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Middle Jurassic bivalves from Geographical Society Ø, North-East Greenland

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Key words: Bajocian, Bathonian, taxonomy, palaeoecology, *Modiolus* (*Strimodiolus*) *milnelandensis* nom. nov.

Abstract. The siliciclastic Bajocian–Bathonian Pelion Formation of Tværdal, Geographical Society Ø, East Greenland, is dominated by shallow-marine sandstones, which yielded 22 bivalve taxa representing 18 genera; these are described and figured here. The type species of the subgenus *Strimodiolus*, *Modiolus* (*Strimodiolus*) *elongatus* Fürsich, 1982, is a junior homonym of *Modiola elongata* Swainson, 1821 and is replaced by *M.* (*Modiolus*) *milnelandensis* nom. nov. Infaunal taxa dominate in terms of abundance and species richness, and several of the semi-infaunal (*e.g.*, *Strimodiolus*, *Cyrtopinna*) and deep-burrowing (*Pleuromya*) bivalves are preserved in life position, suggesting periodical high sedimentation rates below the fair-weather wave-base during deposition of most of the formation.

INTRODUCTION

Middle Jurassic bivalves from East Greenland have been described by a few authors in the past (Madsen, 1904; Ravn, 1911; Spath, 1932), but no comprehensive account exists. The present study adds to our knowledge of the geographic distribution of bivalves in the region by describing the fauna that occurs in the Bajocian–Bathonian Pelion Formation at Tværdal, Geographical Society Ø (Figs. 1, 2). In general, bivalves occur scattered in the sandstone-dominated succession and only rarely form concentrations such as observed for *Pinna*. The taxa are characteristic of shallow-water environments of the Boreal Realm, most of them being also known from Russia, Siberia, and northwestern Europe.

The Middle Jurassic outcrop in Tværdal, Geographical Society Ø was first described by Donovan (1955), who presented a short faunal list, comprising ammonites, bivalves and brachiopods. Price and Whitham (1997) provided general stratigraphic information about the locality. During field campaigns of the Geological Survey of Denmark and Greenland (GGU and GEUS), fossils were collected bed-by-bed, together with stratigraphic and sedimentological data. The aim of the present work is to document the Middle Jurassic bivalve assemblages from Tværdal. The detailed ammonite stratigraphy and report of other fossil groups are outside the scope of the present paper and will be presented elsewhere.

GEOLOGICAL SETTING

The deposition of the Pelion Formation marks the onset of the protracted Middle Jurassic – Volgian rifting phase in East Greenland. The basin margin was controlled towards the west by the main post-Devonian fault of Vischer (1943), and the Jurassic basin essentially comprised a complex of westerly-tilted fault blocks. The supply of sediment to the

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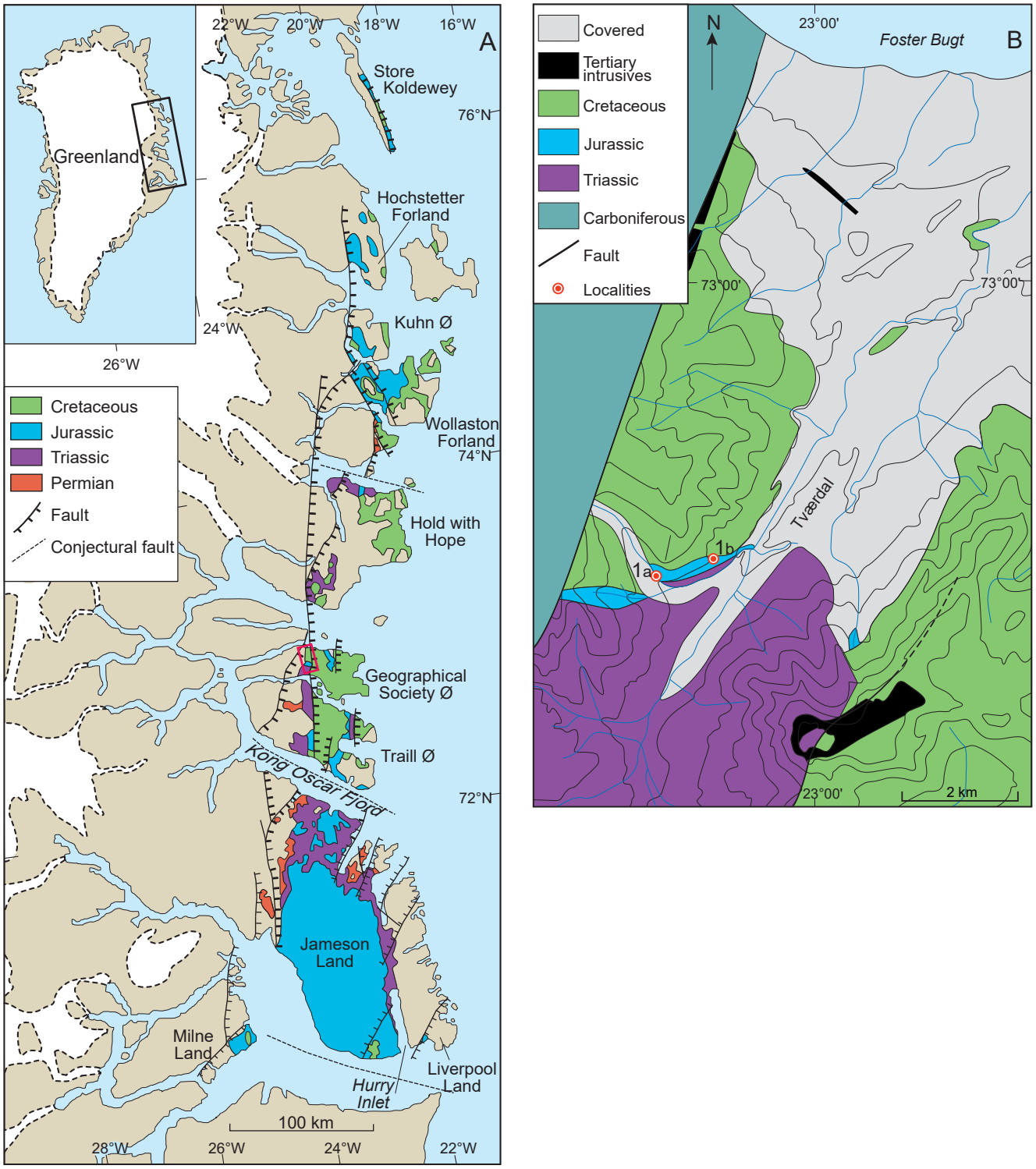

Fig. 1. Geological map of East Greenland

B. Detailed map of the study area of Tværdal on Geographical Society Ø, indicated with a red box in **A**. Modified from Alsen (2015)

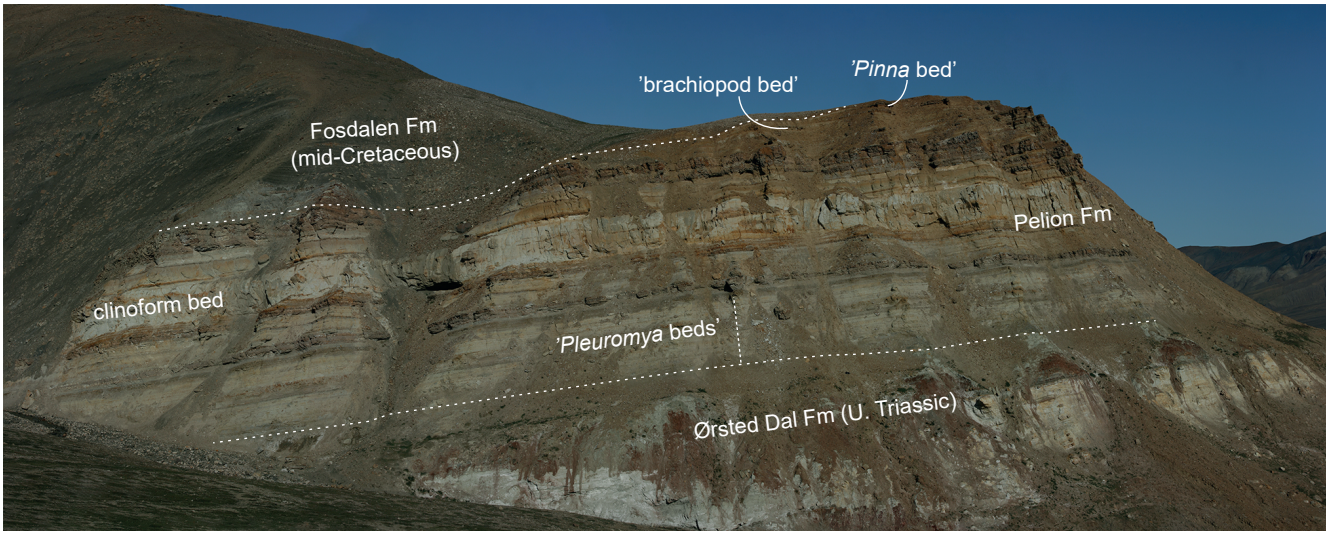

Fig. 2. Field photo of the studied Middle Jurassic succession at locality 1a in Tværdal on Geographical Society Ø

The „*Pleuromya* beds" refer to the ~4.25–11 m interval that is particularly rich in *Pleuromya* specimens, many in life position. The „*Pinna* bed" refers to level 42.6 m of the section. See sedimentological log in Figure 3

shallow-marine and deltaic sand-dominated Pelion Formation was via relay-ramps formed at eastwards *en-echelon* steps of the western main fault (Surlyk, 1977, 1990). The axis of the basin dipped gently towards the south resulting in extensive northwards transgressions during periods of relative sea-level rise. During the Bajocian to Callovian time interval, the basin was thus progressively extended from Jameson Land into the areas north of Kong Oscar Fjord reaching Traill Ø and Geographical Society Ø, Hold with Hope, Wollaston Forland, Kuhn Ø, Hochstetter Forland, and Store Koldewey (Fig. 1). During rifting and associated sea-level rise, the sandy Pelion delta was overlain by offshore marine mudstones of the Fossilbjerget Formation (Surlyk, 1977, 2003). The outcrop of the Pelion Formation in Tværdal on Geographical Society Ø represents a position relatively close to the western Middle Jurassic palaeo-coastline as reflected in the coarser sandstone and conglomeratic beds relative to sections elsewhere in the region (Surlyk, 2003, fig. 17). In-depth descriptions of the geological setting of the Jurassic basin in East Greenland are presented by Surlyk (1977, 2003) and Surlyk *et al.* (2021, 2023).

MATERIAL

Most of the material was collected in the key section at locality 1a (Figs. 1, 2), where the sedimentological log shown in Figure 3 was measured. Material comprising the sample series GEUS 522010 to 522550 was collected during logging of the section and is integrated with the ammonite record. Samples with numbers starting with GEUS 4439-- and 4447-- are from initial reconnaissance visits to the locality and were recorded in a less precisely measured section compared to the log shown in Figure 3. Some samples, however, can be referred to easy recognizable beds and are indicated in the measured section (Fig. 3).

Additional material (samples 522051, 522052, 324598, 324601) came from locality 1b at the north-east end of the outcrop (Fig. 1). Sample 522051 is correlated with the „*Pinna* bed" and sample 522052 with the "Brachiopod bed" in the measured section at locality 1a based on facies and fossil data. The Pelion Formation is rich in species of the ammonite genus *Cranocephalites* indicating the Bajocian and in species of *Arctocephalites* and *Arcticoceras* indicating the Bathonian (PA, unpublished data).

TAXONOMY

The classification scheme follows that of Carter *et al.* (2011). The measurements were taken with a Venier caliper.

Abbreviations used are as follows:

L – length,
H – height,
I – inflation,
LA – anterior length.

In the synonymy lists, only the original reference is given in addition to occurrences of the taxon from boreal areas (*e.g.*, Greenland, northern Russia, Siberia). Illustrated material has been deposited in the Palaeontology Type Collec-

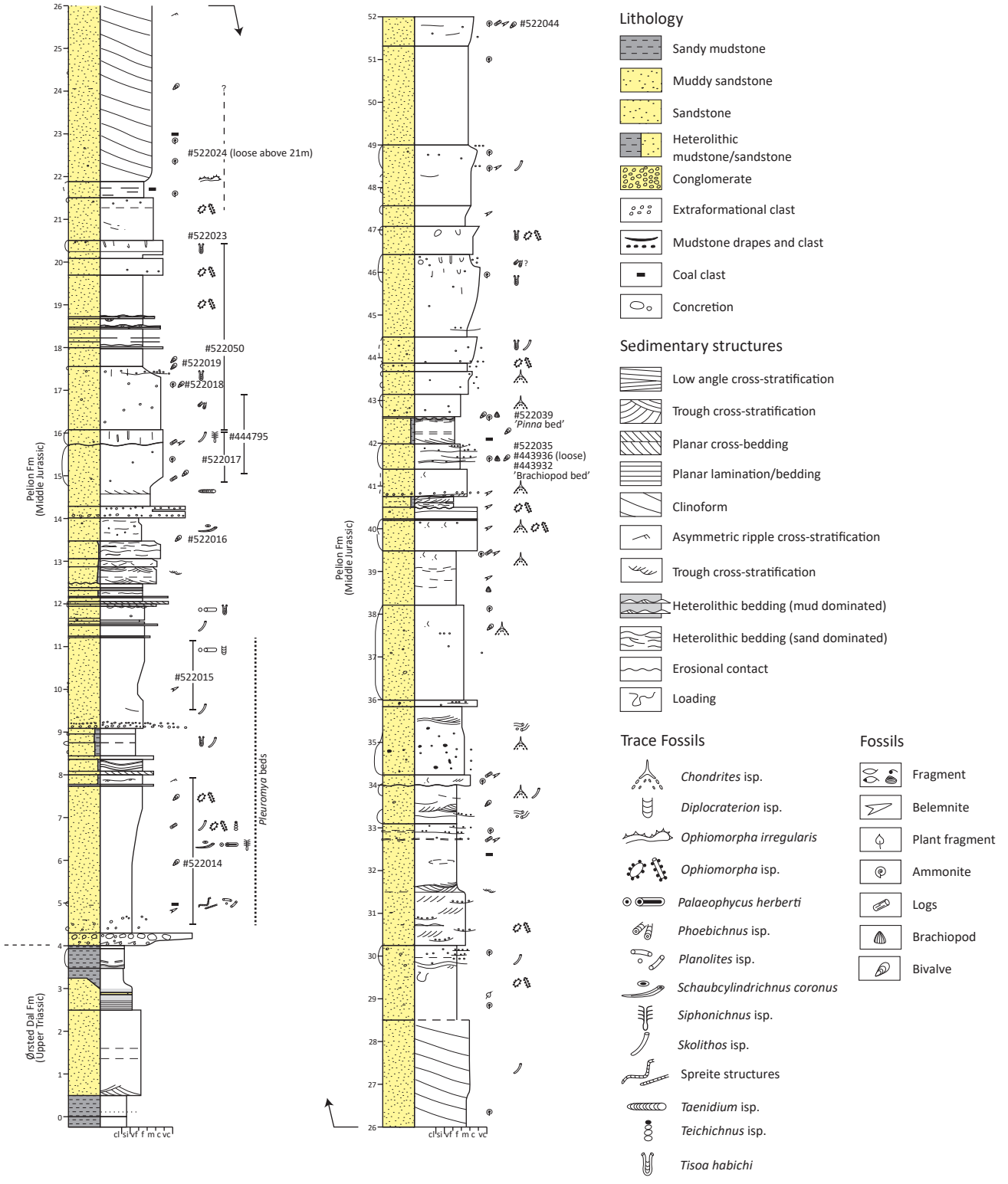

Fig. 3. Section measured at locality 1a, with bivalve levels and sample numbers indicated

Measured by J. Hovikoski

tions of the Natural History Museum of Denmark (prefix: MGUH; Table 1). Other material is housed in the GEUS collection (prefix GEUS).

Class Bivalvia Linnaeus, 1758

Subclass Autobranchia Grobben, 1894

Infraclass Pteriomorphia Beurlen, 1944

Order Mytilida Férussac, 1822

Family Mytilidae Rafinesque, 1815

Genus *Modiolus* Lamarck, 1799

Subgenus *Strimodiolus* Fürsich, 1982

Type species. *Modiolus (Strimodiolus) elongatus* Fürsich, 1982, by original designation.

Remarks. As *Modiolus* (*Strimodiolus*) *elongatus* Fürsich, 1982 is a junior homonym of *Modiola elongata* Swainson, 1821, it is herewith replaced by *Modiolus* (*Strimodiolus*) *milnelandensis* nom. nov.

Modiolus (*Strimodiolus*) *czekanowskii* (Lahusen, 1886)
Fig. 4D–G

1886. *Modiola Czekanowskii* sp.nov. – Lahusen: 5, pl. 2: 2, 2a

1966. *Modiolus czekanowskii* (Lahusen), 1886 – Zakharov: 120, pl. 44: 1

1978. *Musculus* (?) *czekanowskii* (Lahusen), 1886 – Zakharov & Shurygin: 111, pl. 2: 7, 8 (*non* 6)

1982. *Modiolus* (*Strimodiolus*) *czekanowskii* (Lahusen, 1886) – Fürsich: 24, fig. 8C, D

Material. Four fragments of articulated composite moulds from the Bajocian part of the Pelion Formation (GEUS 522014 and 522023).

Description. Incomplete, poorly preserved composite moulds, equivalved, elongated, moderately inflated, slightly conical in outline. Umbones small, subterminal, and prosogyrate. Ventral and dorsal margins nearly straight, anterior and posterior margins well rounded, the posterior part of shell much longer than the anterior one, which is very short. Umbonal ridge very broad, hardly noticeable. Moulds with furrow extending parallel and close to dorsal margin. Surface covered with growth lines and faint growth rugae. Approximately 12 to 15 very faint, closely set, radial striae developed close to dorsal margin, diminishing in strength and disappearing ventrally.

Remarks. The specimens are closest to *Modiolus* (*Strimodiolus*) *czekanowskii* (Lahusen, 1886) as figured by Fürsich (1982) from the Upper Jurassic of Milne Land, East Greenland. In some respect, the specimens resemble the carditoidean *Myoconcha*. Madsen (1904: 179, pl. 6: 8, 9) described the new species *Myoconcha groenlandica* from the Middle Jurassic at Nathorst Fjeld, Jameson Land. *Myoconcha* differs from *Strimodiolus* by its well-developed anterior myophoric buttress and the presence of small cardinal teeth. *M*. (*Strimodiolus*) *strajeskianus* differs from *Myoconcha groenlandica* in outline, ornamentation, and in attaining a larger size.

Most specimens were preserved in life position with their long axis near-vertical.

Order Arcida J. Gray, 1854

Family Parallelodontidae Dall, 1898

Genus *Grammatodon* Meek & Hayden, 1861

Subgenus *Cosmetodon* Branson, 1942

Type species. *Arca keyserlingii* d'Orbigny, 1850, by original designation.

Grammatodon (*Cosmetodon*) *keyserlingii* (d'Orbigny, 1850)
Fig. 4A, B

1846. *Arca elongata* – Keyserling: 305, pl. 17: 1–4 (*non* J. de C. Sowerby, 1825)

1846. *Cucullaea* (*Arca*) *elongata* S. – Rouillier: pl. D: 12. (*non* J. de C. Sowerby, 1825)

1850. *Arca Keyserlingii* d'Orb. – d'Orbigny: 369, no. 357, pl. 44: 6, pl. 45: 2, pl. 49: 3

1883. *Macrodon keyserlingii* (d'Orbigny) – Lahusen: 80, pl. 2: 14, 15

1903. *Macrodon parallelum*. n. sp. – Ilovaisky: 254, pl. 8: 16a–c

1905. *Macrodon Keyserlingii* d'Orb. – Borissjak: 2, pl. 1: 5–9

1905. *Macrodon Lutugini* n. sp. – Borissjak: 5, pl. 1: 10–12, 18

1935. *Parallelodon keyserlingii* (d'Orbigny) – Spath: 58, pl. 15: 7

1936. *Parallelodon* sp. nov.? aff. *P. keyserlingii* (d'Orbigny) – Spath: 112, pl. 43: 3

1955. *Parallelodon keyserlingii* (Orbigny, 1850) – Gerasimov: 46, pl. 1: 19–21

1982. *Grammatodon* (*Cosmetodon*) *keyserlingii* (d'Orbigny, 1850) – Fürsich: 16: 4F, G, I–M, Q, S

Material. Three incomplete left valves and one right valve from the Bajocian–Bathonian part of the Pelion Formation (GEUS 324601, 522023F, and 522051F).

Description. Shells distinctly elongated with posteroventral part slightly produced. Umbones moderately to distinctly protruding beyond dorsal margin, situated approximately one-fifth of shell length from the anterior end, ortho- to slightly

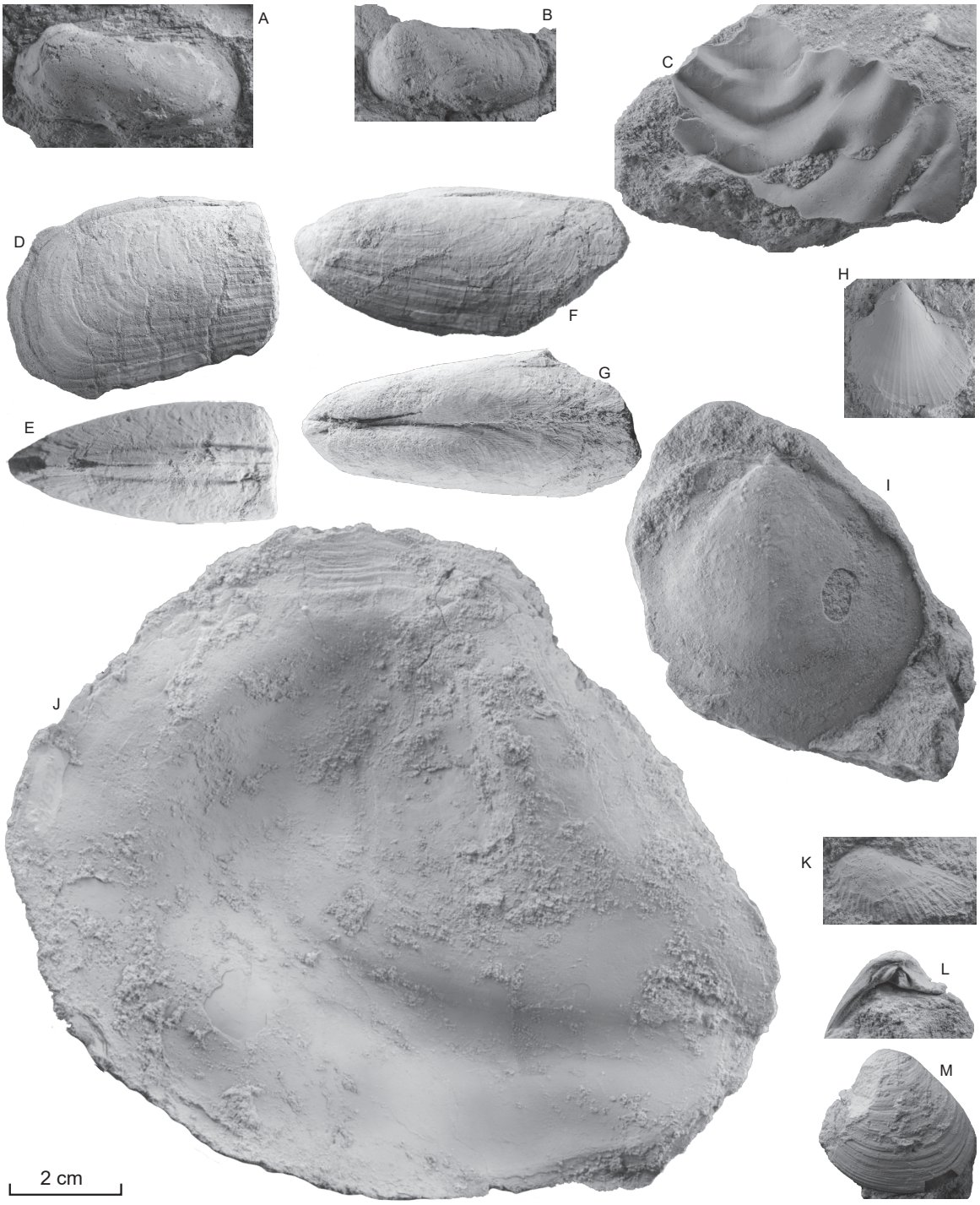

Fig. 4A, B. *Grammatodon* (*Cosmetodon*) *keyserlingii* (d'Orbigny, 1850). A. Internal mould of left valve, MGUH 34777. B. Left valve, MGUH 34778. **C.** *Retroceramus* (*Retroceramus*) sp., fragment of external mould, MGUH 34779. **D–G.** *Modiolus* (*Strimodiolus*) *czekanowskii* (Lahusen, 1886). D–E, posterior half of internal mould of articulated specimen, MGUH 34780; D, right valve view, E, dorsal view; F–G, internal mould of articulated specimen, MGUH 34781; F, left valve view, G, dorsal view. **H, K.** *Oxytoma* (*Oxytoma*) *inequivalve* (J. Sowerby, 1819); H, internal mould of left valve with remains of shell, MGUH 34782. K, internal mould of left valve, MGUH 34783. **I.** *Camptonectes* (*Camptonectes*) sp., internal mould of right valve with remains of shell, MGUH 34784. **J.** *Liostrea* sp., right valve, internal view, MGUH 34785. **L, M.** *Astarte* sp. A, left valve, MMGUH 34786; L, hinge area, M, external view

prosogyrate. Anterior margin not seen, ventral margin faintly sinuous, posterior margin rounded, forming obtuse angle with long, straight dorsal margin. Flank with shallow, slightly posteriorly directed sulcus running from umbo to ventral margin. Broad, rounded posterior umbonal ridge separating concave posterodorsal part of shell from flank. Ornamentation consisting of commarginal growth lines of varying strength crossed by numerous fine radial striae. Only posterior part of hinge seen, consisting of 3–4 teeth of varying length, arranged horizontally to sub-horizontally to hinge margin.

Remarks. The shells can be safely placed in d'Orbigny's species, although they are incomplete. There are several Jurassic species of *Cosmetodon* that closely resemble the present species, differing in the degree of obliquity and in the degree of angularity of the posterodorsal corner. They include *Arca elongata* Sow. of Keyserling (1846: 305, pl. 17: 1–4) and *Cucullaea* (*Arca*) *elongata* S. of Rouillier (1846: 425, pl. D: 12a–d), which seem to differ from *Cucullaea elongata* J. de C. Sowerby (1824: 67, pl. 447: 1), a species that apparently lacks the umbonal sulcus. The various species of *Cosmetodon* that have been described from the Jurassic of northern Russia and Siberia need to be studied in more detail before their relationship and possible synonymy with *G.* (*Cosmetodon*) *keyserlingii* can be firmly established.

Order Myalinida H. Paul, 1939

Family Inoceramidae C. Giebel, 1852

Genus *Retroceramus* Koshelkina, 1957

Subgenus *Retroceramus* Koshelkina, 1957

Type species. *Inoceramus retrorsus* Keyserling, 1848, by original designation.

Retroceramus (*Retroceramus*) *retrorsus* (Keyserling, 1848)

Fig. 5A, B

1848. *Inoceramus retrorsus* – Keyserling: 250, pl. 4: 4–5

1886. *Inoceramus retrorsus* Keys. – Lahusen: 3, pl. 1: 1

1932. *Inoceramus retrorsus* Keyserling – Spath: 110, text-fig. 8

1947. *Inoceramus retrorsus* Keyserling, 1848 – Petrova: 128, pl. 15: 3

1962. *Retroceramus* (*Retroceramus*) *retrorsus* Keyserling, 1848 – Koshelkina: 34, pl. 20: 2, 2a

1963. *Retroceramus* (*Retroceramus*) *retrorsus* (Keyserling, 1848) – Koshelkina: 144, pl. 6: 2a, b

1968. *Retroceramus retrorsus* (Keyserling, 1848) – Efimova *et al.*: 72, pl. 87: 1, 2, pl. 88: 1–4

1992. *Retroceramus retrorsus* (Keyserling, 1848) – Polubotko: 76, pl. 39: 6, pl. 40: 5

Material. Three internal moulds of articulated shells from the Bajocian part of the Pelion Formation (all from GEUS 522014).

Description and remarks. The poorly preserved internal moulds are moderately inflated, comparatively narrow, and obliquely elongated in a posteroventral direction. The tip of the umbo is only preserved in one specimen. The ornamentation consists of spaced, moderately strong, commarginal folds.

The specimens correspond closely to the specimen figured by Spath (1932) under this name and therefore have been referred to that species, despite its poor preservation. A comparable taxon is *Retroceramus* (*Retroceramus*) *porrectus* (Eichwald, 1871) as figured for example by Koshelkina (1962: 33, pl. 20: 1; 1969: 101, pl. 30: 1, 2) from Bathonian rocks of eastern Siberia.

Table 1
Figured specimens, repository numbers and sampling numbers

MGUH	ex GEUS	Sub no's	MGUH	ex GEUS	Sub no's
34777	324601		34801	522051	
34778	522051	F	34802	522051	E
34779	444795		34803	522023	B
34780	522014	I	34804	522014	H
34781	522014	D	34805	522023	
34782	522035	A	34806	522017	
34783	522017	A	34807	522052	C
34784	522014		34808	522051	C
34785	443932		34809	522051	B
34786	324601		34810	324601	
34787	522014		34811	522014	J
34788	522014		34812	522015	C
34789	522052	A	34813	522014	A
34790	522039	B	34814	522013	A
34791	522039	A	34815	522014	F
34792	522039	C	34816	522017	B
34793	443936		34817	522023	A
34794	522023	A	34818	522023	D
34795	522023		34819	522015	B
34796	522051		34820	522014	K
34797	324601		34821	522013	C
34798	522023	C	34822	522050	
34799	324601		34823	522018	A
34800	522017	D	34824	522051	A

Fig. 5A, B. *Retroceramus* (*Retroceramus*) *retrorsus* (Keyserling, 1848), internal moulds of articulated specimens

A. Right valve view, MGUH 34787. **B.** Right valve view, MGUH 34788

***Retroceramus* (*Retroceramus*) sp.**
Fig. 4C

Material. Two specimens, one a shell fragment of a single valve, the other an articulated but poorly preserved, crushed specimen. Both are from the Bajocian part of the Pelion Formation (GEUS 444795 and 522014).

Description and remarks. The single valve is a fragment of a much larger shell and most likely represents a species different from *R.* (*R.*) *retrorsus*. As only a small part of the somewhat irregular, strong commarginal folds is seen, a precise identification is impossible.

Spath (1932: 109, text-fig. 7) figured and described *Inoceramus ambiguus* Eichwald, 1871 from the *Arctocephalites* beds of Jameson Land, a species of comparable size but with less pronounced commarginal folds.

The articulated specimen could be a *R.* (*R.*) *retrorsus* but is too poorly preserved to safely assign it at species level.

Order Ostreida Férussac, 1822

Family Gryphaeidae Vialov, 1936

Genus *Liostrea* Douvillé, 1904

Type species. *Ostrea sublamellosa* Dunker, 1846, by original designation.

***Liostrea* sp.**
Fig. 4J

Material. One right valve from the Bathonian part of the Pelion Formation (GEUS 443932).

Description and remarks. The large, only slightly inflated shell (H: 115.4 mm; L: 134.0 mm) is irregularly suborbicular with a drawn out posteroventral part. The surface is irregular and covered with small growth folds. The ligament area is wide and only faintly impressed. The adductor scar is rounded-subquadrate and situated just posterior of the mid-line of the valve. On the outer surface of the shell there are clusters of acrothoracican borings.

The shell resembles *Liostrea cucurbita* Zakharov (1966: 111, pl. 41: 1, 2, pl. 42: 1) from the Valanginian of Siberia, which is of a similar size but lacks the extended posteroventral area. The studied specimen also exhibits a certain similarity to *Deltoideum delta* (Smith, 1817: 18, fig. 6), which has, however, a much narrower umbonal and ligament area. The shell from Greenland differs from *Ostrea expansa*, which J. Sowerby (1821: 65, pl. 238: 1) had described from the Upper Jurassic of England, in the shape of its adductor scar. *Ostrea explanata* of Goldfuss (1833: 22 pl. 80: 5) from the Middle Jurassic of Bavaria appears to be much thicker-shelled. *Liostrea eduliformis* (Schlotheim, 1820: 233) as figured by Schlippe (1888: 110, pl. 1: 1, 2) also resembles the present specimen, whereas *Ostrea eduliformis* Schlotheim of Madsen (1904: 178, pl. 7: 1–3) from the Middle Jurassic of Nathorst Fjeld probably represents a different species. As only the right valve is available, we refrain from assigning our specimen to a particular species.

Family Pinnidae Leach, 1819

Genus *Pinna* Linnaeus, 1758

Subgenus *Cyrtopinna* Mörch, 1853

Type species. *Pinna incurva* Gmelin, 1791, by original designation.

Remarks. Recently, Koppka (2018) argued that most Jurassic species of *Pinna* belong in fact to the subgenus *Cyrtopinna*, a view that is followed here. Members of the subgenus are characterized by being thin-shelled, having a well-defined median carina, a rhomboidal and in some species even quadrate cross-section, and only weakly developed radial ribs.

Pinna (*Cyrtopinna*) *sublanceolata* Eichwald, 1865
Fig. 6A, D–F

1865. *Pinna sublanceolata* m – Eichwald: 546, pl. 23: 5

Material. Nine articulated specimens, two right and two left valves, all preserved as internal moulds, commonly with remains of shell, from the Bajocian and Bathonian parts of the Pelion Formation (GEUS 324598B, 324601, 443936, 522015G, 522039A-E, 522044, 522051, 522052A, B).

Description. Specimens medium-sized for the genus (maximum height approximately 113 mm), wedge-shaped, thin-shelled, narrow, straight to very faintly curved. Umbones small, situated at anterior end. Dorsal margin straight, ventral margin slightly concave at juvenile stage turning straight to faintly convex posteriorly during growth. Posterior margin broadly rounded to truncated. Valves divided into dorsal and ventral half by median carina running from umbones towards posterior end where it disappears before reaching the posterior margin. Height of dorsal part of shell slightly lower than that of ventral part (height ratio of dorsal and ventral shell parts varying between 0.75 and 0.92). Cross-section of articulated valves rhombic, becoming elliptical towards posterior end, which is gaping in some specimens. Ornamentation consisting of slightly wavy and somewhat puckered radial ribs of variable strength that fade towards posterior end. Number of ribs dorsally of carina approximately ten, ventrally of carina six, the latter restricted to dorsal part of ventral half of shell. Growth lines and commarginal folds, the latter particularly well-developed in ventral part of shell, distinctly curved towards ventral margin but meeting dorsal margin nearly at right angle.

Remarks. There exist numerous names for Jurassic species of *Pinna* (*Cyrtopinna*), which often are based on poorly preserved type material. Spath (1932: 108, pl. 17:. 4) identified a specimen from the *Arcticoceras* beds of Jameson Land as *Pinna sublanceolata* Eichwald, 1865 and we refer the present specimens that come from a close-by area and the same stratigraphic level to this species.

Spath (1936: 108, pl. 44: 4, pl. 45: 5, 6) described *Pinna constantini* de Loriol, 1874 from the Upper Jurassic of Milne Land, East Greenland, which Fürsich (1982: 30, figs. 6A, 11A, D) included in *Pinna* (*P.*) *lanceolata* J. Sowerby, 1821. In this species, the radial ribbing and commarginal folds are far more pronounced than in the present specimens and the ornamentation appears to extend much further in a posterior direction. *Pinna* (*P.*) *lanceolata* is, moreover, narrower than *P.* (*Cyrtopinna*) *sublanceolata*. The number of ribs is comparable, but varies less between specimens than in the case of the Milne Land specimens.

Order Pectinida J. Gray, 1854

Family Pectinidae Rafinesque, 1815

Genus *Camptonectes* Agassiz in Meek, 1864

Subgenus *Camptonectes* Agassiz in Meek, 1864

Type species. *Pecten lens* J. Sowerby, 1818, by subsequent designation of Stoliczka (1871).

Camptonectes (Camptonectes) sp.
Fig. 4I

Material. One internal mould of a right valve with remains of ferruginized shell from the Bajocian part of the Pelion Formation (GEUS 522014).

Description and remarks. The approximately 50-mm-high shell with its suborbicular outline and low convexity is slightly asymmetric, the anterodorsal part of the disk being less convex than the posterodorsal part. The posterior auricle forms an acute angle with the disk, the anterior auricle is only partly preserved. Faint remains of a fine divaricate ornamentation are seen.

The slightly asymmetric disk and traces of a divaricate ornamentation place the specimen in *Camptonectes* (*Camptonectes*), but the poor preservation does not allow an identification at the species level. Spath (1932: 113, pl. 5: 4 and pl. 10: 5) described and figured *Camptonectes rigidus* (J. Sowerby, 1818) from the Bathonian of Mt. Hjørnefjæld, which was placed by Johnson (1984: 125) in the synonymy of *C.* (*Camptonectes*) *laminatus* (J. Sowerby, 1818). The present specimen, coming from a neighbouring area and the same stratigraphic level, may well belong to that species.

Family Oxytomidae Ichikawa, 1958

Genus *Oxytoma* Meek, 1864

Subgenus *Oxytoma* Meek, 1864

Type species. *Avicula muensteri* Bronn, 1830, by original designation.

Fig. 6A, D–F. *Pinna* (*Cyrtopinna*) *sublanceolata* d'Eichwald, 1865. A – internal mould of articulated specimen with remains of shell, right valve view, MGUH 34789; D – internal mould of articulated specimen, right valve view, MGUH 34790; E – internal mould of articulated specimen, left valve view, MGUH 34791; F – internal mould of articulated specimen with remains of shell left valve view, MGUH 34792. **B, C.** *Entolium* (*Entolium*) *corneolum* (Young & Bird, 1828); B – single valve MGUH 34793; C – single valve, MGUH 34794. **G–I.** *Corbicellopsis* cf. *tenera* (de Loriol, 1875); G – left valve, MGUH 34795; H, I – internal mould of articulated specimen, MGUH 34796; H – right valve view, I – dorsal view. **J, K.** *Quenstedtia parallela* (Trautschold, 1866), internal mould of articulated specimen, MGUH 34797; J – right valve view, K – dorsal view. **L, M.** *Quenstedtia bathonica* (Morris & Lycett, 1854), internal mould of articulated specimen, ventral margin partly missing, MGUH 34798; L – right valve view, M – dorsal view. **N.** Lucinid indet., fragment of right valve, MGUH 34799

Oxytoma (*Oxytoma*) *inequivalve* (J. Sowerby, 1819)
Fig. 4H, K

1819. *Avicula inequivalvis*. – J. Sowerby: 78, pl. 244: 2, 3
1883. *Avicula inequivalvis* J. Sowerby – Lahusen: 91, pl. 2: 5
1903. *Avicula* cfr. *Münsteri* Bronn – Ilovaisky: 252, pl. 8: 18, 19 (*non* Bronn)
1909. *Oxytoma inaequivalvis* Sow. – Borissjak: 19, pl. 1: 10
1909. *Oxytoma inequivalvis* var. *borealis* m. – Borissjak: 19, pl. 1: 3–8
1955. *Oxytoma inequivalvis* (Sowerby) – Gerasimov: 88, pl. 18: 1–8
1962. *Oxytoma* ex gr. *inaequivalve* Sow. – Pchelintseva: 37, pl. 6: 13–14
1982. *Oxytoma* (*O.*) *inequivalve* (J. Sowerby, 1819) – Fürsich: 34, fig. 6B–D, F

Material. Internal moulds of two left valves from the Bajocian and Bathonian parts of the Pelion Formation (GEUS 522017A and 522035A).

Description and remarks. The poorly preserved specimens provide only limited morphological information. Their outline varies from suborbicular to posteroventrally elongated-ovate. The short anterior auricle is distinctly set off from the flank, in contrast to the elongated posterior auricle, which is characterized by a deep subauricular sinus. The umbo is situated anteriorly. The ornamentation consists of radial primary ribs between which at least two weaker secondary riblets are intercalated. The specimen 522017A appears distinctly elongated, but this is probably due to the missing ventral part of the valve.

Oxytoma inequivalve is a pandemic bivalve that ranged from tropical to arctic environments and is found throughout the Jurassic. Several species reported from Middle Jurassic strata of high northern latitudes, such as *O*. (*Oxytoma*) *jacksoni* (Pompecki, 1899) of Sey & Kalacheva (1992: 89, pl. 44: 5–7), *O*. (*O.*) *expansum* (Phillips, 1829) of Turbina & Zakharov (1990: 53, pl. 6: 1–5), and *O*. *mclearni* Warren (1932: 16, pl. 1: 26, 27) are probably conspecific with it, but this needs to be confirmed by a detailed study of these taxa. From Volgian strata of East Greenland, Spath (1936: 97, pl. 42: 4–7) had described *Oxytoma expansum* (Phillips, 1829) (= *O. inequivalve* of Fürsich, 1982).

Family Entoliidae Teppner, 1922

Genus *Entolium* Meek, 1865

Subgenus *Entolium* Meek, 1865

Type species. *Pecten demissus* Phillips, 1829, by original designation (as illustrated by Quenstedt (1858, p. 353, pl. 48: 7).

Entolium (*Entolium*) *corneolum* (Young & Bird, 1828)
Fig. 6B,C

1828. *Pecten corneolus* – Young & Bird: 234, pl. 9: 5.
1862. *Pecten demissus* Phillips – Trautschold: 2, pl. 7: 2, 4 (*non* fig. 3)
1883. *Pecten demissus* Phillips – Lahusen: 24, pl. 2: 4
1903. *Pecten vitreus* Röm. – Ilovaisky: 30, pl. 8: 13
1911. *Pecten* (*Entolium*) *demissus* Bean – Ravn: 163, pl. 33: 8
1917. *Pecten demissus* Phillips – Borissjak & Ivanoff: 3, pl. 1: 5, 8, 10, 15, 17
1917. *Pecten spathulatus* Roem. – Borissjak & Ivanoff: 6, pl. 1: 13
1917. *Pecten vitreus* Roem. – Borissjak & Ivanoff: 8, pl. 1: 1, 2, 4, 12, 16
1931. *Pecten* (*Entolium*) cf. *demissus* Phil. – Sokolov & Bodylevsky: 50, pl. 3: 5
1932. *Pecten* (*Entolium*) *demissum* (Phillips) – Spath: 112, pl. 26: 2
1982. *Entolium* (*Entolium*) *corneolum* (Young & Bird, 1828) – Fürsich: 37, fig. 15C

Material. Five single valves from the Bajocian part of the Pelion Formation (GEUS 443936A, B, 522023, 522023G, I).

Description. Shells medium-sized (H of disk ranging from ~30 to 49.5 mm), poorly inflated, equivalved and equilateral. Disk suborbicular, umbonal angle 114–120°. Auricles nearly equal, anterior auricle of right valve slightly larger than posterior one. Dorsal margins of auricles forming an angle of 120–130°. Surface of disk and auricles covered with dense, very fine growth lines.

Remarks. Except for one right valve, the specimens are poorly preserved. Nevertheless, as the characteristic features of the species are seen, there is little doubt that they represent *E*. (*Entolium*) *corneolum*. Specimen 443936A displays regularly arranged growth folds, spaced 3 to 4 mm apart. They resemble to some extent the ornamentation of *Entolium* (*E.*) *orbiculare*, which is widespread in the Upper Jurassic of East Greenland (Fürsich, 1982), but in the latter species the commarginal ribs are much finer and more closely spaced.

Order Carditida Dall, 1889

Family Astartidae d'Orbigny, 1844

Genus *Astarte* J. Sowerby, 1816

Type species. *Venus scotica* Maton & Rackett, 1807, by original designation.

Astarte sp. A
Fig. 4L, M

?1846. *Astarte ovata* Phill. – Rouillier: pl. B: 13a–c. (*non* Phillips, 1871)

?1848. *Astarte ovata* Phill. – Rouillier: 267

?1973. *Astarte* cf. *ovata* Smith – Romanov: 109, pl. 11: 1

Material. Fragment of a left valve from the Bathonian part of the Pelion Formation (GEUS 324601).

Description. Specimen medium-sized (H: 26 mm), rounded-triangular, thick-shelled, anterior part broken off. Umbo depressed, beak prosogyrate. Lunule large, deeply impressed, sharply delimited. Escutcheon long, narrow-lanceolate. Ventral margin evenly curved, posterodorsal margin long, straight, strongly sloping and grading into narrowly rounded posteroventral margin. Interior shell margin not crenulated. Ornamentation abraded, for the first 7 mm consisting of dense, sharp, commarginal ribs that are replaced ventrally by regularly spaced, broad commarginal undulations separated by narrower grooves. Hinge with two cardinal teeth and three sockets to receive cardinals of right valve. Nymph plate followed by long posterior lateral tooth and groove for receiving lateral of right valve. Anterodorsal part of shell missing; thus, information on possible existence of anterior laterals missing.

Remarks. Our specimen closely resembles *Astarte ovata* Phillips of Rouillier (1846: pl. B: 13; 1848: 267) from the Upper Jurassic of Russia. Madsen (1904, p. 182, pl. 6: 14, 15) described *Astarte* sp. cf. *elegans* Sowerby from the Middle Jurassic of Nathorst Fjeld, Jameson Land, which may represent the same species. The outlines of published figures of this species vary considerably and probably represent several species. Cox and Arkell (1949, p. 95) referred *Astarte elegans* J. Sowerby, 1816 to *Neocrassina*. In contrast to the present specimen, *Neocrassina* has only a slightly depressed lunule. For this reason, we keep the specimen from Geographical Society Ø in *Astarte*. As its outline is not fully known, we refrain from placing it in one of the numerous Jurassic species of the genus.

Order Lucinida J. Gray, 1854

Family Lucinidae Fleming, 1828

Lucinidae indet.
Fig. 6N

Material. One fragment of a right valve from the Bathonian part of the Pelion Formation (GEUS 324601).

Description and remarks. The posterior half of the medium-sized (H: ~35.5 mm) and moderately thick shell is missing. The outline appears to be suborbicular, the umbo prosogyrate, the anterodorsal margin is slightly excavated. The partly abraded ornamentation consists of fine commarginal ribs, between which stronger commarginal ribs are intercalated at regular intervals (distance between the latter: 2–3 mm).

Due to the poor preservation, no precise identification of the specimen is possible. The ornamentation and what is preserved of the outline of the shell suggest that it belongs to the family Lucinidae, of which several Jurassic species exhibit a similar ornamentation, such as the Middle Jurassic *Lucina bellona* d'Orbigny of Morris & Lycett (1853, p. 67, pl. 6: 18). The Upper Jurassic lucinids from East Greenland described by Spath (1936) and Fürsich (1982), i.e. *Discomiltha lirata* (Phillips, 1829) and *Discomiltha* (?) sp. A differ by their more produced anterior part of the shell.

Order Cardiida Férussac, 1822

Family Quenstedtiidae Cox, 1929a

Genus *Quenstedtia* Morris & Lycett, 1855

Type species. *Pullastra oblita* Phillips, 1829, by monotypy.

Quenstedtia parallela (Trautschold, 1866)
Fig. 6J, K

1846. *Thracia laevigata* Phillips – Rouillier: pl. B: 7a, b. (*non* Phillips, 1829)

1848. *Thracia laevigata* Phillips – Rouillier: 266

1866. *Pleuromya parallela* n. sp. – Trautschold: 9, pl. 2: 1a–d

1955. *Quenstedtia parallela* (Trautschold) – Gerasimov: 74, pl. 8: 8a, b

1982. *Quenstedtia parallela* (Trautschold) – Fürsich: 80, fig. 31G

Material. One articulated internal mould from the Bathonian part of the Pelion Formation (GEUS 324601).

Description and remarks. The compressed specimen is comparatively small for the genus (L: ~27 mm) and is characterized by subparallel ventral and dorsal margins, submesial, distinctly depressed umbones, and an inconspicuous posterior umbonal ridge that appears to faint towards the posteroventral margin. The anterior and posterior margins are evenly rounded.

The specimen corresponds closely to Trautschold's (1866) figure and description of the species. Trautschold (1866, p. 10) mentions the greatest compression of the shell in the anterior part, which is also the case in the present specimen. As a result, the valves gape distinctly posteriorly. Whether this is a primary feature or a taphonomic artifact is not clear.

Quenstedtia bathonica (Morris & Lycett, 1854)
Fig. 6L, M

1854. *Corbis* (*Corbicella*) *bathonica* – Morris & Lycett: 95, pl. 13: 14

1929b. *Quenstedtia bathonica* (Morris and Lycett) – Cox: 578

Material. One fragmented articulated internal mould from the Bajocian part of the Pelion Formation (522023C).

Description and remarks. The moderately sized specimen (L: 34 mm) is poorly inflated and elongated-ovate. The depressed umbones are situated slightly anteriorly of the mid-line. The greatest inflation is in the area of a broad, only faintly developed posterior umbonal ridge. The antero- and posterodorsal margins are sloping, the anterior and posterior margins are well-rounded, the ventral part of the mould is broken.

The specimen closely resembles *Quenstedtia bathonica*. It is also similar to *Corbicella moraena* (Buvignier) Morris et Lycett of Loriol *et al*. (1872: 257, pl. 15: 3, 4) from the Upper Jurassic of northern France, except that the latter species is more elongated.

Family Tancrediidae F. Meek, 1864

Genus *Corbicellopsis* Cox, 1929b

Type species. *Corbis laevis* J. de C. Sowerby, 1827, by original designation.

Corbicellopsis cf. *tenera* (de Loriol, 1875)
Fig. 6G–I; Tab. 2

cf. 1875. *Corbicella tenera* P. de Loriol, 1875 – Loriol & Pellat: 222, pl. 14: 13a, b.

Material. Two articulated internal moulds from the Bathonian part (GEUS 522051) and one left valve with remains of shell from the Bajocian part of the Pelion Formation (GEUS 522023).

Measurements (in mm). See Table 2.

Table 2
Measurements (in mm) of *Corbicellopsis* cf. *tenera* de Loriol, 1875

Specimen	L	H	I
522051A	23.6	14.4	9.0
522051B	26.0	14.9	9.7
522023	17.2	8.9	–

Description. Specimens small (Table 1), very thin-shelled, poorly inflated, elongated-ovate. Umbones prominent but depressed, beaks orthogyrate. Ligament opisthodetic. Ventral margin broadly arched, anterior margin rounded, posterior margin obliquely truncated. With very inconspicuous posterior umbonal ridge. Shell surface smooth. Internal features not seen.

Remarks. The outline of the specimens is very close to that of *Corbicella tenera* from the Upper Jurassic of the Boulonnais, northern France, but that species is much more compressed. As it is not clear whether this feature has partly been caused by compaction, our specimens are referred to *C. tenera* with doubt. As the left valve of *C. tenera* (de Loriol, 1875: 222) carries two cardinal teeth, it belongs to *Corbicellopsis* rather than *Quenstedtia*.

There are several articulated internal moulds in the collection that most likely either belong to *Corbicellopsis* or *Quenstedtia*. Their poor preservation precludes, however, a precise identification.

Family Unicardiopsidae Chavan, 1969

Genus *Unicardiopsis* Chavan, 1969

Type species. *Unicardium aceste* d'Orbigny, 1850, by original designation.

Unicardiopsis aceste (d'Orbigny, 1850)
Fig. 7A–H, K; Tab. 3

1850. *Unicardium Aceste* d'Orb. – d'Orbigny: 366, no. 307

1936. *Mactromya verioti* (Buvignier) – Spath: 122, pl. 46: 2–3

1982. *Unicardium aceste* d'Orbigny, 1850 – Fürsich: 70, fig. 27G

Material. Ten articulated, two right and two left valves from the Bajocian and Bathonian parts of the Pelion Formation (GEUS 324601, 443936, 444795, 522014, 522017, 522018, 522023, 522044, and 522051). Most of the specimens are internal moulds.

Measurements (in mm). See Table 3.

Table 3
Measurements (in mm) of *Unicardiopis aceste* (d'Orbigny, 1850)

Specimen	LA	L	H	I
522017D	19.2 (57.8%)	33.2	~28.5	19.7
522051	17.6 (49.0%)	35.9	29.5	-
522051E	20.7 (55.0%)	37.6	35.2	24.0
444795	17.0 (52.8%)	32.2	25.1	-
522044	23.0 (60.5%)	38.0	34.6	-
324601	14.6 (50.3%)	29.0	25.3	21.2

The percentage figure relates the anterior length to the total shell length

Description. Medium-sized, moderately inflated shell, equivalved, inequilateral, slightly longer than high. Um-

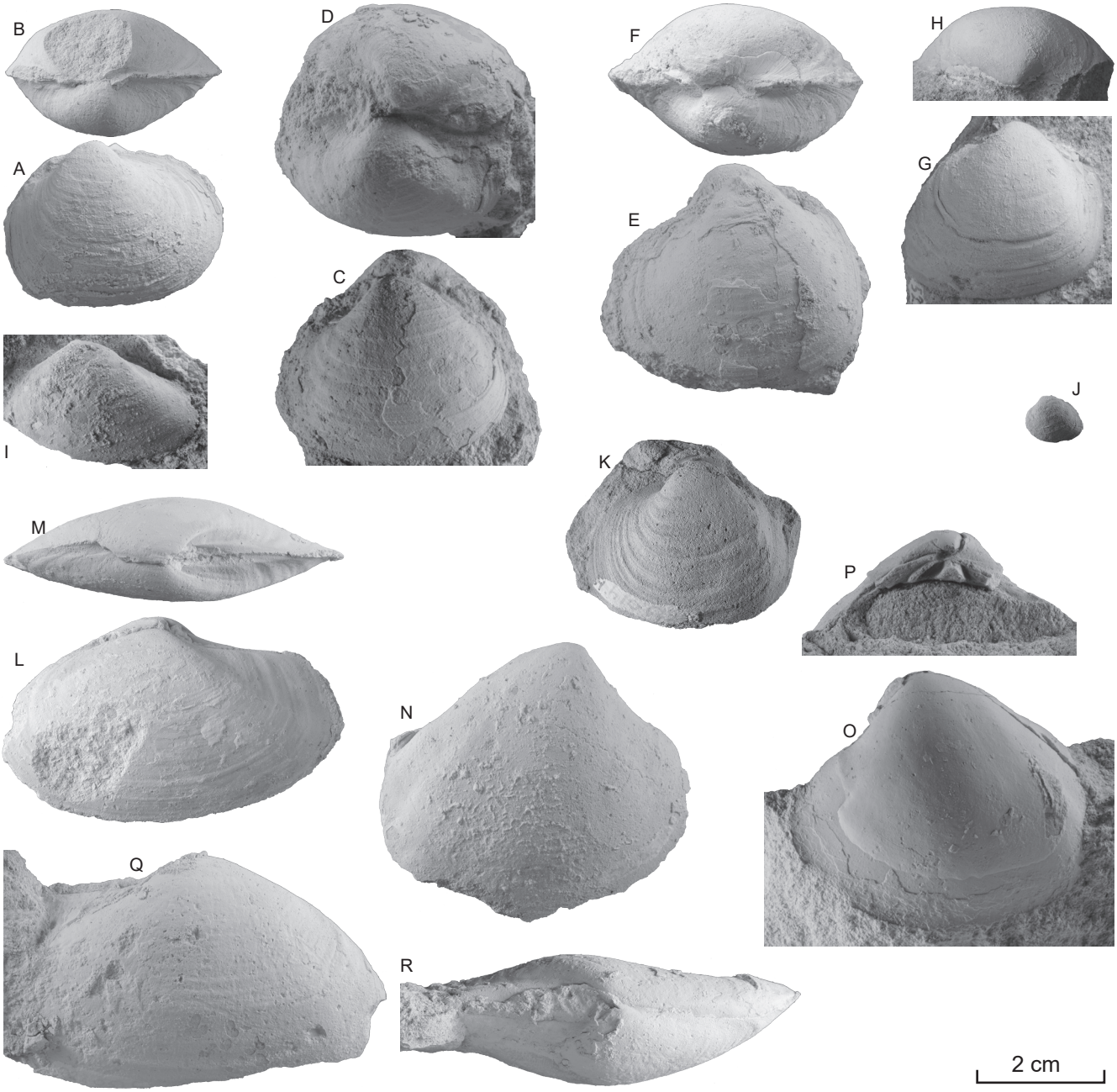

Fig. 7A–H, K. *Unicardiopsis aceste* (d'Orbigny, 1850). A, B – internal mould of articulated specimen, MGUH 34800; A – right valve view, B – dorsal view; C, D – internal mould of articulated specimen, MGUH 34801; C – left valve view, D, dorsal view; E, F – internal mould of articulated specimen, MGUH 34802; E – left valve view, F – dorsal view; G, H – internal mould of left valve, MGUH 34803; G – side view, H – dorsal view; K – internal mould of left valve, MGUH 34804. **I.** *Pronoella?* sp. A, internal mould of left valve, MGUH 34805. **J.** arcticid? indet., internal mould of left valve with remains of shell, MGUH 34806. **L, M, Q, R.** *Thracia amygdaloidea* Lycett, 1863. L, M – internal mould of articulated specimen, MGUH 34807; L – left valve view, M – dorsal view; Q, R – internal mould of articulated specimen, MGUH 34808; Q – right valve view, R – dorsal view. **N–P.** *Pronoella* sp.; N – internal mould of right valve, MGUH 34809; O, P – internal mould of left valve with remains of shell, MGUH 34810; O – external view, P – hinge

bones prominent, slightly prosogyrate, situated 49 to 60% of total shell length from the anterior end (Tab. 2). Anterior margin regularly rounded, grading into broadly curved ventral margin. Posterior margin distinctly truncated, nearly vertical. Dorsal margin nearly straight. Ligament opisthodetic, external. Shell surface covered with prominent growth lines or faint commarginal ribs of varying strength. Internal features not seen.

Remarks. The present specimens closely resemble *Unicardium aceste* d'Orbigny from the Kimmeridgian of France as figured by Cottreau (1927: 122, pl. 16: 26, 27). The species has been recorded from the Volgian of East Greenland by Spath (1936) as *Mactromya verioti* (Buvignier, 1852). It has also been recorded from the Callovian of Russia as *Unicardium laevigatum* by Lahusen (1883: 93, pl. 2: 30).

The comparatively well-preserved specimen GEUS 324601 differs from the remaining ones in being more inflated and in having narrower, more salient, and more strongly prosogyrate umbones. In this respect it resembles species of *Rollierella* Cossmann, 1924 and *Anisocardia* Munier-Chalmas, 1863. However, the resemblance stems mainly from the fact that parts of the posterior and anterodorsal margin of the specimen are missing which changed its outline.

Family Arcticidae R. Newton, 1891

Genus *Pronoella* Fischer, 1887

Subgenus *Pronoella* Fischer, 1887

Type species. *Venulites trigonellaris* v. Schlotheim, 1820, by typification of replaced name.

***Pronoella* sp.**
Fig. 7N–P

Material. Two internal moulds (right valve and left valve, the latter with remains of shell) from the Bathonian part of the Pelion Formation (GEUS 324601 and 522051B).

Description. Specimens medium-sized, triangular-ovate, length exceeding height (L: 50.7 mm, H: 41.6 mm), equivalved. Umbo prosogyrate, situated anteriorly of midline of shell. Anterior margin well-rounded, ventral margin broadly curved, posterior margin slightly truncated. Pallial line simple. Ligament opisthodetic. Hinge of left valve partly preserved, with two cardinal teeth: 2 (strong, knob-like) and 4b (thin, long) and sockets for three cardinal teeth of right valve. Specimen 522051B carrying traces of dense commarginal riblets. Both moulds exhibiting a faint posterior umbonal carina.

Remarks. Most Jurassic shells from Boreal areas with a similar outline and hinge have, in the past, been referred to the genus *Arctica* Schumacher, 1817 (*e.g.*, Warren, 1932; Zakharov, Shurygin, 1978; Fürsich, 1982). The hinge of the present material corresponds, however, better to that of *Pronoella*. Considering that we are dealing with internal moulds, we refrain from assigning the specimens to a particular species. Closely comparable in shape and hinge features is *Arctica sysollae* (Keyserling, 1846) of Fürsich (1982, p. 85, fig. 32A–E) from the Oxfordian Aldinger Elv Member of Milne Land, East Greenland.

***Pronoella*? sp. A**
Fig. 7I

Material. One internal mould of a left valve from the Bajocian part of the Pelion Formation (GEUS 522023).

Description and remarks. The specimen is elongated-trigonal in outline, moderately large (L: 28.7 mm; H: 19.5 mm) and inflated. The prominent umbo (beak broken off) is situated approximately one-fourth of total shell length from the anterior end. The ventral margin is widely curved, the anterior margin is evenly convex, the posterodorsal margin nearly straight and sloping, and the posterior margin is slightly tapering. A weakly developed posterior umbonal carina fades towards the posterior end. No internal features are seen.

As no hinge features are known, the generic assignment is doubtful. The specimen is most closely comparable to *Pronoella nuculaeformis* (Roemer) of Cox (1929a: 184, pl. 6: 9a, b) from the Upper Jurassic of England and to *Cyprina nuculiformis* Pict. of Thurmann & Etallon (1862: 176, pl. 21: 4) from the Upper Jurassic of the Swiss Jura Mountains. Spath (1936, p. 126, pl. 48: 1, pl. 50: 6) figured and described *Pronoella* (?) sp. indet. aff. *nuculaeformis* (Roemer) from the Volgian of Milne Land, East Greenland, which differs in having a distinctly greater height-length ratio. Fürsich (1982) regarded Spath's specimens as crushed individuals of *Pleuromya triangularis* Fürsich, 1982. *Pronoella* (*Pronoella*?) *superjurensis* Fürsich (1982: 94, fig. 32M, N) from the same area and stratigraphic level is more elongated and possesses a distinct posterior umbonal ridge.

Arcticidae? indet.
Fig. 7J

Material. One left valve from the Bajocian part of the elion Formation (GEUS 522017C).

Description and remarks. The small internal mould with remains of shell is longer than high. Part of the umbo is missing as is part of the anterior margin. As a result, the outline shown in Figure 7J is misleading. The shell appears to

be smooth except for faint growth lines. Judging from the slightly forward-directed umbo, the specimen may be a member of the family Arcticidae, but no precise identification is possible.

Order Thraciida Carter, 2011

Family Thraciidae Stoliczka, 1870

Genus *Thracia* J. de C. Sowerby, 1823

Subgenus *Thracia* J. de C. Sowerby, 1823

Type species. *Mya pubescens* Pulteney, 1799, by subsequent designation of Anton (1838).

***Thracia amygdaloidea* Lycett, 1863**
Fig. 7L, M, Q, R; Tab. 4

1863. *Thracia amygdaloidea*, Lyc. – Lycett: 80, pl. 43: 4

Material. Two articulated specimens from the Bathonian part of the Pelion Formation (GEUS 522051C and 522052C).

Measurements (in mm). See Table 4.

Table 4
Measurements (in mm) of *Thracia amygdaloidea* Lycett, 1863

Specimen	LA	L	H	I
522052C	~26	~55	31.8	15.5

Description. Shells elongated-ovate, compressed, inequivalved, right valve higher than left valve. Umbones submesial, depressed. Without lunule but with long, narrow escutcheon.

Anterodorsal margin slightly convex, grading smoothly into well-rounded anterior margin. Ventral margin broadly arched, posterodorsal margin concave, posterior margin truncated. Ridge running from umbo to posteroventral corner. Area of shell posterodorsally of umbonal ridge concave. Shell surface smooth except for growth lines of variable strength.

Remarks. Common species of *Thracia*, such as *T. depressa* (J. de C. Sowerby, 1823) and *T. incerta* (Roemer, 1839), vary considerably in shape but their length-height ratio is generally distinctly smaller than that of the present species, which is very elongated. *T. amygdaloidea* has been described from the Bathonian of southern England and closely fits the specimens from Tværdal. Several records of *T. incerta* (Roemer, 1839) such as those by Thurmann & Etallon (1863, p. 165, pl. 19: 6) from the Kimmeridgian of the Swiss Jura Mountains and Loriol *et al*. (1872, p. 203, pl. 11: 9, 10), Salin (1935, p. 153, pl. 5: 1–8), and Colleté (1996, p. 17, fig. 13) from the Upper Jurassic of northern France also refer to fairly elongated specimens. They more closely resemble *T. amygdaloidea* than *T. incerta*. The specimens from the Upper Jurassic of Milne Land described by Spath as *Thracia incerta* Deshayes (Thurmann) sp. (Spath, 1936, p. 133, pl. 48: 3, pl. 50: 4) and *Thracia* cf. *T. depressa* (J. de C. Sowerby) (Spath, 1936, p. 134, pl. 50: 3) differ in being distinctly shorter. This is also true of the specimens of *Thracia* (*Thracia*) *depressa* (J. de C. Sowerby, 1823) described by Fürsich (1982) from the same area and stratigraphic level.

Order Myida Stoliczka, 1870

Family Pleuromyidae Zittel, 1895

Genus Pleuromya Agassiz, 1843

Type species. *Mya gibbosa* J. de C. Sowerby, 1823, by subsequent designation of Herrmannsen (1847).

***Pleuromya subpolaris* Koschelkina, 1962**
Figs. 8A–J, 9C, D, G, H, K, L; Tab. 5

?1904. *Gresslya gregaria*. (Zieten) Goldfuss. sp. – Madsen: 185, pl. 8: 1, 2

?1904. *Gresslya abducta*. Phillips sp. – Madsen: 186, pl. 8: 3

?1904. *Gresslya peregrina*. Phillips sp. – Madsen: 186, pl. 8: 4

1932. *Pleuromya decurtata* (Phillips) – Spath: 117, pl. 6: 5, pl. 7: 6

1955. *Pleuromya tellina* Agassiz, 1842 – Gerasimov: 75, pl. 9: 3–4.

1962. *Pleuromya subpolaris* n. sp. – Koshelkina: 22, pl. 27: 1, 1a.

1963. *Pleuromya subpolaris* Koshelkina – Koschelkina: 208, pl. 25: 1a, b

1978. *Pleuromya subpolaris* Koshelkina, 1962 – Zakharov & Shurygin: 153, pl. 12: 1, 2

1979. *Homomya gibbosa* (Sowerby) – Wen: 309, pl. 95: 8 (*non* Sowerby)

1987. *Homomya gibbosa* (Sowerby) – Tong: 94, pl. 4: 8, 9 (*non* Sowerby)

Material. Thirty-six articulated specimens from the Bajocian and Bathonian part of the Pelion Formation (GEUS 443936, 522013, 522014, 522015, 522017, 522051, 444795, 324598, 324601). All preserved as composite or internal moulds.

Measurements (in mm). See Table 5.

Description. Elongated-oval composite or internal moulds, moderately inflated, height approximately 60 to 70% of length. Umbo situated 29 to 35% of total shell length from the anterior end. Beaks ortho- to prosogyrate. Outline highly variable. Anterior margin broad, regularly curved, posterior margin slightly tapering, ventral margin ranging from weakly to strongly arcuate, posterodorsal margin

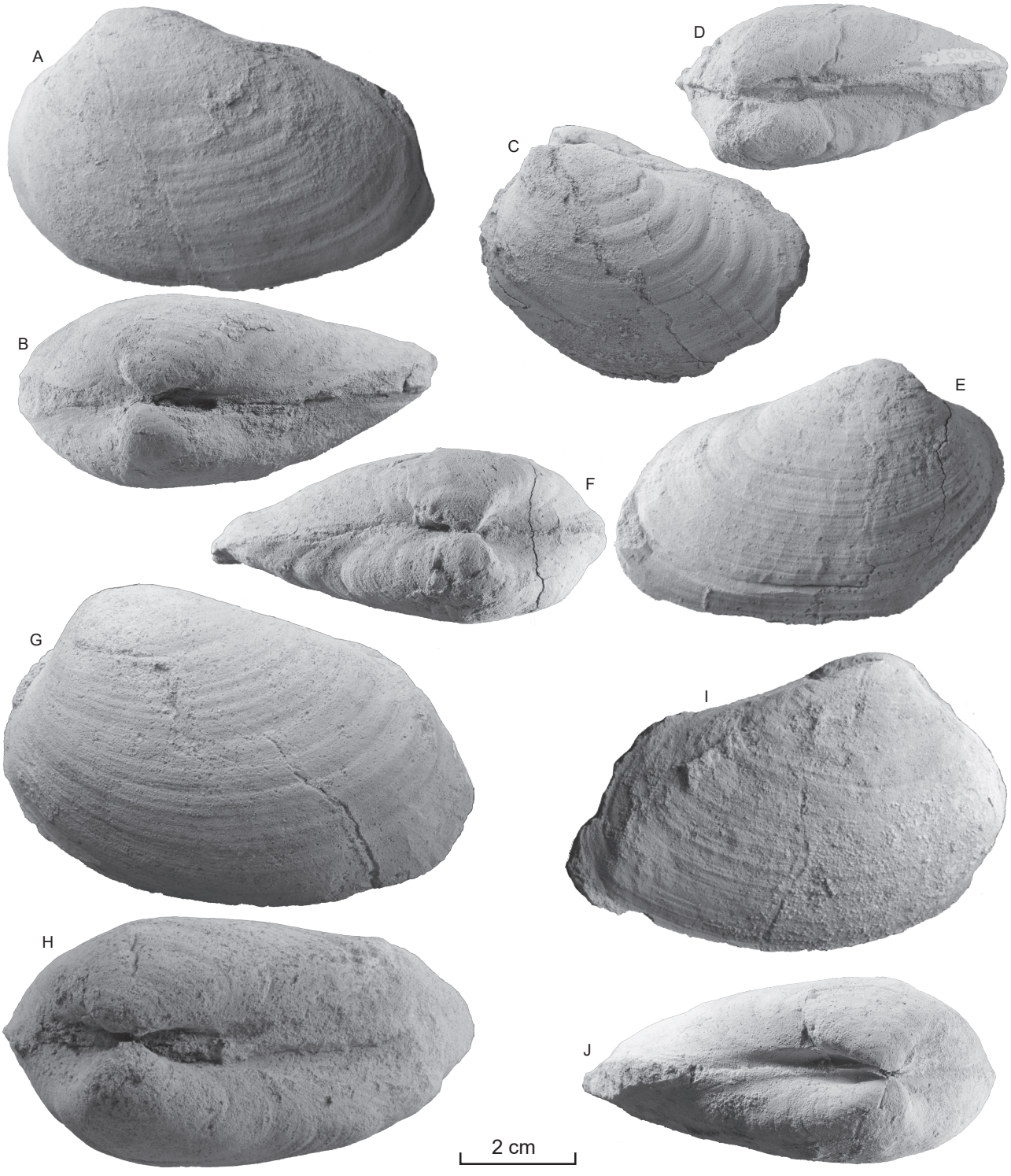

Fig. 8A–J. ***Pleuromya subpolaris*** **Koshelkina, 1962**

All specimens are articulated composite moulds. **A, B.** Specimen with posterior end damaged, MGUH 34811; A – left valve view, B – dorsal view. **C, D.** Distorted specimen, MGUH 34812; C – left valve view, D – dorsal view. **E, F.** Specimen with distorted anteroventral margin, MGUH 34813; E – right valve view, F – dorsal view. **G, H.** Specimen with posterior end missing, MGUH 34814; G – left valve view, H – dorsal view. **I, J.** MGUH 34815; I – right valve view, J – dorsal view

Table 5
Measurements (in mm) of *Pleuromya subpolaris* Koshelkina, 1962

Specimen	LA	L	H	I	Preservation
522014A	20.5	69.8	45.1	28.4	VG
522014C	25.0	–	49.4	35.6	OG
522014E	21.4	~70	49.6	32.1	
522014F	20.5	–	46.3	31.3	
522014G	–	57.0	41.1	29.2	
522014J	23.0	~75	47.3	31.7	VG
522014X	28.5	–	54.2	33.5	VG
522013C	13.8	57.5	46.0	31.5	
522013E	–	–	52.7	36.5	
522013A	18.8	82.8	54.0	42.2	
522013D	12.9	46.6	~32.5	22.2	
324601A	24.6	74.6	44.7	33.7	
522015A	17.2	58.3	43.8	31.4	OG
324598B	~17	–	39.5	27.8	
522017B	20.4	~66.5	35.9	–	
443936	29.2	87.5	54.3	38.9	

V – long axis vertical; O – long axis oblique; G – in growth position

straight, generally sloping. Valves apparently not gaping posteriorly. Surface covered with growth lines and commarginal rugae of variable strength.

Remarks. The specimens occupy a position intermediate between *Pleuromya* and *Homomya* in terms of length-height ratio and shape. Even though they are distinctly larger than most species of *Pleuromya* and in this respect strongly resemble species of *Homomya*, they are placed in *Pleuromya* because their general outline is slightly closer to that genus.

Numerous names exist for Jurassic species of *Pleuromya*. Often, they are based on specimens that display various degrees of distortion and are therefore difficult to compare with the present material. As the Middle Jurassic specimens from East Greenland are closely comparable to *Pleuromya subpolaris* Koschelkina, 1962, they are placed in this species.

Spath (1932: 119, pl. 20: 8) described *Homomya* sp. indet. from Bathonian rocks of Jameson Land, a specimen too poorly preserved to be identified at the species level. Specimens of the species from the same area and stratigraphic level have been identified as *Pleuromya decurtata* (Phillips) by Spath (1932, p. 117, pl. 6: 5, pl. 7: 6). The bivalves from Nathorst Fjeld, Jameson Land, identified as *Gresslya abducta* Phillips and *Gresslya peregrina* Phillips by Madsen (1904) most likely belong to the present species. *Pleuromya uralensis* of d'Orbigny (1845, p. 168, pl. 40: 13, 14) from the Upper Jurassic of northern Russia and East Greenland (Fürsich, 1982, p. 102, figs. 37A–C, 38A–H) differs from *P. subpolaris* in possessing a shallow anterior umbonal sulcus. Similar to *P. subpolaris*, that species occupies a position intermediate between *Pleuromya* and *Homomya* (Fürsich, 1982). *Homomya gibbosa* (Sowerby) of Wen (1979, p. 309, pl. 95: 8) and Tong (1987, p. 94, pl. 4: 8, 9) from the Middle Jurassic of northern Tibet closely resemble the present species in outline and inflation and have been included in the synonymy list.

Pleuromya subpolaris is one of the commonest bivalves in the Middle Jurassic of East Greenland and had an equally wide distribution as the similar *Pleuromya uralensis* (d'Orbigny, 1845) from the Volgian of Milne Land (Fürsich, 1982), which most likely is part of the same evolutionary lineage. Several of our specimens are also similar to species of *Gresslya* such as *Gresslya conformis* Agassiz (1842, p. 211, pl. 13b: 4–6) or *Gresslya laevigata* de Loriol (1896, p. 76, pl. 11: 5, 5a) in having prosogyrate umbones and a convex posterodorsal margin, but these features have usually been caused by compaction (see below). The same is true of apparently inequivalved specimens, a feature that has been caused by shearing of the valves.

Nearly all specimens are preserved articulated and many of them occur in life position. This documents that they did not undergo reworking. Those individuals not occurring in life position probably were reworked while still alive and immediately became buried again, a process that resulted in their death. Alternatively, some may have been displaced by burrowing organisms.

The great variability in the shape of the specimens is due to taphonomic processes and does not necessarily imply that we are dealing with a highly variable species. Distortion is largely due to compaction and varies according to the position of the bivalves within the sediment. Those preserved in life position (*i.e.*, with the anterior-posterior axis more or less vertical) are compressed differently than those embedded with their long axis oblique or horizontal and their commissural plane horizontal, oblique or vertical. Some specimens also display dorso-ventral shear of the valves, which changes the outline, in particular the curvature of margins. Finally, in many specimens the posterior end is incomplete.

Pleuromya uniformis (J. Sowerby, 1813)

Fig. 9A, B, E, F

1813. *Unio uniformis* – J. Sowerby: 83, pl. 33: 4

1845. *Panopaea peregrina* (d'Orb., 1845) – d'Orbigny: 468, pl. 40: 10–12

1895. *Panopaea Toulai* n. sp. – Lundgren: 207, pl. 5: 30a, b

1936. *Pleuromya tellina* Agassiz – Spath: 128, pl. 45: 4a, b, pl. 50: 1a, b

1974. *Pleuromya* aff. *peregrina* d'Orbigny – Zakharov & Mesezhnikov: 158, pl. 37: 2, 3

1978. *Pleuromya uniformis* (Sow.) – Zakharov & Shurygin: 151, pl. 8: 5a–c, pl. 9: 2, 3, pl. 10: 2a, b

Material. Three articulated internal moulds from the Bajocian part of the Pelion Formation (GEUS 522017B and 522023A, B), the latter specimen laterally strongly compacted.

Description and remarks. *Pleuromya uniformis* differs from *Pleuromya subpolaris* by being far more elongated (height of specimen 522023B: 31.0 mm, length: 59.6 mm). The prominent umbo is situated 28% of total shell length

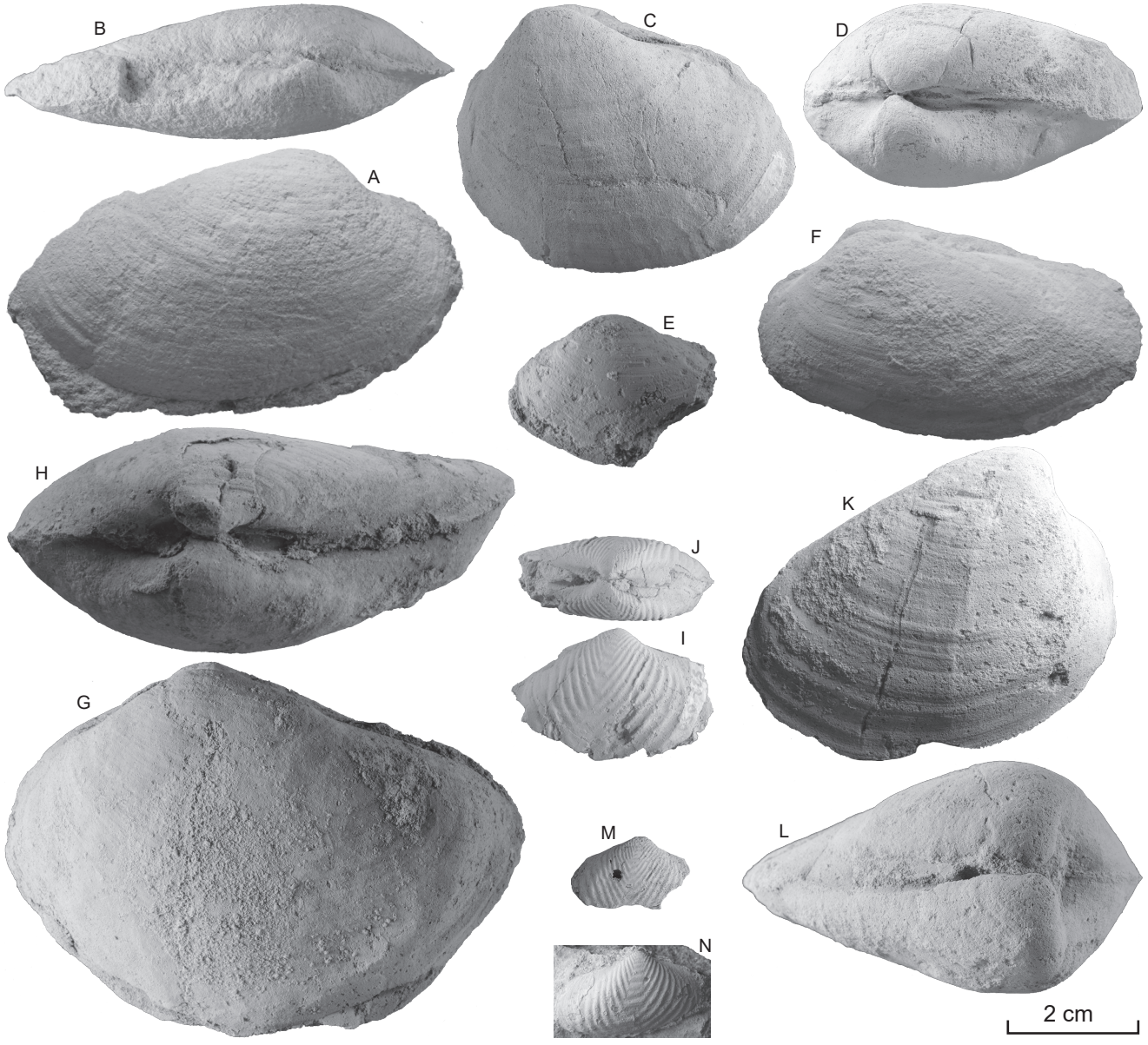

Fig. 9A, B, E, F. *Pleuromya uniformis* (J. Sowerby, 1813); A, B – flattened and slightly sheared articulated composite mould, MGUH 34816; A – right valve view, B – dorsal view; E – articulated internal mould, right valve view, MGUH 34817; F – articulated internal mould, left valve view, MGUH 34818. **C, D, G, H, K, L.** *Pleuromya subpolaris* Koshelkina, 1962; C, D – articulated internal mould; parts of posterior end missing, MGUH 34819; C – left valve view, D – dorsal view; G, H – articulated specimen, MGUH 34820; G – left valve view, H – dorsal view; K, L – distorted articulated composite mould, MGUH 34821; K – right valve view, L – dorsal view. **I, J, M, N.** *Goniomya* (*Goniomya*) *literata* (J. Sowerby, 1819); I, J – incomplete articulated specimen, MGUH 34822; I – right valve view, J – dorsal view; M – composite mould of right valve, MGUH 34823; N – composite mould of right valve, MGUH 34824

from the anterior end. In two of the specimens (522017B, 522023B), the slightly truncated anterior margin is grading smoothly into the broadly curved ventral margin and the regularly curved posterior margin. In the incomplete specimen 522023A, however, the anterior end is somewhat acutely rounded, similar to some specimens figured by Arkell (1935, pl. 45: 3) from the Oxfordian of England.

Pleuromya uniformis is an extremely widespread Jurassic bivalve occurring from tropical to Boreal areas but is comparatively rare in the latter. It is possible that this highly variable species in fact comprises several closely related species which are difficult to tell apart. Of the three species of *Pleuromya* described by Spath (1932) from the Middle Jurassic of East Greenland, *Pleuromya decurtata* (Phillips, 1829) (Spath, 1932, p. 117, pl. 6: 5, pl. 7: 6) is regarded here as belonging to *P. subpolaris*. *Pleuromya securiformis* (Phillips, 1829) of Spath (1932, p. 118, pl. 5: 5, pl. 17: 3) is too worn to allow a precise identification, and the small *Pleuromya* aff. *burnsi* Warren, 1932 (Spath, 1932: 119, pl. 16: 4) may not be a *Pleuromya*.

Order Pholadomyida Newell, 1965

Family Pholadomyidae W. King, 1844

Genus *Goniomya* Agassiz, 1842

Subgenus *Goniomya* Agassiz, 1842

Type species. *Mya angulifera* J. Sowerby, 1819, by subsequent designation of Herrmannsen (1847).

***Goniomya* (*Goniomya*) *literata* (J. Sowerby, 1819)**
Fig. 9I, J, M, N

1819. *Mya*? *literata* – J. Sowerby: 45, pl. 224: 1
1845. *Pholadomya Dubois* – d'Orbigny: 469, pl. 40: 15z, 16
1865. *Goniomya literata* Ag. – Trautschold: 14, pl. 3: 9a, b
1932. *Goniomya v-scripta* (J. Sowerby) – Spath: 120, pl. 7: 4a–c
1955. *Goniomya dubois* Agassiz 1842 – Gerasimov: 83, pl. 19: 1, 2.
1968. *Goniomya dubois* Agassiz, 1843 – Efimova *et al.*: 99, pl. 106: 4
1974. *Goniomya* cf. *dubois* Agassiz – Zakharov & Mesezhnikov: 157, pl. 35: 3
1975. *Goniomya literata* (Sowerby, 1819) – Pugaczewska *in* Birkenmajer & Pugaczewska: 76, pl. 11: 3
1982. *Goniomya* (*Goniomya*) *literata* (J. Sowerby, 1819) – Fürsich: 98, figs. 35E, 36C, D
2014. *Goniomya literata* (J. Sowerby, 1819) – Hryniewicz *et al.*: 43, fig. 19A, B

Material. One articulated shell (GEUS 522050), one fragment of an internal mould of an articulated specimen, and two composite moulds of the right valve (GEUS 522051, 522018A, 522018) from the Bajocian and Bathonian parts of the Pelion Formation.

Description and remarks. Parts of the margins of the elongated shells are broken off. The submesial umbones are slightly prosogyrate. The elongated lunule and escutcheon are smooth and bordered by a ridge. Despite the poor preservation, the shells can be identified at the species level because of their characteristic ornamentation. The surface is covered with V-shaped ribs which are slightly posteriorly directed. In early growth stages, the two bars of the V are separated by a short horizontal bar. The ribs are rounded in cross-section, and their width equals that of the interstices. Towards the ventral margin, the ornamentation appears to fade.

The species is widespread in western Europe and in Boreal areas, although never occurring in great abundances.

PALAEOECOLOGICAL REMARKS

The presence of ammonites, brachiopods, and belemnites, and the composition of the ichnofauna and bivalve fauna point to fully marine conditions. Quantitative samples have not been obtained and some samples span several beds, so no detailed palaeo-community analysis could be carried out. The following comments are, therefore, mainly of a general nature. Sedimentological data such as primary sedimentary structures (very few preserved) and the coarse-grained and partly pebbly nature of the sandstones show that the siliciclastic Bajocian–Bathonian succession of the Pelion Formation at Tværdal records shallow-marine conditions at times above the fair-weather wave-base. This is corroborated by the ichnofauna, which is dominated by ichnotaxa such as *Diplocraterion* and *Ophiomorpha*. Bioturbation and lack of primary sedimentary structures in many of the beds indicate, however, that reworking of sediment was not a constant feature, but breaks in sedimentation, in connection with reduced water energy and low rates of sedimentation, provided time for a benthic macrofauna to colonise the sea floor. The bivalve diversity is fairly low. The two beds with the highest numbers of bivalve taxa at 20.5 and 37.7 m of the section (Fig. 3) contain ten and nine taxa, respectively, and most beds have less than five taxa. This low diversity is unlikely to have been caused by selective dissolution of aragonitic forms, as the shells of 13 out of the 19 taxa described here consisted originally completely of aragonite. These taxa are either preserved as composite/internal moulds or with shell transformed to calcite. The abundance of benthic macroinvertebrates similarly appears to have been low. Apart from a concentration of brachiopods at 41.5 m, there occurs a concentration of articulated *Cyrtopinna sublanceolata* at 42.6 m, the latter repre-

senting an autochthonous occurrence with many of the individuals preserved in life position (Fig. 10). The fact that most infaunal taxa are preserved as closed articulated shells, as are the semi-infaunal, endobyssate *Strimodiolus* and *Cyrtopinna*, points to limited reworking and to the preservation of many faunal elements *in situ*. This is underlined by the deep burrowing *Pleuromya subpolaris* in the basal 11 m of the Bajocian section. There, this bivalve is not only common but invariably preserved in life position with its long axis more or less vertical (Fig. 11). This preservation might reflect either repeated obrution of the bivalves by a rapidly deposited sand unit that suffocated them, or limited erosion of the substrate that did not affect the depth at which the bivalves lived. As *Pleuromya* occurs in life position at different levels in the succession documenting repeated colonization of the substrate, limited reworking and erosion seem to have been the main factors facilitating this kind of preservation. In the case of the endobyssate *Strimodiolus czekanowskii*, in contrast, where most individuals are also preserved in life position, rapid burial seems to have been the reason for the mode of preservation of these semi-infaunal forms. Even more spectacular are levels with *Cyrtopinna* preserved in life position (Fig. 10). Again, relatively rapid influx of sediment must have been responsible for this type of preservation of the endobyssate bivalves. Similar levels with *Pinna* preserved in life position have been documented by Fürsich (1982) from the Middle Volgian Pernaryggen Member of Milne Land, East Greenland.

The epifauna is composed of three byssate taxa (*Retroceramus*, *Camptonectes*, *Oxytoma*), one cemented form (the oyster *Liostrea*), and one free-living form (*Entolium*). The semi-infaunal bivalves were all endobyssate (*Cyrtopinna*, *Grammatodon*, *Strimodiolus*). Whereas the shallow burrower *Unicardiopsis* was most likely a sluggish burrower judging from its inflated shell, other burrowers such as *Thracia* and *Quenstedtia* were fairly rapid burrowers, characterized by smooth and compressed shells. Whereas nearly all bivalves were suspension-feeders, the notable exception being a single chemoautotrophic lucinid, their life habits were more variable (Tab. 6). Of the 19 genera, eleven had an infaunal mode of life, five lived on the substrate, and three were semi-infaunal. Of the infaunal genera, which all were more or less stationary, seven were shallow burrowers (*Unicardiopsis*, *Pronoella*, *Quenstedtia*, *Corbicellopsis*, *Astarte*, Arcticidae indet.) and four deep burrowers (*Pleuromya*, *Goniomya*, *Thracia*, Lucinidae indet.).

Two faunal assemblages can be recognized within the Pelion Formation at Tværdal. A *Pleuromya subpolaris–Retroceramus retrorsus* assemblage seems to characterise the basal part of the formation, whereas an assemblage dominated by *Pinna* (*Cyrtopinna*) *sublanceolata* occurs higher up. Possibly, a third assemblage dominated by *Pronoella* and *Entolium* existed, but the available data are not sufficient to confirm this.

When viewing the taphonomic and palaeoecological attributes of the bivalve fauna, it appears that deposition was

Fig. 10. Field photo of clustered *Pinna* (*Cyrtopinna*) *sublanceolata* in life position, „*Pinna* bed" at level 42.6 m in the sedimentary log (Fig. 3)

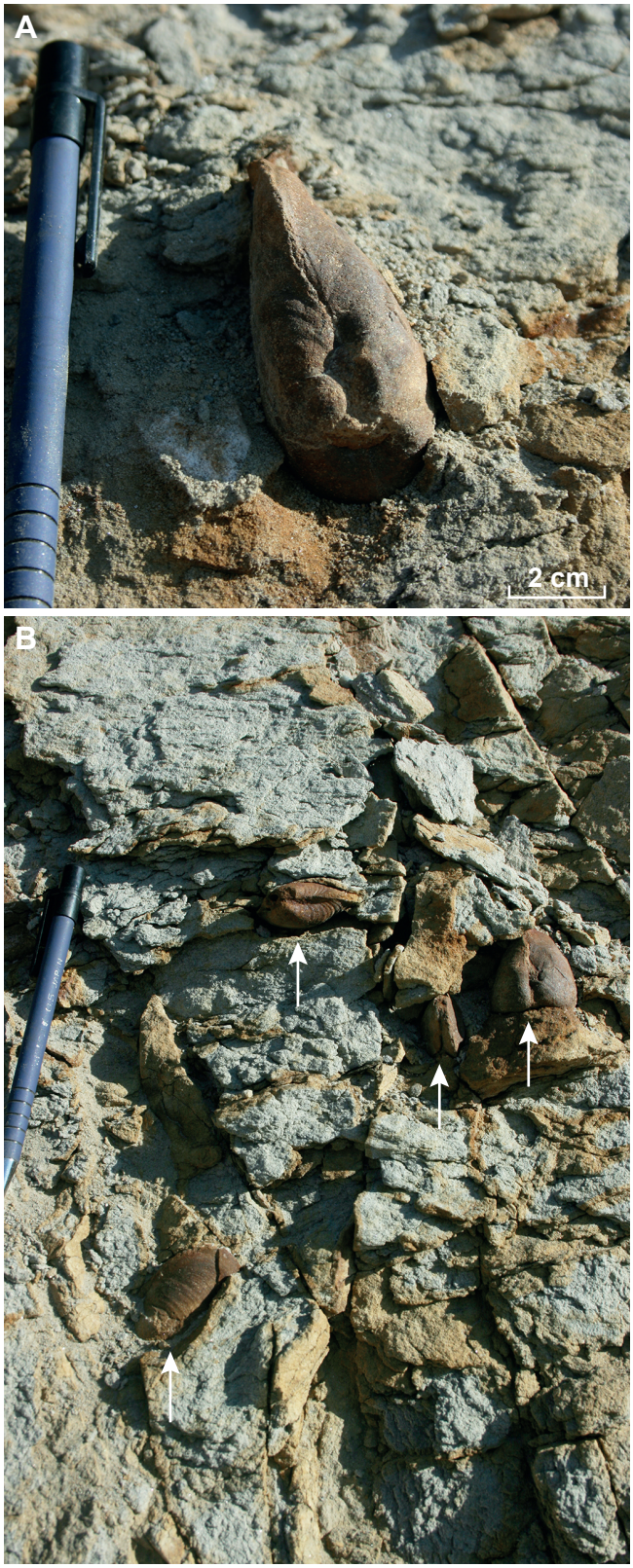

Table 6
List of bivalves occurring in the Bajocian–Bathonian Pelion Formation at Tværdal, Geographical Society Ø

Taxon	Life habit
Modiolus (*Strimodiolus*) *czekanowskii* (Lahusen, 1886)	sb
Grammatodon (*Cosmetodon*) *keyserlingii* (d'Orbigny, 1850)	sb
Retroceramus (*Retroceramus*) *retrorsus* (Keyserling, 1848)	eb
Retroceramus (*Retroceramus*) sp.	eb
Liostrea sp.	ec
Pinna (*Cyrtopinna*) *sublanceolata* d'Eichwald, 1865	sb
Camptonectes (*Camptonectes*) sp.	eb
Oxytoma (*Oxytoma*) *inequivalve* (J. Sowerby, 1819)	eb
Entolium (*Entolium*) *corneolum* (Young & Bird, 1828)	ef
Astarte sp. A	si
Lucinid indet.	di
Quenstedtia parallela (Trautschold, 1866)	si
Quenstedtia bathonica (Morris & Lycett, 1854)	si
Corbicellopsis cf. *tenera* (de Loriol, 1875)	si
Unicardiopsis aceste (d'Orbigny, 1850)	si
Pronoella sp.	si
Pronoella? sp. A	si
arcticid? indet.	si
Thracia amygdaloidea Lycett, 1863	di
Pleuromya subpolaris Koschelkina, 1962	di
Pleuromya uniformis (J. Sowerby, 1813)	di
Goniomya (*Goniomya*) *literata* (J. Sowerby, 1819)	di

di – deep infaunal; si – shallow infaunal; eb – epibyssate; ec – epifaunal cemented; ef – epifaunal free-living; sb – semi-infaunal, endobyssate

episodically under the influence of fair-weather waves, but for its greater part the setting was influenced by storm waves and storm-induced currents, i.e. within the transition zone. The overall net rate of sedimentation appears to have been low. Episodes of sedimentation alternated with phases of erosion and sediment starvation, during which colonization of the sea floor by predominantly infaunal suspension-feeding bivalves resulted in autochthonous concentrations of shells (e.g., *Pinna* bed).

Fig. 11. Bivalves *in-situ* in friable sandstone bed, "*Pleuromya* beds" at 4.25–8 m in the sedimentary log (Fig. 3)

A. *Pleuromya subpolaris* Koshelkina in life position, MGUH 34813, see also Figure 8E, F. **B.** Four specimens (arrowed), the lower three are *P. subpolaris* in life position, the uppermost specimen, *Unicardiopsis aceste* (d'Orbigny) tilted on its side (pen for scale *c.* 15 cm)

CONCLUDING REMARKS

The macrobenthos of the siliciclastic Middle Jurassic Pelion Formation of Tværdal chiefly consists of bivalves that form low-diversity assemblages. These are dominated by either infaunal or semi-infaunal (endobyssate) taxa. The low species diversity appears to be aprimary feature despite the dissolution of aragonitic shells as these are preserved as internal or composite moulds. The comparatively high proportion of deep burrowing and endobyssate individuals preserved in growth position reflects phases of rapid sedimentation in an environment partly above the fair-weather wave-base. The bivalve fauna is composed of taxa that are common elements of the boreal faunal province in the Jurassic.

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1–40 (133–172), pls. 1–4 (58–61), 1931; **20**: 165–184 (173–192), pls. 17–20 (62–65), 1931; **21**: 1–30 (193–222), pls. 1–3 (65–68), 1932.

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