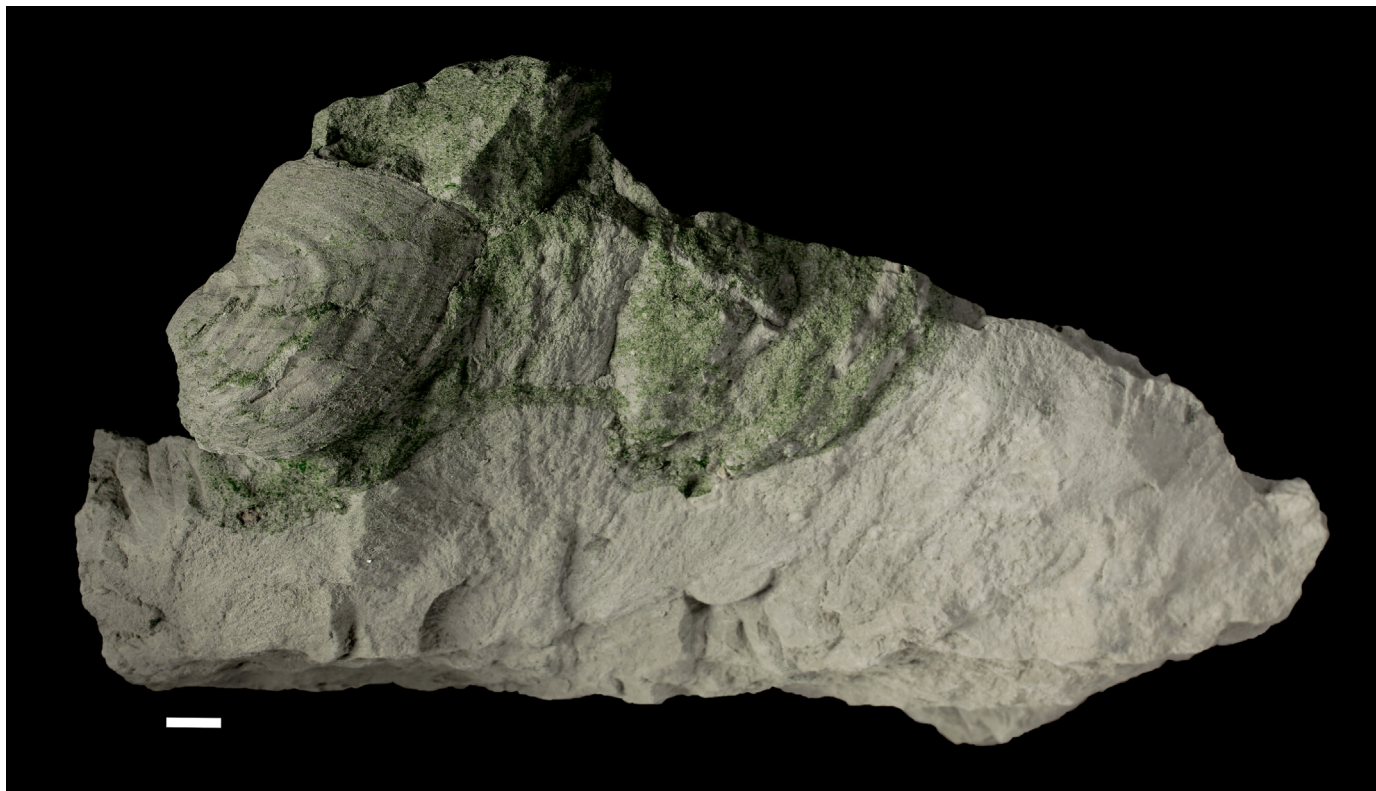


Fig. 14. An articulated specimen of *P. mandibula* (NM O8294) in life position, the glauconitic burrow in stark contrast with the greyish sediment of the underlying bed. Scale bar = 10 mm.

e.g. the presence of habitats preferred by the deep burrowers (McAlester and Rhoads, 1967). The Lower Greensand Bed in the equivalent of the Pecínov locality, Grub section near Roding in Germany (the southern margin of the Mid-European Island), also appears to be associated with a short-term sea-level fall which at least shifted the depositional environment above fair-weather wave base or even back into an emergent setting (Wilmsen et al., 2010).

Furthermore, the P2a sub-unit appears to indicate a slower rate of sedimentation. This is supported not only by the presence of glauconite in the sediment (Odin and Matter, 2003; Amorosi, 2012) but also by the taphonomy of the shells. For instance, the ligament has had sufficient time to decay, resulting in the presence of disarticulated shells and the absence of fragile shells like *Pinna*, which tends to shatter. Additionally, the shells have become encrusted by endobionts, such as bryozoans on the *Plagiostoma* shell (see Fig. 7B). These observations align with the initial description provided by Uličný et al. (1997a), which characterized the unit boundaries as omission surfaces. Moreover, the entire P2a sub-unit appears to represent “Type III shell beds”, as defined by Kidwell (1986), indicating deposition at zero to positive rates of net sedimentation that exceed the rate of input of hard parts.

5.2.2. *Pinna cretacea* in comparison with its recent-living relatives

Recent living members of the *Pinna* genus are widespread in modern oceans. However, the most studied species is *P. nobilis* – as its habitat also seems to closely resemble the one of *P. cretacea*, it was chosen for the comparison in this paper.

P. nobilis lives in present-day Mediterranean; its preferred habitat is the sandy nearshore areas, with a depth range of 0.5–60 m (Basso et al., 2015). Population density is ordinarily directly proportional to the depth up to 15 m depth, afterwards, it sharply declines. García-March et al. (2007) report a density of 1 individual/100 m² in 3 m depth, 6.5 ind./100 m² in 5–10 m and

10.7 ind./100 m² in 10–15 m. In some localities, the deepest living individual dwells in a depth not exceeding 25 m (e.g. Katsanevakis, 2005).

Size/depth depending distribution has also been repeatedly observed in the *P. nobilis* population – that individuals living shallower depth (less than 10 m) grew to a smaller maximum size, while the larger forms (up to 120 cm) preferred deeper habitats (Basso et al., 2015). For example, Katsanevakis (2005) reported the maximum population density of smaller specimens at 4 m depth and larger ones at 12 m. García-March et al. (2007) described a different growth rate and size-dependent mortality in specific depths – at 13 m depth, the smallest specimens (under 30 cm) suffered from the greatest mortality rate, while the larger specimens had a much longer survival rate. On the contrary, specimens living in shallower depths (6 m) were reported to have a faster growth rate for the first 4–5 years of life, up to a total length of 20–30 cm. However, this is followed by a sharp growth decrease limiting their maximum sizes to around 37 cm of total length – it is expected that in the shallowest sites, maximum total sizes are controlled by hydrodynamic stress, causing the death of larger individuals.

The average size of preserved parts of *P. cretacea* specimens from the Pecínov section is 10 cm (median 8.27 cm), while the largest preserved individual is 19.7 cm (all measurements without the posterior ends accounting for at least one-third of the total length). While the Cretaceous genera do not reach the size of *P. nobilis*, its maximum length is about one-third of its recent-living relative, the hydrodynamic stress causing the size/depth depending distribution is expected to be identical. The relatively rich population of small to moderately large specimens collected from the P1 unit seems to indicate a depth of about 15 m, definitely not exceeding 25 m. As there is no relevant statistical data for the Mesozoic species and only several specimens were collected *in situ*, these conclusions should be used with extreme caution. However, as several other

palaeobathymetry indicators are presented in this chapter, and all are in agreement, the overall results are considered accurate.

No specimens of *Pinna* were collected from the P2 unit. This phenomenon is probably linked to: (1) their fully absence; (2) the higher energy and/or slow sedimentary rate – if they were present, the fragile shells would not preserve under such conditions.

5.3. Salinity

Al-Bassam (2018) estimated palaeosalinity ranging from 21.0 to 22.4‰, based on oxygen isotopes. He, however, stated that these conclusions should be regarded with caution, as a) the results could only reflect the situation near the sea bottom and not the whole water column and b) the diagenetic exchange of oxygen isotopes with normal marine water during reworking of the phosphate components might have partially changed the original oxygen isotopic composition. Uličný et al. (1997a) followed Fürsich (1993) in reporting the bivalve association as marine as well as possibly brachyhaline. While it is accurate that most of the bivalve species present at the locality are euhaline and therefore able to withstand the brachyhaline to brackish conditions and some of them are even used as markers of specific to extreme conditions (*Protocardia*, *Entolium*, *Modiolus*, oysters), the association itself does not suggest any other settings apart from normal marine conditions. Low salinity environments are characterised by low diversity, absence of stenohaline fauna and abundance of organisms that were able to adapt (Aberhan, 1994; Brenchley and Harper, 1998). The Pecínov assemblage, in its richness (at least in its lower parts), represents normal marine conditions; accompanying stenohaline organisms (ammonites, nautilids, gastropods, fishes, sharks, echinoids, bryozoans) indicate palaeosalinity over 30‰, approaching the standard numbers around 35‰. Nevertheless, the prevalence of euryhaline species could also support the shallow water environment, as the stenothermal forms usually represent deeper waters (McAlester and Rhoads, 1967).

5.4. Oxidic conditions

Danise et al. (2013) differentiate six stages in the reaction of the benthic organism to the oxygen decrease: (1) base-line: normal benthic oxygen levels, undisturbed communities (2) disrupted environment: decrease in sediment oxygen levels which manifest in a reduction in the diversity of deep infaunal suspension feeders and increase the abundance of deposit feeders (3) disturbed communities living just before the extinction, characterised by opportunistic species tolerant to the extreme conditions (4) anoxia to low-oxygen conditions (5) gradual return to the base-line, colonisation by opportunistic species tolerant to low-oxygen levels (6) re-establishing of the oxygenated conditions; even though the species composition is different from the pre-extinction ones, they are structured in a very similar way.

Considering the well-diversified assemblage, near exclusively dominated by suspension feeders and with a considerable representation of deep infaunal specimens, it is unquestionable that the deposition of the P1 and P2a unit happened under normal oxidic conditions, referred by Danise et al. (2013) as base-line (1).

A considerable decrease in diversity can be seen in sub-unit P2b and upwards. However, as the typical opportunistic species tolerant to the extremely low-oxidic conditions are epifaunal deposit feeders (Brenchley and Harper, 1998), which are near absent in the Pecínov section, it is possible the decline in diversity within the unit P2 does not necessarily represent anoxia but simply an environment

unfavourable by the otherwise dominating infaunal suspension feeders. This part of the section probably represents the disrupted environment (2), as described by Danise et al. (2013).

The upper parts of the P2 unit are characterised by the monospecies clusters of oysters and *Modiolus*. Aberhan (1994) described salinity-controlled environments as assemblages strongly dominated by only a single ecological group. Especially the P2e sub-unit is characterized by a mass occurrence of *Modiolus*, a horizon correlatable within the whole quarry. The Upper Cretaceous species tolerant to anoxia are not well-documented, however, relatives of *Modiolus* are described as opportunistic species able to survive short-time disoxia to anoxia as well as changes in salinity (Baginski and Pierce, 1978; Hammen, 1980; Diaz and Rosenberg, 1995). Modern relatives of *Modiolus* are also well adapted to periodical emerging (Booth, 1975). Lazo et al. (2008) attribute monospecific pavements of *Modiolus* to deviation from either normal salinity or oxidic condition or the combination of both. That would assign the P2e sub-unit to the (3) disturbed community living just before the extinction *sensu* Danise et al. (2013).

The biotopes rapidly change at the top of the P2e sub-unit and within the P2f sub-unit. The majority of ammonite taxa have disappeared (with the exception of a single species *S. gracile*) already in the P2e sub-unit as well as the bivalve assemblages. In this interval, we cannot exclude the role of salinity and especially anoxia as triggering factors in faunal disappearance. The disappearing of entire benthic fauna proves a relatively rapid and drastic palaeoenvironmental change just prior to the peak “b” in the section and, therefore, the maximum of anoxia within the OAE2.

The pioneer benthic fauna occurs around the BH1/BH2 units boundary of the Bílá Hora Fm. (*W. devonense* Zone) and is characterised by inoceramids (*M. puebloensis*) and frequent fragments of *P. vesicularis*. This association indicates biotic recovery in this area and represents a (5) gradual return to the baseline and (6) re-establishing of the oxygenated conditions (Danise et al., 2013).

5.5. Faunal affinities

Kauffman (1973) investigated global bivalve associations and divided them into seventeen subprovinces with thoroughly described boundaries. Part of the assemblage from the Pecínov section is considered cosmopolitan (*Modiolus*, *Pinna*, *Gervillia*, *Nucula*, *Entolium*, *Plagiostoma*, *Pycnodonte*); alternatively, are not strictly cosmopolitan but occur in the Euroamerican region and at least one other region (*Panopea*, *Neithea* (*Neithella*)). Some genera (*Apiotrigonia*, *Nanonavis*, *Pseudoptera*) are considered to directly characterise the north-temperate (=Boreal) realm, or even specifically its Euroamerical region (*Eriphyla*, *Gryphaeostrea*). Hypothetically, the presence of Boreal elements at the onset of the OAE2 could be evidence of the so-called PCE in the Pecínov section. However, as no bivalve genus commonly appearing in the P1 unit is considered connected to the Tethys realm (only rare *R. suborbiculatum* shows affinity to the Tethyan realm), and some of the typically Boreal fauna is abundant throughout the section (e.g. *Pseudoptera*), the general, long-term affinity to the Boreal realm is more likely. That means the area of the BCB is undeniably the palaeobiogeographical boundary between the Tethyan and the Boreal realms in the Cenomanian-Turonian interval with influences of faunas from both realms (Wiese et al., 2004, Košťák et al., 2004, 2020; Krížová et al., 2022). While the late Cenomanian extremely shallow-water rudist taxa represent the Tethyan influx (Krížová et al., 2022), the other benthic bivalves in shallow middle shelf (the depth of 15–30 m) signify Boreal affinity. *R. suborbiculatum*

becoming more prevalent in the P2a unit could be considered as Tethyan influence (e.g. Tröger, 2003) and an indicator of warming (or, more likely, a slightly shallower environment). However, the quantity of specimens implies that it is still appearing within its marginal range in this time interval.

5.6. PCE in the Pecínov section

The PCE is an important late Cenomanian bioevent represented by the incursion of the North Boreal fauna within the middle to the upper part of *M. geslinianum* Zone. The event is characterised by the appearance of Boreal faunistic elements, most notably the belemnite *P. plenus* (Jefferies, 1963). While *P. plenus* has not yet been recorded from the Pecínov member (however, it is well known from the same strata in other parts of the BCB), other indicators were used to point to its location in the section, e.g. chemostratigraphy (closely to the peak “a”, the lower part of unit P2) and the LO of *C. naviculare* which should coincide with the base of the *S. gracile/E. septemseriatum* Sbz (Gale et al., 2005).

Newer findings documented the LO at the base of the P2 unit (see 2.1. Biostratigraphy), which push the event closer to the P1/P2 units boundary, probably occurring in the lower parts of the P2 unit. However, the base of the P2 unit seems to coincide with a sea-level fall, with the depositional setting above the fair-weather wave base (see 5.2. Palaeobathymetry). As was stated in the previous chapter, the shallow waters of the BCB during that time are represented by a strong Tethyan influence, and warmer water temperatures are therefore expected. The Tethyan influence in the P2a sub-unit is supported by the more common appearance of *R. suborbiculatum*. It is possible that the shallow, warm, high-energy environment was not the preferred environment for the incoming boreal fauna, especially for the belemnites. The questions about the preferred habitat of the belemnites, as well as their ecological limitations, are yet to be satisfyingly answered (Hoffmann and Stevens, 2020). However, the *P. plenus* is present in the glauconitic layer (=Lower Greensand Bed) in the equivalent of the Pecínov locality, Grub section near Roding in Germany (the southern margin of the Mid-European Island), where the depositional environment above the fair-weather wave base is also reported (Wilmsen et al., 2010). The belemnite is also described from more than twenty localities in the BCB and is mainly considered as inhabitant of shallower seas (Košťák et al., 2004).

Svoboda (2006) assumed the event occurred as a low counter flow of the cold Boreal water. That is also in agreement with the notion of the water column stratification (Tethys affiliated fauna in the extremely shallow depth vs the Boreal affinity of the benthos from the shallow middle shelf). It is, therefore, possible the occurrence of the *P. plenus* was connected not to specific environmental factors, e.g. depth and temperature, but to the areas with an established cold bottom-water current.

The possible reasons for the absence of the belemnite at Pecínov were discussed by Košťák et al. (2018). It is also notable that there are very few localities (only two) in the BCB where this belemnite co-occurs with ammonites (*M. geslinianum*, Košťák et al., 2004).

Apart from the belemnite *P. plenus* itself, the cooling event is often recognised by the presence of other boreal macro-invertebrates, most notably the serpulid tube *Hamulus* sp., bivalves *Oxytoma seminudum*, *Aequipecten arlesiensis* or serpulid *Ditrupea difformis*. In Germany, the “plenus cold fauna” was historically described as part of the Pennrich Fauna (e.g. Häntzschel, 1933). However, the presence of many of these seems to be more of a matter of local ecology and/or taphonomy, e.g. *E. membranaceum* (the problematic of distinguishing *Entolium* species is discussed in the systematic part) being described as the

warm-water group from the pre-plenus beds in the UK (Jefferies, 1962), while considered as part of the North Temperate Realm in Germany (Tröger, 2003). Most of the species from the Pennrich Fauna are either absent in the Pecínov section or appear across the section, not defining any singular unit (*N. notabilis* reported as a single specimen from the P1 unit, *P. hoperi* and *G. canaliculata* from both P1 and P2 units and *Entolium cf. orbiculare* from P2a).

Thus, deciphering the influence of the PCE within the Pecínov member remains open. The cooling event played an important role in the *M. geslinianum* Zone, but its expression was probably different in extremely shallow and deeper marine environments. However, the influx of cooler water masses may limit the spreading of some fauna, including bivalves and their larvae.

6. Conclusion

The bivalve fauna from the upper Cenomanian – lower Turonian deposits of the Pecínov section, Bohemian Cretaceous Basin represents a relatively rich assemblage with all the main ecospace guilds. Nineteen bivalve species are described, and another seven taxa were left in an open nomenclature at the genus level. In total, the 25 genera, belonging to 21 families and nine orders, are newly described from the locality.

The assemblage is strongly dominated by the infaunal (*Cucullaea*, *Protocardia*, *Panopea*) and semi-infaunal suspension feeders (*Pseudoptera*, *Modiolus*, *Pinna*). Epifaunal suspension feeders (*Oysters*, *Neithea*, *Lima*, *Plagiostoma*) are not common, and infaunal deposit feeders are rare (*Linearia*). The dominant environmental parameters influencing the distribution appear to be the substrate type, water energy and bathymetry.

A significant decrease in taxonomic diversity as well as changes in abundance prior the prominent positive $\delta^{13}\text{C}_{\text{org}}$ peak (the major peak “b” of the OAE2) is suggested to be linked to rapid palaeoenvironmental changes resulting to disappearing the entire benthic communities in the BCB in this interval.

We assume, the upcoming peak of anoxia may play a role in these changes, however, also local environmental factors – e.g. salinity, bathymetry and/or changes in water dynamics triggered decrease in bivalve habitats.

The P1 unit (lower part of the section) of the Peruc-Korycany Fm. (*M. geslinianum* Zone) represent typical shallow marine deposits between the fair-weather wave base and storm wave base. The taphonomy indicates at least episodically higher water energy (e.g. storm waves). The occurrence of articulated epifaunal bivalves suggests rapid episodic burial, most probably in the form of tempestites.

The following P2a sub-unit (upper part of the *M. geslinianum* Zone, *S. gracile/E. septemseriatum* Sbz.) was deposited in a similar environment but in a considerably shallower depth with higher energy. The palaeontological, sedimentological and taphonomical records indicate a slower sedimentary rate.

The benthic fauna occurs in the overlaying BH1 (topmost parts) and BH2 units of the Bílá Hora Fm. (*W. devonense* Zone) and is presented by inoceramids (*M. puebloensis*) and frequent *P. vesicularis*. This association indicates the colonisation by the pioneer fauna and biotic recovery in this area.

The bivalve fauna from the locality consists of worldwide species and the ones with close palaeobiogeographical affinity to the Boreal Realm.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.cretres.2023.105704>.