Faunal dynamics of bivalves and scaphopods in the Bathonian (Middle Jurassic) ore-bearing clays at Gnaszyn, Kraków-Silesia Homocline, Poland

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ABSTRACT:

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The environment at the Gnaszyn section – as deduced from bivalve and scaphopod dynamics – was controlled by the substrate consistency and possibly oxygen deficiency near the sediment-water interface and/or oxygen content fluctuations. The middle part of the section dominated by nuculoid and corbulid bivalves and *Laevidentalium*-type scaphopods probably reflects a soupy substrate and possibly oxygen deficiency in the sediment. Slightly coarser and better-oxygenated silts in the upper and lower parts of the section offered a less soupy substrate consistency, allowing the development of communities dominated by astartids, byssate bivalves, and *Dentalium*- and *Plagioglypta*-type scaphopods.

Key words: Poland; Gnaszyn; Ore-bearing clays; Jurassic; Bathonian; Palaeoecology; Bivalves; Scaphopods.

INTRODUCTION

The bivalves are the group of molluscs that is commonly used to decipher the palaeoenvironment of fossil benthic assemblages (Kaim 1997, 2001 and references therein). This is favoured by the fact that bivalves are fairly common animals in almost all Mesozoic and Cainozoic marine environments. Additionally, bivalve shells in most cases are, at least partially, composed of calcite that usu-

ally preserves well in the fossil record. Furthermore, bivalve shells are relatively easy to extract from the majority of host rocks. The functional morphology and/or ecology of Recent species is well researched, giving us a powerful tool for palaeoecologic investigations (e.g., Stanley 1970). In contrast, scaphopods are much less researched and their Mesozoic fossil counterparts are relatively poorly known. Papers dealing with the taxonomy and phylogeny of Recent scaphopods are

relatively new (Steiner 1992; Lamprell and Healy 1998; Steiner and Kabat 2001; Reynolds 2002) and these topics are still a matter of debate. Additionally, the environmental preferences of particular fossil and Recent scaphopods need further and more detailed studies (compare Reynolds 2002). This paper offers some distribution patterns of both bivalves and scaphopods and attempts to contribute palaeoecological information for reconstruction of the depositional environment of the ore-bearing clays (an informal lithostratigraphic unit comprising marine dark-coloured clay with horizons of siderite concretions) in southern Poland.

MATERIAL AND METHODS

The material analysed herein comes from the large brick-pit "Gnaszyn" located on the western outskirts of Częstochowa (Text-fig. 1). The section exposes mainly Middle Bathonian clays of Subcontractus, Morrisi, and Bremeri zones age (Matyja and Wierzbowski 2006). The samples from Gnaszyn were taken from three different quarry walls (Text-fig. 2). Samples from the north-eastern quarry wall (Text-fig. 2; samples Gns32–38 and Gns1–13) are from the lower and middle part of the succession. Samples from the southern area (Text-fig. 2; Gns24–31) document the uppermost part and samples
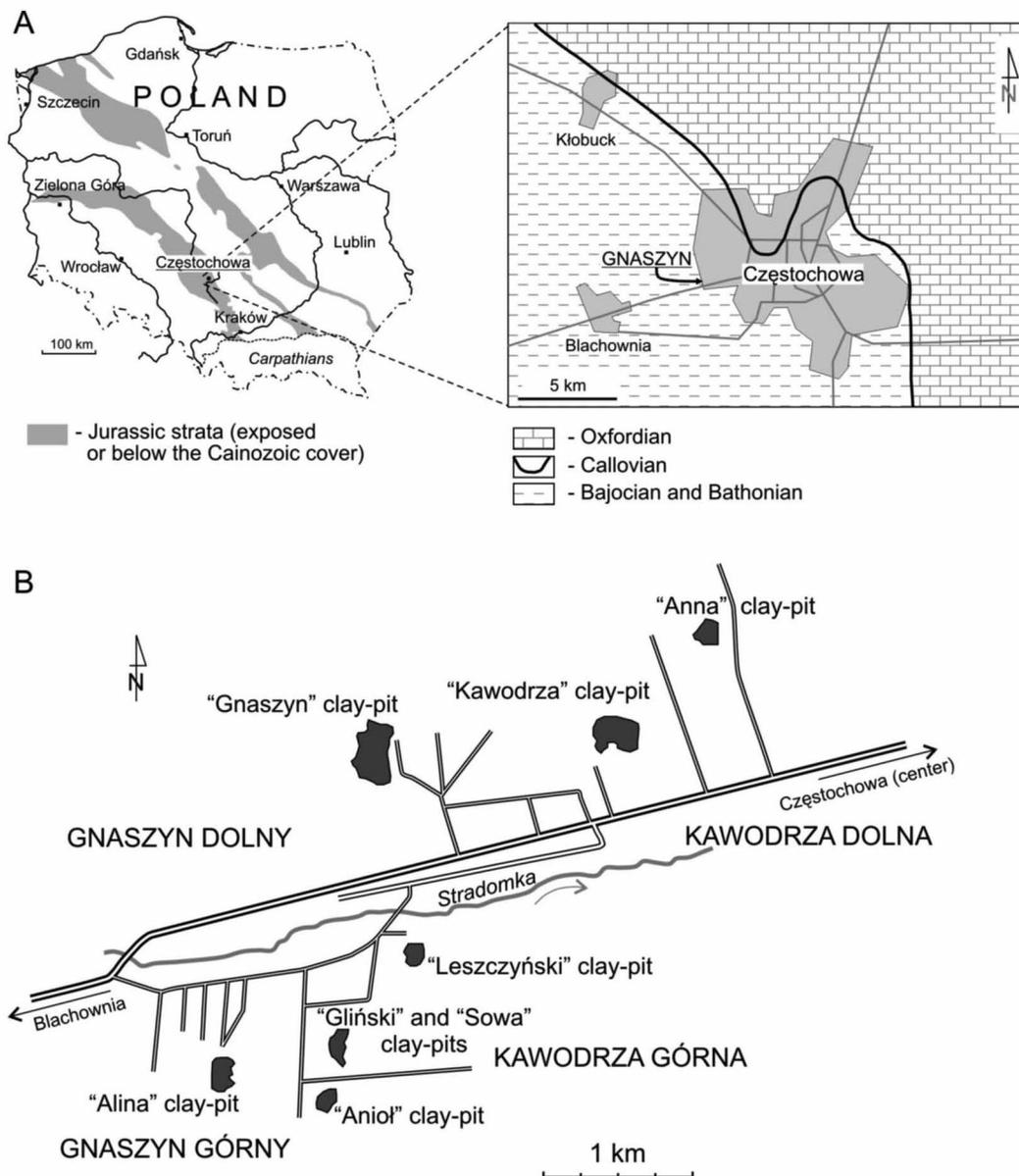
Text-fig. 1. Simplified geological map of the Częstochowa area (A – after Majewski 2000) and location of the Gnaszyn clay-pit (B – after Matyja and Wierzbowski 2003)
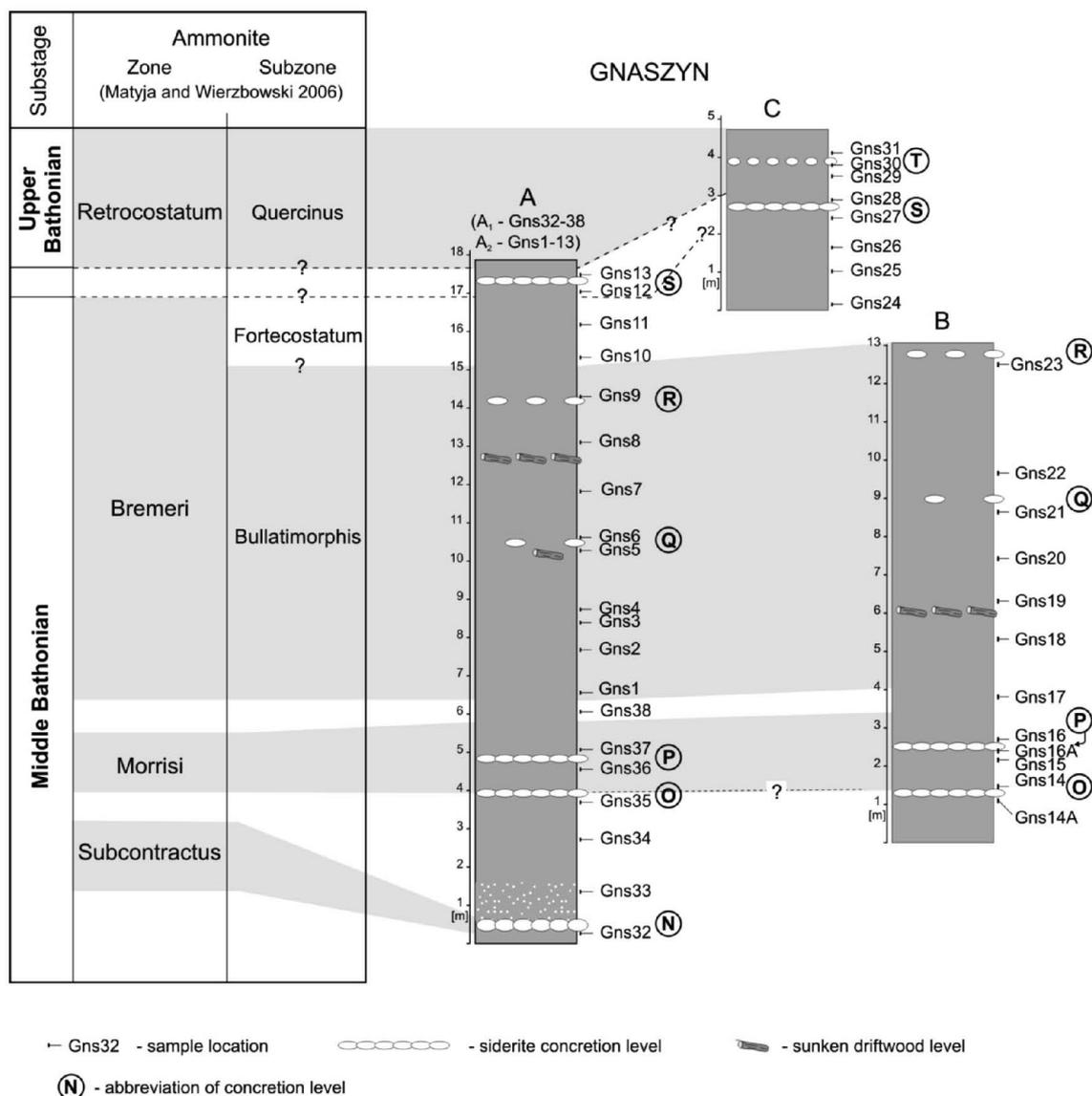
Text-fig. 2. Lithological logs and sampling of the Gnaszyn sections (from Gedl and Kaim 2012)

from the north-western wall (Text-fig. 2; Gns14A–22) duplicate the middle part of the succession. For more details on sample locations see Gedl and Kaim (2012 this issue). The samples (about 5kg each) were taken from each lithologically distinctive horizon of the section. They were washed with hot water and washing powder on a sieve (mesh size 0.375 mm) and the fossils were picked from residues under the microscope. All bivalves were counted and identified to generic and/or family level whenever possible, whereas the scaphopods were divided into four morphological groups. Gastropods and shark teeth from the same samples were the subject of separate studies (Kaim 2012 this issue; Rees 2012 this issue).

THE SUCCESSION OF BIVALVE AND SCAPHOPOD ASSEMBLAGES IN THE GNASZYN SECTION

Bivalves and scaphopods from Gnaszyn are represented by 4715 and 2402 specimens respectively. Bivalves are represented by twelve families and scaphopods have been attributed to four morphological groups (Table 1). In most cases, the shells are preserved with primary microstructure but most of the specimens are juveniles and/or fragmented. Adult or adolescent specimens of both bivalves and scaphopods were found only in the upper part of the succession (samples Gns27–28). Surface collecting was also attempted; however, larger bivalve specimens are very rare and only a few specimens of

Bositra, Pholadomya, *Pinna*, *Pleuromya* and *Goniomya* have been recovered. In some levels (see below), however, some astartids attain larger sizes. A rarefaction analysis performed on the samples from Gnaszyn (Text-fig. 3A) has shown that in the more diverse samples (e.g., Gns14A, Gns27, Gns28, Gns33, Gns34) 75% of taxa are contained in a subsample of 50 to 100 specimens while in the less diverse samples (Gns1, Gns2, Gns4, Gns17, Gns19, Gns20) a subsample size of 30 specimens contains the full diversity. Out of 40 samples investigated, 8 contain less that 30 specimens (Gns6, Gns16A, Gns23, Gns24, Gns26, Gns29, Gns35, Gns37) though even in some of these (e.g. Gns16A) the rarefaction curve flattens off nicely (Text-fig. 3A). On the other hand, some other samples (e.g. Gns26) are clearly too small (Text-fig. 3A) to represent the full diversity at that level. The sample rarefaction curve (Text-fig. 3B) flattens off nicely at the 10th sample, attaining a bivalve diversity of 10 taxa in the Gnaszyn section.
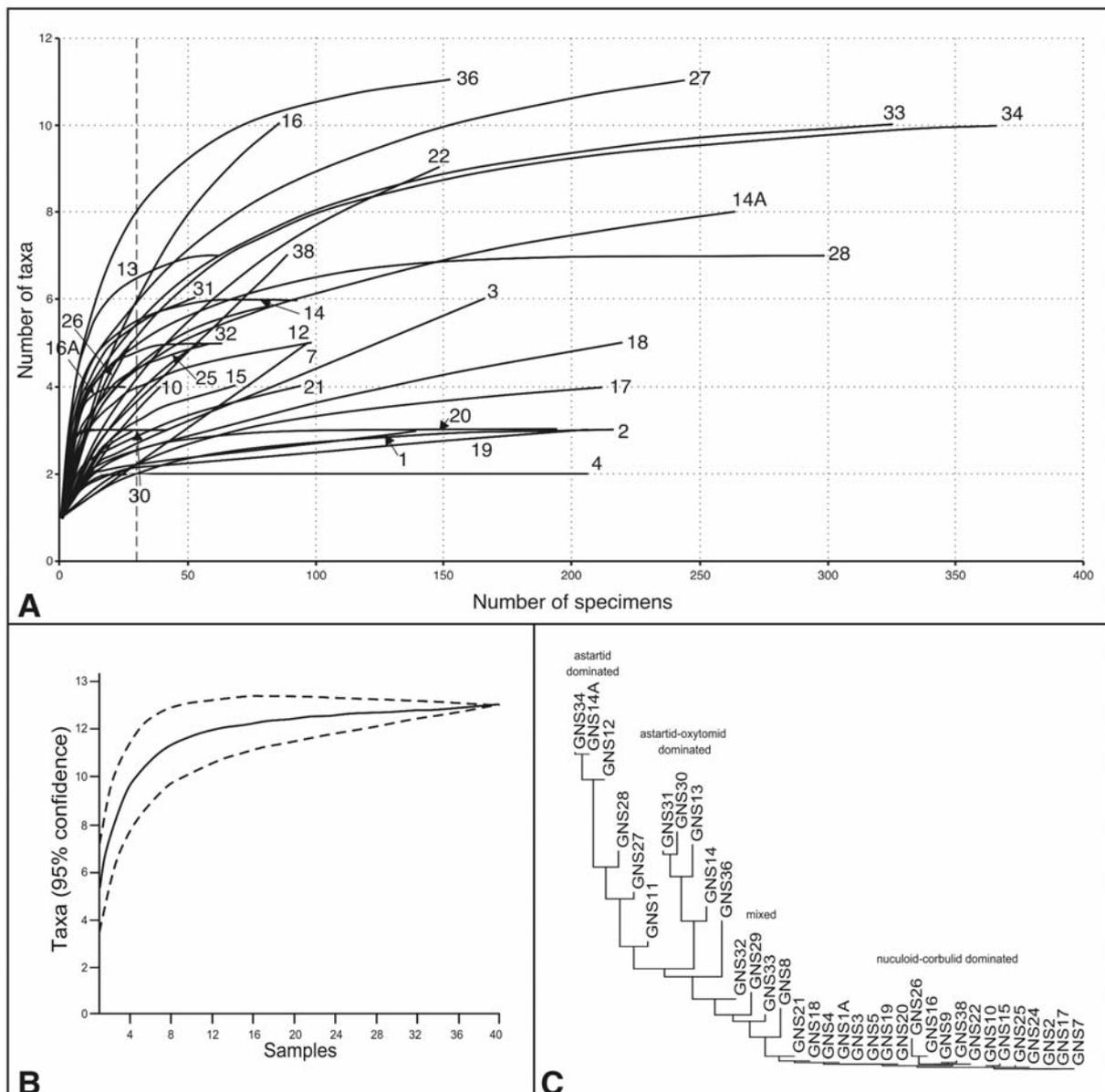
Text-fig. 3. Rarefaction curves and neighbour joining clustering for bivalve samples in Gnaszyn obtained using PAST software (Hammer *et al.* 2001). **A** – Curves for individual samples. Not all curves enumerated, prefix Gns omited from the sample numbers for the clarity of image. Note that nuculid-corbulid-dominated samples (e.g., Gns1, Gns2, Gns4, Gns17, Gns19, Gns20) flatten off at a much smaller sample size and are of lower diversity than astartid-oxytomid-dominated samples (e.g., Gns14A, Gns27, Gns28, Gns33, Gns34). **B** – Sample rarefaction curve of the bivalve samples from Gnaszyn with 95% confidence intervals. Note that the curve flattens off after the 10th sample attaining the diversity of 11 bivalve taxa. **C** – Neighbour joining clustering, Morisita similarity measure with root final branch algorithm. Note good clustering of the astartid-dominated samples next to a cluster containing astartid-oxytomid-dominated samples followed by mixed-composition samples and finally nuculoid-corbulid-dominated samples

Bivalves

Bivalves in the sieved samples: Bivalves in the Gnaszyn section are moderately common, of low diversity, and the number of valves in individual samples ranges from 4 to 366. Many samples yielded only a few bivalves (Gns06, Gns16A, Gns23, and Gns35). Only a few samples provided more than 100 valves (Text-fig. 4) and this usually coincides with the mass occurrence of deposit feeding nuculoids (mainly *Nuculana*, *Mesosaccella* and subordinately *Palaeonucula*) which constitute 60% of all bivalves found in a sample. Less common, but in some samples abundant, are astartids (17%), corbulids (10%), oxytomids (5.2%) and trigonioids (1.2%). The contribution of other groups (arcoids, inoceramids, ostreids, pectinids, pteriids and veneroids other than astartids) is usually less than 1% (Text-fig. 4).

The lower part of the succession (samples Gns32-34 and Gns14A) is dominated by deposit-feeding nuculoids and shallow infaunal suspension-feeding veneroids (mainly astartids) and corbulids, with a significant contribution of epibyssate oxytomids (Text-fig. 4). The higher

samples/taxa	nuculanids	parallelodontids	inoceramids	oxytomids	pectinids	oysters	pteriids	trigoniids	other veneroids	astartids	corbulids	other bivalves	Total bivalves	*Laevidentalium*-type	*Plagioglypta*-type	*Dentalium*-type	*Episiphon*-type	Total scaphopods
Gns13	15			15			10	7		11	2	2	62	29				29
Gns12	29						4	6		58	1		98	14				14
Gns11	27			4	1					23		4	59	18	3			21
Gns10	35			2						1		1	39	24		2		26
Gns9	25		1									3	29					0
Gns8	52	1		4						2	32	4	95	48	6	18		72
Gns7	93		1				1			1	1		97	47	21	43		111
Gns6	7			1							1		9	48	7	6	1	62
Gns5	56										7		63	28	2	1		31
Gns4	176										30		206	29				29
Gns3	143	1			1	1			1		19		166	48				48
Gns2	205			2							9		216	14		2		16
Gns1	124		1								20		145	28		3		31
Gns38	74		1		1				1	1	1	10	89	2				2
Gns37	2			1									3	4		5		9
Gns36	55	1	5	11	3	34	3	7		19	3	12	153	23		26		49
Gns35	10			1							1		12					0
Gns34	44	1	5	14				12	10	269	6	5	366	50	28	33		111
Gns33	176		2	69	4	1		3	8	5	46	12	326	25				25
Gns32	32			3				4		13	11		63					0
Gns31	15		1	21				3		10		3	53	17				17
Gns30	11			16						15			42	2				2
Gns29	13			6	3					3			25	8				8
Gns28	78	4	4	5						103	87	18	299	202	609	41		852
Gns27	77	10	4	8	1	1	3	2	4	58	77	3	244	119	25	251		395
Gns26	19		6		1			1			1		28	11	1	1		13
Gns25	48			2			1	3				1	55	5				5
Gns24	22						1	1					24	4	1			5
Gns23	1		1	2									4					0
Gns22	126	2	4	1			1	2		1	10	2	149	49	7	48		104
Gns21	73	1									18	2	94	55	7	8		70
Gns20	172						5				17		194	54	1	2		57
Gns19	185									1	20		206	17				17
Gns18	183			1					1		33	2	220	15		7		22
Gns17	200	3		1							8		212	19				19
Gns16	67	1	4	3	2		1	1		1	3	3	86	25		5		30
Gns16A	7			3								3	13	1				1
Gns15	59			3						5	1		68	27	1	43		71
Gns14	31			27				3		4	15	12	92	8		17		25
Gns14A	32		1	16	2			1	3	196	13		264	1		3		4
Total	2799	25	37	242	19	37	30	57	27	800	493	100	4668	1118	719	565	1	2403

Table 1. Distribution of bivalves and scaphopods in the Gnaszyn section.

sample (Gns35) is impoverished in the number of specimens, most probably due to diagenesis, as gastropods in the same sample are also rare and usually re-crystallised (Kaim 2012, this issue). The overlying sample (Gns36) contains diverse bivalves (nuculoids, astartids, oxytomids, trigoniids, inoceramids, pectinids, pteriids, corbulids and arcoids), but its most striking feature is an abundant appearance of juvenile ostreids. Higher up, the bivalve fauna is significantly impoverished in taxonomic diversity and heavily dominated by nuculoids and corbulids. This is clearly visible in both sets of samples encompassing this part of the succession (samples Gns37–08 and Gns17–22). Still higher, corbulids decline and

nuculoids are the sole dominant group, with some addition of inoceramids, pteriids, oxytomids and trigoniids (samples Gns09–10 and Gns24–25). Slightly higher (samples Gns11–12 and Gns26–27), similarly to the lowest part of the section (samples Gns32–34 and Gns14A), the astartids become again one of the dominant groups. Also corbulids reappear in this part of section but, surprisingly, only in the southern quarry wall (samples Gns26–27) and not in the north-eastern quarry wall (Gns11–12; Text-fig. 4), showing that there is some lateral variation in this part of the section. In the highest observed part of the section (samples Gns13 and Gns28–31) still dominant are nuculoids, shallow burrowing astartids
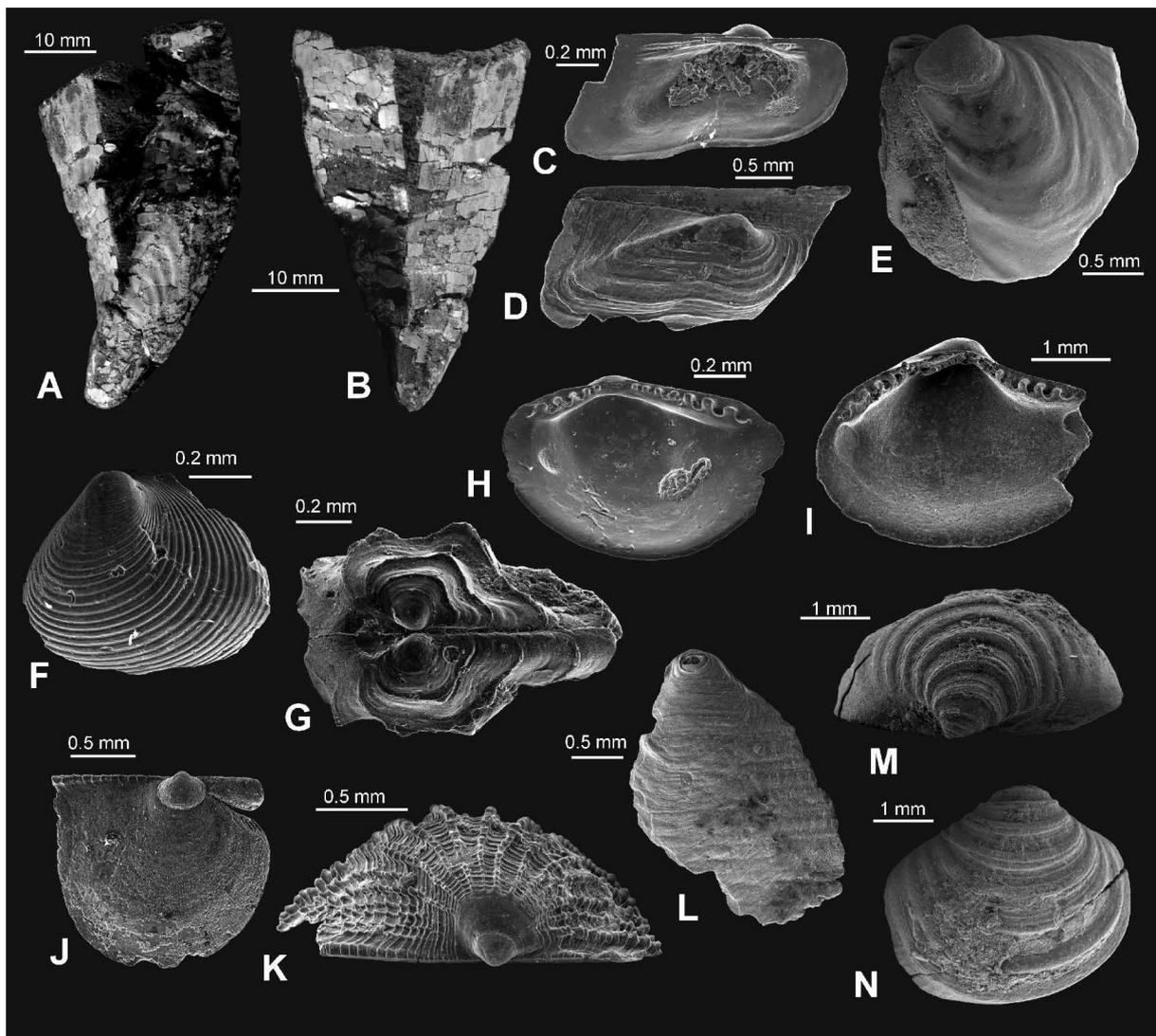
Text-fig. 4. Most common bivalves in the Bathonian (Middle Jurassic) ore-bearing clays in Gnaszyn. **A, B** – *Pinna* sp., subadult specimen collected in life position above sample Gns24; **C, D** – *Grammatodon* (*Cosmetodon*) sp., juveniles from sample Gns17; **E** – *Parainoceramus* sp., juvenile from sample Gns23; **F** – Corbulid (most probably *Varicorbula* sp., juvenile from sample Gns14A; **G** – *Myophorella* sp., juvenile from sample Gns14A; **H** – *Mesosaccella* sp., juvenile from sample Gns16; **I** – *Nuculana* sp., juvenile from sample Gns20; **J** – *Oxytoma* sp., juvenile right valve from sample Gns14; **K** – *Oxytoma* sp., juvenile left valve from sample Gns31; **L** – Unidentified ostreid from Gns24; **M, N** – *Nicaniella* (*Trautscholdia*) sp., juvenile from unregistered sample corresponding to sample Gns27

and byssate oxytomids. Pectinids, pteriids and trigoniids also contribute significantly to the overall diversity of these samples. It should be noted that the astartids in the upper part of the succession are represented by fully grown, complete shells of *Nicaniella* (*Trautscholdia*) spp.

Other bivalves: Some other bivalves have been found but were not observed in the processed samples. These include epibenthic *Bositra* and infaunal bivalves of the genera *Pholadomya*, *Pleuromya* and *Goniomya* (Gedl *et al.* 2003 and our own data). Some of them possess delicate shells which probably could not survive the processing on the sieve. These bivalves, however, are sparsely distributed and do not occur in large numbers. Some bivalves, e.g. hiatellids and epibyssate bakevellids have been found only in the wood-fall associations described from Gnaszyn by Kaim (2011) and Schneider and Kaim (2011).

Scaphopods

The scaphopods in the Gnaszyn section are moderately common apart from samples Gns27–28 where they appear in large numbers (Text-fig. 5). A striking feature of the scaphopods in Gnaszyn is that they usually do not attain large sizes. The only relatively large scaphopod has been found in a sunken wood association (Kaim 2011, fig. 3D) between samples Gns18 and 19. We divided the scaphopods into four morphological groups. The most common is the *Laevidentalium*-type group (46.5% of all scaphopods) which dominate the samples where scaphopods are less numerous (samples Gns38–05, 10–13, 16A–21, 24–26, and 29–31). The *Dentalium*-type group (23.5%) appears in the samples with more numerous scaphopods. It occurs especially in samples Gns34, 37, 07–08, 16A, 21–22, and

27–28, apparently in levels close to siderite concretion horizons (Text-fig. 5). The absence of scaphopods at some concretion horizons (samples Gns35, 09, 16, and 23) resulted, most probably, from diagenetic processes that apparently also affected the bivalves (see above) and gastropods (Kaim 2012, this issue), which are both rare or absent. The *Plagioglypta*-type group (29.9%) is common only in a few samples with the most numerous scaphopod fauna (Gns06–08, 21–22, and 27–28). This group is especially abundant in sample Gns28, where over 600 specimens were counted. The *Episiphon*-type group is represented by a single specimen from sample Gns06.

BIVALVE AND SCAPHOPOD ECOLOGY IN THE GNASZYN SECTION

This chapter summarises information on the ecology of the bivalves and scaphopods occurring in Gnaszyn section by comparisons with their living counterparts.

Bivalves

Nuculoida: Nuculoids are protobranch infaunal bivalves, collecting food using palp proboscides (Reid 1998). We recognised members of two nuculoid families: Nuculidae (*Palaeonucula*) and Nuculanidae (*Nuculana*, *Mesosaccella*). The nuculids burrow to a very shallow depth, remaining close to the sea bottom (Reid 1998). The nuculanids have a foot forming two large lateral flaps which allow rapid burrowing. Detritus feeding might be supplemented by suspension filtration using the gills (Reid 1998). As the ecology of both families is similar we treat them together in our analysis.
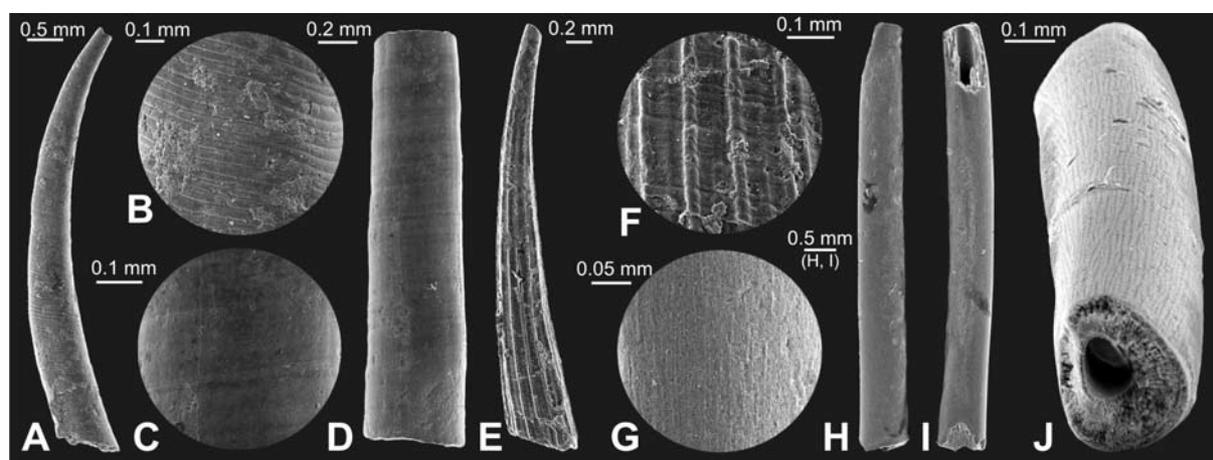
Text-fig. 5. Scaphopod morphologic groups recognised in the Bathonian (Middle Jurassic) ore-bearing clays in Gnaszyn. **A, B** – *Plagioglypta*-type, most probably *Plagioglypta undulata* (Münster, 1844), sample Gns28; **C, D** – *Laevidentalium*-type, sample Gns1; **E, F** – *Dentalium*-type, sample Gns27; **G–J** – *Episiphon*-type, sample Gns6

Arcoida: Arcoids in the Gnaszyn section are represented by members of the family Parallelodontidae (mostly *Grammatodon*). Our arcoids are represented by elongated morphotypes (Text-fig. 6C–D), strongly suggesting an epifaunal mode of life (Stanley 1970), most probably as byssate epifaunal nestlers (Newell 1969; Boyd 1998).

Pterioida: Pteriidae: Pteriids are represented by *Pteria* and some other forms with unidentified generic affiliation. Pteriids possess elongated hinge lines, a character that possibly serves to separate the inhalent and exhalent currents (Stanley 1970). Many of the Recent winged pteriids live on alcyonarians (Stanley 1970) and/or attached to seagrass and clumps of dead shells (Butler 1998).

Pterioida: Inoceramidae: The inoceramids in Gnaszyn are represented by juveniles of *Parainoceramus* sp. (Text-fig. 6E).

Pterioida: Pinnidae: The shells of *Pinna* in Gnaszyn were encountered in two layers (just above Gns14 and in between Gns24 and Gns25) in life position (Text-fig. 6A–B) but they were not found in the rock samples analysed herein.

Ostreoida: Ostreoidea: The ostreids in Gnaszyn are represented mainly by juveniles of both Ostreidae (Text-fig. 6L) and Gryphaeidae (possibly *Liostrea*).

Pectinoida: Oxytomidae: Oxytomids are an extinct group of inequivalve pectinaceans that most probably were byssally attached to the substrate. Duff (1975, 1978) regarded these bivalves as 'pendent' species byssally attached at some distance above the sea floor. He suggested that they could have lived as pseudo-plankton on floating algae (Duff 1978, p. 11), while Oschmann (1994) suggested that oxytomids lived byssally attached to the tests of ammonites resting on the sea floor. Kaim (2001) found that occurrences of oxytomids are strongly correlated with occurrences of cementing oysters. It is thus not necessary to assume a pseudoplanktonic mode of life. Moreover, Stanley (1970) argues that bivalves with inequivalve shells usually rest on one side with the sagittal plane either horizontal, or at an oblique angle to the vertical. Oxytomids are represented in Gnaszyn by *Oxytoma* (Text-fig. 6J–K) and *Meleagrinella*.

Pectinoida: Pectinidae: Pectinids in the Gnaszyn section are represented by *Camptonectes* and some other unidentified forms with auricle asymmetry. This latter character and the low umbonal angle strongly suggest

that these bivalves were byssally attached to the substrate. Johnson (1984) provides an extensive discussion on the ecology of *Camptonectes*, stating that its Jurassic species were apparently byssally suspended (tightly fixed). He also suggests that some species of *Camptonectes* frequently occur in association with *Pinna*, the latter serving as a byssal attachment site.

Trigonioida: Trigoniidae: This family is the only living branch of the Trigonioida, an order that was much more diverse in the Mesozoic (Newell and Boyd 1975; Francis and Hallam 2003). The Recent *Neotrigonia* is a highly active burrowing mollusc that dwells in coarse shallow-marine sediments. It lives with the posterior margin of the valves projecting above the sediment (Darragh 1998; Francis and Hallam 2003). Although the majority of Jurassic trigoniids are interpreted as shallow water, numerous species are considered to have lived in quiet and relatively deep environments (Francis and Hallam 2003). Trigoniids in Gnaszyn are represented by *Trigonia* and *Myophorella* (Text-fig. 6G).

Veneroida: Astartidae: Recent astartids are sluggish shallow-burrowers, active at night (Slack-Smith 1998b). They live with the posterior margin of the shell close to the sediment surface (e.g., Zakharov 1970; Slack-Smith 1998b). Astartids in Gnaszyn are represented by the genera *Astarte*, *Neocrassina* and *Nicaniella* (*Trautscholdia*) (Text-fig. 6M–N). The latter subgenus is known to live in organic-rich muddy environments; its articulated shells were also found associated with a complete plesiosaur skeleton in the Callovian (Middle Jurassic) Oxford Clay (Martill *et al.* 1991). This might suggest that these suspension-feeding bivalves were able to tolerate conditions depleted in oxygen.

Myoida: Corbulidae: Corbulids are shallow burrowers living up to depths of 350 m (Lamprell *et al.* 1998). They commonly build shell-beds slightly beneath the sediment surface (Lewy and Samtleben 1979) which are known in the fossil record since the Triassic (e.g., Kaim 1997). The burrowing rate of corbulids is very low, so they usually have difficulties in escaping after a burial event (Lewy and Samtleben 1979) but otherwise they are opportunists which are capable of coping with different adverse conditions e.g., salinity, oxygen and turbidity (Lewy and Samtleben 1979; Homes and Miller 2006; Hrs-Brenko 2006; Wesselingh 2006). The corbulids in Gnaszyn are represented by *Corbulomima* and *Varicorbula* (Text-fig. 6F), which are believed to have been attached to the substratum by byssal threads (Duff 1978).
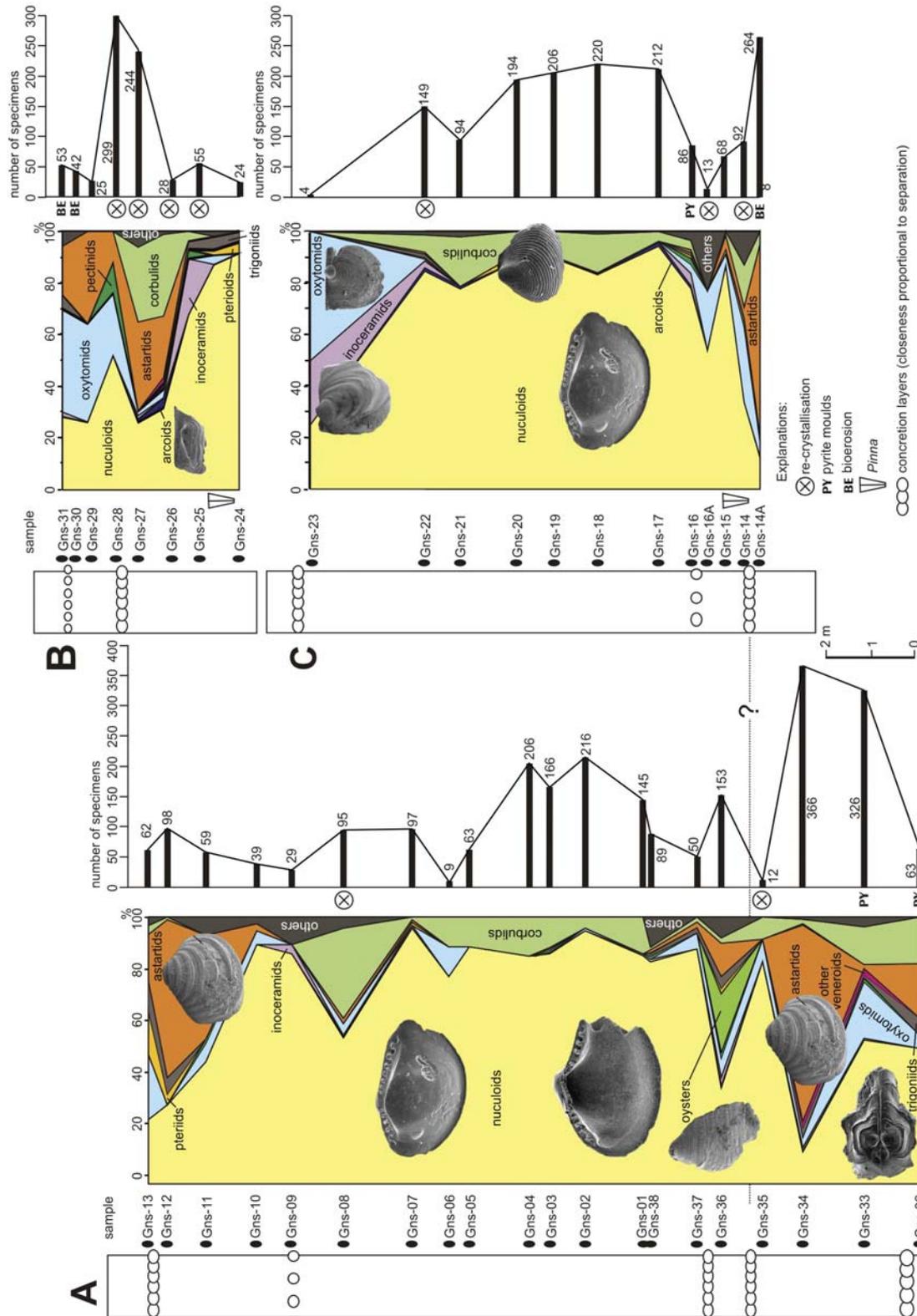
Text-fig. 6. Sample size and vertical variations in relative abundance (%) of the most common bivalves in the ore-bearing clays in Gnaszyn; for stratigraphy see Matyja and Wierzbowski (2006) and Gedl and Kaim (2012). **A** – Section A; **B** – Section C; **C** – Section B
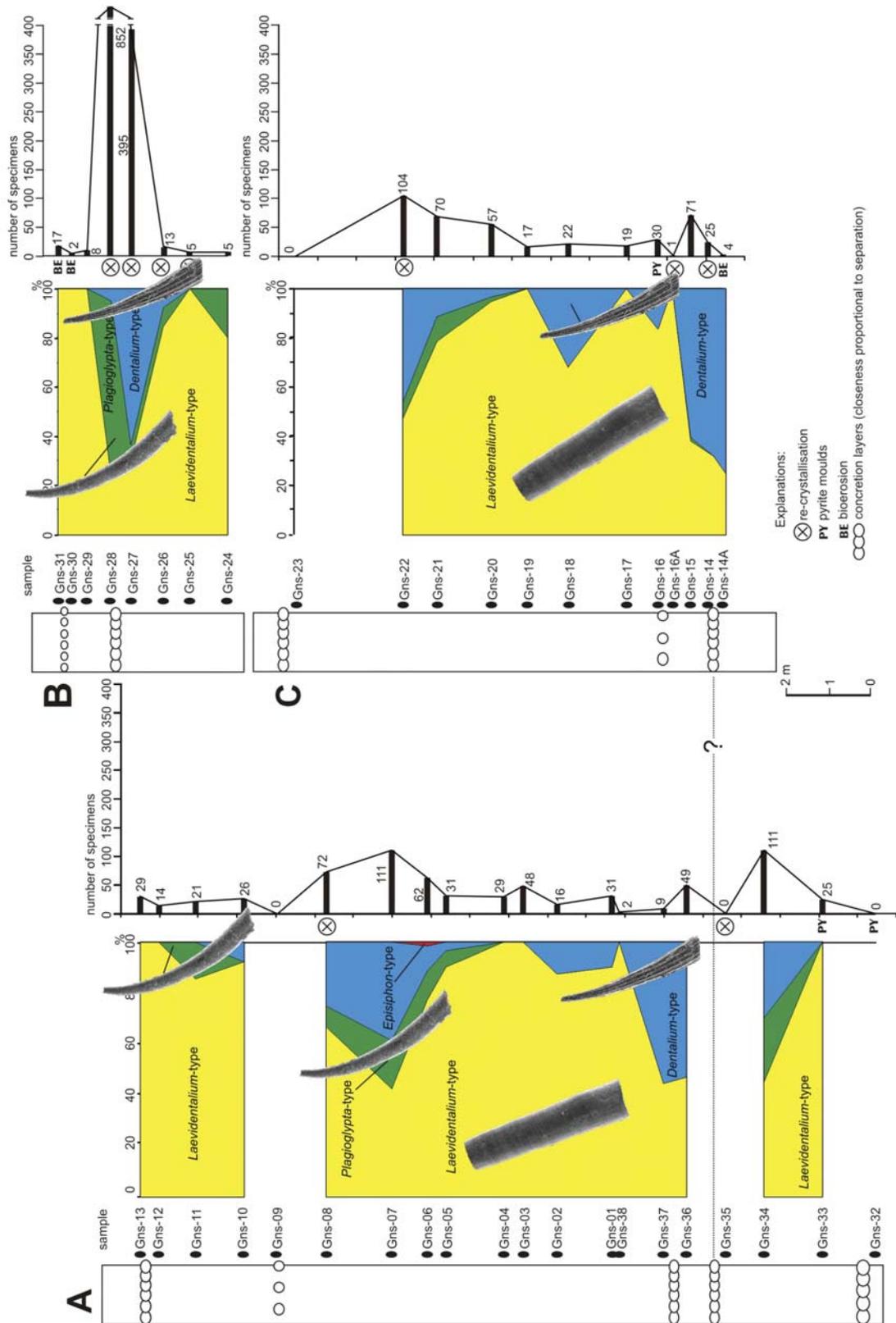
Text-fig. 7. Sample size and vertical variation in relative abundance (%) of scaphopods divided into morphological groups in the ore-bearing clays in Gnaszyn; for stratigraphy see Matyja and Wierzbowski (2006) and Gedl and Kaim (2012). **A** – Section A; **B** – Section C; **C** – Section B

Scaphopods

Detailed taxonomical study of the scaphopods from the Gnaszyn section is still pending. The most common are scaphopods with smooth shells (with only growth lines visible), weakly curved, increasing slowly in diameter, and widely elliptical in cross-section. We referred this group to the *Laevidentalium*-type (Text-fig. 7C–D). The scaphopods with longitudinal ribs we referred to the *Dentalium*-type (Text-fig. 7E–G), and small, strongly curved shells, slightly triangular in cross-section in the anterior part and ornamented with dense, inclined anterior annulations, we referred to the *Plagioglypta*-type (Text-fig. 7A–B). The fourth, *Episiphon*-type (Text-fig. 7G–J) group, is represented by a single specimen having a small shell, triangular in cross-section and with an irregularly longitudinal pattern on its surface. All scaphopods are euhaline benthic microcarnivores inhabiting all types of soft bottom environments (Palmer and Steiner 1998). Scaphopods range from the littoral to the abyssal zones (Palmer and Steiner 1998) and most of them consume foraminifers (Dinamani 1964; Reynolds 2002). Duff (1975) noted negative correlation between the abundance of scaphopods and foraminifers in the Oxford Clay. A similar pattern was observed by Kaim (2001) in Valanginian clays from Poland. According to Wignall (1990), scaphopods decline rapidly in abundance in organic-rich facies, suggesting low tolerance to oxygen depletion. On the other hand, some scaphopods are known to be associated with ichthyosaur skeletons (Martill 1987) and methane seeps (Goedert and Squires 1990).

PALAEOECOLOGY OF THE BOTTOM ENVIRONMENT AS INFERRED FROM THE SUCCESSION OF BIVALVE AND SCAPHOPOD ASSEMBLAGES

The full-marine salinity of the section is proved by the continuous presence of diverse echinoderms (Gedl *et al.* 2003, 2006) including crinoids, ophiuroids, asteroids, holothurians and echinoids. Gedl (2012, this issue) argues that subtle changes in dinoflagellate cyst distribution in the middle part of the section may reflect slightly reduced salinity in the surface waters but it seems that it did not affect the bottom waters, which remained fully marine. Although the depth of the basin is a matter of discussion (Gedl *et al.* 2003; Wierzbowski and Joachimski 2007), it seems that the clays were deposited on the outer shelf below the photic zone (Gedl *et al.* 2003). The sediment surface was well-oxygenated, as suggested by the continuous presence of scaphopod molluscs (apart from samples Gns9, 23, 32, and Gns35,

in which the absence of scaphopods is most likely due to diagenetic processes). Moreover, the majority of geochemical environmental indices: (TOC/S, Ni/Co, V/Cr, U/Th, (Cu+Mo)/Zn ratios, the content of authigenic uranium, and the relationship between TOC-Fe-S), point to oxic conditions of the sediment surface (Szczepanik *et al.* 2007). Though the surface layer seems to have been oxygenated, the deeper parts of the sediment were most likely dysoxic/anoxic, as has been suggested by the DOP (degree of pyritisation) and V/V+Ni indices (Szczepanik *et al.* 2007). It is also likely that there was some seasonal variation in oxygenation level (higher levels of organic production in summer promote lower levels of bottom oxygen), as proposed for the Kimmeridge Clay by Oschmann (1994). It seems that the presence of a relatively thin layer of oxygenated sediment might be responsible for the small size of the molluscs (e.g. scaphopods) inhabiting the sea bottom. Such reduction in size of the animals in stressed environments is known from modern communities (Gray 1989). Nevertheless we could not observe any convincing indications of stunting by adverse conditions, as proposed for the Bathonian of England by Johnson *et al.* (2007), albeit we cannot dismiss it unequivocally with the data to hand.

The bivalve associations in Gnaszyn section are dominated by nuculoids. This group of deposit-feeding protobranchs is present in all the samples analysed. This dominance is especially well pronounced in the middle part of the section, where nuculoids contribute to over 80% of the bivalve association. The other group present there are corbulids. These bivalves are rather slow infaunal suspension feeders with low capability to escape after a burial event. It seems that the sedimentation rate was low enough to allow development of the corbulid communities. In periods with dominance of nuculoid and corbulid bivalves the scaphopods are represented mainly by *Laevidentalium*-type species.

The nuculid-corbulid domination in the middle part of the section suggests that the sediment they inhabited was very soft, possibly with some variation in oxygen content. The soupy bottom surface and oxygen-deficient deeper sediment is also consistent with the sedimentological and ichnological observations of Leonowicz (2012, this issue) who found out that the middle part of the section contains the lowest amounts of the sandy fraction, small amounts of shell detritus and the ubiquitous occurrence of the ichnofossils *Chondrites* and *Trichichnus*, considered as indicators of oxygen-poor environments (Ekdale and Mason 1988; Löwemark 2003). The soupy sediment-water interface could also have been responsible for the general paucity of the epibenthic fauna (e.g., Rhoads and Young 1970; Etter

1990). The presence of a few laminated horizons (albeit secondarily obliterated by bioturbation) (Leonowicz 2012, this issue) and the uncommon occurrence of the bivalve *Bositra* may suggest that, at least temporarily, the bottom waters were deoxygenated (see e.g. Oschmann 1994; Wignall 1994).

The composition of the bivalve and scaphopod associations in the upper and lower parts of the sequence is clearly different from that of the associations of the middle part. The associations in the upper and lower parts are dominated by astartid bivalves, with some contribution of byssate oxytomids and a predominance of *Dentalium*- and *Plagioglypta*-type scaphopods. The occurrence of astartid-rich associations correlates well with the coarsening of the sediment; Leonowicz (2012, this issue) reported the highest amounts of the sandy fraction in the uppermost and lowermost parts of the succession. Moreover, the ichnofossil assemblages show the highest diversity in these intervals. We noted also the presence here of larger bivalves, including the mud-sticking *Pinna* in life position as well as the infaunal *Pholadomya*, *Pleuromya* and *Goniomya*, though we have not encountered them in the analysed samples. The samples displaying the domination of astartid bivalves are also the most distinct both in neighbour joining clustering (Text-fig. 3C) and principal component analysis (PCA; Text-fig. 8). In the neighbour joining the astartid-rich samples form a distinctive cluster (Text-fig. 3C) which consists of samples Gns11, Gns12, Gns14A, Gns27, Gns28 and Gns34. A sister cluster contains astartid-oxytomid samples (Gns13, Gns14, Gns30, Gns 32) next to mixed samples (Gns8, Gns29, Gns32, Gns33, Gns36). The remaining samples form a nuculoid-corbulid cluster. The PCA shows a distinct grouping of astartid-dominated samples along the astartid loading, especially clearly visible in the PC1-PC2 graph (shaded area in Text-fig. 8A). The remaining samples are distributed almost linearly along the nuculoids loading. Therefore, it seems to be plausible that the factors controlling the distribution of astartids and nuculoids are the most important for sample composition. The first two components in the PCA are responsible for as much as 92.83% of the entire variation (Text-fig. 8D).

The abundance of heavily-ornamented sluggish astartids suggests that the water-sediment interface was not soupy, though still soft. The appearance of byssate bivalves and ostreids in some samples apparently indicates the appearance of substrates for their attachment. Moreover, Witkowska (2012, this issue) argues that the iron carbonate concretion layers in Gnaszyn, which precipitated from pore fluids of the host sediment during early diagenesis, correspond to periods of better bottom oxygenation and a lower sedimentation rate.

COMPARISON TO OTHER BENTHIC ASSOCIATIONS

Comparison of assemblages obtained from Gnaszyn with published ones is somewhat difficult due to the different sampling strategy. Quantitative palaeoecological studies are usually based on surface collecting (e.g. Duff 1975; Wignall 1990; Oschmann 1994), which are usually biased towards larger specimens (see discussion in Brayard *et al.* 2011). Only rarely do the data come from sieving the samples (Kaim 2001, 2011). Nevertheless, it seems that the bivalve associations from Gnaszyn fit well into the pattern known from other Jurassic bivalve black-shale associations. The most similar is the Kimmeridgian–Tithonian Kimmeridge Clay associations from England (Wignall 1990; Oschmann 1994). It seems that the astartid-dominated associations in Gnaszyn are similar to the A14 (*Corbulomima*/*Neocrassina*) or B3 (*Trautscholdia*/*Corbulomima*) associations of Wignall (1990) and correspond well to the bivalve associations from the lowermost Upper Valanginian of Poland (Kaim 2001).The nuculoid-corbulid-dominated samples in Gnaszyn are more similar to the "Nuculacean shell bed biofacies" of Duff (1975) from the Callovian Oxford Clay. The latter association comes from shell beds which are interpreted as omission surfaces and therefore biased by time-averaging. The presence of *Bositra* and laminated sediment in some layers (though not found in the analysed samples) strongly suggests temporary dysoxic/anoxic conditions, as suggested from analogous Lower Jurassic clays in Switzerland (Etter 1995, 1996) and some horizons in the Kimmeridge Clay (Oschmann 1994). Judging from the samples analysed herein and in Kaim (2001), there is a distinct sequence in the occurrence of small bivalves in clay sediments in relation to increasing oxygenation and/or substrate consistency. The most dysoxic/anoxic conditions are characterised by the dominance of *Bositra*, which is subsequently replaced by nuculoids, followed by astartids and then arcoids.

CONCLUSIONS

The bivalve and scaphopod assemblages in Gnaszyn section suggest an outer shelf environment. The middle part of the section is dominated by nuculoid and corbulid bivalves and *Laevidentalium*-type scaphopods. The clay in this part contains only a small admixture of the sandy fraction and shell detritus (Leonowicz 2012). The abundant presence of deposit-feeding nuculids associated with corbulids and the general paucity of epibenthic bivalves strongly suggests a soupy water-sediment inter-
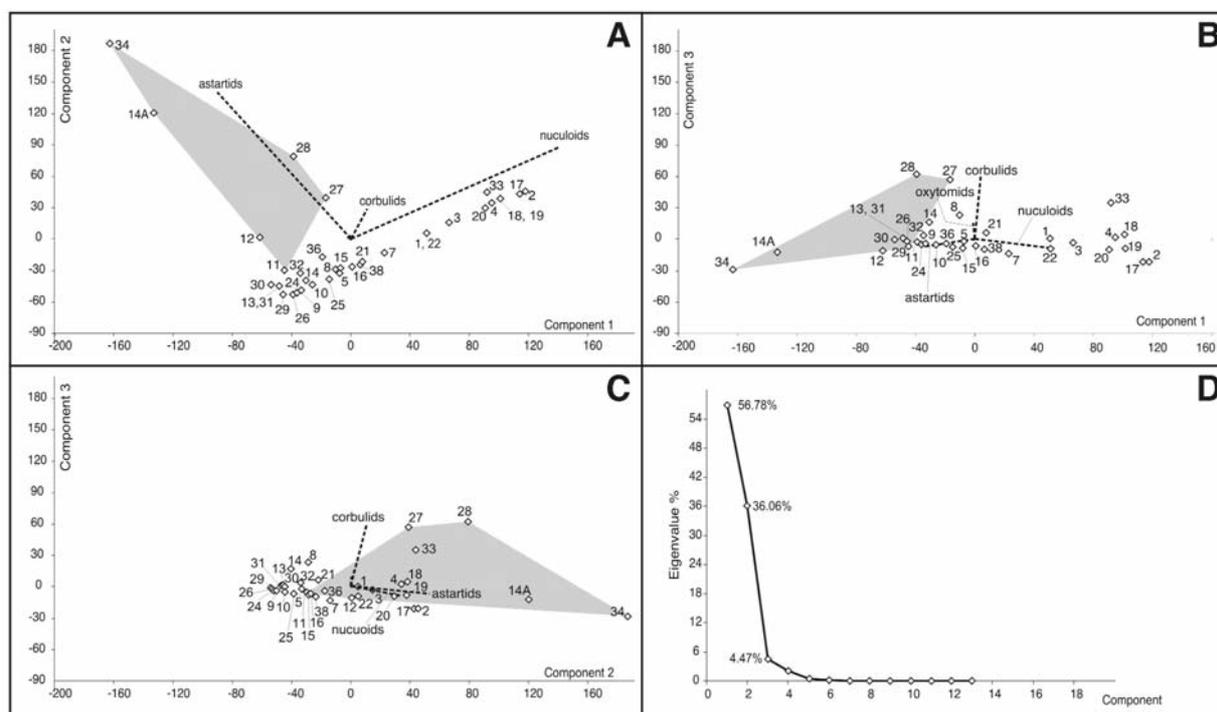
Text-fig. 8. Principal component analysis (PCA) of the bivalve assemblages from Gnaszyn, Poland, performed using PAST software (Hammer *et al.* 2001). **A–C** – Biplots of scores and loadings of principal component analysis (PCA) on the variance-covariance matrix with singular value decomposition (SVD). Dashed lines indicate loadings for particular taxa used in the analysis. Shaded convex hull indicates the smallest convex polygon containing all astartid dominated samples (upper left cluster in Text-fig. 3C). Prefix Gns omitted from sample numbers for image clarity. **D** – Scree plot showing the variance in the dataset as explained by each principal component. PC1 explains 56.78%, PC2 36.06%, and PC3 4.47% of the variation

face. Moreover, it is quite likely that there were also some restrictions and/or fluctuations of oxygen content in the sediment. The continuous presence of small scaphopod molluscs suggests, however, that at least the surface part of the sediment was oxygenated. Such a scenario is well supported by the geochemical (Szczepanik *et al.* 2007), sedimentological and ichnological (Leonowicz 2012, this issue) data. The lower and upper part of the succession is dominated by astartid bivalves and *Plagioglypta*- and *Dentalium*-type scaphopods. These molluscs inhabited slightly coarser sediment with a higher admixture of the sandy fraction and shell detritus. The latter and also the presence of larger animals (e.g. *Pinna*) on the seafloor allowed development of more diverse epibenthic communities dominated by oxytomid bivalves. The presence of larger bivalves and ubiquity of scaphopods suggest a firmer substrate and a thicker layer of oxygenated sediment.

REFERENCES:

Boyd, S.E. 1998. Order Arcoida. In: P. L. Beesley *et al.* (Eds), Mollusca: The Southern Synthesis. Fauna of Australia 5, 253–261. CSIRO Publishing, Melbourne.

Brayard, A., Nützel, A., Kaim, A., Hautmann, A., Escarguel, G., Bucher, H., Stephen, D.A., Bylund, K.G. and Jenks, J. 2011. Gastropod evidence against the Early Triassic Lilliput effect: reply. *Geology*, **39**, e233.

Butler, A.J. 1998. Order Pterioida. In: P. L. Beesley *et al.* (Eds), Mollusca: The Southern Synthesis. Fauna of Australia 5, 261–267. CSIRO Publishing, Melbourne.

Darragh, T. A. 1998. Order Trigonioida. In: P. L. Beesley *et al.* (Eds), Mollusca: The Southern Synthesis. Fauna of Australia 5, 294–296. CSIRO Publishing, Melbourne.

Dinamani, P. 1964. Feeding in *Dentalium conspicuum*. *Proceedings of the Malacological Society of London*, **36**, 1–5.

Duff, K.L. 1975. Palaeoecology of a bituminous shale – the Lower Oxford Clay of central England. *Palaeontology*, **18**, 443–482.

Duff, K.L. 1978. Bivalvia from the English Lower Oxford Clay (Middle Jurassic). *Palaeontographical Society Monographs*, **132**, 1–137.

Ekdale, A.A. and Mason, T.R. 1988. Characteristic trace-fossil associations in oxygen-poor sedimentary environments. *Geology*, **16**, 720–723.

Etter, W. 1990. Paläontologische Untersuchungen im unteren Opalinuston der Nordschweiz. Dissertation Universität Zürich, 151 pp.

Etter, W. 1995. Benthic diversity patterns in oxygenation gradients: an example from the Middle Jurassic of Switzerland. *Lethaia*, **28**, 259–270.

Etter, W. 1996. Pseudoplanctonic and benthic invertebrates in the Middle Jurassic Opalinum Clay, northern Switzerland. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **126**, 325–341.

Francis, A.O. and Hallam, A. 2003. Ecology and evolution of Jurassic trigoniid bivalves in Europe. *Lethaia*, **36**, 287–304.

Gedl, P. 2012. Organic-walled dinoflagellate cysts from Bathonian ore-bearing clays at Gnaszyn, Kraków-Silesia Homocline, Poland. *Acta Geologica Polonica*, **62** (3), 439–461.

Gedl, P. and Kaim, A. 2012. An introduction to palaeoenvironmental reconstruction of Bathonian (Middle Jurassic) ore-bearing clays at Gnaszyn, Kraków-Silesia Monocline, Poland. *Acta Geologica Polonica*, **62** (3), 267–280.

Gedl, P., Kaim, A., Boczarowski, A., Kędzierski, M., Smoleń, J., Szczepanik, P., Witkowska, M. and Ziaja, J. 2003. Rekonstrukcja paleośrodowiska sedymentacji środkowojurajskich iłów rudonośnych Gnaszyna (Częstochowa) – wyniki wstępne. *Tomy Jurajskie*, **1**, 19–27.

Gedl, P., Boczarowski, A., Dudek, T., Kaim, A., Kędzierski, M., Leonowicz, P., Smoleń, J., Szczepanik, P., Witkowska, M. and Ziaja, J. 2006. Stop B1.7 — Gnaszyn clay pit (Middle Bathonian-lowermost Upper Bathonian). Lithology, fossil assemblages and palaeoenvironment. In: A. Wierzbowski *et al.* (Eds), Jurassic of Poland and adjacent Slovakian Carpathians. Field trip guidebook of 7th International Congress on the Jurassic System. 155–156. Polish Geological Institute, Warszawa.

Goedert, J.L. and Squires, R.L. 1990. Eocene deep-sea communities in localized limestones formed by subduction-related methane seeps, southwestern Washington. *Geology*, **18**, 1182–1185.

Gray, J.S. 1989. Effects of environmental stress on species rich assemblages. *Biological Journal of the Linnean Society*, **37**, 19–32.

Hammer, Ø., Harper, D.A.T., and P.D. Ryan, 2001. PAST: Paleontological Statistics Software Package for Education and Data Analysis. *Palaeontologia Electronica*, **4**, 1–9.

Holmes, S. and Miller, N. 2006. Aspects of the ecology and population genetics of the bivalve Corbula gibba. *Marine Ecology. Progress Series*, **315**, 129–140.

Hrs-Brenko, M. 2006. The basket shell, *Corbula gibba* Olivi, 1792 (bivalve mollusks) as a species resistant to environmental disturbances: A review. *Acta Adriatica*, **47**, 49–64.

Johnson, A.L.A. 1984. The palaeobiology of the bivalve families Pectinidae and Propeamussiidae in the Jurassic of Europe. *Zitteliana*, **11**, 1–235.

Johnson, A.L.A., Liquorish, M. and Sha, J. 2007. Variation in growth-rate and form of a Bathonian (Middle Jurassic) oyster in England, and its environmental implications. *Palaeontology*, **50**, 1155–1173.

Kaim, A. 1997. Brachiopod-bivalve assemblages of the Middle Triassic Terebratula   Beds, Upper Silesia, Poland. *Acta Palaeontologica Polonica*, **42**, 333–359.

Kaim, A. 2001. Faunal dynamics of juvenile gastropods and associated organisms across the Valanginian transgression-regression cycle in central Poland. *Cretaceous Research*, **22**, 333–351.

Kaim, A. 2011. Non-actualistic wood-fall associations from Middle Jurassic of Poland. *Lethaia*, **44**, 109–124.

Kaim, A. 2012. Faunal dynamics of gastropods in the Bathonian (Middle Jurassic) ore-bearing clays at Gnaszyn, Kraków-Silesia Monocline, Poland. *Acta Geologica Polonica*, **62** (3), 367–380.

Kaim, A. and Schneider, S. 2012. A conch with a collar: early ontogeny of the enigmatic fossil bivalve *Myoconcha*. *Journal of Paleontology*, **86**, 652–658.

Lamprell, K.L. and Healy, J.M. 1998. A revision of the Scaphopoda from Australian Waters (Mollusca). *Records of The Australian Museum, Supplement*, **24**, 1–189.

Lamprell, K.L., Healy, J.M. and Dyne, G.R. 1998. Superfamily Myoidea. In: P.L. Beesley *et al.* (Eds), Mollusca: The Southern Synthesis. Fauna of Australia 5, 363–366. CSIRO Publishing, Melbourne.

Leonowicz, P. 2012. Sedimentology and ichnology of Bathonian (Middle Jurassic) ore bearing clays at Gnaszyn, Kraków-Silesia Homocline, Poland. *Acta Geologica Polonica,* **62** (3), 281-296.

Lewy, Z. and Samtleben, C. 1979. Functional morphology and palaeontological significance of the conchiolin layers in corbulid pelecypods. *Lethaia,* **12**, 341–351.

Löwemark, L. 2003. Automatic image analysis of X-ray radiography: a new method for ichnofabric evaluation. *Deep-Sea Research I*, **50**, 815–827.

Majewski, W. 2000. Middle Jurassic concretions from Częstochowa (Poland) as indicators of sedimentation rates. *Acta Geologica Polonica*, **50**, 431–439.

Martill, D.M. 1987. A taphonomic and diagenetic case-study of a partially articulated Ichtyosaur. *Palaeontology*, **30**, 543–556.

Martill, D. M., Cruickshank, A. R. I. and Taylor, M. A. 1991. Dispersal via whale bones. *Nature*, **351**, p. 193.

Matyja, B.A. and Wierzbowski, A. 2003. Biostratigrafia amonitowa formacji Częstochowskich iłów rudonośnych (najwyższy bajos-górny baton) z odsłonięć w Częstochowie. *Tomy Jurajskie*, **1**, 3–6.

Matyja, B.A. and Wierzbowski, A. 2006. Stop B1.7 – Gnaszyn clay pit (Middle Bathonian-lowermost Upper Bathonian). Ammonite biostratigraphy. *In*: A. Wierzbowski *et al.* (Eds), Field trip guidebook of 7th International Congress on the Jurassic System. 154–155. Polish Geological Institute, Warszawa.

Newell N.D. 1969. Classification of Bivalvia. In: R.C. Moore and C. Teichert (Eds), Treatise on Invertebrate Paleontology. Part N, Volume 1 (of 3), Mollusca 6, Bivalvia. 205–224. The Geological Society of America and The University of Kansas, Lawrence.

Newell, N.D. and Boyd, D.W. 1975. Parallel evolution in early trigonacean bivalves. *Bulletin of the American Museum of Natural History*, **154**, 53–162.

Oschmann, W. 1994. Der Kimmeridge Clay von Yorkshire als ein Beispiel eines Fossilien Sauerstoff-kontrollierten Millieus. *Beringeria*, **9**, 1–153.

Palmer, C.P. and Steiner, G. 1998. Class Scaphopoda. Introduction. In: P. L. Beesley *et al.* (Eds), Mollusca: The Southern Synthesis. Fauna of Australia, 5, 431–438. CSIRO Publishing, Melbourne.

Rees, J. 2012. Palaeoecological implications of neoselachian shark teeth from a Bathonian (Middle Jurassic) section at Gnaszyn, Poland. *Acta Geologica Polonica*, **62** (3), 397–402.

Reid, R.G.B. 1998. Subclass Protobranchia. In: P.L. Beesley *et al.* (Eds), Mollusca: The Southern Synthesis. Fauna of Australia 5, 235–247. CSIRO Publishing, Melbourne.

Reynolds, P.D. 2002. The Scaphopoda. *Advances in Marine Biology*, **42**, 137–236.

Rhoads, D.C. and Young, D.K. 1970. The influence of deposit-feeding organisms on sediment stability and community trophic structure. *Journal of Marine Research*, **28**, 150–178

Schneider, S. and Kaim, A. 2011. Early ontogeny of Middle Jurassic hiatellids from a wood fall association: implications for phylogeny and paleaoecology of Hiatellidae. *Journal of Molluscan Studies*, **78** (1), 119–127.

Seilacher, A. 1984. Constructional morphology of bivalve: evolutionary pathways in primary versus secondary soft-bottom dwellers. *Palaeontology*, **27**, 207–237.

Slack-Smith, S.M. 1998a. Superfamily Carditoidea. In: P.L. Beesley *et al.* (Eds), Mollusca: The Southern Synthesis. Fauna of Australia 5, 322–325. CSIRO Publishing; Melbourne.

Slack-Smith, S.M. 1998b. Superfamily Crassatelloidea. In: P.L. Beesley *et al.* (Eds), Mollusca: The Southern Synthesis. Fauna of Australia 5, 325–328. CSIRO Publishing, Melbourne.

Stanley, S.M. 1970. Relation of shell form to life habits of the Bivalvia (Mollusca). *Geological Society of America Memoir*, **125**, 1–296.

Steiner, G. 1992. Phylogeny and classification of Scaphopoda. *Journal of Molluscan Studies*, **58**, 385–400.

Steiner, G. and Kabat, A.R. 2001. Catalogue of supraspecific taxa of Scaphopoda Mollusca). *Zoosystema*, **23**, 433–460.

Szczepanik, P., Witkowska, M. and Sawłowicz, Z. 2007. Geochemistry of Middle Jurassic mudstones (Kraków-Częstochowa area, southern Poland): interpretation of the depositional redox conditions. *Geological Quarterly*, **51**, 57–66.

Wesselingh, F.P. 2006. Evolutionary ecology of the Pachydontinae (Bivalvia, Corbulidae) in the Pebas lake/wetland system (Micoene, western Amazonia). *Scripta Geologica*, **133**, 395–417.

Wierzbowski, H. and Joachimski, M. 2007. Reconstruction of late Bajocian–Bathonian marine palaeoenvironments using carbon and oxygen isotope ratios of calcareous fossils from the Polish Jura Chain. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **254**, 523–540.

Wignall, P.B. 1990. Benthic palaeoecology of the late Jurassic Kimmeridge Clay of England. *Special Papers in Palaeontology*, **43**, 1–74.

Wignall, P.B. 1994. Black shales. *Geology and Geophysics Monographs*, **30**, 1–130.

Witkowska, M. 2012. Palaeoenvironmental significance of iron carbonate concretions from the Bathonian (Middle Jurassic) ore-bearing clays at Gnaszyn, Kraków-Silesia Homocline, Poland. *Acta Geologica Polonica*, **62** (3), 307–324.

Zakharov, V.A. 1970. Late Jurassic and early Cretaceous bivalves of Northern Siberia and their ecology, Part 2, Fam. Astartidae. *Transactions of the Institute of Geology and Geophysics, Siberian Branch of the Academy of Sciences of the USSR*, **113**, 1–144.