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Faunal dynamics of juvenile gastropods and associated organisms across the Valanginian transgression-regression cycle in central Poland

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The Valanginian fossil assemblages at Wąwał in central Poland are dominated by juvenile gastropods with planktotrophic, mostly pelagic larvae, their occurrence thus being largely independent of local bottom environment in their distribution. The gastropod-dominated associations show a pattern of species turnover that is surprisingly consistent with a eustatic cycle and changes in biogeographic provincialism, both also strongly expressed in the distribution of ammonites. The Valanginian sea expanded into central Poland from the north, bringing cold waters with boreal faunas, and on the deepening sea-bottom the diversity of benthonic macro-organisms decreased. During the early Late Valanginian highstand, the seaway connecting the North European sea with the Carpathian ocean expanded enough to allow migration of Tethyan organisms into central Poland. In the late Late Valanginian this eustatic trend reversed and Boreal faunas again replaced those from the Tethys. The isotope record in benthonic foraminiferal tests suggests that, despite the sea-level changes, the bottom-water temperatures remained relatively stable.
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Key Words: cycles; gastropods; juveniles; palaeobiogeography; palaeoecology; Valanginian; Poland.

1. Introduction

Organisms are generally more sensitive to subtle environmental changes than physical or geochemical parameters. In fact, they tend to be too sensitive to make their fossil record useful for detailed palaeoenvironmental studies: even minor changes in a sedimentary regime may result in the complete replacement of bottom assemblages. This problem can be largely avoided by focusing on pelagic organisms, especially those that are numerous and occur continuously in thick sections. In the Mesozoic, molluscan larval conchs attached to juvenile teleoconchs provide such opportunities. Among them gastropods are the most diverse and their juvenile individuals are quite easy to identify.

The study discussed herein concerns fossil assemblages that are dominated by larval and juvenile gastropod shells to track environmental changes associated with one of the most prominent eustatic events of the Mesozoic, the Valanginian expansion of the North European epicontinental sea and its connection with the Tethys. In central Poland, the eustatic episode resulting in a highstand sea-level during the early Late Valanginian is well represented by a black clay with abundant aragonitic fossils. The best exposure of this clay is at Wąwał, near Tomaszów Mazowiecki (105 km SW of Warsaw).

Quantitative palaeoecological analysis of benthonic assemblages and recruitment in pelagic gastropod larvae with stable isotope records ($\delta^{13}C$, $\delta^{18}O$) provided by associated benthonic foraminifers are combined in this paper. The results presented offer new insights into the biogeographic evolution of the European marine basin during the Valanginian.

2. Geological setting and methods

The clay pit at the village of Wąwał is located 2 km east of Tomaszów Mazowiecki. It exposes a section of Valanginian age. Although the clay is quarried continuously, the section has never been exposed completely. Kutek *et al.* (1989) assembled all data known until 1987. The lowermost part of the Valanginian was briefly accessible in the 1960s. According to Kutek *et al.* (1989) the succession starts with a conglomerate consisting of calcareous pebbles (unit 1; see Figure 1) which overlies Jurassic limestone. The ammonite *Karakashiceras quadristrangulatum* (Sayn, 1907), which proves a Valanginian age for the conglomerate (Kutek *et al.*, 1989), was found in a pebble

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by Pruszkowski (1962). The units directly overlying the conglomerate include a clayey sand (unit 2) and silt with ferruginous ooids (units 3–5). The sequence higher up is mostly muddy, with ferruginous ooids and phosphate nodules in its lower part (units 6–8) and only an admixture of silt and sand in its upper part (units 9–12). In the middle part of unit 11, the clay is almost pure, with phosphate nodules in some horizons. A silt coarsening upwards completes the section (unit 13). A characteristic horizon of calcareous nodules up to 20 cm thick (unit 14) terminates the fossiliferous part of the succession.

Three series of samples have been taken for this study from accessible parts of the section. The first series (samples S1–A1; Figure 1) starts at the top of unit 8 and ends in the lowermost part of unit 11. The second set of samples (F2–A2) was collected from the middle part of unit 11 and the third (samples D5–A3) encompasses the lowermost part of unit 11, unit 12 and part of unit 13 (see Figure 1). The succession between these series was not exposed during sampling, resulting in two gaps. Each of the samples was about 2.5 kg in weight. They were washed with hot water on a sieve (mesh size 0.5 mm) and the fossils were picked from the residue under a microscope. All specimens were counted, and identified to species level (gastropods), generic level (bivalves, foraminifers), or morphologic groups (ostracods).

The fossils from Wąwał have been reported in numerous papers on particular taxonomic groups including ammonites (Lewiński, 1932; Kokoszyńska, 1956; Pruszkowski, 1962; Witkowski, 1967, 1969; Dzik, 1990; Ploch, 1999), ostracods (Sztejn, 1957; Kubiatowicz, 1976, 1983), foraminifers (Sztejn, 1957), decapod crustaceans (Collins, 1969), oysters (Pugaczewska, 1975), bryozoans (Dzik, 1975), holothurian sclerites (Kubiatowicz & Matyja, 1977), gastropods (Schröder, 1995) and nannofossils (Mutterlose, 1993). Still awaiting taxonomic treatment are bivalves (except oysters), echinoderms (except holothurian sclerites), scaphopods, serpulids, cirripeds, brachiopods, fish otoliths, and teeth.

3. Succession of fossil assemblages in the Valanginian of Wąwał

During sedimentation of the Valanginian clays at Wąwał a profound restructuring of the fossil assemblages took place. In the lowermost fossiliferous sample gastropods are uncommon and preserved only as internal moulds. Aragonite was probably removed during late diagenesis. In this sample and somewhat higher (samples S1–Q1) ornate ostracod carapaces, bivalves and echinoderm ossicles are most common (Figure 1, Table 1). In sample P1 foraminifers have their first mass occurrence. Smooth ostracods dominate and comprise mainly *Apatocythere*, *Cytherella*, and *Dolocythere*. The ornate ostracods belong mainly to procythereids. Immediately above (O1–M1) foraminifers became less important. The organisms that flourished instead were first bivalves (P1–M1), then gastropods (L1–K1). The following assemblage (J1–H1) shows a balanced contribution from bivalves, ornate ostracods and foraminifers with unusual and rare gastropods. This brief episode is followed to the top of the sampled part of the section (B1), by assemblages dominated by gastropods and foraminifers, with some participation of scaphopods.

It is noteworthy that on both sides of the first gap in sampling (A1–F2) the composition of assemblage is closely similar in being dominated by smooth ostracods. This kind of assemblage seems to continue across the second gap in sampling (A2–D5), and the turnover is connected with the transition from beds 11 to 12 (B5–A5). In the uppermost part of the section bivalves (oysters especially) and gastropods dominate (D3–C3). Serpulids only become abundant high in the sampled part of the section. They are mostly represented by fragments of tubes but in one sample (C3) lumps of articulated tubes also occur.

There is some pattern to the distribution of ostracods in the Wąwał section. Among the ostracods with ornate carapaces, *Protocythere hechti* Triebel, 1938 appears exclusively in the upper part of the section (samples G3–A3) whereas *Protocythere helvetica* Oertli, 1966 and *Pseudoprotocythere aubersonensis* Oertli, 1966 dominate in the lower part (samples S1–A5). This is consistent with data presented by Kubiatowicz (1983).

A few samples in the upper part of the section (D3, E3, H3) are completely devoid of ostracods. At some levels in the lower part of the clay unit 11 (C1, F2, E2, C2, B2, A2, D5, C5) only smooth ostracod carapaces are present. Ornate ostracods are most common in the lower part of the section, whereas smooth ostracods are most common in the middle part. In the upper part of the section both ornate and smooth ostracods are uncommon (Figure 1).

Echinoderms are uncommon, represented primarily by disarticulated ossicles of echinoids, asteroids, ophiuroids, crinoids, and holothurian sclerites. They have been found in all samples except for A2.

Fish otoliths are not numerous. Nevertheless, they are diverse and occur continuously throughout the section. They are most common in the lower and upper parts. Fish teeth are much less common and randomly distributed.

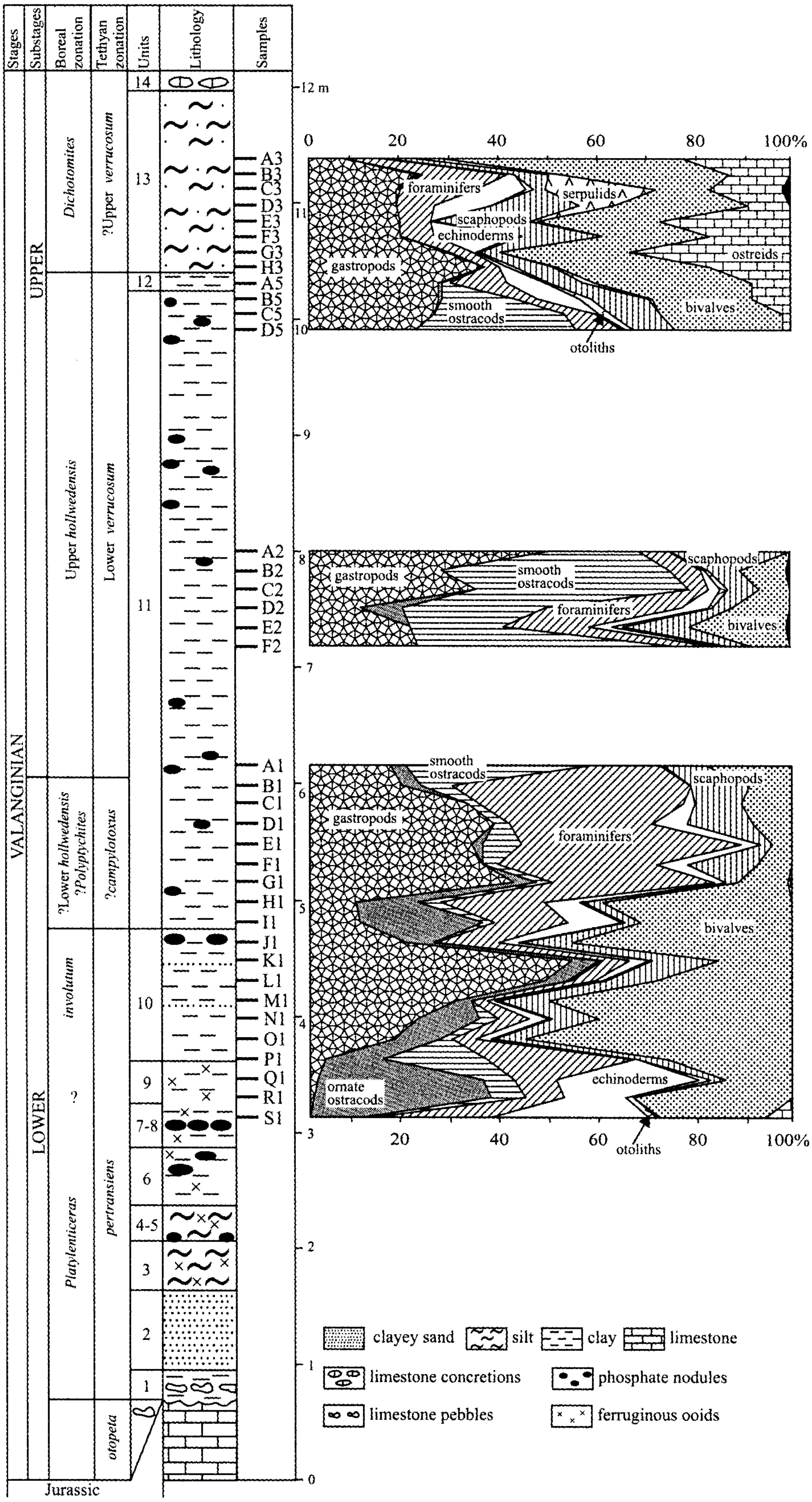

Figure 1. Locations of samples in the Valanginian of the Wąwał section (stratigraphy after Kutek *et al.*, 1989) and logs of relative abundance (%) for the main fossil groups.

Table 1. Distribution of fossils in the Wąwał section.

Sample	Gastropods	Ornate ostracods	Smooth ostracods	Foraminifers	Echinoderms	Otoliths	Scaphopods	Serpulids	Bivalves (ostreids excluded)	Ostreids	Cirripeds	Brachiopods	Bryozoans	Teeth	Ammonoids	Total
A3	336	6	4	364	21	20	320	256	2342	1066				1		4736
B3	1079	51	30	863	51	29	341	94	1702	633			1			4874
C3	692	13	25	603	397	49	90	880	443	562	5	45	12			3816
D3	499			202	309	12	481	200	741	232	3					2679
E3	616			211	11	27	651	49	831	884				4		3284
F3	843	2	8	309	759	56	738	17	993	738						4463
G3	2446	35	41	442	36	63	359	9	2310	2886				5		8632
H3	1821			126	99	92	388	12	1581	832		1	1			4953
A5	320	11	18	141	92	10	86	27	389	91						1185
B5	150	4	82	25	50	10	67	2	116	42				1		549
C5	59		62	15	1	6	23		58	4						228
D5	54		80	22	2	5	20		55	3						241
A2	8		3				4									15
B2	87		148	19	4	3	19		30	1				2		313
C2	55		69	6	4	3	10		10							157
D2	56	46	163	151	31	4	22		64						1	538
E2	187		176	162	49	19	121		188	1				1	4	908
F2	112		262	39	12	2	24		41							492
A1	86	16	200	74	2	1	45		92					1		517
B1	2117	448	717	5585	3	18	1374		958							11 220
C1	1549		89	1998	131	8	430		495							4700
D1	765	2	66	585	148	2	274		152	1						1995
E1	1299	88	312	1759	164	1	108		140	2						3873
F1	840	7	66	763	158	4	338		158	6						2340
G1	2200	265	163	1757	115	25	124		553	22				2		5226
H1	326	425	146	736	240	15	149		1296	3				2		3338
I1	511	1235	140	731	536	37	149		1537	1						4877
J1	366	100	18	240	63	17	194		831							1829
K1	262	27	5	26	18	6	63		74					1		482
L1	475	45	10	43	18	12	96		274							973
M1	639	53	8	61	38	14	220		1050							2083
N1	466	265	74	139	76	30	199		819							2068
O1	266	146	31	68	49	18	95		823	1						1497
P1	154	671	1121	1642	40	22	305		1378	3				8		5344
Q1	38	963	170	246	810	56	91		368	6				2		2750
R1	13	1038	192	238	361	23			925	1						2791
S1		102	17	215	290	17	3		192	53						889
Total	21 792	6064	4716	20 606	5188	736	8021	1546	24 009	8074	8	46	14	30	5	100 855

Among other fossils eight scutae of cirripeds (samples C3–D3), 46 valves of brachiopods (samples C3–H3), and 14 colonies of cyclostomate bryozoans have been found.

4. Systematic palaeontology

Taxonomic treatment of the gastropods of Wąwał was presented by Schröder (1995). He described 27 species of gastropods. During my research I identified about 50 species. Their taxonomy will be published separately apart from one new species, which is described below because it is discussed extensively in the following sections.

Order: Cerithiimorpha Golikov & Starobogatov, 1975
Superfamily: ?Cerithioidea Férussac, 1819
Family: uncertain

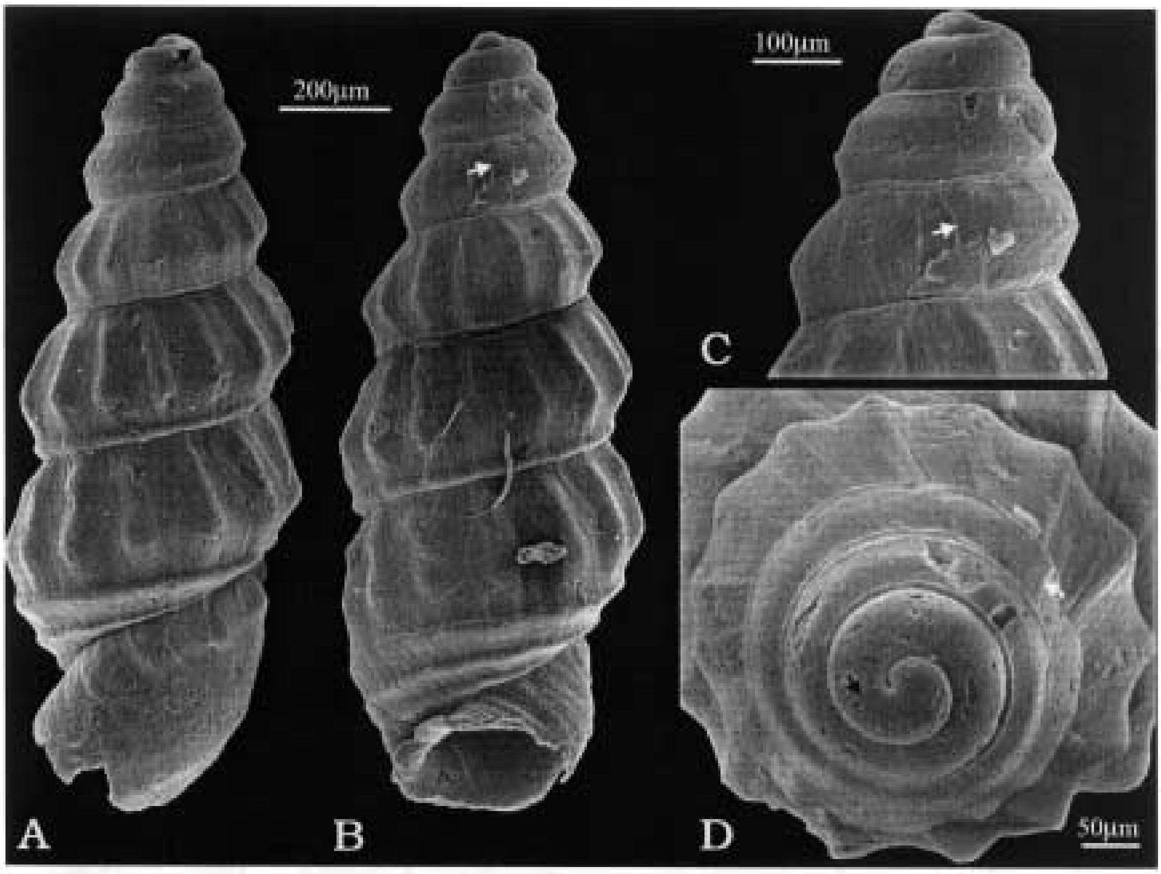

Figure 2. *Tomaszoviella polonica* gen. et sp. nov. from the Valanginian of Wąwał; holotype, ZPAL Ga.9/1. Black arrows show the suture between embryonic and larval conchs; white arrows show the suture between protoconch and teleoconch.

Tomaszoviella gen. nov.

Derivation of name. After the town of Tomaszów Mazowiecki, located near the type locality.
Type species. *Tomaszoviella polonica* gen. et sp. nov.

Diagnosis. Protoconch with two spiral keels on the last whorl of the shell, the lower distinct and the upper one weak. Ornamentation of the teleoconch with tight axial ribs. Last whorl deviates from the helix axis.

Tomaszoviella polonica sp. nov.
Figure 2

Derivation of name. After the type locality.
Holotype. ZPAL Ga.9/1 (Figure 2); specimen housed at the Institute of Palaeobiology, Polish Academy of Sciences, Warsaw.
Type locality. Wąwal near Tomaszów Mazowiecki, central Poland.
Stratigraphic horizon. Boundary bed between the *Platylenticeras* and *Polyptychites* horizons, Lower Valanginian, Lower Cretaceous.

Material. 199 well-preserved specimens.

Diagnosis. Micromorphic gastropod with height of adult conch about 1.4 mm. Protoconch high-spired with three whorls. The connection between protoconch and teleoconch is clearly visible and opisthocyrtic. The teleoconch possesses four whorls with tight axial ribs. The ribs on the third whorl are ornamented with two blunt nodes on the upper and lower parts of the rib.

Description. Embryonic conch has half of the whorl and is 0.1 mm in diameter. Maximum diameter of the larval conch is about 0.3 mm and its height is 0.33 mm. Maximum diameter of the teleoconch is 0.54 mm. The last uncoiled whorl has no sculpture, except for dense growth lines.

Remarks. The protoconch of the species is most similar to protochonchs of procerithiids with short planktotrophic development (for example *Xystrella* sp. from Wąwał). The two spiral ribs on the protoconch are typical for procerithiid gastropods, but the teleoconch ornamentation of *Tomaszoviella polonica* is of a kind unknown among the procerithiids. The loosely coiled whorls are typical for vermetid gastropods. According to Bandel & Kowalke (1997) the vermetids evolved from cerithiid gastropods in the Jurassic. *T. polonica* possibly represents an early stage in vermetid evolution.

5. Evolution of the bottom environment as inferred from the succession of benthonic assemblages

The cause of the profound faunal shifts recognized in the succession of faunal assemblages at Wąwał may be clarified to some degree by focusing on benthonic organisms with close Recent analogues. This can be done especially with bivalves. Bivalve faunas of the Polish Valanginian have not yet been treated taxonomically, but identification of genera seems to be reliable enough to match Recent counterparts for many forms found in the material.

The presence of juvenile oysters (diameter up to 2 cm) in the basal and top parts of the section was undoubtedly related to the availability of hard substrata for the settlement of larvae. The coexistence of oysters with the deposit-feeders *Neilonella* and *Nuculoma* (Figure 3) suggests that juvenile oysters utilized secondary (skeletal debris) rather than primary (lithified bottom) substrates. Many specimens of oysters show xenomorphic imprints of bivalves and gastropods on their valves, but many others were cemented to unidentified objects. These same objects were probably used as a substrate by the byssally attached *Oxytoma* and *Meleagrinella*. Duff (1975, 1978) regarded these inequivalve pectinaceans as 'pendent' species, byssally attached at some distance above the sea floor. He suggested that they could have lived as pseudoplankton on floating algae. In the Wąwał section the presence of *Meleagrinella* is strongly correlated with abundant cementing oysters (Figure 3). It is thus not necessary to assume a pseudoplanktonic mode of life.

In the lowermost part of the section, specimens of the noetiid *Arcopsis* dominate. Extant species of this genus vary in their ecology and mode of life. Stanley (1970, p. 22) pointed out that arcid and noetiid species with a shell length (L) to height (H) ratio (L/H) above 1.35 are epifaunal, and that taxa with an L/H ratio below 1.35 are infaunal. The species of *Arcopsis* from Wąwał lacks a byssal sinus and has an L/H ratio ranging from 1.32 to 1.41. The variation is mostly of ontogenetic origin, and it seems probable that *Arcopsis* at Wąwał was a shallow burrower with a weak byssus anchored in the loose sediment. A similar mode of life was proposed by Duff (1978) for arcids in the Oxford Clay of England. The heterodont *Neomiodon* associated with *Arcopsis* in this part of the section is inferred to have been a rapid burrower, because the shells of *Neomiodon* are round and lack ornamentation. This suggests that the sediment in the lower part of the section was loose and the rate of sedimentation was rather slow.

At the base of unit 11 the *Arcopsis-Neomiodon* assemblage is replaced by an astartid assemblage. According to Zakharov (1970, p. 23), most of the Mesozoic astartids were shallow burrowers with the posterior end of the shell slightly elevated above the sediment.

Not far above (samples F1–B1), the astartids are almost completely replaced by the *Corbulomima-Neomiodon* assemblage. According to Duff (1978), *Corbulomima* was an infaunal, siphonate suspension-feeder. It probably built banks slightly beneath the sediment surface in a manner similar to Recent corbulids (Lewy & Samtleben, 1979). *Corbulomima* is also believed to have been attached to the substratum by byssal threads (Duff, 1978). Banks built by corbulids are often found as thin pavements of shells in clayey or silty rocks of the Triassic (Kaim, 1997), Jurassic (Oschmann, 1988; Wignall, 1990), and Tertiary (Lewy & Samtleben, 1979). The burrowing rate of corbulids is very low, so they cannot escape after a burial event (Lewy & Samtleben 1979). The rate of sedimentation must, therefore, have been extremely low in the part of the section in which their shells are abundant.

In the middle part of the section astartids dominate again; the deposit-feeding nuculids *Neilonella* and *Nuculoma* are also common there. These bivalves are believed to have fed on the organic material from within the sediment (Duff, 1978). This suggests that the sediment was organic-rich and soft.

Neomiodon, with some contribution from *Corbulomima*, dominates again in a narrow zone near the base of the upper series of samples (D5–B5). The composition of the assemblage is similar to the *Corbulomima*-dominated assemblage in the lower horizon, except that juvenile oysters are more common. The occurence of *Neomiodon* ends with the change to the more silty unit 13, which is rich in oysters.

An important group of benthonic molluscs in the Wąwał section are scaphopods. They are present in virtually all of the samples except for R1. They have not been treated taxonomically, but the number of species seems to be higher in the upper part of the section. Many shells there are sculptured with

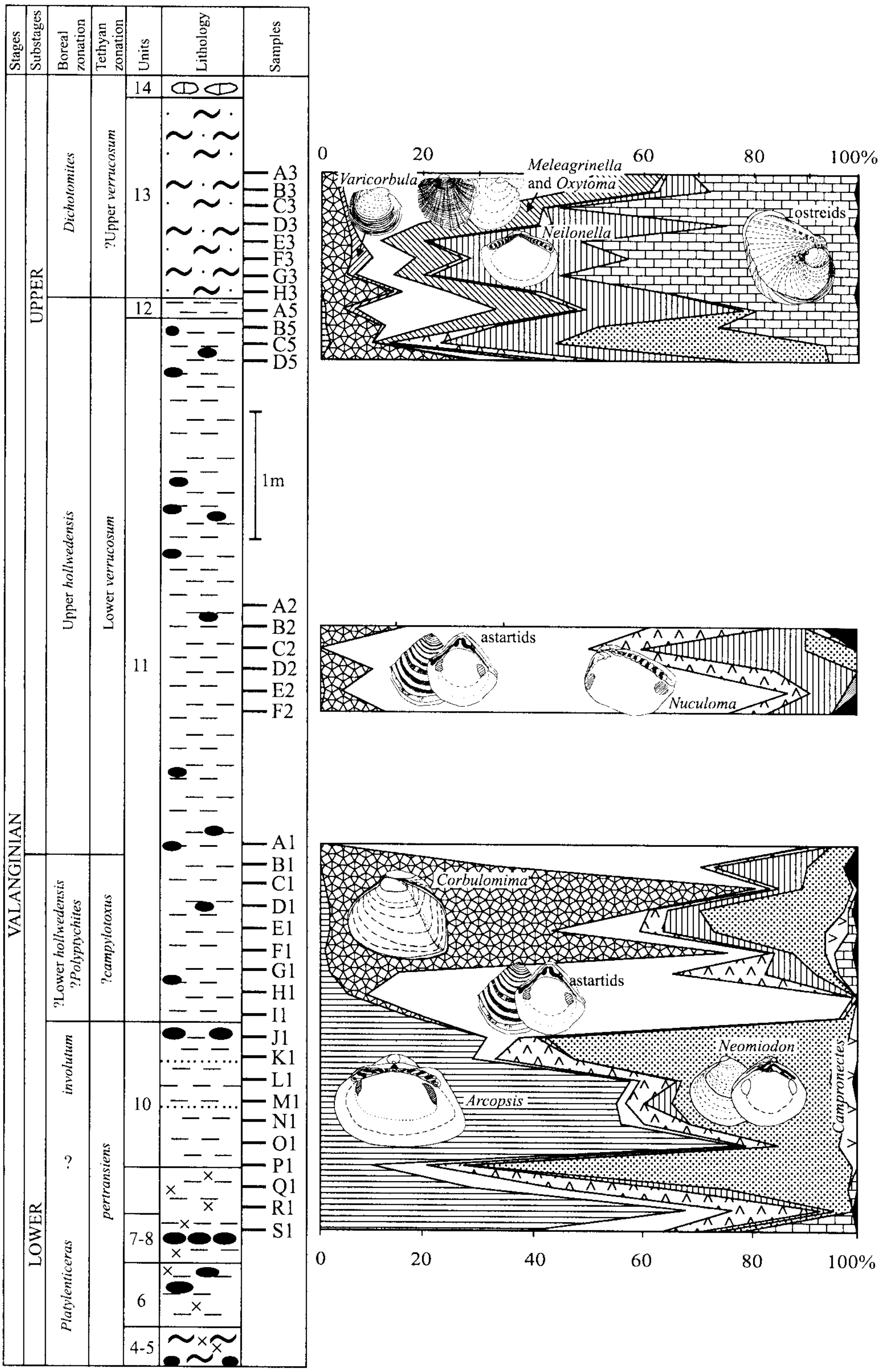

Figure 3. Vertical variations in relative abundance (%) of the most common genera of bivalves in the Valanginian of Wąwał.

costae and striae, whereas in the lower part they are smooth. Recent scaphopods are microcarnivores and many of them consume foraminifers (Dinamani, 1964). Duff (1975) noted a negative correlation between the abundance of scaphopods and foraminifers in the Oxford Clay. A similar pattern is observed in the Wąwał section. According to Wignall (1990) scaphopods rapidly decline in abundance in organic-rich facies, suggesting low tolerance to oxygen depletion. The relative abundance of the scaphopod shells throughout the section suggests that the surface layer of the sediment was rather well oxygenated.

Benthonic foraminifers may also provide important hints about the bottom environment. Almost all samples throughout the section are dominated by *Lenticulina* species group 1 [mainly *L. nodosa* (Reuss, 1863), with an admixture of *L. gaultina* (Berthelin, 1880) and *L. muensteri* (Roemer, 1839)]. They comprise over 90% of all foraminiferal specimens found in the samples (Figure 4). The genus *Lenticulina* was regarded by Koutsoukos *et al.* (1990) as an epifaunal/shallow infaunal active deposit feeder. In the lower part of the section specimens of *Citharina* sp. 1 and *Frondicularia* are also common, and in the upper part *Epistomina* sp. 1 comprises about 25% of the foraminiferal assemblage. *Citharina* and *Frondicularia* are regarded as infaunal deposit feeders and *Epistomina* as an epifaunal/shallow infaunal active deposit feeder (Koutsoukos *et al.*, 1990). *Lenticulina* species group 2 and *Citharina* sp. 2 occur exclusively in the upper part of the section (samples A5–A3). Other foraminifers are only subordinate. The maximum number of specimens in a single sample was 5536 (sample B1). The mass presence of epifaunal/shallow infaunal *Lenticulina* along with the absence of infaunal *Citharina* and *Frondicularia* suggest a slow sedimentation rate and well-oxygenated bottom waters (compare Jorissen *et al.*, 1995). Significantly, the mass appearance of foraminifers at Wąwał is confined to the samples that are also characterized by the *Corbulomima-Neomiodon* assemblage and abundance of scaphopods.

In summary, during the Valanginian the benthonic assemblages at Wąwał were controlled by features of the sedimentary environment. Throughout deposition of the succession the substrate was soft and rich in organic matter, but its surface layer was well oxygenated. The rate of sedimentation was rather low and decreased even more during transgressions, when the distance to food sources increased. The *Corbulomima-Neomiodon*-foraminifer assemblage may have arisen during such an episode of very slow sedimentation. The presence of small oysters in this part of the section is consistent with the inferred low sedimentation rate. In the part of the section representing the early Late Valanginian high stand (samples F2–A2) benthonic fossils are relatively rare. Apart from astartids only the deposit-feeders *Nuculoma* and *Neilonella* are common. This suggests that the bottom waters were poor in nutrients. After shallowing of the basin, the availability of nutrients improved and the sedimentation rate was not high. It is likely that winnowing counterbalanced the increased influx of coarser sediment. This would have allowed the oyster assemblage to colonize the site despite the soft bottom conditions. The oysters utilized shells of other animals.

6. Succession of gastropod assemblages at Wąwał

Gastropods are represented in the Wąwał collection by 21,792 specimens of about 50 species (Table 2). In all samples apart from S1 their shells are preserved as primary aragonite. The number of specimens in individual samples ranges from eight (A2) to 2446 (G3). The number of species ranges from six (A2, R1) to 24 (E1). In most samples, the number of specimens is only roughly correlated with the number of species. The gastropods in the Wąwał section are represented by juvenile individuals for which larger adult or subadult forms are also known (e.g., aporrhaid sp. 1, *Haustator polonicus*), by individuals of minute species (*Tomaszoviella polonica* gen. et sp. nov., *Palaeorissoina wonwalensis* Gründel, 1999, *Ringicula* sp.), and by species known only from juveniles. The most abundant are three cerithioidean species (*Procerithium kulickii* Schröder, 1995, *Procerithium tricuspis* Schröder, 1995, and *Xystrella* sp.), which together comprise 61.8% of the gastropod assemblage (Figure 5). Other important groups include mathildids (13%), and the opisthobranch genus *Actaeon* represented by two species: *Actaeon gazdzickii* Schröder, 1995 and *Actaeon* sp. 1 (12.5%). The lowermost part of the section (samples S1–O1) includes deposits that are dominated by *A. gazdzickii* and interfinger with a horizon rich in *P. kulickii* (Figure 5). *Carinathilda microstriata* (Schröder, 1995) and *Mathilda orthocosta* Schröder, 1995 are common in the middle and upper parts of the lower sampled unit. *Schroederium valanginense* (Schröder, 1995) shows three low peaks of appearance (Figure 6). The first (sample I1) is connected with an abundance of micromorphic *Tomaszoviella polonica*. In the middle part of the section, the dominant gastropod is *Xystrella* sp. *Mathilda wonwalensis* Schröder, 1995 and *Mathilda tomaszina* Schröder, 1995 are restricted to this part of the succession,

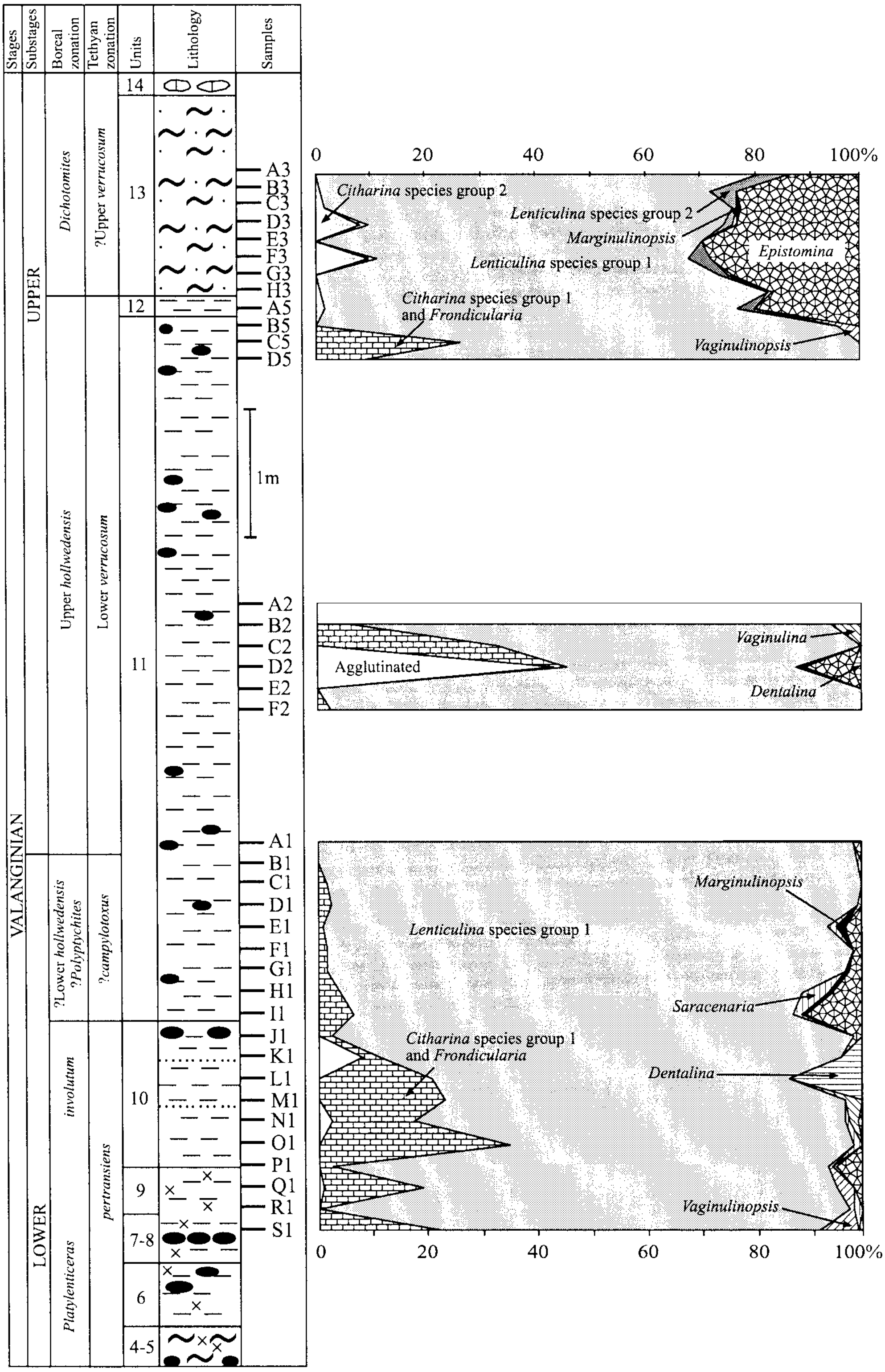

Figure 4. Vertical variations in relative abundance (%) of the most common taxonomic groups of foraminifers in the Valanginian of Wąwał.

Table 2. Distribution of gastropods in the Wąwał section.

Sample	*Procerithium kulickii*	*Xystrella* sp.	*Procerithium tricuspis*	*Schroederium valanginense*	*Tomaszoviella polonica*	*Mathilda orthocosta*	*Mathilda wonwalensis*	*Mathilda tomaszina*	*Carinathilda microstriata*	*Carinathilda* cf. *tectispira*	*Gegania seriaformis*	Apor-1	Apor-5	*Palaeorissoina wonwalensis*	*Pseudomelania* sp.	*Actaeon gazdzicki*	*Actaeon* sp. 1	*Bandellina laevissima*	Others	Total
A3			312							1			2	2	2		9		8	336
B3			995							3			8				45		28	1079
C3			566							2			10		1		100		13	692
D3			247							6			2	5	2		220		17	499
E3			242							17			6	61			282		8	616
F3			228							17			13	224			343		18	843
G3			1484							15			40	458	2		424		23	2446
H3		1	1373	1						18			21	122			250		35	1821
A5		2	198			3	2			4	1	6	1	34	1	3	54		11	320
B5		6	83			2	7			1	5			18		8	13		7	150
C5		18	7			6	8	1			6	2				11				59
D5		3	12			3	9	2			2	1		4		15	3			54
A2		1				1	3				2					1				8
B2		55				4	5	1			4	9				9				87
C2		34				4	4	1			3	6				3				55
D2		34				4	4	2			1	6				5				56
E2		132				7	9	8			6	10				13			2	187
F2		87				5	5	1			1	5				7			1	112
A1	60	4				2		1	11		1	2	5							86
B1	1515			32		9			356		20	20	78		33	26		2	26	2117
C1	899	1				3			501		8	11	81		15	5			25	1549
D1	529					6			162		6	5	32		6	7			12	765
E1	620			80		4			410		14	7	75		18	31		2	38	1299
F1	424			40					254		7	9	46	2	17	12			29	840
G1	1840			5		9			114		13	19	61		17	78		5	39	2200
H1	180			6	56	12			28			10			4	11		1	18	326
I1	173			27	142	13			92			13			9	19		5	18	511
J1	129			5	1	26			121		5	3	4		6	53		2	11	366
K1	138					22			41		6		1		9	44			1	262
L1	200			1		52			97		8	2			10	98			7	475
M1	311					75			82		8	17	11		13	112			10	639
N1	292					26			28			7	7		13	88			5	466
O1	2					17			14		7		14		7	203			2	266
P1	1					9			11		5		9		3	94		5	17	154
Q1	17					1			2			3				14			1	38
R1	2											1			2	6		2		13
Total	7332	378	5747	197	199	325	56	17	2324	84	139	174	527	930	190	976	1743	24	430	21 792

whereas *Mathilda orthocosta*, *Actaeon gazdzickii*, *Gegania seriaformis* Schröder, 1995 and APOR-1 of Schröder (1995) are infrequent. This assemblage continues to the base of the upper part of section. It is replaced above by an assemblage dominated by *P. tricuspis*, *Actaeon* sp. 1, and *Palaeorissoina wonwalensis*. Among the mathildids only *Carinathilda* cf. *tectispira* (Schröder, 1995) and two species of *Gymnothilda* are present.

The key for understanding this seemingly chaotic succession of more or less distantly related gastropod species lies in their larval biology, interpreted below based on analogies with Recent species (compare Jablonski & Lutz, 1980).

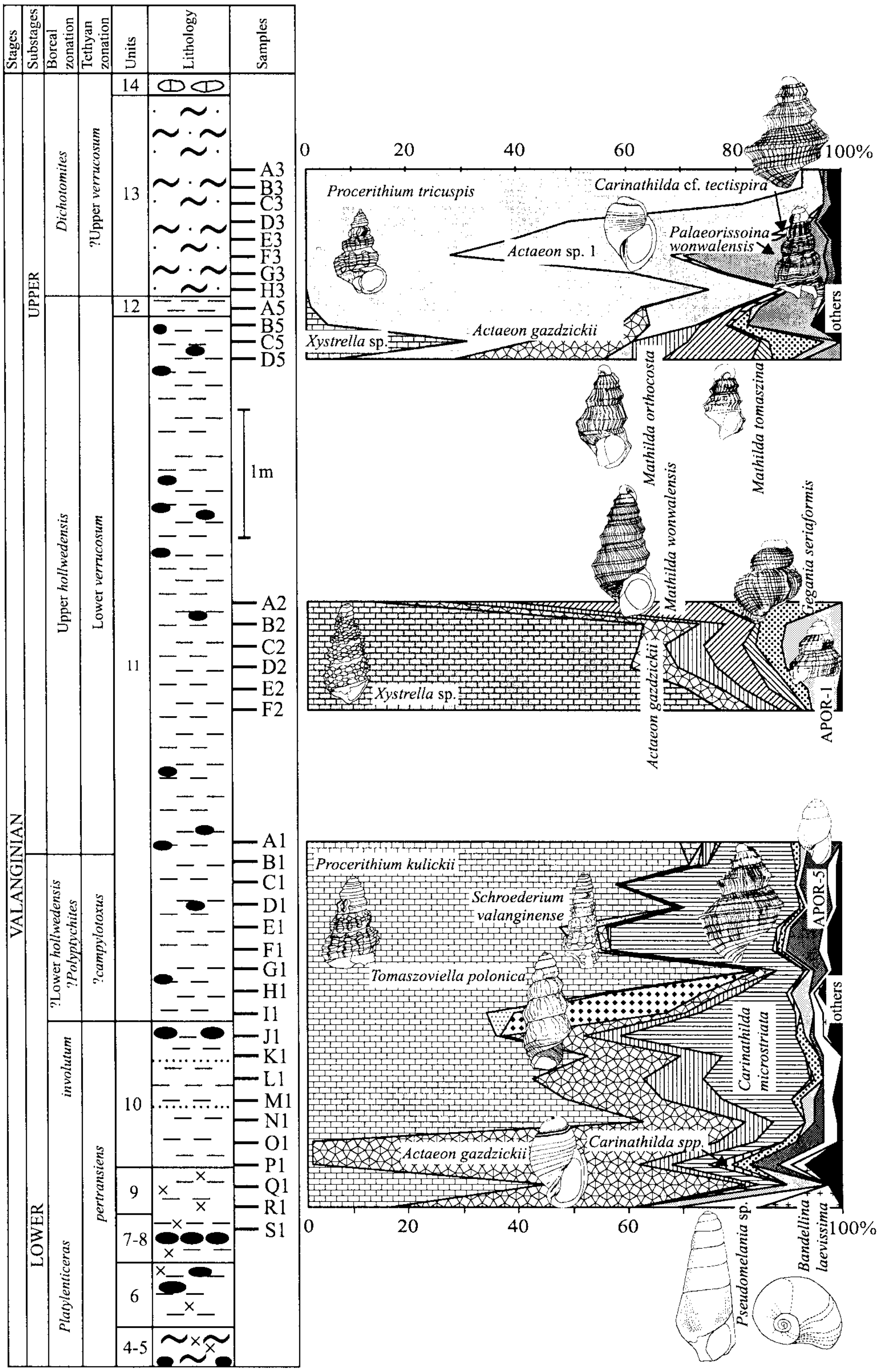

Figure 5. Vertical variations in relative abundance (%) of the most common species of gastropods in the Valanginian of Wąwał.

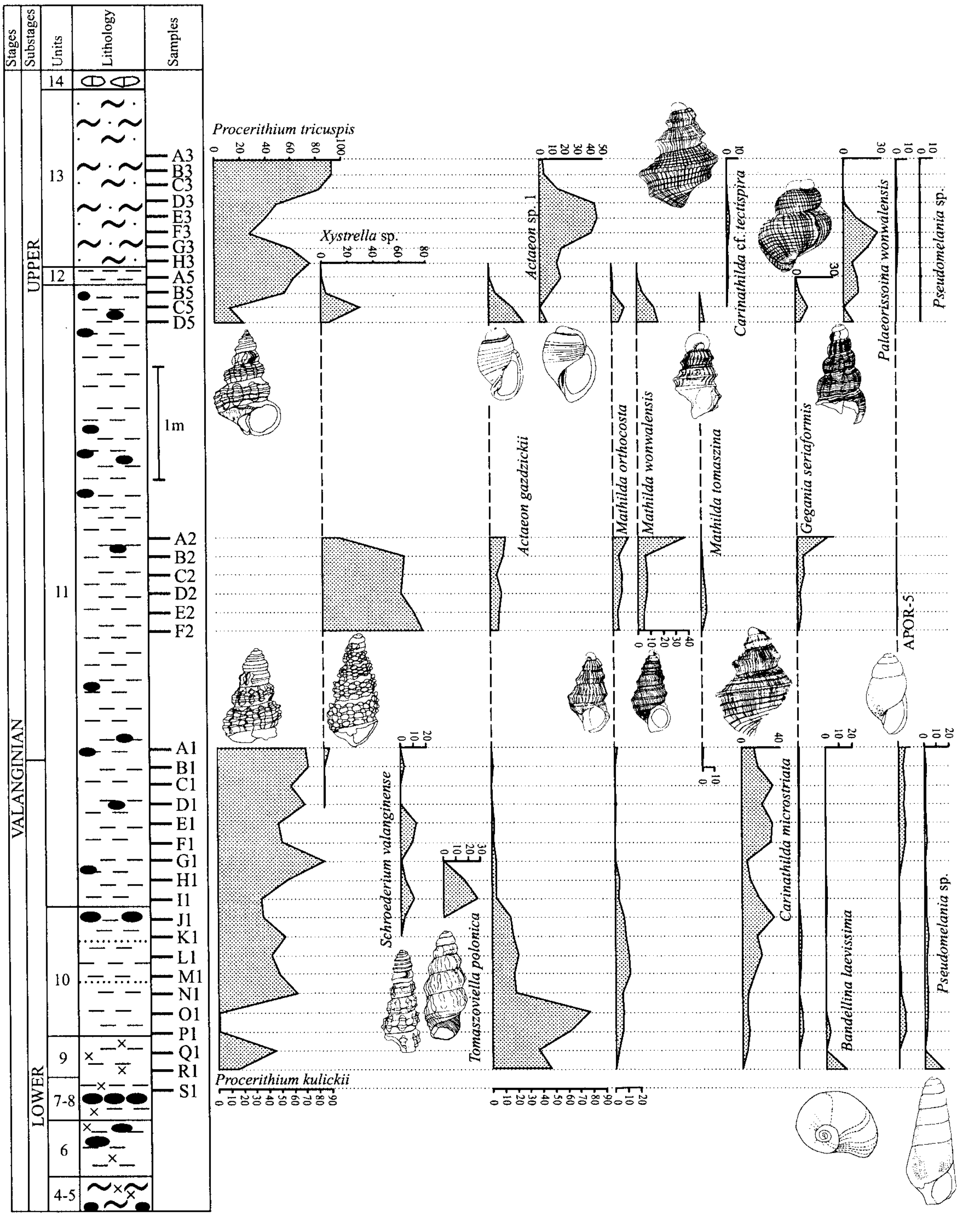

Figure 6. Faunal dynamics of the Valanginian gastropods of Wąwał; note that the gaps in sampling are within zones of relative stability.

7. Larval gastropod ecology and evolution of pelagic environment at Wąwał

The larval shell (protoconch) is composed of the embryonic shell (Protoconch I) and the larval whorls (Protoconch II) secreted by larvae after hatching or brooding. After metamorphosis of the larva is completed, the teleoconch (postlarval shell) is laid down. According to the widely accepted classifications of Thorson (1950) and Shuto (1974) (Jablonski & Lutz, 1980, and references therein) two main types of larval development are distinguished. A large yolky food supply is present in larvae with nonplanktotrophic development whereas it is absent in larvae with planktotrophic development. Larvae with nonplanktotrophic development are further subdivided into lecithotrophic and brooded larvae. Lecithotrophic larvae are nourished by the yolk of the eggs from which they develop. Brooded larvae develop within the parent and emerge as metamorphosed juveniles. This kind of development is characteristic of ovoviviparous species.

The dichotomy in larval adaptation affects egg size and is reflected in the morphology of the larval shell. Large rounded and paucispiral protoconchs indicate nonplanktotrophic larvae or larvae with a short planktotrophic stage. By contrast, planktotrophic larvae are indicated by narrow, polygyrate protoconchs (see Jablonski & Lutz, 1980).

Planktotrophic larvae may swim as veligers in surface waters feeding on smaller planktic organisms (pelagic larvae) or swim/crawl in the water close to, or on, the sediment, feeding on organic detritus (demersal larvae; Jablonski & Lutz, 1980). The pelagic stage lasts 2–6 weeks in temperate-water species (Thorson, 1961) but some tropical species (so-called teleplanic larvae) can remain in the plankton for six months or more (Scheltema, 1971).

Among Wąwał gastropods two species of *Procerithium* (Figure 5) are dominant. These have a high spired protoconch with a small embryonic shell (*P. kulickii* shows four whorls and *P. tricuspis* five), and apparently their development was planktotrophic. It is likely that the two species were able to spend a long period in the pelagic environment as planktonic feeding larvae and were distributed widely. In contrast, the protoconch of *Xystrella* sp. from Wąwał had only three low-spired whorls. It is highly probable that it spent much less time as a swimming larva than the two species of *Procerithium*. Another cerithioidean in the Wąwał section is *Schroederium valanginense*. The protoconch of this species has 4–5 very high-spired whorls. Its larval aperture clearly exhibits a sinusigera lip. This feature accommodates the extended velar lobes and is best developed in teleplanic larvae (Jablonski & Lutz, 1980, and references therein). This adaptation makes it possible for the larva to float in plankton for months, although many exceptions are known of long-lived larvae that lack an apertural projection; e.g., as for the Cassoidea and within the Janthinoidea (K. Bandel, pers. comm. 2000).

The first peak of abundance of *S. valanginense* (see above) coincides with the occurrence of the small *Tomaszoviella polonica*. This minute gastropod probably represents the Cerithioidea (see above, section 4). It has a high-spired protoconch with three whorls. The teleoconch possesses four whorls with tight axial ribs. The last whorl is uncoiled and has no sculpture, except for dense growth lines. These two co-occuring species have the highest-spired larval shells of all of the Wąwał prosobranch gastropods (Figure 7). Apparently, these species had a long pelagic life and may have been able to migrate from distant regions during an episode of favourable climatic and/or hydrogeographical conditions. Often such a small cerithioideans living today (e.g., *Alaba* and *Bittium*) are opportunistic and explode in blooms of algae (K. Bandel, pers. comm. 2000).

By contrast, the aporrhaid sp. 1 has the largest and most turbiniform larval shell among the Wąwał gastropods (Figure 7). This species is probably related to the Jurassic genus *Pietteia*. All other Wąwał prosobranchs show similar ranges in the ratio diameter/numbers of coils, i.e., from 0.1 to 0.2 (Figure 7), but the numbers of protoconch coils vary from 1.25 (*Pseudomelania* sp.) to 5.5 (*Haustator polonicus*).

Pseudomelania sp. is the only common species of prosobranch gastropods at Wąwał that is inferred to have had a short pelagic or lecithotrophic larval type. The adult form had a smooth, tightly coiled, turreted shell similar to shells of parasitic eulimid gastropods (e.g., *Melanella orphanensis* Clarke, 1974). It is probable that *Pseudomelania* sp. had a similar mode of life. Most of the Recent eulimids are parasites on echinoderms (Warén, 1980) but the occurrences of *Pseudomelania* sp. and echinoderm ossicles are rather roughly correlated (Figure 8). The second presumed parasitic gastropod is an unnamed pyramidellid species similar to *Liostomia clavula* (Lovén, 1846).

The Wąwał palaeorissoinid APOR-3 described by Schröder (1995), and redescribed by Gründel (1999) as *Palaeorissoina wonwalensis* Gründel, 1999, and other gastropods (APOR-1, APOR-5) related to palaeorissoinids (Gründel, 1999) and ?*Dicroloma* sp., had more coils in their larval shells than *Pseudomelania* sp. All palaeorissoinid-like gastropods are interpreted here as gastropods with planktotrophic development. This homogeneity in protoconch morphology (Figure 7) suggests that most of the prosobranch gastropods from Wąwał had similar dispersal abilities. The only exceptions are discussed above: *S. valanginense* and *T. polonica* with very high dispersal and the possible parasite *Pseudomelania* sp.

The only certain representative of the Aporrhaidae at Wąwał is the rare aporrhaid sp. 1. Extant species of these gastropods are largely infaunal or seasonal burrowers (Barnes & Bagenal, 1952; Perron, 1978). Recent aporrhaids graze on diatoms and decaying

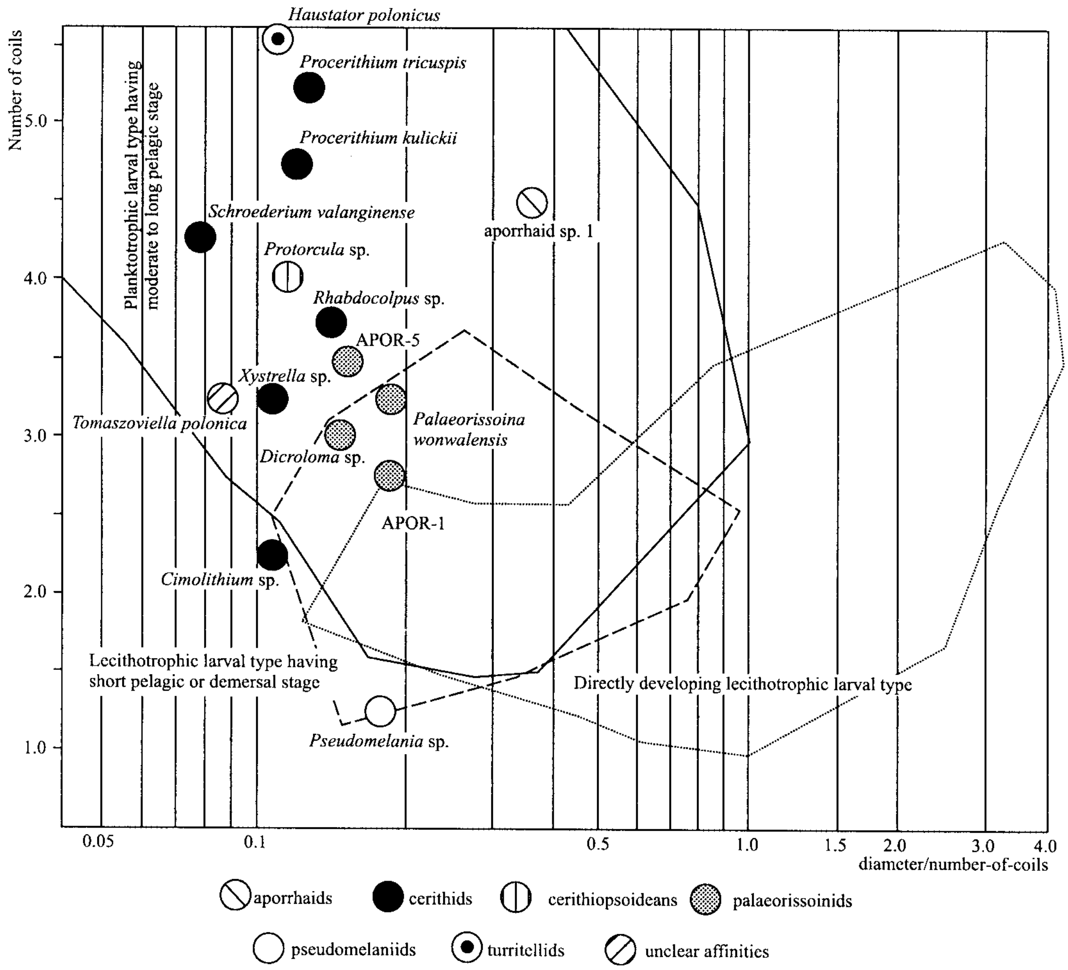

Figure 7. Geometry of the Wąwał gastropod larval conchs and their correspondence to fields of different ecological groups (from Shuto, 1974).

remains of macroalgae (Perron, 1978). It is likely that their Mesozoic ancestors had a similar feeding behaviour and fed on decaying remains of macroalgae.

Most of the Recent cerithiid species are algal-detritus feeders and graze on diatoms and microscopic benthonic algae (Houbrick, 1992). The Valanginian cerithiids probably also grazed on microscopic benthonic algae.

By contrast, most mathildids are carnivorous. They feed on coelenterates (Bandel, 1995) whereas actaeonids specialize in preying upon polychaete annelids and other burrowing, sediment-dwelling animals (Rudman, 1972; Gosliner, 1994, p. 279). Tubes of serpulid worms are common in the upper part of the section and their appearance roughly correlates with the distribution range of *Actaeon* sp. 1 (Figure 9). Coelenterates and sediment-dwelling polychaetes are not recorded at Wąwał.

I found a single specimen of *Globularia* (*sensu* Schröder, 1995) in the Wąwał section. This is likely to be related to the Naticoidea, predators with drilling abilities. Twenty specimens of perforated bivalve and gastropod conchs, probable victims of drilling gastropods, have been also collected. The Recent turritellids are filter-feeders (Graham, 1938). Among the gastropods at Wąwał the only turritellid is *Haustator polonicus* Schröder, 1995, which is presumed to have behaved in a manner similar to Recent taxa. Archaeogastropods are almost absent at Wąwał. Only three specimens of *Discohelix bandeli* Schröder, 1995 were found. Neogastropods are not known in the section.

It appears, therefore, that the distribution of gastropods is not random in the Wąwał section. Most of the prosobranch gastropods had a planktotrophic development and similar dispersal ability. The species with lecithotrophic development are rare and were restricted to near the beginning and end of the Valanginian eustatic episode. The gastropods with a very high pelagic dispersal ability appeared for only short periods. To further explore this intriguing

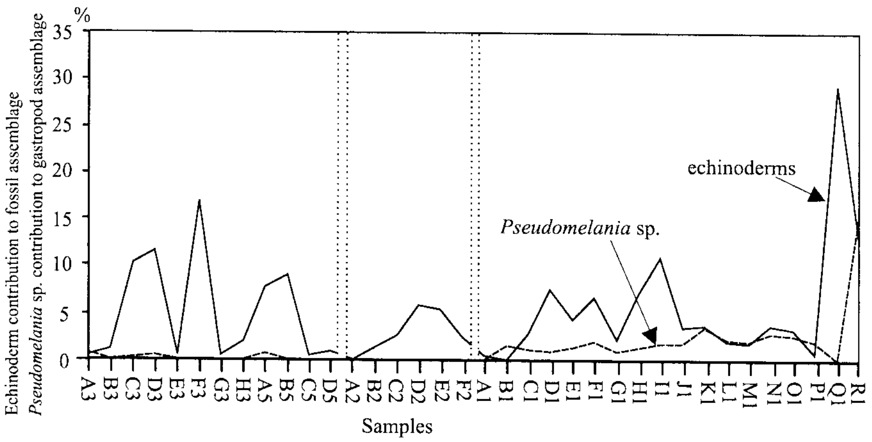

Figure 8. Correlation between frequency of echinoderm ossicles and conchs of the gastropod *Pseudomelania* sp. (probable echinoderm parasite); distances between samples not to scale.

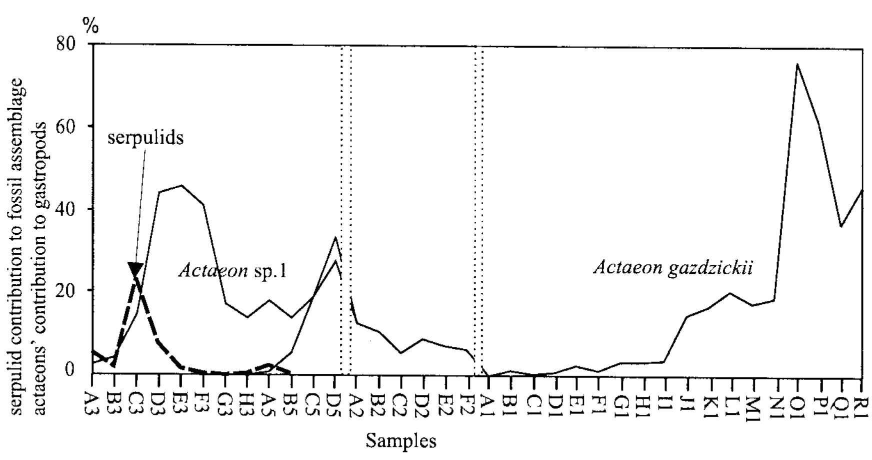

Figure 9. Correlation between frequency of serpulids and two acteonid species, which probably preyed on them; distances between samples not to scale.

pattern, stable isotopes of carbon and oxygen were analyzed in calcitic tests of foraminifers.

8. Stable isotopes $\delta^{13}C$ and $\delta^{18}O$

Stable isotope ratios were determined in empty calcitic tests of the benthonic *Lenticulina* species group 1. Specimens of this group are present in all samples apart from A2, and in sample C2 the number of specimens was insufficient to perform the analysis. The isotope ratios of each sample were measured on about 20 *Lenticulina* tests. The tests, hand-picked from under a binocular microscope, were ground in agate mortar to <63 µm. Calcite was converted to CO_2 by treating with anhydrous orthophosphoric acid ($d = 1.90\ gcm^{-1}$, at 25°C overnight under vacuum (McCrea, 1950). The CO_2 for isotopic analysis was purified by cryogenic distillation. The isotopic analysis was performed on mass spectrometer FinniganMat Delta Plus at the Institute of Palaeobiology, Polish Academy of Sciences, working in dual inlet mode with a universal triple collector. All δ values were corrected by a factor of 1.01025 and for ^{17}O using the standard procedure of Craig (1957). Isotopic ratios are expressed in δ notation relative to the V-PDB standard. Analytical reproducibility of the in-house standard was better than ± 0.05‰ and ± 0.1‰ for $\delta^{13}C$ and $\delta^{18}O$, respectively.

The variation in the $\delta^{18}O$ values does not exceed 1‰ throughout the section (Figure 10). This suggests an almost stable temperature in the bottom waters. If there was some bottom-to-surface temperature gradient in the basin, to keep the bottom temperature stable during transgressive sea-level rise, the

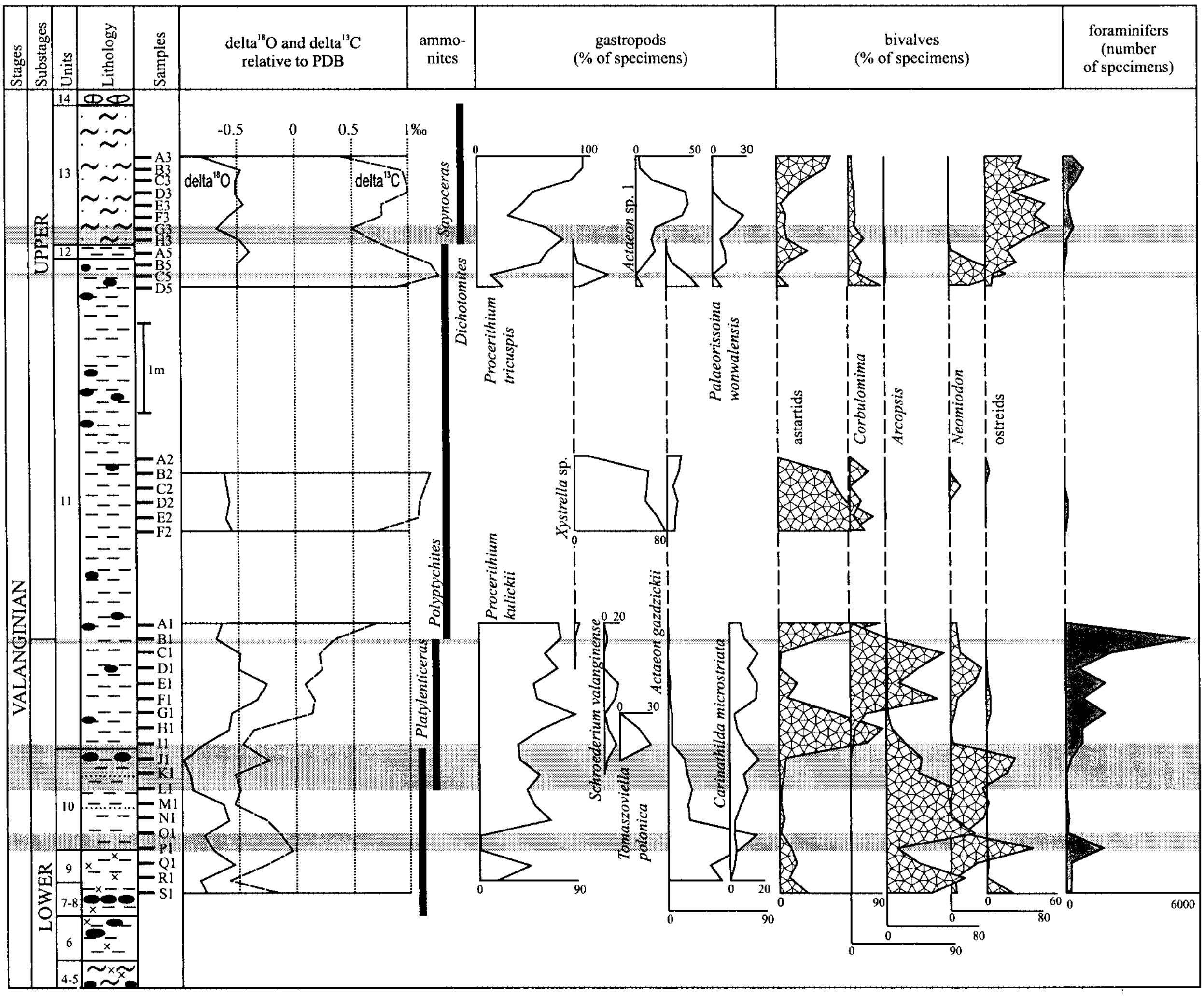

Figure 10. Depletion in $\delta^{18}O$, enrichment in $\delta^{13}C$, and their correlation with changes in relative abundance of particular fossil groups in the Valanginian of Wąwał. Shaded horizontal zones indicate proposed ecological events.

temperature of the surface waters had to increase whereas during the subsequent regression the temperatures had to decrease. The most notable positive excursion of $\delta^{18}O$ is observed in the lower part of the section, from sample J1 ($-$ 0.98‰) to E1 ($-$ 0.26‰). A notable shift towards higher $\delta^{13}C$ values parallels this and extends even further to sample A1. The values change from $-$ 0.46‰ in sample I1 to 0.71‰ in sample A1. The $\delta^{13}C$ values reach the stable level in the middle and upper parts of the section. Notable negative excursions both in $\delta^{13}C$ and $\delta^{18}O$ are recorded in the upper part of the section (samples G3 and A3).

Both $\delta^{13}C$ and $\delta^{18}O$ values received from benthonic foraminifers in the Wąwał section are consistent with the overall $\delta^{13}C$ and $\delta^{18}O$ trends for the Valanginian recorded in belemnites (Podlaha *et al.*, 1998).

9. Evolution of the Polish part of the North European Basin during the Valanginian

According to Kutek *et al.* (1989) and Mutterlose (1992), the Polish part of the Valanginian sea was connected through the German Basin with the North Sea Basin. Moreover, it was connected with the Tethys throughout the Valanginian (Kutek *et al.*, 1989; Mutterlose, 1992). Thus the area of Wąwał was located within a seaway connecting the Boreal and Tethyan realms. Its excellent fossil record provides a basis for detailed analysis of the environmental evolution at this key palaeogeographic region during the Valanginian.

The Early Cretaceous palaeogeographic map of Decourt *et al.* (1993) places central Poland at a latitude of around 37–38°N. The climate of the surrounding lands was probably warm as inferred for the English Wealden (Sladen & Batten, 1984; Watson & Alvin 1996).

The existence of stenohaline echinoderms throughout the Wąwał section testifies that the salinity of the Polish part of the North European sea was fully marine. A transgressive/regressive cycle is recorded in the Wąwał section. The lower, transgressive part of the section reveals unstable hydrological conditions with several profound faunal reorganisations (Figure 10). The first pronounced change is the replacement of the dominant herbivorous gastropod *P. kulickii* by the carnivorous gastropod *A. gazdzickii*, and the concurrent replacement of the shallow-burrowing bivalve *Arcopsis* by the bivalve *Neomiodon*, which presumably represented a somewhat deeper infauna (samples P1–O1).

The next environmental change, beginning with sample L1, probably marks the continuing of expansion of the Boreal Sea. According to Kutek *et al.* (1989), the Boreal ammonite *Polyptychites* appears in this part of the section (Figure 10). The rise of $\delta^{13}C$ values parallels the sea-level rise. The early diagenetic phosphatic concretions (Łącka *et al.*, 1989) prove that conditions were apparently anoxic within the sediment but that its surface and the water column were well oxygenated. Oxygen sensitive scaphopods are present in the whole section. The ubiquity of the cerithioidean gastropods *Procerithium kulicki* and *P. tricuspis* (samples S1–A1 and D5–A3 respectively) that presumably fed on algal detritus suggests shallow-water conditions near the photic zone.

The progressing transgression also allowed long distance travellers, the teleplanic larvae of the gastropod *Schroederium valanginense*, to immigrate. A further sea-level rise (early Late Valanginian highstand) widened a connection with the Tethys (sample B1) throughout southern Poland. During that time the Tethyan ammonite *Saynoceras* replaced the Boreal *Polyptychites* (Kutek *et al.*, 1989). Among the gastropods, probably *Xystrella* sp. and the two species of probable mathildid coelenterate feeders (Bandel, 1995) appeared whereas *Schroederium valanginense* and *Carinathilda microstriata* disappeared. The actaeonid gastropods, predators of polychaetes (Rudman, 1972; Gosliner, 1994), are uncommon in this part of the sequence. Specimens of *Xystrella* sp. are often found as complete adult individuals, which strongly suggests that conditions were favourable for this species. However, this gastropod occurs in the part of the sequence that accumulated when the depth of water reached its maximum. There are two possible ways to explain this: a pseudoplanktonic mode of life on drifted vegetation or a feeding behaviour different from that of other cerithiids.

In the middle part of the section (samples F2–A2), interpreted here as having been deposited during the early Late Valanginian highstand, the faunal dynamics stabilized and fossils are not numerous. With the sea-level fall, the hydrological situation became unstable again. The first signs of the event are observed in a narrow zone close to the top of unit 11 (sample C5; Figure 10). A much more pronounced expression of the event is recorded at the base of unit 13 (H3–G3): both $\delta^{18}O$ and $\delta^{13}C$ values drop abruptly, the clayey sedimentation was replaced by silty deposition, and the Tethyan ammonite *Saynoceras* was replaced by the Boreal ammonite *Dichotomites*. The abrupt change in lithology was connected with changes in the composition of the fauna (gastropods, bivalves, ammonites, ostracods, and foraminifers). This suggests a profound hydrographic event. It can be ascribed to a global lowstand in late *verrucosum* time, as suggested by Hoedemaeker (1984) and Kutek *et al.* (1989). A little later the sea retreated from the Wąwał area.

10. Conclusions

Frequency distribution logs for particular species of fossils sampled at Wąwał almost always show the same pattern: a gradual increase in contribution to samples, a more or less prolonged stasis, and then gradual decrease up to complete disappearance (Figure 6). Such a fusiform frequency distribution is typical for the fossil record in stratigraphically continuous successions (Cisne & Rabe, 1978). This suggests that the Wąwał section offers a precise and complete record of ecological events during the Valanginian eustatic cycle of the north European sea. The fusiform pattern of species-time distribution also has some bearing on biostratigraphy: this means that only a quantative approach provides a basis for assessing the reliability of observed range limits (qualitative presentations of ranges are much more sensitive to sample size: Marshall, 1991; Dzik, 1994).

When analyzed quantitatively, the benthonic faunas of Wąwał show a close correspondence with the evolution of an abiotic environment inferred from stable isotopes and biogeographic evidence. The gastropods appear to have been distributed according to their feeding mode and larval ecology. Moreover, the distribution of gastropod species can be correlated to some degree with Boreal/Tethyan provincialism expressed in the Wąwał section by the distribution of ammonoids. The two species of gastropods, with presumably the longest pelagic life cycle, were present in the area only during the initial phase of the eustatic sea-level rise. The long period spent as feeding planktonic larvae made these gastropods sensitive to environmental changes. The series of peaks in their appearance may possibly reflect some kind of cyclicity.

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