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Taphonomy of Eemian marine molluscs and acorn barnacles from eastern Arkhangelsk region, northern Russia

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Abstract

Marine Eemian deposits along the Pyoza river and its tributary Varchuska, Arkhangelsk region, constitute successions of muddy and sandy facies with rich macrobenthic fauna dominated by bivalves and barnacles. Taphonomic features formed by abrasion, disarticulation, dissolution, fragmentation, bioerosion and encrustation define taphofacies for a palaeoenvironmental model. Five bivalve taphofacies and three barnacle taphofacies could be distinguished. Both bivalves and barnacles are poorly preserved in foreshore/shoreface environments, as the shells were subjected to extensive transportation by currents. The shells were best preserved in offshore environments, where rapid episodic sedimentation enabled within-habitat preservation, in some cases even preservation in life position. Barnacles are absent from the most clay-rich offshore deposits, probably because of clogging of filters by turbidity and lack of suitable substrate. Such dissimilarities suggest that the number and distribution of taphofacies may depend on which fossil groups are used. Interspecific variability may exist within the individual taphofacies. The barnacles, for example, tend to be better preserved than the mussel *Mytilus edulis*, although both are fixosessile suspension feeders. This indicates that not only life habits but also intrinsic shell properties influence preservation. Thus, taphofacies analyses should combine data on taphonomic features, specific life habit and shell properties to determine overall preservation patterns. In that way, taphofacies analyses may form a powerful tool for palaeoenvironmental analyses of marine deposits.

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1. Introduction

During the last interglacial (Eemian) the sea inundated the north Russian lowlands up to a distance of 400 km from the present coast forming a multitude of shallow-marine environments

(Devyatova and Loseva, 1964; Biske and Devyatova, 1965; Devyatova, 1982; Funder et al., 2002). The sediments from this so-called Boreal Transgression are exposed in cliffs along rivers and coasts, and are noted for their rich macrobenthic shell faunas with a number of boreal species. The boreal species presently have their northern limits along the coast of Norway and the Kola Peninsula, and do not live in the White Sea (Funder et al., 2002). No similar palaeofaunas are known from other Late Cainozoic marine de-

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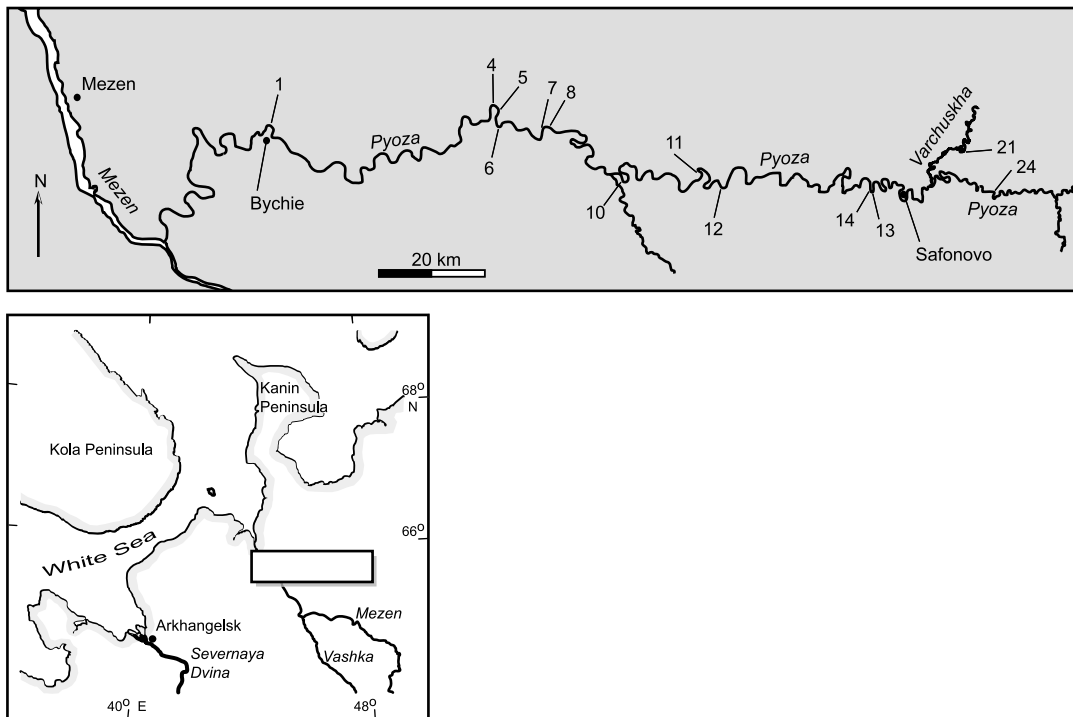


Fig. 1. Localities with Eemian marine deposits along the Pyoza river.

posits in northern Russia (Zharkidze and Samoilovich, 1989), and the 'Boreal Transgression' thus is an important marker horizon across the region.

Shells of molluscs and acorn barnacles (balanomorpha barnacles) are widely distributed in marine sediments of the 'Boreal Transgression', but only minor notes on their preservation were given by Devyatova and Loseva (1964), and no other taphonomic studies have been conducted on the boreal palaeofauna, despite its importance for Russian Quaternary stratigraphy. This paper presents a taphonomic analysis for the Pyoza river area in the Arkhangelsk region that may provide further insight into the palaeoenvironmental conditions during the Eemian (Figs. 1 and 2). Also, the intention is to study interspecific differences in preservation. The sections studied have been described by Houmark-Nielsen et al. (2001).

2. Geological setting

Stratigraphic setting, altitude, and faunal char-

acteristics indicate that the marine sediments exposed in the Pyoza river area all belong to the same transgressive–regressive cycle, the Eemian 'Boreal Transgression' (Houmark-Nielsen et al., 2001; Fig. 3). The marine successions are here divided into two main facies.

(1) An offshore fine-grained facies that consists of grey mud with silt–sand laminae or sand layers (Fig. 4). At most localities the mud is structureless. At locality 11, it is discontinuously laminated and indistinctive trace fossils indicate that it has been moderately bioturbated. The lower boundary of this facies is exposed at localities 6, 7 and 10, where the mud overlies glaciomarine diamicton or till. The facies reaches a thickness of 9 m and is well exposed at localities 1, 7, 8 and 10–12.

(2) Sandy and gravelly yellowish facies represents a shoreface/foreshore environment that succeeds the muddy facies (Fig. 5). The sands are planar stratified, or with small-scale and large-scale trough cross-stratification. The gravels are structureless, and occasionally offshore mud is in-

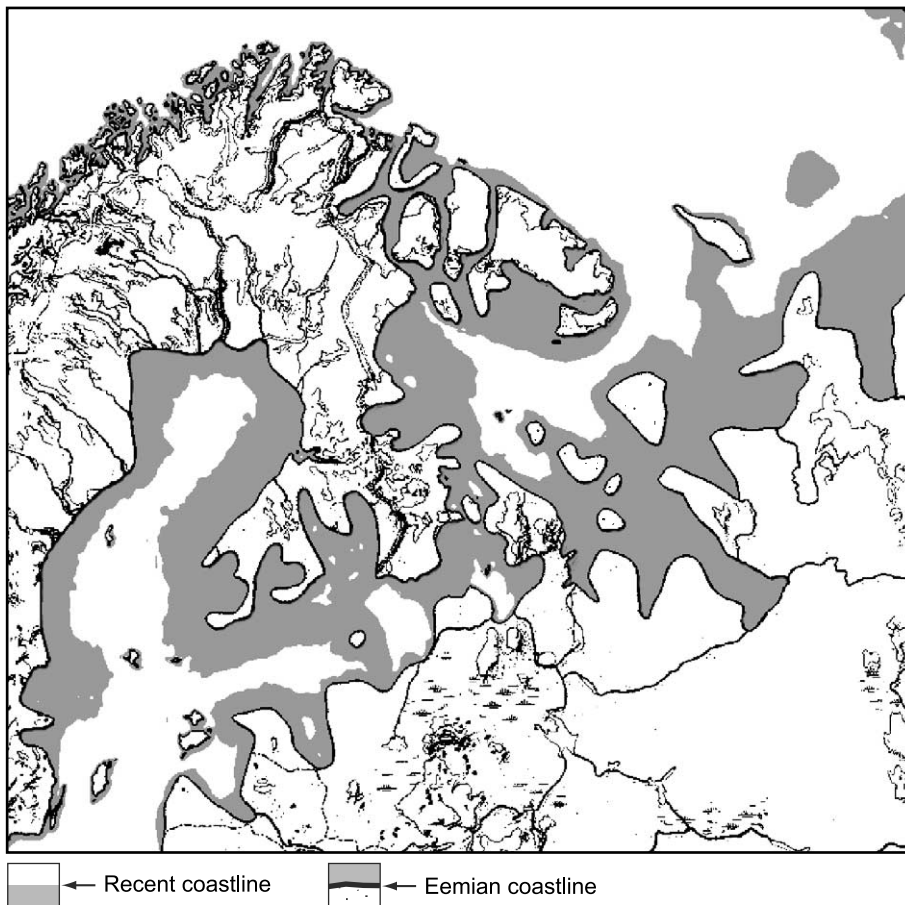


Fig. 2. Maximum distribution of the Eemian sea in the Arkhangelsk region. Recent lowlands were covered by the sea (grey). Adapted from [Funder et al. \(2002\)](#).

corporated as intraclasts. Trace fossils belonging to *Diplocraterion* sp. and *Thalassinoides suevicus* are sporadically present in a stratigraphic interval dominated by sandy beds at locality 6 (Fig. 6). *T. suevicus* maintains a smooth muddy wall lining when it is enclosed in sandy sediment. The facies, which has a maximum thickness of 9 m, is exposed between c. 20 and 60 m above present sea level at localities 1, 4–6, 12–14, 21 and 24.

The two facies are separated by a sharp and erosive boundary or by a gradual transition. The gradual transition coarsens gently upwards to sand, or consists of an interbedded sequence of mud and sand.

Taken together, these features indicate that the muddy facies was deposited below the fair-weather

er wave base in a low-energy offshore environment interrupted by deposition of sheet sands during storms. Thus, the fair-weather muds alternate with silt-sand laminae or sand beds deposited during storms (see [Elliott, 1986](#)). The sandy facies was deposited above the fair-weather wave base in a high-energy shoreface/foreshore and, presumably more landward, environment. The change in facies found at localities 1, 6, 11 and 12 represents a coarsening-upward and shallowing-upward succession. During the Weichselian glaciation the marine sediments were covered by proglacial, lacustrine-fluvial, ice-marginal and fluvial deposits. However, the marine sediments remained glaciotectonically undisturbed, except at locality 21 ([Houmark-Nielsen et al., 2001](#)).

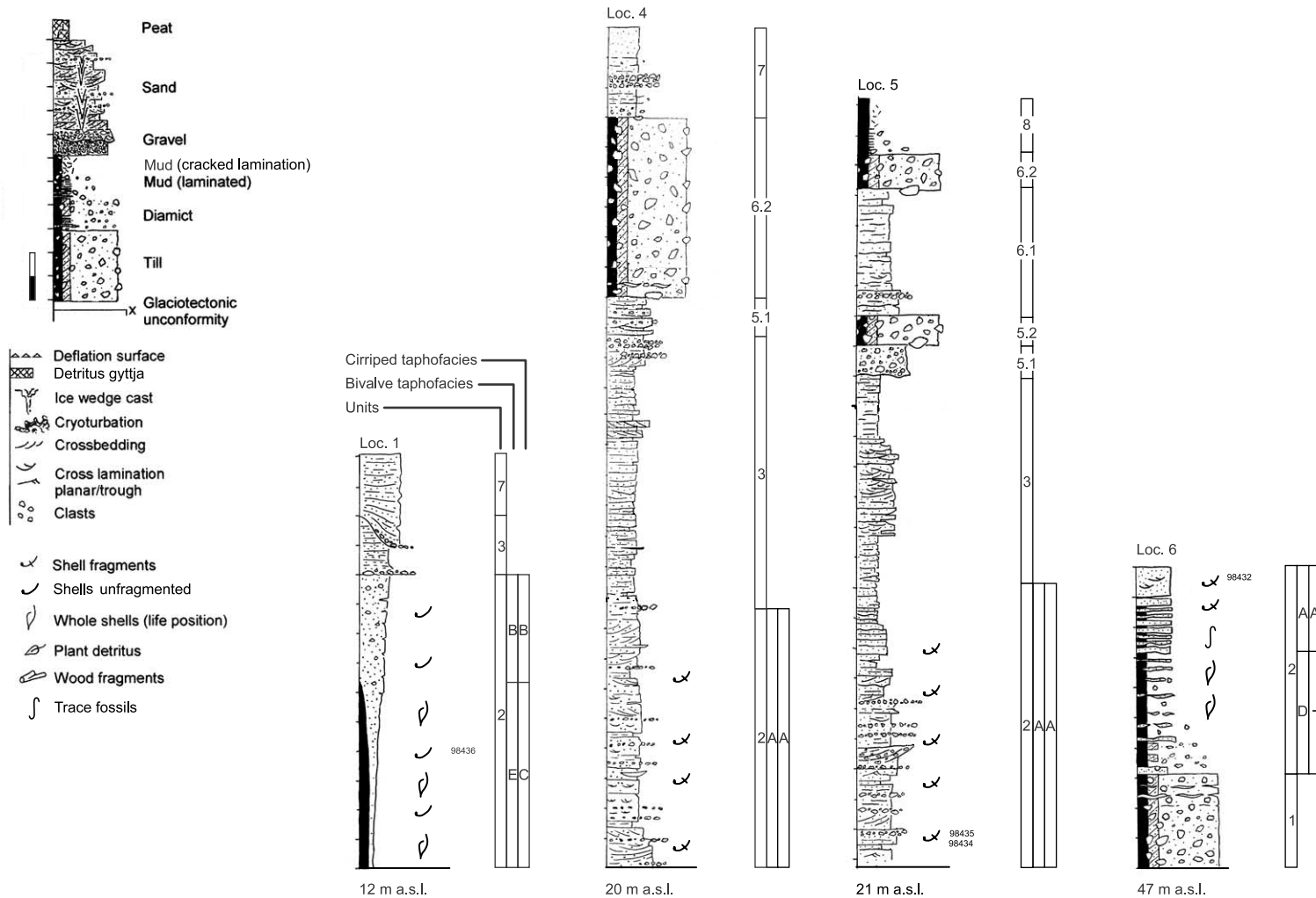


Fig. 3. Sedimentological logs for the localities selected for this study. Adapted and partly redrawn from Houmark-Nielsen et al. (2001). Sample numbers, bivalve taphofacies and barnacle taphofacies are added here to the right of each sedimentological log. Stratigraphic units: 1, Saalian glaciation; 2, marine Eemian; 3, proglacial Weichselian; 4, lacustrine and fluvial; 5.1, glaciofluvial; 5.2, Yolkino Till; 5.3, glaciolacustrine; 6.1, ice marginal; 6.2, Viryuga Till; 7, fluvial; 8, Holocene.

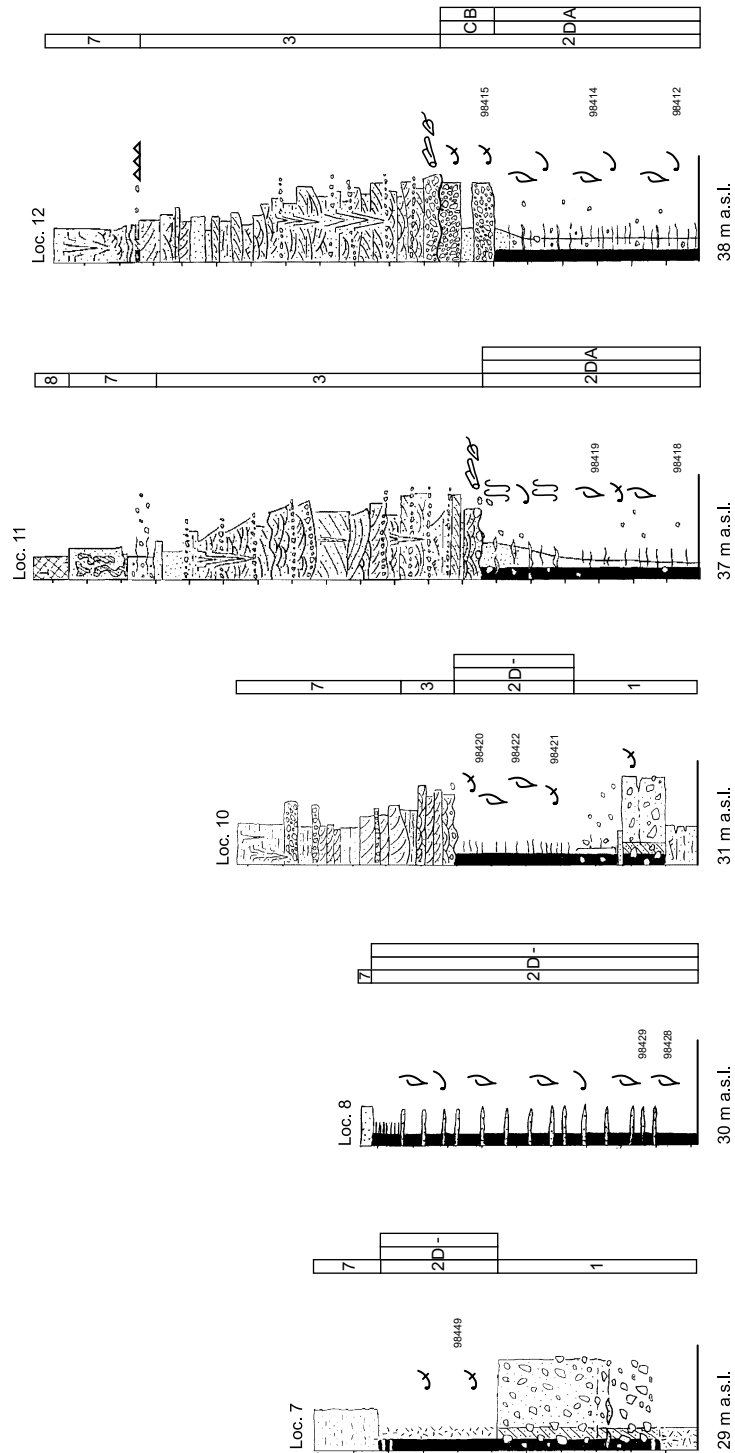


Fig. 3 (Continued).

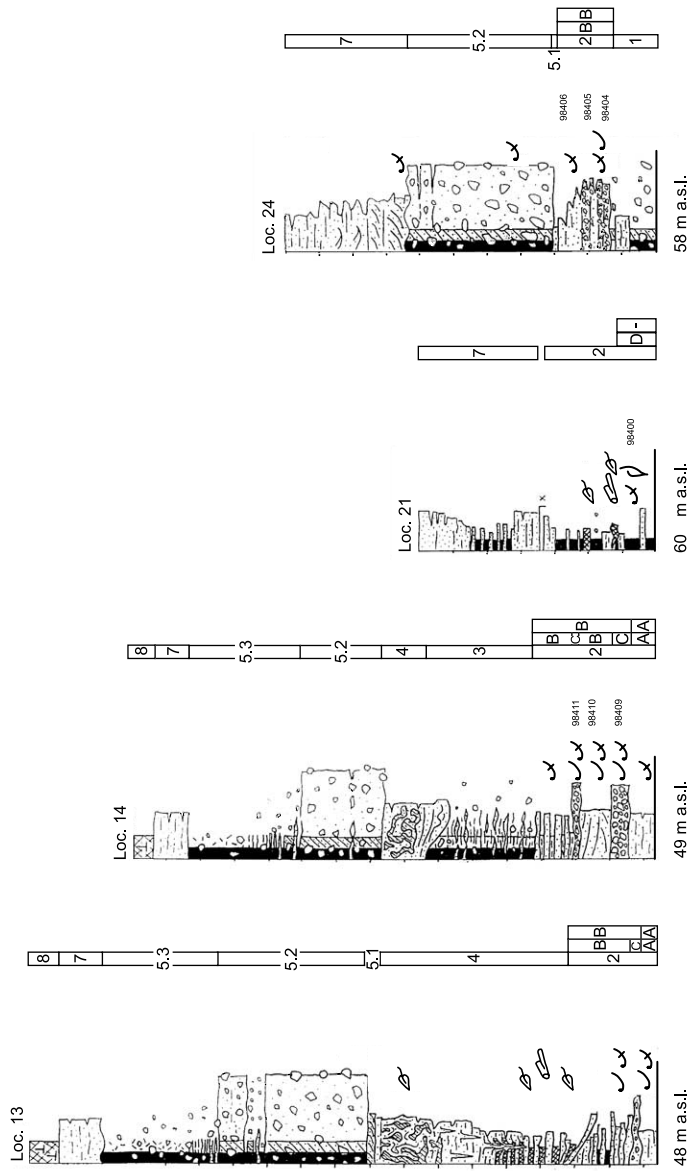


Fig. 3 (Continued).



Fig. 4. Discontinuously laminated mud (between arrows) of the muddy facies. Locality 12, level 38–44 m a.s.l.

3. Materials and methods

3.1. Samples

The localities constitute a 150 km long east–west transect studied in 1997 and 1998 (Fig. 1). A total of eight bulk samples and 14 hand-picked samples form the basis of this study. The bulk samples were 16 l in volume before wet sieving through a mesh of 0.7 mm. Inevitably, size bias is introduced when hand-picking shells, leading to underrepresentation of small species (Boucot, 1981). However, hand-picking enables the shells to be studied at site prior to sample transportation and cleaning with water, because shells may be artificially disarticulated and broken during sample processing. Shells of barnacles and molluscs were identified to the lowest possible taxonomic level and are deposited in the Collection of Quaternary Geology and Palaeobotany in the

Geological Museum, Copenhagen. The systematic arrangement and taxonomic nomenclature for barnacles and molluscs follow Newman and Ross (1976) and Le Renard (1997), respectively. Distinction between different species of barnacles is based on Broch (1924) and Stephensen (1933). Molluscs were identified using Tebble (1976), Kafanov (1980), Poppe and Goto (1991, 1993), Bogdanov and Sirenko (1993), Golikov (1995) and collections at the Geological and Zoological Museums, Copenhagen.

3.2. Taphonomic analysis

Taphonomy of the shells was studied in the field and under binocular and scanning electron microscopes. Taphonomic features formed by abrasion, bioerosion, disarticulation, dissolution and fragmentation were recorded, in addition to biofabric (i.e. shell orientation and density).

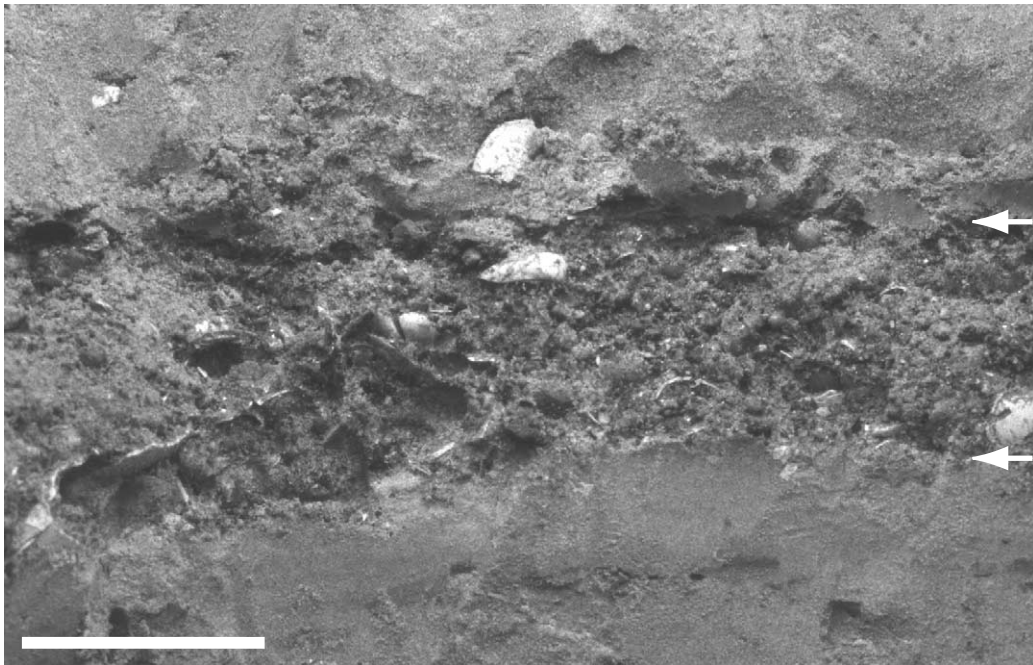


Fig. 5. Sands and shell-rich gravel (between arrows) of the sandy facies. Locality 14, level 51 m a.s.l. Scale bar = 10 cm.

Terminology for biofabric characterisation follows [Kidwell \(1991b\)](#) and [Kidwell and Holland \(1991\)](#).

A three-level scheme of taphonomic grades, which was adopted from [Kowalewski et al. \(1995\)](#) and [Hallman et al. \(1996\)](#), was applied to each of the shells to indicate the degree of taphonomic alteration. Grades 0, 1 and 2 refer to no, moderate and high alteration, respectively. Grade 2 indicates alteration of greater than 20% shell surface. The 20% level was selected as the boundary between grades 1 and 2 for all taphonomic features, with the exception of 50% for fragmentation. The scheme is sustained by verbal descriptions and ‘flash cards’ of shells displaying the three taphonomic grades for bioerosion (see [Hallman et al., 1996](#); [Figs. 7 and 8](#)). The ‘flash cards’ show differently shaped species and enable an easy assessment of taphonomic alteration.

The overall patterns of preservation were recorded separately for barnacle and bivalve assemblages by using the scheme of taphonomic grades. Distinction between bivalves and barnacles is

made because they differ in shell configuration and commonly in life habit. Barnacles are fixose-sile in their final life stage, where they have a multi-element skeletons in which the base attaches directly to a hard substrate ([Fig. 8](#)). In some species, the base is membranous and only consists of organic matter ([Anderson, 1994](#)). Most of the bivalves live endobenthically ([Fig. 7](#)).

The scheme of taphonomic grades was applied both to the most common selected species of bivalves and barnacles, viz. *Mytilus edulis* (Mytilidae), *Arctica islandica* (Arcticidae), *Mya truncata* (Myidae), *Hiatella arctica* (Hiatellidae), *Balanus balanus* and *Balanus crenatus* (Balanidae) ([Fig. 9](#); [Table 1](#)). The grades of taphonomic features were recorded for individual shells in any one sample, and then were averaged for individual taphonomic features over the entire sample. Such averaged values present a generalised estimate of taphonomic alteration, and have proven useful in previous taphonomic studies ([Flessa et al., 1993](#); [Nebelsick and Kowalewski, 1999](#); [Nebelsick, 1999](#)).

Table 1
Life habits and ecological requirements for recent members of species selected for detailed taphonomic analysis^a

Species	Shell form			Habitat		Life habit		
	Shell outline	Obesity	Ornamentation	Shallowest depth	Substrate	Tiering	Mobility	Trophic
<i>Mytilus edulis</i>	Elongated subtriangular	Moderately inflated	Fine concentric lines	Foreshore/tidal zone	Hard	Epibenthic	Byssate, fixosessile	Suspension feeder
<i>Arctica islandica</i>	Subcircular	Inflated	Fine concentric lines	Foreshore/tidal zone	Soft	Endobenthic, shallow	Burrower	Suspension feeder
<i>Mya truncata</i>	Oval, posterior end truncated	Inflated	Fine concentric lines	Foreshore/tidal zone	Soft	Endobenthic, deep	Burrower	Suspension feeder
<i>Hiatella arctica</i>	Elongated oval to subrectangular	Moderately inflated	Slender concentric ridges	Foreshore/tidal zone	Soft to firm	Endo-/epibenthic, shallow	Burrower	Suspension feeder
<i>Balanus balanus</i>	Volcano-shaped compartment	–	Uneven surface with irregular folds or regular angular folds ^b	Shoreface	Hard	Epibenthic	Cemented, fixosessile	Suspension feeder
<i>Balanus crenatus</i>	Variable shape of compartment ^c	–	Uneven surface or irregular folds	Shoreface	Hard	Epibenthic	Cemented, fixosessile	Suspension feeder

^a Based on Tebble (1976), Thomsen and Vorren (1986), Peacock (1993), Poppe and Goto (1993) and Funder et al. (2002).

^b Commonly the folds provide a star-shaped cross-section.

^c Commonly high and slender.



Fig. 6. Example of the trace fossil *Diplooretion* isp. Locality 6, level 55 m a.s.l. Scale bar = 5 cm.

4. Results

4.1. Palaeofauna

Shells occur throughout the marine sediments. Molluscs and barnacles dominate the fauna, which is richer and more thermophilous than the present-day fauna in the same region (Devyatova and Loseva, 1964; Biske and Devyatova, 1965; Houmark-Nielsen et al., 2001; Funder et al., 2002) (Table 2). Other macrofaunal elements occur very sparsely and include bryozoans, regular sea urchins and serpulid worms.

Generally, the sandy facies contains rich, warm-water assemblages with boreal species in abundance. The muddy facies is characterised by cold-water assemblages with low diversity and

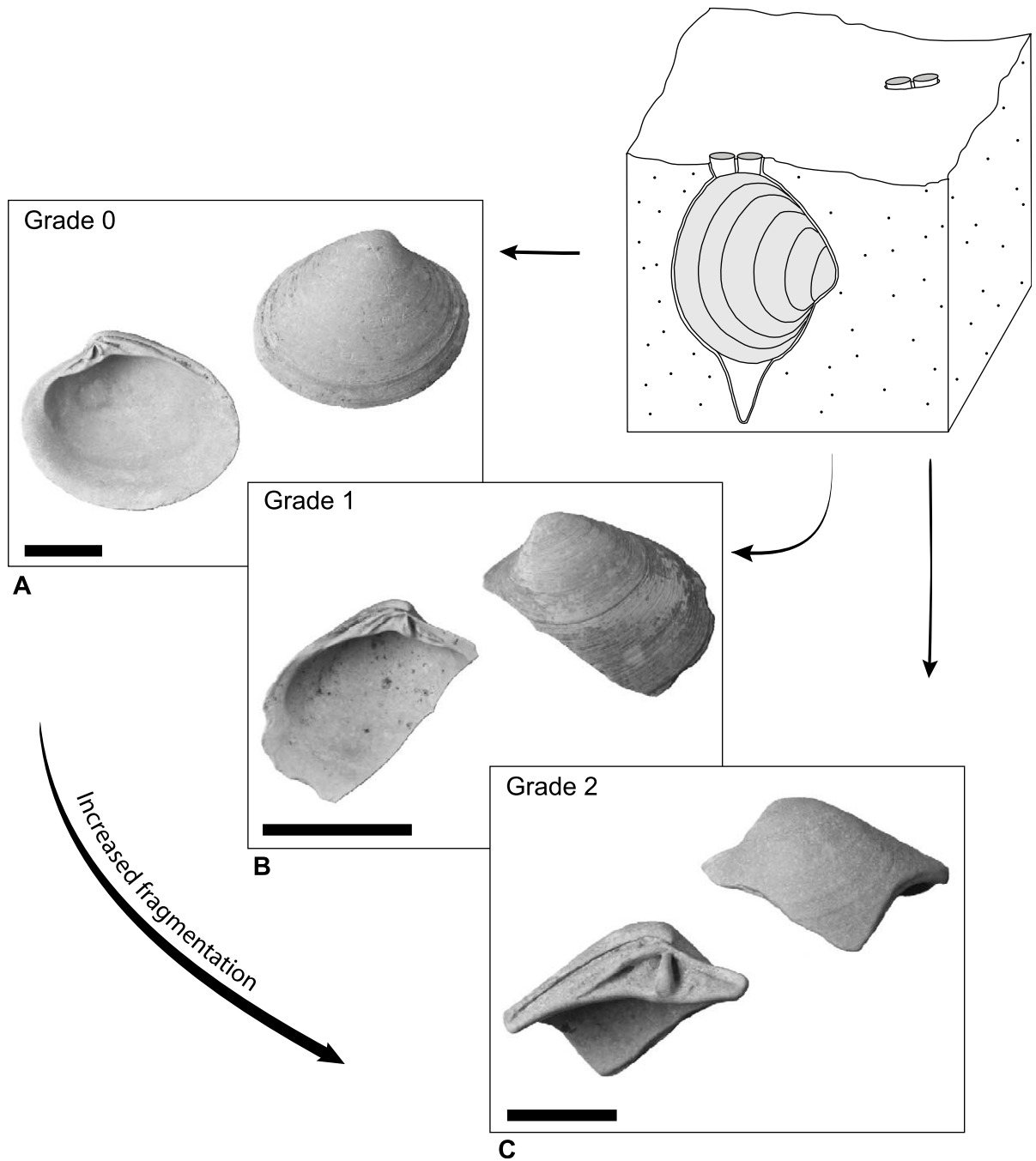


Fig. 7. Variability in preservation states of bivalves, corresponding to the taphonomic grades 0, 1 and 2 of fragmentation. Exemplified by *Arctica islandica* (sample 98410).

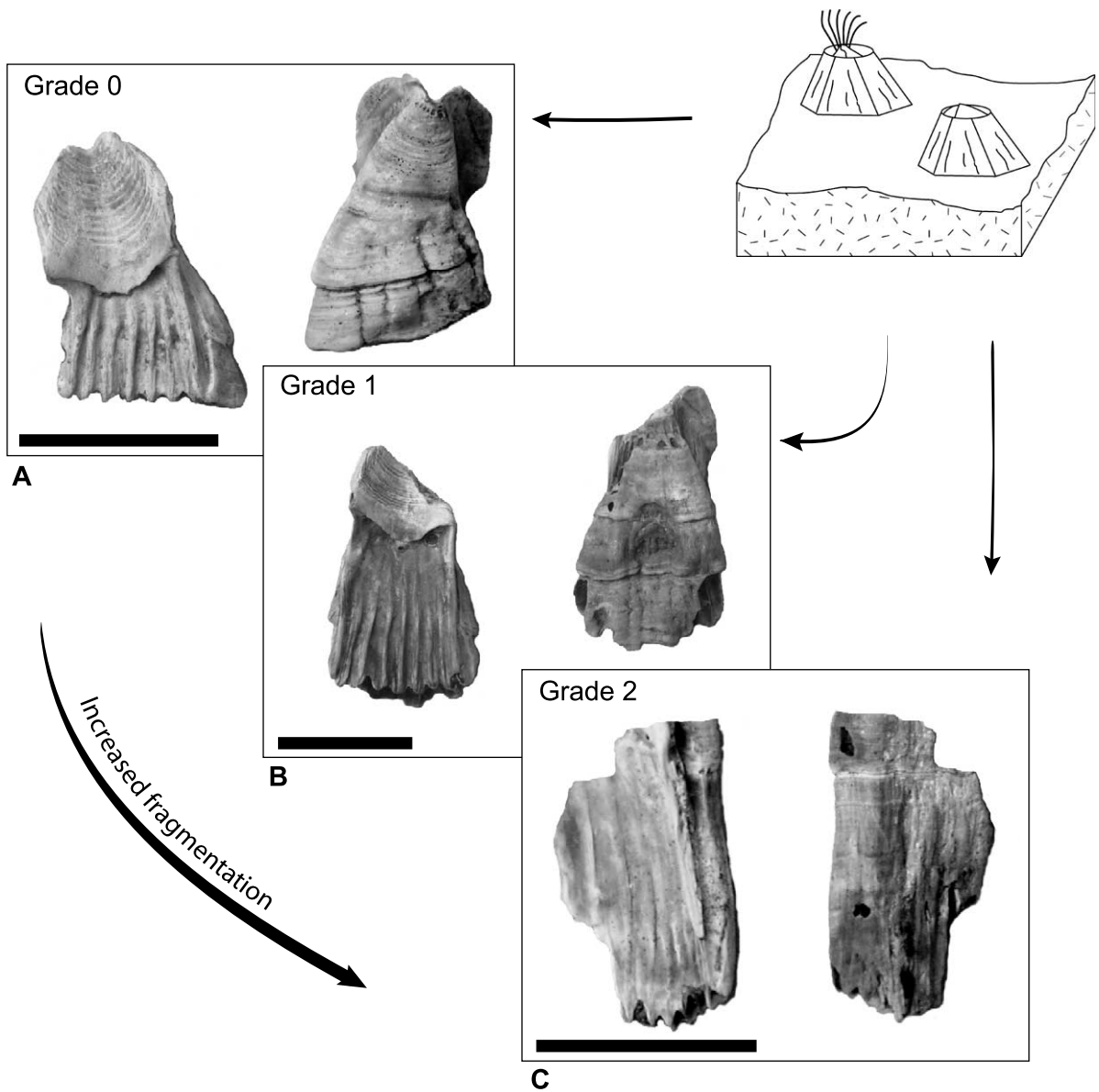


Fig. 8. Variability in preservation states of barnacles, corresponding to the taphonomic grades 0, 1 and 2 of fragmentation. Exemplified by *Balanus crenatus* (sample 98415).

only a small element of boreal species. Although deposition took place during the ‘Boreal Transgression’, not all Eemian localities contain boreal species. At these localities the water temperature might have been too low and prevented larval settlement of boreal species (Houmark-Nielsen et al., 2001). This is likely to have affected the

species content in assemblages and their distribution.

4.2. Taphofacies

Speyer and Brett (1986) and Brett and Baird (1986) coined the term taphofacies, i.e. tapho-

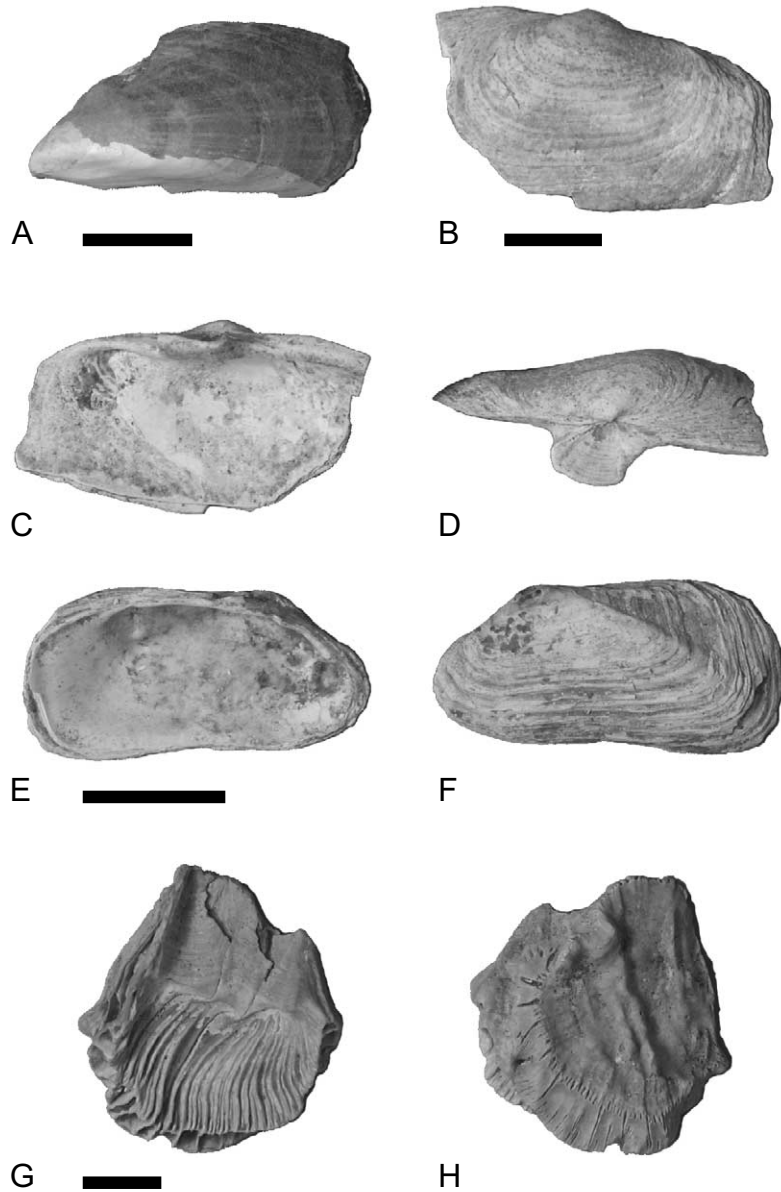


Fig. 9. Species of bivalves and barnacles selected for a closer taphonomic study. For *Arctica islandica* and *Balanus crenatus* see Figs. 7 and 8. (A) *Mytilus edulis*. (B–D) *Mya truncata*. (E,F) *Hiatella arctica*. (G,H) *Balanus balanus*. From samples 98419, 98432, 98420 and 98409, respectively. Scale bars = 1 cm.

nomic facies, which was redefined by Speyer and Brett (1988, p. 227) as “a stratigraphic body of rock which is distinguished from other vertically and laterally related bodies of rock on the basis of its particular suite of taphonomic properties”. In-

terpretation of environmental parameters may be enhanced by means of taphofacies, and taphofacies are therefore defined herein, leading to a set of five bivalve taphofacies and a set of three barnacle taphofacies (Table 3). Comparison of

Table 2

List of palaeofauna recorded in bulk samples and hand-picked samples from studied localities^{a,b}

Localities Samples (98-) Sample size ^c	Bulk samples ^a									Hand-picked samples ^b														
	5	5	6	12	14	24	24	24	24	1	7	8	8	10	10	10	11	11	12	12	14	14	21	
	434	435	432	415	410	404	405	406		436	449	428	429	421	422	420	418	419	412	414	409	411	400	
										196	11	52	99	117	5	69	82	46	106	60	189	154	32	
POLYPLACOPHORA																								
Sp. indet.					3													1						
GASTROPODA																								
<i>Margarites costalis</i> (Gould in Abbott, 1841)				S						1														
<i>Littorina littorea</i> (Linné, 1758)				S	C												1		1		1			
<i>Natica clausa</i> Broderip and Sowerby, 1829										5									1					
<i>Euspira pallida</i> (Broderip and Sowerby, 1829)				F	S					1							3	1	2	1	1			
<i>Amauropsis islandica</i> (Gmelin, 1791)				F	F																	2		
<i>Buccinum undatum</i> Linné, 1758				C	C					2										1		5		
<i>Neptunea despecta</i> (Linné, 1758)				1						1									1					
<i>Oenopota pyramidalis</i> (Ström, 1788)					F																			
<i>Oenopota nobilis</i> (Møller, 1842)					C																			
<i>Oenopota viridula</i> (Møller, 1842)					S																			
<i>Oenopota harpa</i> (Dall, 1884)					F																			
<i>Oenopota</i> sp. indet.				F	S					1												1		
<i>Obesotoma simplex</i> (Middendorff, 1849)					S																			
<i>Onoba</i> sp. indet.					3																			
<i>Amaura candida</i> Møller, 1842					S																			
<i>Retusa pertenuis</i> (Mighels, 1843)					C																			
<i>Cylichna alba</i> (Brown, 1827)					C	C																2		
BIVALVIA																								
<i>Ennucula tenuis</i> (Montagu, 1808)					1									10			2		9	11				
<i>Nuculana pernula</i> Müller, 1779				F	S					5			2				9	4	6	17				
<i>Yoldia hyperborea</i> Torell, 1859					S							1							21	3				
<i>Portlandia arctica</i> (Gray, 1824)																			4					
<i>Crenella decussata</i> (Montagu, 1808)					F	F															4	3		
<i>Mytilus edulis</i> Linné, 1758					F	F	S	2	S	11							7	4	10		15	18		
<i>Chlamys islandica</i> (Müller, 1776)		1					S			1														
<i>Heteranomia squamula</i> (Linné, 1758)					1														?					
<i>Axinopsis orbiculata</i> (Sars, 1878)					1																			
<i>Thyasira flexuosa</i> (Montagu, 1803)										2											1			
<i>Mysella bidentata</i> (Montagu, 1803)					C	F													1					
<i>Astarte borealis</i> (Schumacher, 1817)		?	C	F	D	1				3												10	3	
<i>Astarte elliptica</i> (Brown, 1827)					2																	2	1	3

Table 2 (Continued).

Localities Samples (98-) Sample size ^c	Bulk samples ^a								Hand-picked samples ^b													
	5 434	5 435	6 432	12 415	14 410	24 404	24 405	24 406	1 436	7 449	8 428	8 429	10 421	10 422	10 420	11 418	11 419	12 412	12 414	14 409	14 411	21 400
<i>Astarte montagui montagui</i> (Dillwyn, 1817)				S																		5
<i>Astarte sulcata</i> (da Costa, 1778)						C	S		18											2		6
<i>Cerastoderma edule</i> (Linné, 1758)				F	F	?S									2		6		2	?1	1	
<i>Ciliatocardium ciliatum</i> (Fabricius, 1780)									16		1						1					
<i>Serripes groenlandicus</i> (Mohr, 1786)				S					2						3					5	1	
<i>Spisula elliptica</i> (Brown, 1827)			1	D	F		?1									2		?1	12	16		
<i>Macoma balthica</i> (Linné, 1758)	S	D		D	C	F	S		2						7	5	7	6	2	7		
<i>Macoma calcarea</i> (Gmelin, 1791)				F	D	F	C	S	32		22	33		1	4	16	12	25	14	1	3	2
<i>Abra prismatica</i> (Montagu, 1803)					F															2		
<i>Arctica islandica</i> (Linné, 1767)			3	D	F	F	F		3											56	36	6
<i>Pisidium</i> sp. indet.					2																	
<i>Mya truncata</i> Linné, 1758				F	F	F	C	C	3			5	5		3	26	16	10	5	10	8	7
<i>Hiatella arctica</i> (Linné, 1767)				F	S	C	S	1	2	11	30	57	102	4	61					4	2	
<i>Panomysia norvegica</i> (Spengler, 1793)									3						1						1	2
<i>Zirphaea crispata</i> (Linné, 1758)			1	3		3														1	1	
<i>Lyonsia norvegica</i> (Gmelin, 1791)									22													
SCAPHOPODA																						
<i>Pulsellum lofotense</i> (Sars, 1865)									3													
CIRRIPEDIA																						
<i>Balanid</i> sp. indet.	F	D	D	D	D	D	F	F	19						4	1	2		33	53		
<i>Verruca stroemia</i> (Müller, 1776)					F	2	2	2												1		
<i>Chirona hameri</i> (Ascanius, 1767)						C																
<i>Semibalanus balanoides</i> (Linné, 1767)					C	D	C	3	8											3		
<i>Balanus balanus</i> (Linné, 1758)				F	S	D	S	S	34											7		
<i>Balanus crenatus</i> Bruguière, 1789					D	F	2	1												1		
<i>Balanus improvisus</i> Darwin, 1854					C	F	S		8											4		
CRABS				2	C																	
BRYOZOANS					?3		2		8													
SEA URCHINS					C																	
SERPULIDA					3																	
FISH REMAINS		1		3	C																	
TRACE FOSSILS ^d																						
<i>Caulostrepsis taeniola</i> Bromley and D'Alessandro, 1983		+	+	+	+				+											+	+	
<i>Entobia</i> isp.						+																
<i>Leptichmus peristroma</i> Taylor et al., 1999					+				+											+		

Table 2 (Continued).

Localities Samples (98-) Sample size ^c	Hand-picked samples ^b																										
	Bulk samples ^a																										
5	5	6	12	14	24	24	24	1	7	8	8	10	10	10	10	10	10	11	11	11	12	12	12	14	14	21	
434	435	432	415	410	404	405	406	436	449	428	429	421	422	420	418	419	412	414	409	411	400	412	414	409	411	400	
								196	11	52	99	117	5	69	82	46	106	60	189	154	32						
<i>Oichnus simplex</i> Bromley, 1981								+																			
<i>Oichnus paraboloides</i> Bromley, 1981								+																			

^a Identifiable valves and fragments in bulk samples by number 1–3; S, sparse = 4–10; C, common = 11–20; F, frequent = 21–50; D, dominant > 50; ?, identification uncertain.
^b Identifiable valves and fragments in hand-picked samples by absolute number.
^c Total number of identifiable valves and fragments in hand-picked samples.
^d Identifiable bioerosion structures by presence (+).

bivalve and barnacle taphofacies sets has not previously been conducted. Previous taphonomic studies have been done separately on barnacle and mollusc assemblages (e.g. Donovan, 1988, 1989, 1993; Meldahl and Flessa, 1990; Staff and Powell, 1990; Banerjee and Kidwell, 1991; Doyle et al., 1996).

4.2.1. *Bivalve taphofacies A*

Description: This taphofacies is characterised by poorly preserved shell remains that usually are no larger than 10 mm. Besides being disarticulated, the shells are highly fragmented and abraded, and a few are bioeroded. Among borings, the holes and pits of predaceous gastropods are predominant; these are assigned to the trace fossil *Oichnus paraboloides* (Bromley, 1981; Nielsen and Nielsen, 2001). The shells are moderately dissolved and not encrusted. The density of shells is low and sporadic in the coarse-grained sands and gravels. The shells comprise less than 1% of the clastic components of the sediment.

Interpretation: This taphofacies represents the worst state of bivalve preservation in the area studied. The extensive abrasion is evidence of significant transport of shells together with abrasive sediment by currents in a high-energy setting such as a foreshore environment (Brett and Baird, 1986; Speyer and Brett, 1988). The shells may have been reworked repeatedly by waves. The lack of encrustation could reflect either removal of possible existing encrusters by abrasion, or a limited time of exposure to larval settlements, as suggested by the low frequency of borings.

Comparison: Meldahl and Flessa (1990) examined the variability in taphonomy of molluscs from recent intertidal and shallow shelf environments in Provincetown Harbor, Cape Cod. The beach environment shows many similarities to the bivalve taphofacies A. Both are characterised by high abrasion and fragmentation and moderate dissolution, whereas bioerosion and encrustation are low to absent. High-energy environments such as beaches tend to be high in abrasion, fragmentation and edge rounding due to wave energy and coarse grain size (Parsons and Brett, 1991). However, beach environments in tropical reef-lagoon systems show less similarity, i.e. high bio-

Table 3
Summary of intensity of taphonomic features in each taphofacies^a

Taphonomic features	Bivalve taphofacies					Barnacle taphofacies		
	A	B	C	D	E	A	B	C
Abrasion	2 (1–2)	1 (0–1)	0 (0–1)	0 (0–1)	0 (0–1)	2 (1–2)	0 (0–1)	0 (0–1)
Bioerosion	1 (0–1)	1 (0–1)	1 (0–1)	0 (0–1)	1 (0–1)	0 (0–1)	0 (0–1)	0 (0–1)
Disarticulation	2 (2)	2 (2)	2 (2)	1 (0–2)	0 (0–2)	2 (1–2)	2 (1–2)	1 (0–1)
Dissolution	1 (1–2)	1 (1–2)	1 (0–1)	1 (1–2)	0 (0–1)	1 (0–2)	1 (0–2)	0 (0–1)
Encrustation	0 (0)	0 (0)	0 (0–1)	0 (0)	1 (0–1)	0 (0–1)	1 (0–1)	1 (0–1)
Fragmentation	2 (0–2)	1 (0–2)	1 (0–2)	0 (0–1)	0 (0–1)	2 (0–2)	1 (0–2)	0 (0–1)
Biofabric								
Shell packing	Dispersed	Dispersed	Very dense	Dispersed	Dispersed	Dispersed	Dispersed	Dispersed
Preferential orientation	None	None	Concavo-convex	None	None	None	None	Lumped in clusters
Shells in life position	None	None	None	Common	Abundant	None	None	Abundant

Key: 0, no alteration; 1, low; 2, high. Grade 2 indicates alteration greater than 20% shell surface, except the 50% boundary for fragmentation.

^a Three-level scheme of taphonomic grades was applied to the shells in general to indicate the prevailing degree of taphonomic alteration. The total ranges in individual shell preservation are given in parentheses.

erosion and low abrasion (Parsons, 1989; Parsons and Brett, 1991).

4.2.2. Bivalve taphofacies B

Description: The bivalves are fairly well preserved but most of them are disarticulated, moderately fragmented, and smaller than 30 mm. A small number of shells have somewhat abraded edges and projections. Generally, the abrasion and bioerosion is moderate; the latter represented by *Oichnus paraboloides*, *Caulostrepsis taeniola* and microborings. A polychaete annelid, *Polydora* sp., probably formed the *C. taeniola* (Boekschooten, 1967; Bromley and D'Alessandro, 1983), which only is situated in the posterior end of *Astarte* shells. Encrustation is absent. The shell preservation varies widely. Small shells tend to be less fragmented and abraded than the larger ones. Also, shells of endobenthic species are commonly better preserved than epibenthic species. The loosely dispersed shells seem not to have a preferred orientation in the coarse-grained sediment of sands and gravels. Less than 1% of the clastic components of the sediment are shells.

Interpretation: Some of the shells were subjected to abrasion for a short period of time and only transported short distances. The moderate fragmentation indicates an environment with moderate to high wave or current energy and sedimentation rate, probably a sandy and gravelly shoreface environment. Some shells may have been transported from other habitats such as a foreshore. This could cause the varied preservation. However, life habit and shell size also influenced the preservation as indicated above. This is apparently related to the hydrodynamic properties of shells, as small shells are likely to be held in suspension (Driscoll, 1970).

Comparison: Bivalve taphofacies B is characterised by a wide variability in preservation. Similar mixtures of relatively taphonomically unaltered and altered shells comprise inner shelf assemblages off the coast of Texas. The mixtures are attributed to the temporal frequency of storms, mortality and final burial (Staff and Powell, 1990). A comparative study by Staff and Powell (1990) showed that such mixtures are not present in a microtidal inlet examined by Davies et al.

(1989). The inlet contains nearly exclusively altered shells, indicating frequent reworking due to high energy.

4.2.3. *Bivalve taphofacies C*

Description: The bivalves are fairly well preserved and fragmentation is absent to moderate. Although disarticulation is high, many shells have preserved remnants of their periostracum. Few shells have somewhat abraded shell edges and projections. Borings similar to *Oichnus paraboloides* and *Caulostrepsis taeniola* occur moderately. The latter is restricted to *Astarte* shells. Microborings may be situated in the shells as well (Nielsen and Maiboe, 2000, fig. 1). Rarely, scarce encrustation of bryozoans and barnacles is present on large shells. Otherwise, encrustation is absent. The shells, which usually are no larger than 120 mm, are very densely packed in the gravelly sediment. They comprise less than 10% of the clastic components. Shells of centimetre size are typically oriented parallel to bedding planes and have a convexo-concave orientation, preferentially in a convex-up orientation. Smaller shells have a more random orientation.

Interpretation: This taphofacies comprises shell concentrations, i.e. concentrations of biomineralised invertebrate remains more than 2 mm in size (Kidwell, 1991b; Fürsich, 1995). The shell concentrations bear close resemblance to proximal storm flow concentrations (proximal tempestites) defined by Fürsich and Oschmann (1993). These are distinguished from other shell concentrations by signs of low physical destruction and high physical concentration in addition to sharp erosive-based beds and preferentially convex-up orientation of shells (Fürsich and Oschmann, 1993; Fürsich, 1995). Disarticulation and fragmentation, in combination with abrasion and orientation, indicate that the shells in bivalve taphofacies C are allochthonous and deposited during high-energy conditions in a nearshore environment. Thus, the bivalve taphofacies C is interpreted as deposited by a proximal storm flow. The deposition probably occurred above storm wave base, but somewhat below fair-weather wave base (see Fürsich and Oschmann, 1993, fig. 5).

Comparison: Banerjee and Kidwell (1991)

studied different types of shell beds within the Lower Cretaceous Mannville Group of Canada and recognised a systematic distribution of them in relation to parasequence flooding surfaces. Some of the shell beds situated at the top of parasequences, i.e. shallowest water part of a parasequence, resemble the bivalve taphofacies C in biofabric and taphonomic features. These shell beds were formed in an environment above average storm wave base (Banerjee and Kidwell, 1991), consistent with the interpretation of the bivalve taphofacies C.

Proximal storm flow concentrations have been recognised in many studies. For example, such shell concentrations are common in the Jurassic Chari Formation (Fürsich and Oschmann, 1993) and the Cretaceous Habur Formation (Fürsich, 1995), both in western India. Shell concentrations in the Chari Formation may contain highly fragmented and abraded shells, which were interpreted as acquired at an earlier stage of reworking, i.e. before transportation and deposition by storm flow. This is not the case of the bivalve taphofacies C, as the shells show no signs of previous reworking. Although bivalve taphofacies C resembles bivalve taphofacies B, the former is somewhat better preserved and has considerably higher shell density.

4.2.4. *Bivalve taphofacies D*

Description: Bivalves of this taphofacies are generally well preserved, though commonly disarticulated. Some shells may even be preserved in life position with the valves closed or slightly opened. Fragmentation is absent to moderate, and evidence of abrasion and encrustation is absent. Borings are few and only *Oichnus paraboloides* occurs. The degree of dissolution ranges from moderate to high between different localities. Poorly preserved unidentifiable shells occur rarely, and these are highly fragmented and abraded. All shells are distributed sporadically in muddy sediment. Typically, the shells are smaller than 80 mm in length and comprise less than 1% of the clastic components.

Interpretation: The well-preserved shells, some even in life position, indicate within-habitat preservation in an environment characterised by low

background sedimentation and current energy interrupted by rapid episodic burial (Brett and Baird, 1986; Speyer and Brett, 1988). This interpretation is consistent with the enclosing fine-grained sediment with discontinuous lamination. Bioturbation and, perhaps, predation are likely to have caused the disarticulation and fragmentation. Fragmentation produced by bioturbators and predators may be indistinguishable (Brett, 1990). Together, the taphonomic features indicate that the environment was an offshore muddy sea bottom. Conversely, the poorly preserved shells are considered allochthonous, as suggested by the high grade of abrasion, and these shells derived from a high-energy environment, probably a shoreface or foreshore.

Comparison: Bivalve taphofacies D differs from bivalve taphofacies E by the absence of encrustation and fewer poorly preserved shell fragments. It differs from bivalve taphofacies A, B and C by the lack of abrasion and extensive fragmentation.

4.2.5. Bivalve taphofacies E

Description: This taphofacies is characterised by excellent preservation. Many shells are articulated and still preserve ligament and periostracum. The shells are loosely dispersed and usually no larger than 120 mm. They constitute less than 1% of the clastic components. Some are in life position in the muddy sediment. Fragmentation is absent or moderate and abrasion is absent. Dissolution ranges from absent to moderate. The moderate bioerosion produced borings similar to *Oichnus paraboloides* and *Leptichnus peristroma*. *Leptichnus peristroma* encompasses multiseriate arrangements of etched pits formed by ctenostome bryozoans (Taylor et al., 1999), while some pits are covered by bryozoan skeletal material. A small number of bivalves are moderately infested by various combinations of encrusters. The most prevalent encrusters are barnacles, while the next most important are an unidentified species of calcareous bryozoans. Calcareous tubes of serpulid worms are much less common. The barnacles include species of the genera *Balanus* and *Verruca*. In addition, poorly preserved fragments of bivalves, which are neither articulated nor encrusted, occur sporadically. These fragments are

moderately to highly abraded and moderately dissolved.

Interpretation: The high number of articulated shells in living position and with ligament preserved is the result of preservation in life position. Other well-preserved shells are only slightly displaced and clearly within-habitat preserved as indicated by the absence of abrasion and limited fragmentation. The intensity of encrustation is closely related to the duration of shell exposure on the seafloor and implies a slow rate of sedimentation, although episodes of high sedimentation cannot be precluded. Highly abraded bivalve fragments were transported from another habitat and could have been subjected to repeated reworking on a foreshore. This evidence suggests a deeper-water setting, i.e. a muddy sea bottom in an upper offshore environment, into which poorly preserved shell fragments were transported from shallow-water areas nearby.

Comparison: Preservation similar to this taphofacies has previously been reported from the Plio–Pleistocene Waccamaw Formation in North Carolina (Ward and Hall, 1999; Hall and Ward, 2000). This palaeofauna, which indicates a near-shore open marine environment, is dominated by molluscs and corals that show no signs of significant post-mortem transport. Encrustation is common and suggests that epibionts infested the shells for a considerable period of time before burial (Ward and Hall, 1999). Unlike the bivalve taphofacies E, the palaeofauna appears not to contain abraded shell fragments.

4.2.6. Barnacle taphofacies A

Description: Barnacles in this taphofacies are poorly preserved, i.e. the plates are disarticulated, highly fragmented, and usually less than 10 mm in size. In addition, the plates are moderately to highly abraded and commonly unidentifiable. Dissolution is generally moderate, ranging from absent to high. *Oichnus paraboloides* and microborings are rare. Encrustation, which consists of other barnacles, is absent to moderate. The distribution of barnacles is sporadic in the coarse-grained sediment, and the density varies from place to place.

Interpretation: All of these features imply high-

energy conditions in a shoreface or foreshore environment, and the barnacle plates are allochthonous. Abrasion suggests extensive transport along with sediment, and the coarser grain size of enclosing sediment may indicate a high rate of sedimentation.

Comparison: Doyle et al. (1996) defined eight types of ‘preservational-state assemblages’. To some extent, barnacle taphofacies A resembles their type 6, comminuted shell beds, that is characterised by remains no larger than 10 mm and comprising more than 50% of the clastic components of the sediment. However, this is not the case in the present study, as barnacle taphofacies A contains less than 1%. Preservational-state assemblage type 7 of Doyle et al. (1996) consists of less than 10% isolated valves and plates, but this type is often associated with barnacle stubs (their type 3).

4.2.7. Barnacle taphofacies B

Description: The state of preservation is variable. Most barnacles, which roughly are 5–30 mm in size, are moderately well preserved. Nearly all plates are disarticulated. In general, the plates are moderately fragmented and dissolved. Fragmentation and dissolution may range from absent to high within a single sample. A small number of plates show moderate abrasion of plate edges and projections. *Oichnus paraboloides* and microborings are rare. The grade of encrustation (by other barnacles) is moderate. The barnacle remains, which occur in sands and gravels, are loosely dispersed, although the density of barnacles may be locally variable.

Interpretation: The barnacles are clearly allochthonous and have been subjected to some transport. The high variability in preservation indicates that the barnacle remains are either time-averaged or underwent taphonomic processes for different time periods (cf. Kidwell and Bosence, 1991; Nebelsick, 1999). One or more parameters may have caused this preservation pattern. For example, continuous production and release of barnacles to the taphonomically active zone. Also bioturbational mixing of the remains before final burial could generate a similar preservation pattern (Nebelsick, 1999). The latter is less likely,

as barnacle taphofacies B is not associated with bioturbation structures. The variable density is probably closely related to local conditions, such as original population density, sedimentation rate and hydrodynamic energy at burial. A nearshore environment, probably a shoreface, is proposed.

Comparison: Barnacle taphofacies B bears a resemblance to ‘preservational-state assemblage’ type 5, barnacle-rich beds, defined by Doyle et al. (1996). Both consist of barnacle remains of the same size, and are not associated with clusters in life position. However, type 5 differs by having no abraded remains and comprising more than 50% of the clastic components. Barnacle taphofacies B comprises less than 1%.

4.2.8. Barnacle taphofacies C

Description: Barnacles, which usually are no larger than 25 mm, are generally in an excellent state of preservation and attached to hard substrates, especially shells of epifaunal molluscs, e.g. *Buccinum undatum* and *Neptunea despecta*. As such, the barnacles have a lumped distribution. Opercular plates, i.e. plates covering orifice, are even present in some specimens. In other specimens, some disarticulation of the opercular and wall plates may have occurred. Orifices of barnacles attached to hard substrates display a range of orientation. Borings similar to *Oichnus paraboloides* are rarely present. The extent of encrustation is moderate, although some barnacles have grown on top of one another. Also, more poorly preserved fragments occur loosely dispersed in the fine-grained sediment. These fragments are moderately abraded and dissolved, and may contain microborings.

Interpretation: The well-preserved barnacles still attached to their substrate can be regarded as inhabitants of benthic islands (Seilacher, 1982; Zuschin et al., 1999). A number of the islands are apparently preserved in life position, as indicated by the orifices. The shells were subjected to rapid episodic burial prior to disarticulation, which has preserved them completely or almost completely articulated (Brett and Baird, 1986; Speyer and Brett, 1988). The poorly preserved fragments occurring between the benthic islands are allochthonous and probably deposited from

Table 4
Taphonomic variation in selected bivalves^a

Species		Bivalve taphofacies				
		A	B	C	D	E
<i>Arctica islandica</i>	Abrasion	1.3	0.6	0.0–0.2	0.2	0.0
	Bioerosion	0.0	0.0–0.2	0.2	0.0	0.0
	Disarticulation	2.0	2.0	2.0	1.3	0.3
	Dissolution	1.0	1.0	0.1	1.3	0.0
	Fragmentation	1.3	0.9–1.2	0.5–0.8	0.3	0.0
<i>Hiatella arctica</i>	Abrasion	1.6	0.6–0.8	0.3	0.0	0.0
	Bioerosion	0.2	0.0–0.2	0.0–0.2	0.0–0.2	0.0
	Disarticulation	2.0	2.0	2.0	1.0–1.5	0.0
	Dissolution	1.2	1.0–1.2	0.1–0.4	1.0–2.0	0.5
	Fragmentation	1.6	0.9–1.3	0.5–0.6	0.2–0.5	0.0
<i>Mya truncata</i>	Abrasion	1.5	0.8–1.0	0.1–0.2	0.0–0.2	0.3
	Bioerosion	0.3	0.3	0.2–0.4	0.0–0.2	0.0
	Disarticulation	2.0	2.0	2.0	0.0–1.0	0.3
	Dissolution	1.0	1.0	0.0–0.2	1.0	0.0
	Fragmentation	1.8	1.0–1.5	0.9–1.1	0.1–0.8	0.3
<i>Mytilus edulis</i>	Abrasion	1.2	0.8	0.2–0.4	0.3–0.8	0.0
	Bioerosion	0.6	0.3–0.7	0.4–0.6	0.0–0.5	0.3
	Disarticulation	2.0	2.0	2.0	2.0	0.3
	Dissolution	1.6	1.3–1.5	0.5–1.0	1.3–1.8	0.3
	Fragmentation	2.0	2.0	1.2–1.8	0.6–1.0	0.7
Samples (98-)		432	404, 405, 406, 410	409, 411, 415	400, 412, 414, 418, 419, 420, 421, 422, 428, 429, 449	436 ^b

^a The scheme of taphonomic grades was applied to individual shells and averaged for each sample. These averaged values are referred to the corresponding taphofacies. For key see Table 3.

^b Selected bivalves were only encountered sparsely.

suspension or transported along the seafloor by storms. Their state of preservation and the lithology of enclosing sediment make it clear that the depositional environment into which the shallow-water faunal elements were transported from nearby was below wave base.

Comparison: Doyle et al. (1996) described a ‘preservational-state assemblage’ type 1 consisting of clusters in life position. They interpreted such clusters as preservation in life position within a shallow-water, intertidal habitat. Their type 2 comprised displaced clusters (i.e. not in original life position), as indicated by the differently oriented orifices. The barnacles are relatively intact, and as such the barnacle taphofacies C represents a mixture of Doyle et al.’s (1996) types 1 and 2.

4.2.9. Distribution of the two sets of taphofacies

The taphofacies show wide differences in taphonomic alteration for different localities and stratigraphical levels (Fig. 3). These are mapped with

respect to averaged taphonomic grades for single taphonomic features. Taphonomic alteration is highest in parts of the sandy facies as indicated by the bivalve taphofacies A and barnacle taphofacies A. The bivalve taphofacies B and C and barnacle taphofacies B show intermediate alteration and tend to be restricted to discrete strata of the sandy facies. These taphofacies may alternate in their distribution, as observed at locality 12. Taphonomic alteration is lowest in the muddy facies, where the bivalve taphofacies D and E and barnacle taphofacies C prevail.

Vertical transitions between the taphofacies are sharp and coincide with stratigraphic boundaries. It is noteworthy that the sharp transitions within the set of bivalve taphofacies do not always coincide with those of the barnacle taphofacies set. For example, barnacle taphofacies B may co-exist with bivalve taphofacies B or C. On the other hand, bivalve taphofacies E only occurs together with barnacle taphofacies C. As such the two sets

Table 5
Taphonomic variation in selected barnacles^a

Species		Barnacle taphofacies		
		A	B	C
<i>Balanus balanus</i>	Abrasion	1.7	0.5–0.7	0.2
	Bioerosion	0.1	0.0–0.2	0.1
	Disarticulation	1.8	1.6–1.8	0.5
	Dissolution	1.3	1.0–1.1	0.2
	Fragmentation	1.8	1.0–1.3	0.1
<i>Balanus crenatus</i>	Abrasion		0.7	
	Bioerosion		0.0–0.1	
	Disarticulation		1.6	
	Dissolution		0.9–1.1	
	Fragmentation		1.1–1.3	
Samples (98-)		432	410, 415	436

^a The scheme of taphonomic grades applied to individual shells and averaged for each sample, referred to the corresponding taphofacies. For key see Table 3.

of taphofacies provide complementary information on the patterns of taphonomic alteration.

Lateral transitions between the taphofacies have not been found within the same site. However, it is likely that gradual transitions occur, as indicated by the presence of poorly preserved allochthonous fragments among autochthonous whole shells in bivalve taphofacies E, where the allochthonous fragments may be derived from the depositional environment of bivalve taphofacies A.

4.3. Preservation of selected species

The intensity of taphonomic features (abrasion, bioerosion, disarticulation, dissolution, fragmentation) has been investigated for some of the most common bivalve and barnacle species (Tables 4 and 5). Investigation of specimens of different species, even within the same sample, shows that significant variability in preservation may exist between the species.

The majority of *Mytilus edulis* shells are disarticulated and highly fragmented, resulting in many small fragments. Its inner shell layer of nacre is usually lacking, probably from dissolution. *Mytilus edulis* from the bivalve taphofacies A, B and C (sandy facies), is commonly moderately abraded and may contain microborings. A small number of articulated whole *M. edulis* shells were

obtained from the bivalve taphofacies E (muddy facies). None were collected from other taphofacies.

Mya truncata, which has thick valves, has less tendency to fracture than *Mytilus edulis*. The former tends to fracture across the shell between the ventral margin and dorsal margin close to the ligament pit. The shells from the bivalve taphofacies A, B and C (sandy facies) are not abraded or are moderately abraded. Additionally, these shells may contain *Oichnus paraboloides* together with microborings. Articulated pristine shells can be found in the bivalve taphofacies D and E (muddy facies).

Arctica islandica and *Hiatella arctica* have thick solid shells, which generally are fairly well preserved. Typically, these species are less fragmented than *Mytilus edulis* and *Mya truncata*. *Arctica islandica* and *H. arctica* have been subjected to less bioerosion than the other species investigated. Articulated pristine shells of *A. islandica* and *H. arctica* may occur in the bivalve taphofacies D and E. As such, the preservation of *H. arctica* is quite similar to *A. islandica*. However, the former may be highly chalky and disintegrated in the bivalve taphofacies D, probably due to severe dissolution by pore water. Another interspecific difference is seen in the periostracal coverage. The thick periostracum of *A. islandica* is better preserved than the thinner periostraca of *Mya truncata* and *Mytilus edulis*. The studied specimens of *H. arctica* lack periostracum.

Balanus balanus and *Balanus crenatus* have a similar preservation. Both species are mostly disarticulated and somewhat fragmented in the barnacle taphofacies A and B. They seem to be more resistant to disarticulation and fragmentation than the co-occurring shells of *Mytilus edulis*. Also, the barnacles tend to be less bioeroded than *M. edulis*, but borings are more common in the barnacles than in the infaunal *Arctica islandica* and *Hiatella arctica*. Where the barnacle taphofacies A coincides with the bivalve taphofacies D, *B. balanus* and *B. crenatus* tend to be more fragmented and abraded than the co-occurring infaunal bivalves. Articulated whole specimens of *B. crenatus* dominate the barnacle taphofacies C. Their preservation is comparable to the pres-

ervation in the corresponding bivalve taphofacies E.

5. Discussion

5.1. *Taphofacies models*

A complex combination of taphonomic processes is apparent in the Eemian bivalve and barnacle faunas of the Pyoza river area, and distinct patterns in the distribution of taphonomic features are evident. Although the taphofacies facilitate a stratigraphic survey, significant broad patterns are present, which could reveal the environmental implications of the taphofacies (Speyer and Brett, 1986, 1988; Brett and Baird, 1986; Brett and Speyer, 1990; Staff and Powell, 1990; Brett, 1995). Taphonomy of shell accumulations exhibits characteristic trends along onshore–offshore transects and within depositional sequences (Kidwell et al., 1986; Kidwell, 1991a; Fürsich and Oschmann, 1993; Fürsich, 1995; Krawinkel and Seyfried, 1996). Recognition of these trends is the foundation of our taphofacies model.

The model proposed in Fig. 10 suggests that the taphofacies were produced over a siliciclastic shallow gently sloping shelf, where predominantly biological local shell accumulation occurred in offshore environments, while pronounced deterioration of shells by physical processes proceeded in nearshore environments. The simplest explanation is that the taphofacies represent intermediates in a taphonomic continuum along a transect from upper offshore to foreshore. This model fits with the lower altitudes for the muddy facies compared to the sandy facies. Furthermore, the model is consistent with the dispersed occurrence of poorly preserved shell fragments in the muddy facies. The fragments, which are typical for the sandy facies, were probably transported seaward by currents caused by tides or storms, forming sediment–water mixtures along the seafloor or higher up in the water column (Coniglio and Dix, 1992). The abundant silt–sand laminae and sand beds indicate that seaward-returning storm gradient currents initiated discontinuous

sediment discharges, leading to episodic silty or sandy sedimentation. The buried shells in life position in the offshore muds suggest deposition by storms and not turbidites (Aigner and Reineck, 1982; Elliott, 1986; Johnson and Baldwin, 1996).

No barnacles, and thus no barnacle taphofacies, are present in the most fine-grained strata of the muddy facies (Figs. 3 and 10). This absence may be for several reasons. Firstly, the strata would have to be formed so far offshore that barnacle remains could not be brought out there by storms. Secondly, insufficient substrate may have prohibited larval settlement. Thirdly, the suspended fine-grained particles may have clogged up and taken the life of larvae. These causes may also explain the low diversity and density of bivalves.

The taphofacies model in Fig. 10 indicates that marked variety in taphonomic patterns does not require significant change in water depth. The key elements in the taphofacies model appear to be grain size, sedimentation pattern, and sedimentation rate. As relationships between sedimentary facies and taphofacies exist, the distribution pattern of taphofacies is expected to resemble those of sedimentary facies (Speyer and Brett, 1986, 1988; Staff and Powell, 1990; Brett, 1995). Following Walther's law of facies, taphofacies occurring in a conformable vertical succession were formed in laterally adjacent environments characterised by distinct combinations of taphonomic processes. For example, the gradual vertical transition from bivalve taphofacies E and barnacle taphofacies C to bivalve taphofacies B and barnacle taphofacies B at locality 1 indicates a lateral shift in environments through time due to a prograding coast. It is possible that the progradation happened during a period of unchanged or falling sea level.

Only a few pioneering studies have focused on the taphonomy of barnacles (e.g. Donovan, 1988, 1989, 1993; Doyle et al., 1996), although the barnacles are common in late Cainozoic shallow-marine deposits (Foster and Buckeridge, 1987), for example in the Miocene of southern Spain (Doyle et al., 1996), Pliocene of West Indies (Donovan, 1989, 1993), Plio–Pleistocene of East Anglia (Do-

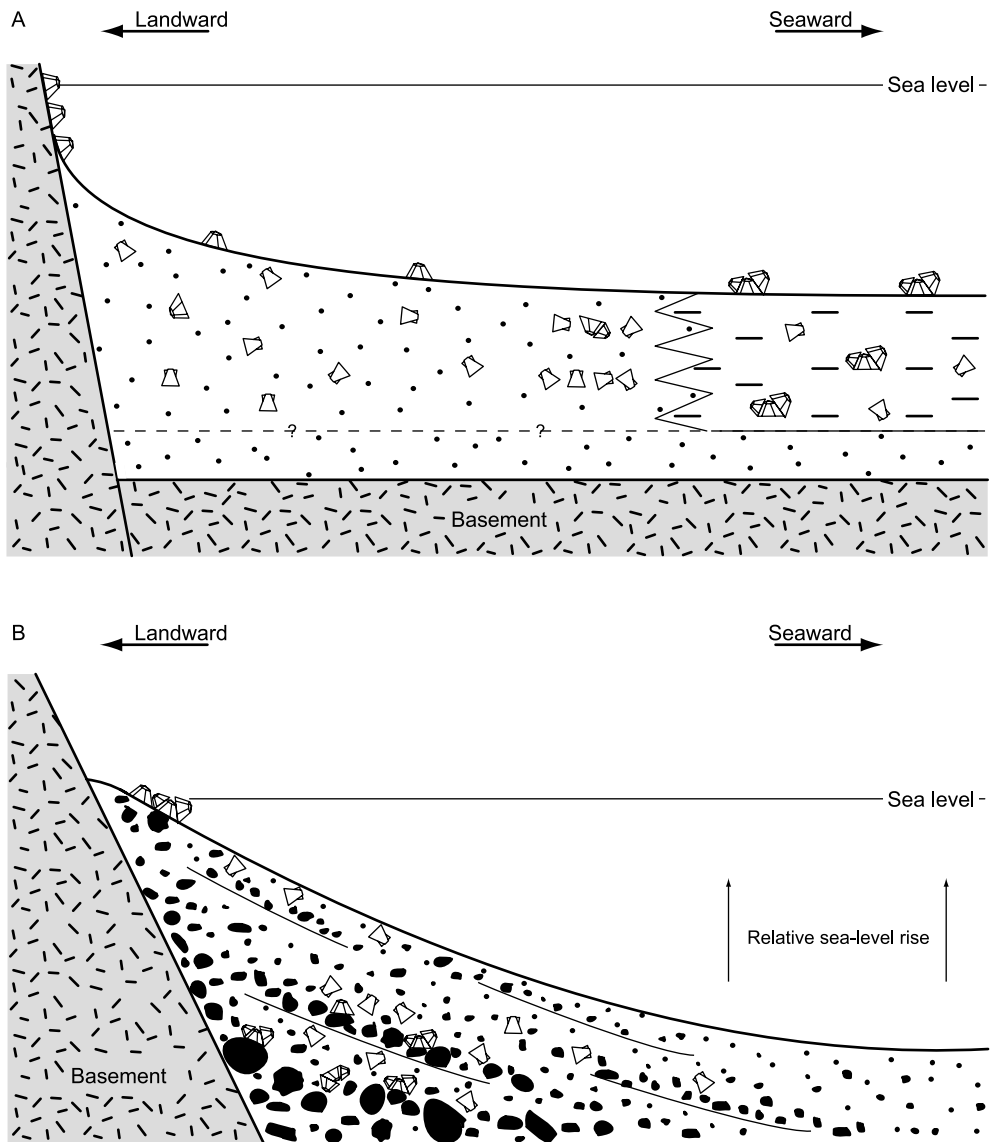


Fig. 11. Schematic palaeoenvironmental reconstructions showing the distribution and preservation of barnacles in different geological settings (see Fig. 10 for key). (A) Rocky coast (modified from Donovan, 1989, 1993). (B) Partly submerged fan conglomerates in intermontane basin, deposited during transgression (based on Doyle et al., 1996).

novan, 1988) and Pleistocene to Holocene of Greenland (Bennike et al., 2000). Living barnacles are abundant in many shallow-marine environments, especially on rocky shorelines (e.g. Donovan, 1993). Due to the wide distribution of barnacles, knowledge of their taphonomy is particularly important for palaeoenvironmental modelling. For example, Donovan (1989, 1993)

proposed a model for steep rocky coasts (Fig. 11A), showing that the shells are better preserved in muddy sediments deposited seaward, where clusters of articulated shells occur. Closer to the rocky foreshore, the shells are not so well preserved in sandy sediments, although some plates are articulated. The model, however, represents only rocky coasts, where stones and boulders

are absent in the transition from solid rocky foreshore to sand sea bottom.

Doyle et al. (1996) defined eight monospecific ‘preservational-state assemblages’ of the intertidal *Megabalanus tintinnabulum* collected from previously submerged fan conglomerates in an intermontane basin. A model based on this study is put forward here (Fig. 11B). The coarse-grained clastic sediments, which were submerged in the intertidal zone, provided a suitable substrate for barnacles. The shells are well preserved and clusters are present. In contrast, conglomerates deposited further seaward contain only disarticulated and often fragmented shells. Their model is based on the assumption that *M. tintinnabulum* lived in the intertidal zone. The model must be used with caution, especially interpreting specimens in life position, because other studies indicate that this and other species of Megabalaninae mostly live in shallow subtidal environments (Foster, 1978; Buckeridge, 1983; Senn and Glasstetter, 1989).

Our taphofacies model is the first for siliciclastic gently sloping coasts, and a comparison of our taphofacies model with those for rocky coasts and fan conglomerates shows different preservational patterns. The model by Doyle et al. (1996) predicts an opposite foreshore–offshore trend in preservation compared to our model, which bears a resemblance to the model by Donovan (1989, 1993).

The taphonomy of fossil assemblages is related closely to sea-level changes, as taphonomic processes are linked to rate of burial and environmental energy (Banerjee and Kidwell, 1991; Fürsich and Oschmann, 1993; Brett, 1995; Fürsich, 1995). In shallow-water siliciclastic areas, late phases of highstand deposition are associated with increasing sedimentation rate. Shallowing leads to higher energy conditions as the aggrading seafloor approaches levels of storm and fair-weather wave base. Excellent preservation of intact multi-element shells and skeletons is characteristic during mid-highstand progradation and caused by rapid sedimentation (Brett, 1995; see also Kidwell, 1991a; Speyer and Brett, 1991). Our bivalve taphofacies D and E and barnacle taphofacies C are characterised by similar preservation. During late highstand or regression re-

working is expected to increase, resulting in increased abrasion, disarticulation and fragmentation. Approaching a lowstand, increasingly poorly preserved shells are deposited in very shallow-water areas. The shells are highly fragmented, abraded and reworked (Brett, 1995). Our bivalve taphofacies A and barnacle taphofacies A have this style of preservation. Highly corroded and fragmented shells typify erosive lowstand and early transgression (Brett, 1995).

The taphonomic pattern outlined above for shallowing-upward successions is recognised in the Pyoza river area at localities 1, 6, 11 and 12, where the preservation of shells differs stratigraphically upward. At these localities the muddy facies is overlain by the sandy facies. The muddy facies is characterised by better-preserved shells than the sandy facies. In that way the taphonomy indicates that the deposits were formed during a period of upward shallowing.

5.2. Variability within taphofacies

Species of major taxa may differ consistently in preservation potential (Flessa and Brown, 1983; Brett, 1990; Parsons and Brett, 1991; Dent, 1996; Best and Kidwell, 2000). This is also recognised in the present study. The selected species from the Pyoza river area may differ markedly in abrasion, bioerosion, fragmentation and periostracal coverage. Notably, there may be differences between species with similar life habits. For example, *Mytilus edulis* tends to be more poorly preserved than both *Balanus balanus* and *Balanus crenatus*, although all three species are part of the fixosessile epifauna. However, *M. edulis* is byssate, thin-shelled and may be more easily detached from the substrate and subjected to taphonomic processes, while the barnacles remained attached by cement for longer.

Also, preservational differences exist among the bivalves. Fragmentation is most prevalent in *Mytilus edulis*. Resistance to fragmentation of *Arctica islandica* and *Hiatella arctica* may be related to several aspects of shell morphology and composition, including shell size, thickness, architecture, microstructure and organic matrix (Currey and Taylor, 1974; Walker, 1979; Emig, 1990; Hall-

man et al., 1996; Parsons et al., 1997). For example, fracture surfaces tend to follow pre-existing lines of weakness, such as growth lines and organic matrix between microstructural elements. In that way, fragmentation can yield consistent shapes of fragments (Taylor and Layman, 1972; Brett, 1990). Also, the life position of infaunal bivalves within the sea bottom may be important in decreasing exposure time to taphonomic processes relative to epifaunal bivalves (Driscoll, 1970; Aguirre and Farinati, 1999; Best and Kidwell, 2000). The intensity of bioerosion relies on surficial exposure time. Bioerosion may interact with other taphonomic processes, as this process can weaken the shells sufficiently to enhance processes such as dissolution and fragmentation (Roy et al., 1994). However, the present study gives no clues on interaction between these processes.

The taphofacies concept and its applications to palaeofaunas are still matters for debate. Taphofacies may be characterised in two ways. The taphofacies may be based on the taphonomy of individual species or on many species together, corresponding to the ‘target species’ and the ‘pooled species’ approaches (Dent, 1996). The ‘target species’ approach may lead to taphofacies which differ from those based on ‘pooled’ species. The difference is related to specific shell properties of the examined species (Dent, 1996; Best and Kidwell, 2000). Thus, in analysing the palaeoenvironmental significance of mollusc and barnacle assemblages, it is important to recognise that differential preservation apparently is a very common phenomenon in the fossil marine record. As the present study shows, however, the use of the ‘pooled species’ approach does not detract from the usefulness of taphofacies.

Time-averaging is another possible source of variability in taphofacies. The magnitude of time-averaging depends on several factors such as sedimentation rate, hydrodynamic energy, bioturbation, input and transport of shell material as well as preservation potential (Fürsich and Aberhan, 1990; Kidwell and Bosence, 1991; Flessa et al., 1993; Kowalewski, 1996). The magnitude of time-averaging is difficult to determine, as suitable dating methods are unavailable for Eemian pa-

laeofaunas to resolve possible time-averaging over hundreds or perhaps thousands of years.

5.3. *Taphofacies in the light of ichnofacies*

The theory of recurrent taphofacies is based on repeated patterns in distribution of taphonomic features in palaeoenvironments. It seems possible that taphofacies may have not only a geographically and stratigraphically local application, but also an archetypical one like ichnofacies.

Ichnofacies, which are defined on ethology of trace fossils and type of substrates, have, unlike taphofacies, a formal status and are considered as archetypes. The theory of recurrent ichnofacies was developed by Seilacher (1964, 1967), who established it on the basis of co-occurring ichnogenera in numerous formations, combined with analyses of ethologic groups. Two important components are integrated into ichnofacies, viz. biological contributions and taphonomic losses (Bromley and Asgaard, 1991; Bromley, 1996). The behaviour of tracemakers, which resulted in the formation of distinct ichnofacies, may have been influenced by several dynamic parameters, e.g. substrate consistency, sedimentation rate, hydrodynamic energy, oxygen concentration, salinity and availability of food (Ekdale, 1988; Frey et al., 1990). However, the complexity of these restricting parameters does not impede the use of ichnofacies for palaeoenvironmental interpretations (Ekdale and Mason, 1988; Bromley and Asgaard, 1991; McCann, 1993). Ichnofacies can only be interpreted in terms of palaeobathymetry when specific combinations of environmental parameters are related to depth (Ekdale, 1988; Frey et al., 1990). This may also be the case with body-fossil taphofacies.

The formation of ichnofacies is related to environmental parameters that also affect organisms with skeletal parts. Skeletonised organisms may even be potential tracemakers. Similarities thus may exist in the distribution of ichnofacies, biofacies and taphofacies. Nevertheless, the distributions may not coincide, as trace fossils produced by bioturbators rarely can be reworked and survive, whereas skeletal parts commonly are reworked.

At present, the status of taphofacies is informal, although an archetypical usefulness is preferred. It would require that the origin of taphonomic features be interpreted. For example, the taphonomic effects of differential intrinsic properties of shells have to be separated from the effects of palaeoenvironmental parameters. A logical next step in future studies is to focus on shell properties in the genesis of taphonomic features.

6. Conclusions

Separate sets of taphofacies, which are established on different groups of marine invertebrates, are a useful tool for evaluating the Eemian succession in northern Russia in palaeoenvironmental terms. It is confirmed that the distribution patterns of taphonomic features are closely interrelated with the sedimentary facies. However, a general theory of recurrent taphofacies requires taking relative time and interspecific differences, such as shell architecture, shell structure and life habit into account. In particular, the distinction between endobenthic and epibenthic faunas seems important.

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